

Body size modulates demographic patterns of top predators and their native and invasive prey: A biomathematical approach

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ABSTRACT. The arrival of invasive species in native communities impacts the structure and functioning of ecosystems, and is considered a critical indicator of loss of biodiversity. Exploring the effects of new species in communities presents challenges addressable through theoretical ecology. Species body size not only shapes trophic relationships, but may also impact predator success and facilitate species coexistence. However, little attention has been paid to the effects of differences in species body size on interactions between native and invasive primary consumers, which could be relevant to their coexistence with higher-level predators. Our aim is to investigate demographic patterns using a dynamic, mechanistic model of two age-structured primary consumers (one invasive and one native) sharing a plant resource and preyed upon by a common predator. In our model, we highlight three crucial phenomena: the structuring of primary consumers into adults and juveniles, reproduction occurring in discrete pulses, and the seasonal addition of new individuals to the population. Hence, the success of one species over the other relies on its reproductive capacity to incorporate individuals in each reproductive cycle. Our simulations reveal that abundance patterns are influenced by body size, suggesting that changes in predator body size could serve as key indicators of shifts in community structure.

[Keywords: biological invasion, impulsive model, trophic chain, predation, body size]

RESUMEN. La masa corporal modula los patrones demográficos de depredadores superiores y sus presas nativas e invasoras: Un enfoque biomatemático. La llegada de especies invasoras a comunidades nativas impacta en la estructura y el funcionamiento de los ecosistemas, y se la considera un indicador crucial de la pérdida de biodiversidad. Explorar los efectos de nuevas especies en comunidades plantea desafíos que se pueden abordar desde la ecología teórica. Además de estructurar las relaciones tróficas, el tamaño corporal de las especies puede influir en el éxito de los depredadores e, incluso, favorecer la coexistencia entre especies. Sin embargo, se le ha prestado poca atención a los efectos de las diferencias en el tamaño corporal de las especies en las interacciones entre consumidores primarios nativos e invasores. Esto puede ser relevante para su coexistencia con los depredadores de nivel superior. Nuestro objetivo es estudiar patrones demográficos mediante un modelo dinámico y mecanicista de dos consumidores primarios estructurados por edad (uno invasor y otro nativo) que comparten un recurso vegetal y son presa de un depredador común. En nuestro modelo destacamos tres fenómenos cruciales: la estructuración de los consumidores primarios en adultos y juveniles, la reproducción en pulsos discretos y la incorporación estacional de nuevos individuos a la población. De esta manera, el éxito de una especie sobre la otra radica en su capacidad reproductiva para incorporar individuos en cada ciclo reproductivo. Nuestras simulaciones revelan que los patrones de abundancia se ven influenciados por el tamaño corporal, lo que sugiere que cambios en el tamaño corporal de los depredadores podrían ser indicadores claves de cambios en la estructura comunitaria.

[Palabras clave: invasión biológica, modelo impulsivo, cadena trófica, depredación, tamaño corporal]

INTRODUCTION

Body size influences community structure through its impact on species interactions (Schmidt-Nielsen and Knut 1984; Yodzis and Innes 1992; Marquet et al. 2002; Weitz and Levin 2006; Séguin et al. 2014; Cruz and Pires 2022). These demographic changes are also a consequence of the introduction of new species, such as the case of beavers (*Castor canadensis*) in Tierra del Fuego (Anderson et al. 2009), or the local extinction followed

by the reintroduction of wolves (*Canis lupus*) in Yellowstone National Park, USA (Ripple and Larsen 2000; Ripple et al. 2001; Ripple and Beschta 2003). Model-focused research analyzing how population traits (body size) influence community composition often overlooks the age structure of invasive and native species, as well as the variation in predator body size, which impacts their respective abundances (Green et al. 2022; Ortiz et al. 2023).

Species capable of breaking natural biogeographic barriers, whether by intentional or unvoluntary human intervention, are termed exotic species (Essl et al. 2018). Upon establishing themselves within specific habitats and exhibiting regular reproductive patterns, certain of these species thrive in their new ecological niches. Instances where these exotic species produce substantial adverse impacts on the environment, economy or public health in introduced areas warrant their designation as invasive species (IUCN 2000; Pyšek et al. 2020). Invasive species, due to variations in their life histories, could have a competitive advantage over their native counterparts (Pyke et al. 2008). Consequently, the prevailing expectation is that extinctions will predominantly affect larger-bodied species, potentially decreasing population densities across higher trophic levels. Subsequently, this could precipitate augmented populations of intermediate prey, prompting the overexploitation of food sources such as plants or shrubs and consequent alterations in the local vegetation structure (Ripple et al. 2014; Monk et al. 2022; Shedden-González et al. 2023). This phenomenon, known as a trophic cascade (Ripple and Beschta 2004; Ritchie et al. 2012), exercises a top-down regulatory influence on the ecosystem. For example, Pumas (*Puma concolor*), commonly referred to as mountain lions, rank among the focal feline species in conservation efforts (Dickman et al. 2015). However, a comprehensive understanding of the interactions between pumas (*Apex predator*), native and invasive herbivores (primary consumers) and vegetation (resource) remains elusive regarding their implications for ecosystem functionality (Wilmers et al. 2013).

The extinction of native mammalian predators yields significant effects, notably increasing mesopredator abundance by up to fourfold (Ritchie and Johnson 2009; Gigliotti et al. 2023). At the ecosystem level, the introduction of exotic mammals impacts food web functionality, triggering cascading effects on carnivore, herbivore, and resource abundance (Beschta and Ripple 2009; Ripple and Beschta 2012). Exotic mesopredators can function as seed dispersers, potentially altering long-term population abundance (Hasting et al. 2007; Anderson et al. 2009; Davis et al. 2010; Hatton et al. 2019). Conversely, increased predation pressure exerted by a generalist predator following

the introduction of an invasive alternative prey could incite apparent competition between native and exotic prey (Courchamp et al. 2000; Roemer et al. 2001; Ringler et al. 2015). Invasive species establish novel trophic relationships for native carnivores, potentially achieving positive effects by providing additional food sources, as documented in neotropical carnivore diets (Buenavista and Palomares 2018; Osorio et al. 2020). Despite the complexity of these interactions and the limited available data on population densities, the cyclic dynamics between hares and one of their primary predators, the Canada lynx (*Lynx canadensis*), have been identified in the Kluane region, southwestern Yukon, Canada (Gobbin et al. 2022). These dynamics can be modeled using mathematical tools inspired by real case studies.

An illustrative case study is found in a natural experiment conducted in Australia, suggesting that the introduction of a superior predator, the Tasmanian devil (*Sarcophilus harrisi*), constrains the abundance of wildcats (*Felis catus*) by increasing consumer predation rates (Cunningham et al. 2019, 2020). Another case study, involving the introduction of exotic mammals to South Pacific islands, offers valuable information on the impacts of introduced predators on natural ecosystems: the coati (*Nasua nasua*) was introduced to the Juan Fernández Islands (33°38'29" S - 78°50'28" W, southern Pacific Ocean) to control a rodent plague but ended up preying on native bird eggs (Colwell 1989). Additionally, Osorio et al. (2020) reported on exotic prey facilitating the coexistence between pumas and culpeo foxes in the central Chilean Andes. In this instance, predation may foster the coexistence of native and exotic herbivores, potentially subsidizing native carnivore populations such as pumas.

However, empirical methods seldom manage to capture the temporal aspect of interactions adequately and assess the effects of body size on demographic patterns and coexistence dynamics (Campillay et al. 2021, 2022). Consequently, both resource productivity and dietary changes, thus body size, influence demographic patterns (van de Wolfshaar et al. 2006; Rogers et al. 2018). Recent theoretical studies (Damuth 1993; Marquet 2002; Weitz and Levin 2006; Delong 2012; Delong et al. 2014; Cruz and Pires 2022) have addressed the role of species body size in community dynamics. However, the relationship between body mass and community structure remains

incompletely explored, necessitating a more comprehensive theoretical understanding of the demographic implications of body size and its impact on trophic networks involving invasive species (e.g., exotic prey and native wild carnivores, Osorio et al. 2020) to examine ecological community structure.

Our main goal encompasses two essential aspects: firstly, to investigate the implications of changes in the body size of apex predators on community structure; secondly, to explore long-term coexistence patterns between native and invasive prey species through simulations of realistic scenarios akin to those documented by Osorio et al. (2021). Additionally, through simulations within dynamic systems, we demonstrate how modeling age structure provides a foundation for understanding the long-term demographic patterns observed in natural environments (Gobin et al. 2022). In a broader context, this theoretical research holds the potential to integrate academic disciplines in both basic and applied sciences, significantly contributing to the comprehension of invasion biology (Lebreton et al. 1992; Ballari et al. 2016).

MATERIALS AND METHODS

We assessed the body size effects on demographic patterns, incorporating the body mass variable when modeling the parameters that affect interspecific interactions. We considered a three-level trophic web including: 1) a native predator species (P Figure 1), and its body mass (in kg, m_p); 2) two age-structured populations of invasive (A , Figure 2) and native (C , Figure 3) primary consumers, and 3) the producers (R) consumed by both native and exotic herbivorous species. Native adults are denoted by C_a , with body size (kg) m_{c_a} ; and juveniles by C_j , with body size (kg) m_{c_j} . Adult invaders are denoted by A_a , with body size m_{a_a} (kg); and juveniles, by A_j , with body size (kg) m_{a_j} . The definition and description of the variables and parameters are summarized in Table 1. The conceptual model is presented in Figure 4 and is based on an ecological community studied in central-southern Chile by (Osorio et al. 2021). The production rates, predation rates, conversion coefficients and all traits present in the model parameters depend on body size and are based on general principles as proposed by metabolic theory (Marquet 2022; Delong 2014).

Model formulation

Here, we use a dynamic model describing a three-level trophic chain of native species, to which we couple an equation in the second trophic level (primary consumers) representing invasive species structured in juveniles and adults. Additionally, we modeled the seasonal births through a succession of discrete times, which generates a discontinuity in the abundance curves, differentiating the demographic patterns of each species. This system of differential equations is known as an impulsive system and provides a theoretical framework that captures this phenomenon (Samoilenko and Perestyuk 1995; González and Pinto 1996; Haki et al. 2017; Pinto et al. 2018; Castillo et al. 2019; Lu et al. 2022). The following set of ordinary differential equations (ODEs) describes the interactions and dynamics except in the time succession $\{t_0, t_1, \dots, t_k, \dots\}$, representing the seasonal births occurring in regular pulses, as presented by Gobin et al. (2022):

$$\begin{aligned} & (e_{p_{A_j}} \phi_{[P A_j]} A_j + e_{p_{A_a}} \phi_{[P A_a]} A_a) P - d_{[P]} P \\ P' = & (e_{p_{C_j}} \phi_{[P C_j]} C_j + e_{p_{C_a}} \phi_{[P C_a]} C_a) P + \end{aligned} \quad \text{Equation 1}$$

$$C_j' = - (d_{[C_j]} - \gamma_{[C]} + P) C_j, \quad \text{Equation 2}$$

$$C_a' = \gamma_{[C]} C_j - (d_{[C_a]} + \phi_{[P C_a]} P) C_a, \quad \text{Equation 3}$$

$$A_j' = - (d_{[A_j]} - \gamma_{[A]} + P) A_j, \quad \text{Equation 4}$$

$$A_a' = \gamma_{[A]} A_j - (d_{[A_a]} + \phi_{[P A_a]} P) A_a, \quad \text{Equation 5}$$

$$R' = rR \left(1 - \frac{R}{K}\right) - (\phi_{[C_j R]} C_j + \phi_{[C_a R]} C_a) R - (\phi_{[A_j R]} A_j + \phi_{[A_a R]} A_a) R \quad \text{Equation 6}$$

The abundance curves of the mesopredator (A, C) are modified at the instants $\{t_0, t_1, \dots, t_k, \dots\}$ and we represent them as follows:

$$\Delta P(t_k) = 6, \quad \text{Equation 7}$$

$$\Delta C_j(t_k) = 0, \quad \text{Equation 8}$$

$$\Delta C_a(t_k) = b C_j(t_k^-) R(t_k), \quad \text{Equation 9}$$

$$\Delta A_j(t_k) = 0, \quad \text{Equation 10}$$

$$\Delta A_a(t_k) = c A_j(t_k^-) R(t_k), \quad \text{Equation 11}$$

$$\Delta R(t_k) = 40. \quad \text{Equation 12}$$

where, the variation discrete is defined $\Delta N(t_k) = N(t_k) - N(t_k^-)$ with $N \in \{P, C, A, R\}$. Products $b C_j(t_k^-) R(t_k)$, and $c A_j(t_k^-) R(t_k)$, represent the intake of resource R by primary consumers with intensity b and c . In this way, we replace the continuous reproduction of the model

with discrete pulses of birth. Thus, the model we present is recognized as an impulsive system of differential equations that describes natural and artificial environments. In this investigation we provide simulations of the model. From a mathematical perspective, the presence of impulsiveness gives a mixed character to the system, both continuous and discrete, generating a conceptual and technical richness that its presentation exceeds the scope of the analysis. purpose of our research. We assume that the basal resource has logistic growth with growth rate r and carrying capacity K in the absence of predators, while predation rates per unit resource are represented by $\phi[ij]$ for native consumers, invasive consumers, and predation, where ij corresponds to the notation presented in equations (1)-(6). The conversion efficiency and mortality rate for species are denoted by e_i and d_i (with $i \in \{C, A, P\}$), respectively. The codes utilized in this research can be found in the Supplementary Material.

Body size dependence of parameters

The growth rate r is proportional to $m_R^{\alpha-1}$, where the allometric exponent α is a number between 2/3 and 1 (Brown et al. 1995; Savage et al. 2004; Hatton et al. 2019). Meanwhile, the maximum number of individuals that the base resource population, K , can support is proportional to $m_R^{-\alpha}$ (Damuth 1993). The conversion efficiency e_i , with $i \in \{C, A\}$, is proportional to the ratio of the mass m_R/m_i . That is, if the consumed species is larger than its predator, the conversion efficiency increases. The mortality rate, d_i , with $i \in \{C, A, P\}$, is proportional to $m_i^{\alpha-1}$ (Brown et al. 1995; savage et al. 2004). Through theoretical and empirical investigations, these allometric relationships have been corroborated for many species (Hatton et al. 2019). On the other hand, the predation rate, $\phi[ij]$, of a species $i \in \{C, A, P\}$ per unit prey of species $j \in \{R, C, A, P\}$ is the product between the probability of successfully killing a prey given a mass ratio

$\frac{m_i}{m_j}$: $Q\left(\frac{m_i}{m_j}\right)$, and the interaction rate per unit density of the predator: $I(m_i, m_j)$ (Weitz and Levin 2006). In mathematical terms, this is expressed as follows.

$$\phi_{ij} = f_{ij} Q\left(\frac{m_i}{m_j}\right) I(m_i, m_j) / (1 + j/H_0(m_i, m_j))$$

Equation 13

$$\text{where } H_0(m_i, m_j) = \frac{n_0 m_i^{\alpha-1}}{e_i \left(\frac{m_i}{m_j}\right) f_{ij} Q\left(\frac{m_i}{m_j}\right) I(m_i, m_j)}$$

To carry out the simulations and the analytical study, we considered

$$Q\left(\frac{m_i}{m_j}\right) = 1 - e^{-\left(\frac{m_i}{m_j}\right)^2}$$

$$\text{and } I(m_i, m_j) = m_j^\beta + m_i^\beta$$

where β represents the intensity of predation, and the parameters $f[ij]$ is positive theoretical constants. The predation rate model described above was proposed by Weitz and Levin (2006). Our biomathematical modeling approach has been used to unify metabolic scaling theory, demographic theory, and coexistence theory to model the demographic patterns of species (Campillay et al. 2021, 2022).

Impulses effect on species abundances

In our model, $\Delta N(t_k) = N(t_k) - N(t_k^-)$, with $N \in \{P, C, A, R\}$, indicates a discrete derivative at time instant $\{t_k\}$. This type of model is very useful for incorporating discrete events that don't fully fit in continuous systems. Here, we model the fact that the top predators can persist even when species A and C become extinct. The puma, for example, is an opportunistic predator that can search for food resources elsewhere and, therefore, manages to keep its abundance, so $\Delta C(t_k) = B > 0$. Likewise, the dynamics of the basal resource (i.e., plants) is influenced by climatic factors, and at certain times, its abundance increases, which is represented by $\Delta R(t_k) = 40$. Note that, for the abundances of juveniles in each primary consumer species, they do not show discrete changes in their abundances, since they cannot increase their abundances due to their biological state: $\Delta C_j(t_k) = 0$ y $\Delta A_j(t_k) = 0$. Finally, to couple predator births to the system, we consider that $\Delta P(t_k) = 6$.

The impulse equations we propose allow us to represent the success of an invasive species compared to the native species. Here, we have considered three scenarios to model and visualize the abundances of the parameters species, which depend on the b and c incorporated in the impulse instants in species A_a and C_a . The invasion conditions are as follows: 1) $b > 1$ and $c < 1$: the native species has an advantage over the invasive species because the increase in abundances of the invasive species is less than the native species at the instant of time t_k , and 2) $b > 1$ and $c > 1$: indicates that the product between the abundance of the base resource and the abundance of adult primary consumers increases by a factor greater than 1 at the instant of time t_k .



Figura 1. Fotos de Puma en la región del Maule. Fotografías: Christian Osorio and Tomás Urrutia.

Figure 1. Photos of Puma in the Maule region. Photographs: Christian Osorio and Tomás Urrutia.



Figura 3. Fotos de vizcacha (nativa) en la región del Maule. Fotografía: Carlos Castro-Pastenes.

Figure 3. Photos of vizcacha (native) in the Maule region. Photography: Carlos Castro-Pastenes.



Figura 2. Fotos de lagomorfos liebre (*Lepus europaeus*) y conejo (*Oryctolagus cuniculus*) en la región del Maule. Fotografías: Christian Osorio.

Figure 2. Photos of hare (*Lepus europaeus*) and rabbit (*Oryctolagus cuniculus*) lagomorphs in the Maule region. Photographs: Christian Osorio.

We have implemented the system of equations in Matlab (2023), applied ODE45 and incorporated the impulsive effect. We used the parameter values shown in Table 2. The body sizes for native species are: juveniles $m_{C_j} = 1$ kg and adults $m_{C_a} = 2.5$. For invasive species, we consider: for juveniles $m_{A_j} = 0.8$ kg and for adults $m_{A_a} = 1.5$ kg. For the base

resource, we consider between 0.04 kg and 15 kg. Finally, due to the great variability of the body masses of the puma throughout its range of distribution, the simulated values between 50 kg or 100 kg (Grigione et al. 2002; Jansen et al. 2011).

RESULTS

Simulations were conducted using the model to represent various scenarios aimed at assessing the demographic patterns of native and invasive species, alongside the impact of predator body mass and the availability of the basal resource. In instances where native species exhibited an advantage over invasives ($b > 1$ and $c < 1$), a specific dynamic was observed, as depicted in Figure 5. The native species persisted among predators with body masses of 50, 70, and 80 kg, whereas for those with 100 kg, the native species was displaced, leaving only the invasive species. Conversely, when the product of the basal resource abundance and that of adult primary consumers increased ($b > 1$ and $c > 1$), a distinct pattern emerged, illustrated in Figure 6. Under these conditions, only the native species managed to establish among 50 kg predators, while the invasives prevailed among body masses of 70, 80, and 100 kg. This illustrates the impact of impulsive effects on abundance dynamics.

The variation in basal resource availability, represented by changes in its body mass, was

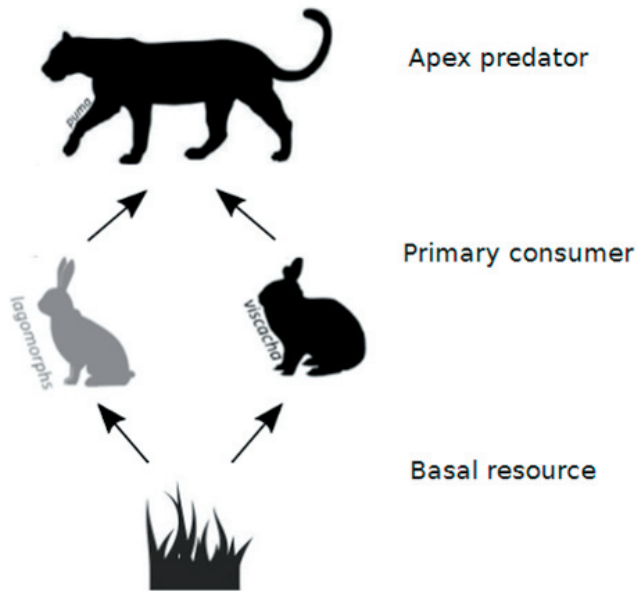


Figure 4. Simplified food web presented as a conceptual scheme for the three-level food chain apex predator-primary consumers-basal resource, centered in the central zone of Chile, reported by Osorio et al. (2020). The native species (vizcacha) and the invasive one (rabbit) are prey to the puma.

Figura 4. Red alimentaria simplificada presentada como un esquema conceptual para la cadena alimentaria de tres niveles depredador superior-consumidores primarios-recurso basal, centrado en la zona central de Chile, reportado por Osorio et al. (2020). La especie nativa (vizcacha) y la invasora (conejo) son presa del puma.

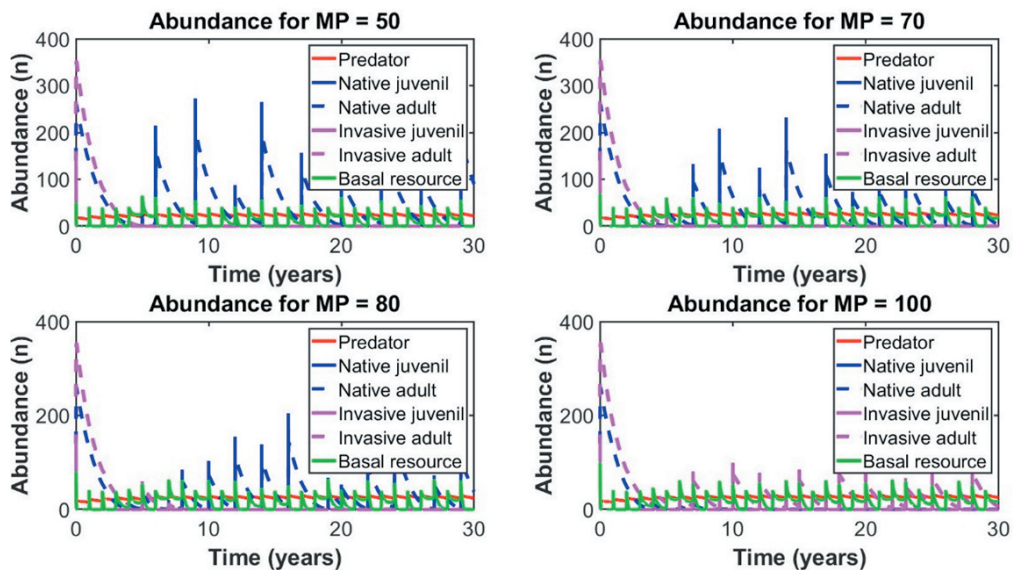


Figure 5. Simulations of the biomathematical model with $b = 3.2$ y $c = 0.7$. Body sizes for the native species were: juveniles $m_{c_j} = 1$ kg and adults $m_{c_a} = 2.5$. For the invasive species, we considered: juveniles $m_{a_j} = 0.8$ kg and for adults $m_{a_a} = 1.5$ kg. For the base resource we considered $m_R = 0.5$ kg. The body sizes for the top predator were 50, 70, 80 and 100 kg.

Figura 5. Simulaciones del modelo biomatemático con $b = 3.2$ y $c = 0.7$. Los tamaños corporales para las especies nativas fueron: juveniles $m_{c_j} = 1$ kg y adultos $m_{c_a} = 2.5$. Para las especies invasoras consideramos: juveniles $m_{a_j} = 0.8$ kg y adultos $m_{a_a} = 1.5$ kg. Para el recurso base consideramos $m_R = 0.5$ kg. Los tamaños corporales para los depredadores superiores fueron 50, 70, 80 y 100 kg.

analyzed within the $b > 1$ and $c < 1$ scenario. Figure 7 revealed that only the invasive species could establish when the resource availability was 0.7 kg, contrasting with scenarios where the native species predominated and became the sole prey of the superior predator. Finally, Figure 8 explores the $b > 1$ and $c > 1$ scenario,

with a constant body mass of the superior predator (100 kg) and temporal variations in basal resource availability, coexistence between native and invasive species was observed as a resource for the superior predator in the initial 10 seasons, aligning with prior findings (Osorio et al. 2021).

Tabla 1. Definición y descripción de las variables y parámetros incluidos en el modelo.
Table 1. Definition and description of variables and parameters included into model.

Variable	Description (name, meaning)
P	Abundance of predator
C_j and C_a	Abundance of juvenile and adult native herbivores
A_j and A_a	Abundance of juvenile and adult invasive herbivores
R	Abundance of base resource
r	$r_0 m_R^{\alpha-1}$, population growth rate of base resource
K	$K_0 m_R^{-\alpha}$, Damuth's rule for base resource
$\gamma_{[i]}$	$\gamma_{0i} m_{ia}^{0.27}$ with $i \in \{C, A\}$, maturation rate
$d_{[i]}$	$d_{0i} m_i^{\alpha-1}$ with $i \in \{C_j, C_a, A_j, A_a, P\}$, mortality rate
$e_{[i]}$	$\frac{m_i}{e_{0i} m_R}$ with $i \in \{C_j, C_a, A_j, A_a\}$, efficiency of conversion
$e_{[P,i]}$	$\frac{m_i}{m_P}$ with $i \in \{C_j, C_a, A_j, A_a\}$, efficiency of conversion
$\phi_{[ij]}$	$f_{[ij]} Q \left(\frac{m_i}{m_i} \right) I(m_0, m_i)$ with $i \in \{C_j, C_a, A_j, A_a, P\}$, predation rate

Tabla 2. Parámetros utilizados en el modelo dinámico. En este caso se ha considerado: α, r_0, d_0 (Hatton et al. 2019), β (Weitz and Levin 2006), los valores de e_{0i}, e_{Pi} y $f[ij]$ se proponen en esta investigación.

Table 2. Parameters used in the dynamic model. In this case it has been considered: α, r_0, d_0 (Hatton et al. 2019), β (Weitz and Levin 2006), the e_{0i}, e_{Pi} and $f[ij]$ are proposed in this research.

Parameter	Values
α	0.75
β	0.5
r_0	2.7
K_0	15.2
d_{0i}	0.74 with $i \in \{C_j, C_a, A_j, A_a, P\}$
e_{0i}	0.2;0.7;0.5;0.4 with $ij \in \{PC_j, PC_a, PA_j, PA_a\}$
γ_{0i}	53 with $i \in \{C, A\}$
$f_{[ij]}$	0.3;0.1;0.5;0.2;0.4;0.4;0.4;0.4 with $ij \in \{PC_j, PC_a, PA_j, PA_a, C_jR, C_aR, A_jR, A_aR\}$
C	0.7 or 2.5
B	3.2 or 4

However, in the long term, the native species establishes itself as the predominant one. These findings underscore the complexity of species interactions, the critical influence of predator body mass, and its role in community dynamics. They emphasize the importance of considering this pivotal trait in understanding species co-existence and succession within ecosystems.

DISCUSSION

We investigated the effects of body size on the community dynamics of three trophic levels: top predators, primary consumers,

and the basal resource. Primary consumers were structured by age, and seasonal births that modify abundance curves were modeled for all species.

Previous studies on food chains (Binzer et al. 2012; Sentis et al. 2017) suggest that species may face extinction due to climatic factors. However, there is evidence that significant changes in body size can occur before extinction, including the replacement of the top predator by an exotic predator (Hasting et al. 2007; Anderson et al. 2009; Davis et al. 2010). As body size increases, predator conversion efficiency and predation

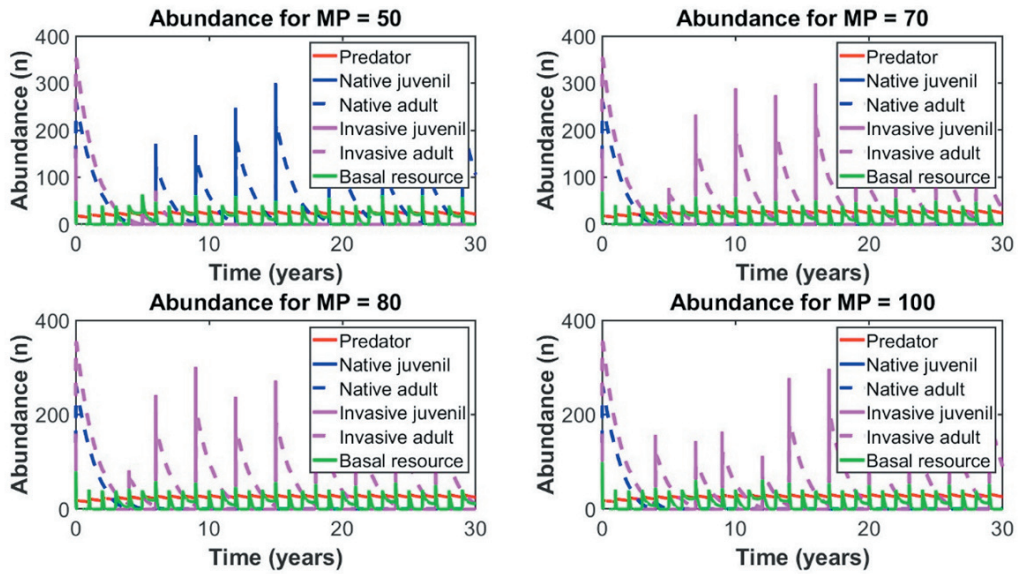


Figure 6. Simulations of the biomathematical model with $b = 4$ y $c = 2.5$. Body sizes for the native species were: juveniles $m_{C_j} = 1$ kg and adults $m_{C_a} = 2.5$. For the invasive species, we considered: juveniles $m_{A_j} = 0.8$ kg and adults $m_{A_a} = 1.5$ kg. For the base resource, we considered $m_R = 0.5$ kg. The body sizes for the top predator were 50, 70, 80 and 100 kg.

Figura 6. Simulaciones del modelo biomatemático con $b = 4$ y $c = 2.5$. Los tamaños corporales para las especies nativas fueron: juveniles $m_{C_j} = 1$ kg y adultos $m_{C_a} = 2.5$. Para las especies invasoras consideramos: juveniles $m_{A_j} = 0.8$ kg y adultos $m_{A_a} = 1.5$ kg. Para el recurso base consideramos $m_R = 0.5$ kg. Los tamaños corporales para los depredadores superiores fueron 50, 70, 80 y 100 kg.

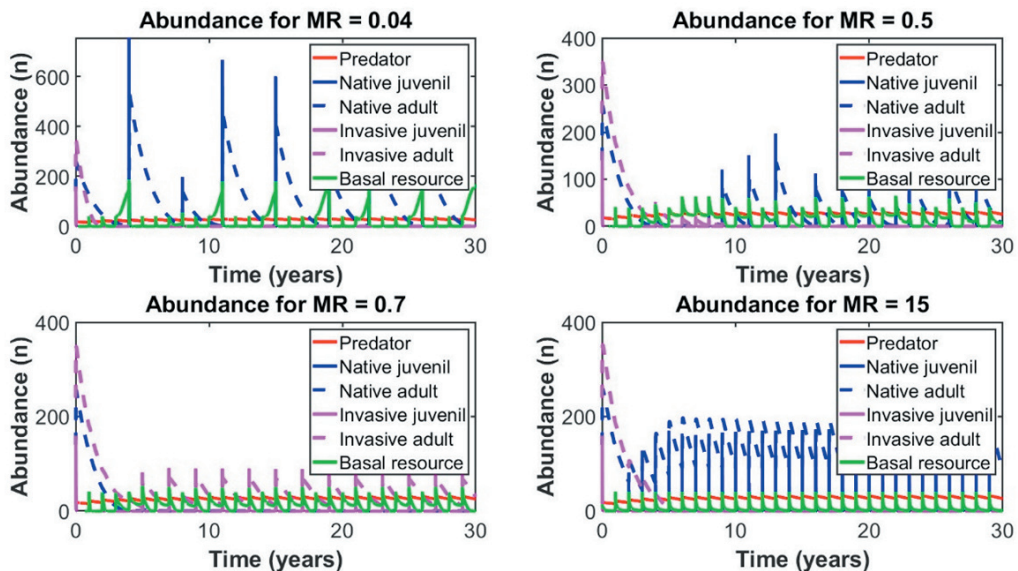


Figure 7. Simulations of the biomathematical model with $b = 3.2$ y $c = 0.7$. Body sizes for the native species were: juveniles $m_{C_j} = 1$ kg and adults $m_{C_a} = 2.5$. For the invasive species, we considered: juveniles $m_{A_j} = 0.8$ kg and adults $m_{A_a} = 1.5$ kg. For the base resource, we considered $m_P = 100$ kg. The body sizes for the resource were 0.04, 0.5, 0.7 and 15 kg.

Figura 7. Simulaciones del modelo biomatemático con $b = 3.2$ y $c = 0.7$. Los tamaños corporales para las especies nativas fueron: juveniles $m_{C_j} = 1$ kg y adultos $m_{C_a} = 2.5$. Para las especies invasoras consideramos: juveniles $m_{A_j} = 0.8$ kg y adultos $m_{A_a} = 1.5$ kg. Para el recurso base consideramos $m_P = 100$ kg. Los tamaños corporales para el recurso fueron 0.04, 0.5, 0.7 y 15 kg.

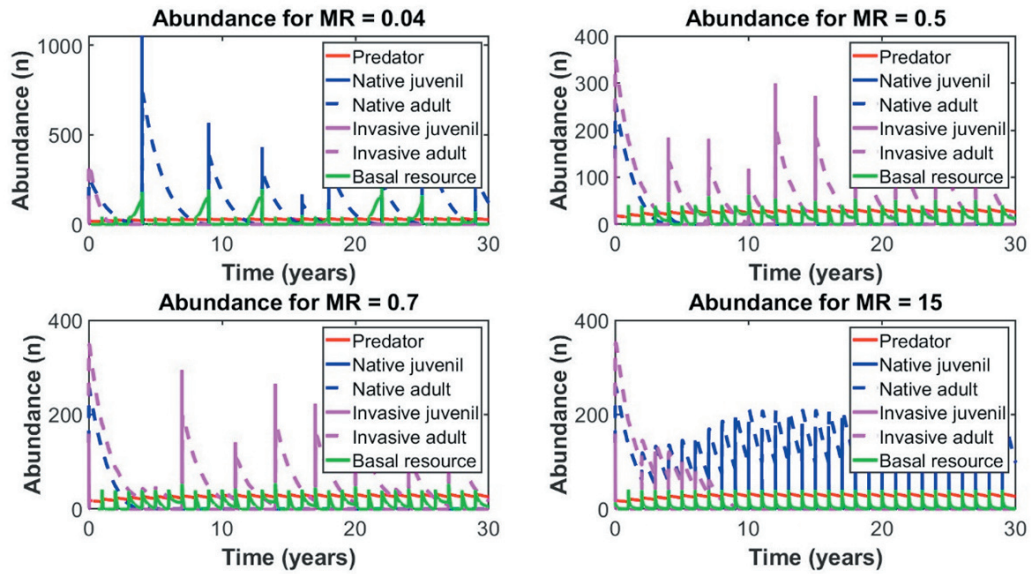


Figure 8. Simulations of the biomathematical model with $b = 4$ y $c = 2.5$. Body sizes for the native species are: juveniles $m_{c_j} = 1$ kg and adults $m_{c_a} = 2.5$. For the invasive species, we consider: for juveniles $m_{A_j} = 0.8$ kg and for adults $m_{A_a} = 1.5$ kg. For the base resource we consider $m_p = 100$ kg. The body sizes for the resource were 0.04, 0.5, 0.7 and 15 kg.

Figura 8. Simulaciones del modelo biomatemático con $b = 4$ y $c = 2.5$. Los tamaños corporales para las especies nativas fueron: juveniles $m_{c_j} = 1$ kg y adultos $m_{c_a} = 2.5$. Para las especies invasoras consideramos: juveniles $m_{A_j} = 0.8$ kg y adultos $m_{A_a} = 1.5$ kg. Para el recurso base consideramos $m_p = 100$ kg. Los tamaños corporales para el recurso fueron 0.04, 0.5, 0.7 and 15 kg.

rate increase, while the mortality rate between consumers and predators decreases. Owing to the age structure, the abundance of primary consumers is bolstered by the addition of new adult individuals: coupled with seasonal births, this resembles the observed demographic patterns in our simulations. We also demonstrate that theoretical invasion conditions represent realistic scenarios for the central-southern region of Chile (e.g., Osorio et al. 2020), and variations in body sizes of top predators lead to a sequence of abundance pattern configurations (Figures 5 through 8).

Our modeling approach may be relevant for research endeavors seeking to identify realistic demographic patterns (Gobin et al. 2022) or to make general predictions about how the species community structure evolves in the long term concerning body size. This becomes particularly pertinent in human-wildlife conflict scenarios (Inskip and Zimmermann 2009), where theoretical models offer novel insights into domestic animal control policies (Beltrami et al. 2021) and native species conservation strategies.

Despite the limitations of our model, such as the lack of representation of competition among primary consumers and the absence of spatial variables or random processes that

influence reproduction or mortality rates due to environmental conditions, the impulsive effect significantly enhances its realism. This impulsive feature enables the integration of life-history traits, such as seasonal births, in the studied species without compromising its general applicability. Our simulations successfully replicated the observed dynamics in nature in the Yukon region, Canada, owing to the impulsive effect embedded in our model (Gilg et al. 2003; Peckarsky et al. 2008; Kreps et al. 2018; Gobin et al. 2022).

The simulations presented in this article, supported by previously published empirical data (Osorio et al. 2020; Gobin et al. 2022), provide a valuable tool for conservation: impulsive models stand out for their ease of application, relying on generally available data and accessible parameters, such as body weight and reproductive features. These models allowed us to anticipate the outcome of species introductions, encompassing their establishment in the environment, the potential coexistence with native competitors, or their invasive potential, which might lead to the extinction of these competitors. Moreover, they could provide a framework for investigating which ranges of body size could drive the extinction of native predators in future studies.

Therefore, impulsive models offer a simple, yet powerful, and effective conceptual framework to study and predict the likely outcomes of invasive species introductions, providing a crucial tool for wildlife managers and policy makers in allocating funds or planning research and management efforts. Furthermore, theoretical models, such as the one discussed in this article, can be effectively integrated with statistical (i.e., empirical) models and analyses, as demonstrated by studies like Beltrami et al. (2020) (free-ranging dogs and native wild carnivores) and Osorio et al. (2020) (exotic prey and native wild carnivores), to explore biological invasions.

In conclusion, species interactions, strongly influenced by body sizes, shape the demographic patterns within communities by modulating conversion efficiency, predation rates, reproduction, and mortality rates. Therefore, body size emerges as a crucial phenotypic trait that helps establish relationships responsible for determining

community structure, even in the context of incorporating invasive species.

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REFERENCES

- Anderson, C. B., G. M. Pastur, M. V. Lencinas, P. K. Wallem, M. C. Moorman, and A. D. Rosemond. 2009. Do introduced North American beavers *Castor canadensis* engineer differently in southern South America? An overview with implications for restoration. *Mammal Review* 39(1):33-52. <https://doi.org/10.1111/j.1365-2907.2008.00136.x>.
- Ballari, S. A., C. B. Anderson, and A. E. Valenzuela. 2016. Understanding trends in biological invasions by introduced mammals in southern South America: a review of research and management. *Mammal Review* 46(3):229-240. <https://doi.org/10.1111/mam.12065>.
- Beltrami, E., N. Gálvez, C. Osorio, M. J. Kelly, D. Morales-Moraga, and C. Bonacic. 2021. Ravines as conservation strongholds for small wildcats under pressure from free-ranging dogs and cats in Mediterranean landscapes of Chile. *Studies on Neotropical Fauna and Environment* 58(1):1-17. <https://doi.org/10.1080/01650521.2021.1933691>.
- Beschta, R. L., and W. J. Ripple. 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biological Conservation* 142(11):2401-2414. <https://doi.org/10.1016/j.biocon.2009.06.015>.
- Binzer, A., C. Guill, U. Brose, and B. C. Rall. 2012. The dynamics of food chains under climate change and nutrient enrichment. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367(1605):2935-2944. <https://doi.org/10.1098/rstb.2012.0230>.
- Buenavista, S., and F. Palomares. 2018. The role of exotic mammals in the diet of native carnivores from South America. *Mammal Review* 48(1):37-47. <https://doi.org/10.1111/mam.12111>.
- Butchart, S. H., M. Walpole, B. Collen, A. Van Strien, J. P. Scharlemann, R. E. Almond, and R. Watson. 2010. Global biodiversity: indicators of recent declines. *Science* 328(5982):1164-1168. [10.1126/science.1187512](https://doi.org/10.1126/science.1187512). <https://doi.org/10.1126/science.1187512>.
- Byrnes, J. E., P. L. Reynolds, and J. J. Stachowicz. 2007. Invasions and extinctions reshape coastal marine food webs. *PLOS ONE* 2(3):e295. <https://doi.org/10.1371/journal.pone.0000295>.
- Campillay-Llanos, W., F. Córdova-Lepe, and F. N. Moreno-Gómez, F. N. 2022. Coexistence, energy, and trophic cascade in a three-level food chain integrating body sizes. *Frontiers in Ecology and Evolution* 10:821176. <https://doi.org/10.3389/fevo.2022.821176>.
- Campillay-Llanos, W., V. Saldaña-Núñez, F. Córdova-Lepe, and F. N. Moreno-Gómez. 2021. Fish catch management strategies: Evaluating the interplay between body size and global warming. *Natural Resource Modeling* 34(4):e12331. <https://doi.org/10.1111/nrm.12331>.
- Castillo, S., M. Pinto, and R. Torres, R. 2019. Asymptotic formulae for solutions to impulsive differential equations with piecewise constant argument of generalized type. *Electronic Journal of Differential Equations*. URL: hdl.handle.net/10877/14749.
- Colwell, R. K. 1989. Hummingbirds of the Juan Fernández Islands: natural history, evolution and population status. *Ibis* 131(4):548-566. <https://doi.org/10.1111/j.1474-919X.1989.tb04790.x>.
- Cruz, L. R., and M. M. Pires. 2022. Body mass ratios determine dietary patterns and help predicting predator-prey interactions of Neotropical Carnivora. *Mammal Research* 67(3):255-263. <https://doi.org/10.1007/s13364-022-00631-9>.
- Cunningham, C. X., C. N. Johnson, and M. E. Jones. 2020. A native apex predator limits an invasive mesopredator

- and protects native prey: Tasmanian devils protecting bandicoots from cats. *Ecology Letters* 23(4):711-721. <https://doi.org/10.1111/ele.13473>.
- Cunningham, C. X., C. N. Johnson, T. Hollings, K. Kreger, and M. E. Jones. 2019. Trophic rewilding establishes a landscape of fear: Tasmanian devil introduction increases risk-sensitive foraging in a key prey species. *Ecography* 42(12):2053-2059. <https://doi.org/10.1111/ecog.04635>.
- Damuth, J. 1993. Cope's rule, the island rule and the scaling of mammalian population density. *Nature* 365(6448): 748-750. <https://doi.org/10.1038/365748a0>.
- Davis, N. E., D. M. Forsyth, and G. Coulson. 2010. Facilitative interactions between an exotic mammal and native and exotic plants: hog deer (*Axis porcinus*) as seed dispersers in south-eastern Australia. *Biological Invasions* 12(5):1079-1092. <https://doi.org/10.1007/s10530-009-9525-1>.
- DeLong, J. P. 2012. Experimental demonstration of a 'rate-size' trade-off governing body size optimization. *Evolutionary Ecology Research* 14(3):343-352.
- DeLong, J. P., T. C. Hanley, and D. A. Vasseur. 2014. Predator-prey dynamics and the plasticity of predator body size. *Functional Ecology* 28(2):487-493. <https://doi.org/10.1111/1365-2435.12199>.
- Dickman, A. J., A. E. Hinks, E. A. Macdonald, D. Burnham, and D. W. Macdonald. 2015. Priorities for global felid conservation. *Conservation Biology* 29(3):854-864. <https://doi.org/10.1111/cobi.12494>.
- Essl, F., S. Bacher, P. Genovesi, P. E. Hulme, J. M. Jeschke, S. Katsanevakis, and D. M. Richardson. 2018. Which taxa are alien? Criteria, applications, and uncertainties. *BioScience* 68(7):496-509. <https://doi.org/10.1093/biosci/biy057>.
- Gigliotti, L. C., L. Keener, L. H. Swanepoel, C. Sholto-Douglas, A. Hunnicutt, and G. Curveira-Santos. 2023. Positive but un-sustained wildlife community responses to reserve expansion and mammal reintroductions in South Africa. *Biological Conservation* 287:110277. <https://doi.org/10.1016/j.biocon.2023.110277>.
- Gilg, O., I. Hanski, and B. Sittler. 2003. Cyclic dynamics in a simple vertebrate predator-prey community. *Science* 302(5646):866-868. <https://doi.org/10.1126/science.108750>.
- Gobin, J., T. J. Hossie, R. E. Derbyshire, S. Sonnega, T. W. Cambridge, L. Scholl, and D. L. Murray. 2022. Functional responses shape node and network level properties of a simplified boreal food web. *Front Ecol Evol* 10:898805. <https://doi.org/10.3389/fevo.2022.898805>.
- González, P., and M. Pinto. 1996. Asymptotic behavior of impulsive differential equations. *The Rocky Mountain Journal of Mathematics* 26(1):165-173. URL: jstor.org/stable/44238007.
- Green, S. J., C. B. Brookson, N. A. Hardy, and L. B. Crowder. 2022. Trait-based approaches to global change ecology: moving from description to prediction. *Proceedings of the Royal Society B* 289(1971):20220071.
- Grigione, M. M., P. Beier, R. A. Hopkins, D. Neal, W. D. Padley, C. M. Schonewald, and M. L. Johnson. 2002. Ecological and allometric determinants of home-range size for mountain lions (*Puma concolor*). *Animal Conservation* 5(4):317-324. <https://doi.org/10.1017/S1367943002004079>.
- Hakl, R., M. Pinto, V. Tkachenko, and S. Trofimchuk. 2017. Almost periodic evolution systems with impulse action at state-dependent moments. *Journal of Mathematical Analysis and Applications* 446(1):1030-1045. <https://doi.org/10.1016/j.jmaa.2016.09.024>.
- Hastings, A., J. E. Byers, J. A. Crooks, K. Cuddington, C. G. Jones, J. G. Lambrinos, and W. G. Wilson. 2007. Ecosystem engineering in space and time. *Ecology Letters* 10(2):153-164. <https://doi.org/10.1111/j.1461-0248.2006.00997.x>.
- Hatton, I. A., A. P. Dobson, D. Storch, E. D. Galbraith, and M. Loreau. 2019. Linking scaling laws across eukaryotes. *Proceedings of the National Academy of Sciences* 116(43):21616-21622. <https://doi.org/10.1073/pnas.1900492116>.
- Inskip, C., and A. Zimmermann. 2009. Human-felid conflict: a review of patterns and priorities worldwide. *Oryx* 43(1): 18-34. <https://doi.org/10.1017/S003060530899030X>.
- IUCN (International Union for Conservation of Nature). 2017. The IUCN Red List of Threatened Species. IUCN, Gland.
- Jansen, B. D., and J. A. Jenks. 2011. Estimating body mass of pumas (*Puma concolor*). *Wildlife Research* 38(2):147-151. <https://doi.org/10.1071/WR10109>.
- Krebs, C. J., R. Boonstra, A. J. Kenney, and B. S. Gilbert. 2018. Hares and small rodent cycles: a 45-year perspective on predator-prey dynamics in the Yukon boreal forest. *Australian Zoologist* 39(4):724-732. <https://doi.org/10.7882/AZ.2018.012>.
- LaBarge, L. R., M. J. Evans, J. R. Miller, G. Cannataro, C. Hunt, and L. M. Elbroch. 2022. Pumas *Puma concolor* as ecological brokers: a review of their biotic relationships. *Mammal Review* 52(3):360-376. <https://doi.org/10.1111/mam.12281>.
- Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62(1):67-118. <https://doi.org/10.2307/2937171>.
- Lu, W., M. Pinto, and Y. Xia. 2022. Smooth stable manifolds for the non-instantaneous impulsive equations with applications to Duffing oscillators. *Proceedings of the Royal Society A* 478(2259):20210957. <https://doi.org/10.1098/rspa.2021.0957>.
- Marquet, P. A. 2002. Of predators, prey, and power laws. *Science* 295(5563):2229-2230. <https://doi.org/10.1126/science.1070587>.
- Monk, J. D., J. A. Smith, E. Donadio, P. L. Perrig, R. D. Crego, M. Fileni, and A. D. Middleton. 2022. Cascading effects of a disease outbreak in a remote protected area. *Ecology Letters* 25(5):1152-1163. <https://doi.org/10.1111/ele.13983>.
- Ortiz, E., R. Ramos-Jiliberto, and M. Arim. 2023. Prey selection along a predators' body size gradient evidences the role of different trait-based mechanisms in food web organization. *PLOS ONE* 18(10):e0292374.

- Osoerio, C., A. Muñoz, N. Guarda, C. Bonacic, and M. Kelly. 2020. Exotic prey facilitate coexistence between Pumas and Culpeo Foxes in the Andes of central Chile. *Diversity* 12(9):317. <https://doi.org/10.3390/d12090317>.
- Peckarsky, B. L., P. A. Abrams, D. I. Bolnick, L. M. Dill, J. H. Grabowski, B. Luttbeg, and G. C. Trussell. 2008. Revisiting the classics: considering nonconsumptive effects in textbook examples of predator-prey interactions. *Ecology* 89(9): 2416-2425. <https://doi.org/10.1890/07-1131.1>.
- Pinto, M., R. Torres, and D. Sepulveda. 2018. Exponential periodic attractor of impulsive Hopfield-type neural network system with piecewise constant argument. *Electronic Journal of Qualitative Theory of Differential Equations* 2018(34): 1-28. <https://doi.org/10.14232/ejqtde.2018.1.34>.
- Pyke, C. R., R. Thomas, R. D. Porter, J. J. Hellmann, S. Dukes, D. M. Lodge, and G. Chavarria. 2008. Current practices and future opportunities for policy on climate change and invasive species. *Conservation Biology* 22(3):585-592. <https://doi.org/10.1111/j.1523-1739.2008.00956.x>.
- Pyšek, P., P. E. Hulme, D. Simberloff, S. Bacher, T. M. Blackburn, J. T. Carlton, and D. M. Richardson. 2020. Scientists' warning on invasive alien species. *Biological Reviews* 95(6):1511-1534. <https://doi.org/10.1111/brv.12627>.
- Ripple, W. J., and R. L. Beschta. 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. *Forest Ecology and Management* 184(1-3):299-313. [https://doi.org/10.1016/S0378-1127\(03\)00154-3](https://doi.org/10.1016/S0378-1127(03)00154-3).
- Ripple, W. J., and R. L. Beschta. 2004. Wolves and the ecology of fear: Can predation risk structure ecosystems? *BioScience* 54(8):755-766. [https://doi.org/10.1641/0006-3568\(2004\)054\[0755:WATEOF\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2004)054[0755:WATEOF]2.0.CO;2).
- Ripple, W. J., and R. L. Beschta. 2012. Trophic cascades in Yellowstone: the first 15 years after wolf reintroduction. *Biological Conservation* 145(1):205-213. <https://doi.org/10.1016/j.biocon.2011.11.005>.
- Ripple, W. J., and E. J. Larsen. 2000. Historic aspen recruitment, elk, and wolves in northern Yellowstone National Park, USA. *Biological Conservation* 95(3):361-370. [https://doi.org/10.1016/S0006-3207\(00\)00014-8](https://doi.org/10.1016/S0006-3207(00)00014-8).
- Ripple, W. J., J. A. Estes, R. L. Beschta, C. C. Wilmers, E. G. Ritchie, M. Hebblewhite, and A. J. Wirsing. 2014. Status and ecological effects of the world's largest carnivores. *Science* 343(6167):1241484. <https://doi.org/10.1126/science.12414>.
- Ripple, W. J., E. J. Larsen, R. A. Renkin, and D. W. Smith. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biological Conservation* 102(3):227-234. [https://doi.org/10.1016/S0006-3207\(01\)00107-0](https://doi.org/10.1016/S0006-3207(01)00107-0).
- Ritchie, E. G., and C. N. Johnson. 2009. Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters* 12(9):982-998. <https://doi.org/10.1111/j.1461-0248.2009.01347.x>.
- Ritchie, E. G., B. Elmhagen, A. S. Glen, M. Letnic, G. Ludwig, and R. A. McDonald. 2012. Ecosystem restoration with teeth: What role for predators? *Trends in Ecology and Evolution* 27(5):265-271. <https://doi.org/10.1016/j.tree.2012.01.001>.
- Rogers, T. L., T. C. Gouhier, and D. L. Kimbro. 2018. Temperature dependency of intraguild predation between native and invasive crabs. *Ecology* 99(4):885-895. <https://doi.org/10.1002/ecy.2157>.
- Samoilenko, A. M., and N. A. Perestyuk. 1995. *Impulsive differential equations*. World Scientific. <https://doi.org/10.1142/2892>.
- Schmidt-Nielsen, K., and S. N. Knut. 1984. *Scaling: why is animal size so important?* Cambridge University Press. <https://doi.org/10.1017/CBO9781139167826>.
- Séguin, A., É. Harvey, P. Archambault, C. Nozais, and D. Gravel. 2014. Body size as a predictor of species loss effect on ecosystem functioning. *Scientific Reports* 4(1):1-5. <https://doi.org/10.1038/srep04616>.
- Sentis, A., C. Gémard, B. Jaugeon, and D. S. Boukal. 2017. Predator diversity and environmental change modify the strengths of trophic and nontrophic interactions. *Global Change Biology* 23(7):2629-2640. <https://doi.org/10.1111/gcb.13560>.
- Shedden-González, A., B. Solórzano-García, J. M. White, P. K. Gillingham, and A. H. Korstjens. 2023. Drivers of jaguar (*Panthera onca*) and puma (*Puma concolor*) predation on endangered primates within a transformed landscape in southern Mexico. *Biotropica* 55(5):1058-1068. <https://doi.org/10.1111/btp.13253>.
- Van de Wolfshaar, K. E., A. M. De Roos, and L. Persson. 2006. Size-dependent interactions inhibit coexistence in intraguild predation systems with life-history omnivory. *The American Naturalist* 168(1):62-75. <https://doi.org/10.1086/505156>.
- Weitz, J. S., and S. A. Levin. 2006. Size and scaling of predator-prey dynamics. *Ecology Letters* 9(5):548-557. <https://doi.org/10.1111/j.1461-0248.2006.00900.x>.
- Wilmers, C. C., Y. Wang, B. Nickel, P. Houghtaling, Y. Shakeri, M. L. Allen, and T. Williams. 2013. Scale dependent behavioral responses to human development by a large predator, the puma. *PLOS ONE* 8(4):e60590. <https://doi.org/10.1371/journal.pone.0060590>.
- Yodzis, P., and S. Innes. 1992. Body size and consumer-resource dynamics. *The American Naturalist* 139(6):1151-1175. <https://doi.org/10.1086/285380>.