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Coexistence, Energy, and Trophic Cascade in a Three-Level Food Chain Integrating Body Sizes

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Predation is a biological interaction that influences demographic patterns by modifying community structure. In the current ecological crisis, there is a need to better understand the conditions of coexistence between predators, prey and their resources. The body size is considered a key feature to explain community-scale phenomena, energetic, and evolutionary constraints. This raises the question of how species body size directly or indirectly affects the demographic patterns that enable coexistence. Considering the above, we conducted a theoretical study that implements a Rosenzweig-MacArthur type model, which represents a three-level chain that integrates body sizes and includes a Holling type I functional response. In this model, we characterize coexistence through body size-dependent net reproductive rates. Our results suggest that the body sizes of consumer species strongly affect the size-density relations and energy requirements. We obtain the negative relationship between body size and density of intermediate consumers and discuss the energy equivalence rule. Furthermore, larger predators have a more significant impact on the intensity of the trophic cascade than smaller predators. Finally, we discuss potential extensions and applications of our modeling approach.

Keywords: community structure, food chain, population density, coexistence, energy use, trophic cascade, allometry, body size

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1. INTRODUCTION

Predation is a biological interaction that impacts community structure (Marquet, 2002; Hatton et al., 2015; Brose et al., 2019) and due to the extinction of large carnivores (Ripple and Beschta, 2007; Atkins et al., 2019) it is reasonable to expect profound modifications to ecosystems (Ripple et al., 2014). Predator density is usually limited by metabolic rate and prey abundance (Carbone and Gittleman, 2002), and the coexistence between predators and prey requires mechanisms that allow for the maintenance of an adequate level of resources for each species to persist (Chesson, 2000). Thus, characterizing population fluctuations through demographic patterns (Barbier and Loreau, 2019) allows assessing the energy requirements used by a community (Damuth, 1987, 1993; Brown, 1995), and the indirect effects of top predators on the basal resource through interaction with some intermediate species, i.e., trophic cascade (Terborgh et al., 2001, 2010). Determining how these phenomena arise from energetic, evolutionary and physiological constraints and inter-species interactions is necessary to understand community structuring processes (Pawar et al., 2015; Momo, 2017; Piovia-Scott et al., 2017).

It has been recorded that body size is allometrically related with basal metabolism, reproduction rate, mortality rate and population abundance. Mathematically it can be expressed as: $Y = b \cdot m^{\alpha}$, where Y is one these biological attributes of interest, b is a species-dependent factor, m is the body size and α is the allometric exponent (Kleiber, 1932; Damuth, 1981; Hatton et al., 2019). For instance, a demographic pattern recorded in empirical research is the "size-density relationship," which indicates a negative relationship between density and average body size (Damuth, 1987, 1993, 2007; Marquet et al., 1990). Interestingly, a recent study suggests that the relationship between body size and population density has changed over a relatively short period of time, a change that the allometric exponent can capture (Santini and Isaac, 2021). This could eventually change body size-dependent coexistence conditions, even impacting the energy requirements used by the species. Furthermore, the indirect phenomena produced in food webs could intensify (Delong et al., 2015). Barbier et al. (2021), using a macroecological approach performed a meta-analysis of predator-prey pairs (mammals, birds and reptiles), and showed that predation rates at the macro level differ from that presented in Lotka-Volterra-type models (the probability of encounters grows as the product of the density of the predator and its prey).

On the other hand, predator-prey interactions have been intensively studied through mathematical modeling (May, 1973; Yodzis and Innes, 1992). Weitz and Levin (2006) using a Rosenzweig-MacArthur type model, incorporating body masses in the parameters obtained the size-density relationship with allometric exponent 3/4. There are strong similarities between empirical patterns and those predicted by mathematical models for carnivorous mammals (Carbone and Gittleman, 2002; Weitz and Levin, 2006; DeLong and Vasseur, 2012). Extending the modeling approach to a three-level food chain (apex predator-consumer-prey) may allow to improve the understanding of fundamental aspects of community structuring, such as species coexistence and the effect of indirect interactions (Rinaldi and De Feo, 1999; Terborgh et al., 2010; Abdala-Roberts et al., 2019).

Size-density relationships are essential for understanding ecosystem functioning, and dynamic models provide us with an adequate description of natural systems. This study presents a theoretical exploration using mathematical models, considering the law of mass action, that integrates species body sizes into a dynamic representing a three-species food chain. The relationships between species' body sizes eventually determine species' coexistence and energetic requirements. In addition, this trait allows identifying the influence and control that species from higher trophic levels exert on species at lower trophic levels. Through mathematical modeling, it is possible to show relationships in simple terms that allow the notions of coexistence, energy and intensity of the trophic cascade to be studied. This contributes to a better understanding of the factors that determine the structuring of communities.

The article is structured in six sections. The second section deals with the presentation of the model. The third section focuses on the dynamic analysis of the model and the determination of coexistence conditions. The fourth section presents a type of invasion criterion and the trophic cascade intensity phenomenon. The fifth section contains the results of the coexistence analysis, energy requirements and trophic cascade intensity. Finally, the sixth section corresponds to a discussion of the results obtained.

2. THE MODEL

We analyze a three-level system of equations of the Rosenzweig-MacArthur-type model. Consider a food chain in the following energy transfer sequence: Resource Consumer Predator, with respective body mass sizes m_R, m_C and m_P and, abundances functions in time represented by $R(\cdot)$, $C(\cdot)$ and $P(\cdot)$, respectively. We write the change in population densities as follows: $dX/dt = G_X \cdot X$, with $X \in \{R, C, P\}$. Where G_X is the per capita growth rate and is described in detail in the following terms:

- **Resource**:

$$\frac{dR}{dt} = G_R \cdot R, \quad G_R := \mathcal{L}(m_R, R) - f_{CR} \cdot \phi(m_C, m_R) \cdot C, \quad (1)$$

where $\mathcal{L}(m_R, R) = r(m_R) \cdot \{1 - R\,/\,K(m_R)\}$ is the logistic type per capita resource rate. The parameters $r(m_R)$ and $K(m_R)$, also denoted by r and K, are considered proportional to $m_R^{\alpha_r - 1}$ and $m_R^{-\gamma}$ respectively (Damuth, 1993), where scale exponents α_r and γ are number in the interval $[2/3, 1]$. In addition, the parameter f_{CR} is linked to consumer predation of the resource but independent of their body sizes or abundances.

- **Consumer**:

$$\begin{aligned} &\tfrac{dC}{dt} = G_C \cdot C, \\ &G_C := e_C \cdot \tfrac{m_R}{m_C} \cdot f_{CR} \cdot \phi(m_C, m_R) \cdot R \\ &-\delta_C \cdot d(m_C) - f_{PC} \cdot \phi(m_P, m_C) \cdot P, \end{aligned} \quad (2)$$

where parameters e_C (related to conversion efficiency) and δ_C (related to mortality) are not masses depend. Moreover, f_{PC} is associated with the top-predation of the consumer and does not depend on their body sizes or abundances. For example, the parameters f_{CR} and f_{PC} are linked to the behavior of the predator and the prey, the hunting strategies of the predator, the movement of the prey, the anti-predator behavior or the physiological stress that the predator exerts on the prey (Schmitz, 2017).

- **Predator**:

$$\frac{dP}{dt} = G_P \cdot P, \quad G_P := e_P \cdot \frac{m_C}{m_P} \cdot f_{PC} \cdot \phi(m_P, m_C) \cdot C - \delta_P \cdot d(m_P), \quad (3)$$

where e_C and e_P are not body sizes depend.

Equations (1–3) articulated in a three-level chain allow to address trophic interactions across different scales of body sizes. This approach contribute to the understanding of complex processes that take place in different ecosystems (Abdala-Roberts et al., 2019). For a better understanding of the results, let's consider the following direction of energy transfer from X to Y, i.e., $X \quad Y$ ($R \quad C$ or $C \quad P$). The conversion efficiency of species Y (C or P)

it is proportional to the quotient, m_X/m_Y, with e_Y as the constant of proportionality. In addition, the per capita mortality rate is proportional, with constant of proportionality δ_Y, to a mass-dependent term $d(m_Y)$ equals to $m_Y^{\alpha_d-1}$, with $2/3 \leq \alpha_d \leq 1$ (Loeuille and Loreau, 2005). These parametric relationships have been corroborated by theoretical and empirical investigations in the context of the metabolic theory of ecology (West et al., 2001; Brown et al., 2004; Savage et al., 2004; Hatton et al., 2019).

In a link $X \quad Y$, the consumption is at a non-negative per capita rate proportional to $\phi(m_Y, m_X) \cdot X$ called a functional response, that allow us to relate predation rate with the abundance of the consumer species, encapsulating physiological and behavioral aspects (Holling, 1959). In empirical research, it has been recorded that these functions also depend on the body sizes of the species (Weitz and Levin, 2006; Kalinkat et al., 2013; Ortiz and Arim, 2016; Pawar et al., 2019).

The parameter $\phi(m_Y, m_X)$ represents the mass-dependent component in the capture efficiency. It is constructed as the product between the probability, $\Pi(m_Y/m_X)$, of successfully killing a prey of body size m_X consumed by a predator of body size m_Y (the probability increases as the predator has more body size) and $I(m_Y, m_X)$ is the interaction rate per unit predator density (Weitz and Levin, 2006; Campillay-Llanos et al., 2021). So, it is

$$\phi(m_Y, m_X) = \Pi(m_Y/m_X) \cdot I(m_Y, m_X). \tag{4}$$

This product has been proposed by Weitz and Levin (2006) and described in detail in Campillay-Llanos et al. (2021). The interaction rate $I(m_Y, m_X) = m_Y^{\beta} \cdot F(m_Y/m_X)$, is a product where β represents the intensity of the predator mass in the interaction and the factor $F(\cdot)$, a positive value, is a scaling function that describes the behavior of the interaction rate relative to the quotient m_Y/m_X. In two extreme cases (domain boundary), $F(\cdot)$ has the necessary properties to ensure that: If $m_Y \ll m_X$ (read the $\ll$ sign as "much less than"), then we have $I(m_Y, m_X) \sim f_0\, m_X^{\beta}$ and on the other extreme, if $m_X \ll m_Y$, we must have $I(m_Y, m_X) \sim f_\infty\, m_Y^{\beta}$, where f_0 and f_∞ are positive constant. In this study, we consider $F(\nu) = f_0/\nu^{\beta} + f_\infty$ and $\Pi(\nu) = 1 - e^{-\nu^2}$, therefore the $\phi(m_Y, m_X)$ model that we will follow for graphics and simulations is:

$$\phi(m_Y, m_X) = (1 - e^{-(m_Y/m_X)^2})[f_0\, m_X^{\beta} + f_\infty\, m_Y^{\beta}].$$

On the other hand, in the absence of apex predators ($P = 0$), the model is expressed by Equations (1) and (2), which is the called Rosenzweig-MacArthur model (Rosenzweig and MacArthur, 1963), that has been proposed and studied by Weitz and Levin (2006). While, in the absence of intermediate consumers and apex predator ($C = P = 0$), the basal resource grows logistically, represented by $dR/dt = \mathcal{L}(m_R, R) \cdot R$.

Table 1 provides a summary of variables and the parameters presented.

TABLE 1 | Definition and description of variables and parameters included into the model.

Variable	Description (name, meaning)
P	Abundance of predators.
C	Abundance of intermediate consumer.
R	Abundance of basal resource.
B_X	$\rho_X \cdot m_X^{\alpha}$. Basal metabolic rate of species X.
r	$r_0 \cdot m_R^{\alpha_r-1}$. Population growth rate.
K	$K_0 \cdot m_R^{-\gamma}$, Damuth's Rule.
$d(m_X)$	$m_X^{\alpha_d-1}$. Mortality rate of species X.
δ_X	Mortality rate of species X when $m_X = 1$.
e_C	Efficiency of conversion of species C when $m_R = m_C$.
e_P	Efficiency of conversion of species P when $m_C = m_P$.
$\phi(m_Y, m_X)$	$\Pi(m_Y/m_X) \cdot I(m_Y, m_X)$. Capture efficiency of species (Y).
$\Pi(\nu)$	$1 - e^{-\nu^2}$. Probability of capturing and killing a body size prey m_X.
$I(m_Y, m_X)$	$m_Y^{\beta} \cdot F(m_Y/m_X)$. Predation intensity on a body size species m_X.
$F(\nu)$	$f_0 + f_\infty \nu^{-\beta}$. Factor that models the size difference between the predator and its prey.
$\Gamma(\nu)$	$(\nu)^{\beta-\alpha} \cdot \Pi(\nu) \cdot F(\nu)$. Regulation factor.
$\mathcal{R}_Y(X)$	$[e_Y \cdot \{m_X/m_Y\} \cdot \phi(m_Y, m_X)] \cdot [\delta_Y \cdot d(m_Y)]^{-1} \cdot X$. Reproductive number.
$\mathcal{R}_R(R, C)$	$\mathcal{L}(m_R, R) \cdot [f_{CR}\phi(m_C, m_R)C]^{-1}$. Effective reproductive number of resource.
G_X	with $X \in \{R, C, P\}$. Per capita growth rate.
$X \quad Y$	Direction of energy transfer from X to Y

3. ANALYSIS OF THE DYNAMICS DEFINED BY MODEL

Let us introduce the reproductive number $\mathcal{R}_Y(X)$ as the average number of predators type Y that one predator leaves while it lives when X is the abundance of prey. Considering this conceptualization, we can mention that the population of apex predators Y (we refer to P or *resp.* C when $P = 0$) increases if $\mathcal{R}_Y(X) > 1$, and decreases if $\mathcal{R}_Y(X) < 1$. More precisely, we have $\mathcal{R}_Y(X) := \mathcal{R}_Y(1) \cdot X$, with

$$\mathcal{R}_Y(1) := \underbrace{[e_Y \cdot \{m_X/m_Y\} \cdot f_{YX} \cdot \phi(m_Y, m_X)]}_{\text{Per-capita natality rate of } Y \text{ if } X = 1} \cdot \underbrace{[\delta_Y \cdot d(m_Y)]^{-1}}_{\text{Average lifetime of a type } Y \text{ animal}} . \tag{5}$$

We also introduce $\mathcal{R}_R(R, C) := \mathcal{L}(m_R, R) \cdot [f_{CR}\phi(m_C, m_R)C]^{-1}$, corresponds to the effective reproductive number of a resource unit when abundance is R and there are C consumers.

In order to have a better control over the signs of the derivatives (increase, balance or decrease) of the system represented by Equations (1–3) we perform algebraic operations to obtain an equivalent system, but in terms of the reproductive numbers:

TABLE 2 | Steady states, existence and positive conditions for the system (Equation 6) with type I functional response.

Name	Equilibria	Existence	Local behavior
Null	$(0, 0, 0)$	Always	Always unstable
Axial	$(K, 0, 0)$	Always	$\mathcal{R}_C(K) < 1$ stable
Predator-free	$(R_*, C_*, 0)$	$\mathcal{R}_C(K) > 1$	$\mathcal{R}_P(C_*) < 1$ stable
Coexistence	(R^*, C^*, P^*)	$\mathcal{R}_C(K) > 1$ & $\mathcal{R}_P(C_*) > 1$	Always stable

$$\begin{cases} \frac{dR}{dt} = G_R \cdot R \; = \; \left\{\mathcal{L}(m_R, R)\left(1 - \frac{1}{\mathcal{R}_R(R,C)}\right)\right\} \cdot R, \\ \frac{dC}{dt} = G_C \cdot C \; = \; \left\{\delta_C \cdot d(m_C) \cdot \left(\mathcal{R}_C(R) - 1\right) - f_{PC} \cdot \phi(m_P, m_C) \cdot P\right\} \cdot C, \\ \frac{dP}{dt} = G_P \cdot P \; = \; \left\{\delta_P \cdot d(m_P) \cdot \left(\mathcal{R}_P(C) - 1\right)\right\} \cdot P, \end{cases} \tag{6}$$

where the state space for the variable (R, C, P) is the set $\Delta = [0, K(m_R)] \times [0, \infty) \times [0, \infty)$.

3.1. Equilibria of Coexistence

In summary, there are at most four equilibrium points, as shown in **Table 2**. According to the per capita growth rate, extinction equilibrium is expected to exist, the absence of the two predators leads to the carrying capacity of the basal resource, the absence of the apex predator generates a two-species dynamic. Finally, the algebraic structure of the equations allows to obtain a unique equilibrium of coexistence. The null equilibrium which is unstable in the $(1, 0, 0)$ direction. The equilibrium $(K, 0, 0)$ is locally asymptotically stable if only if $\mathcal{R}_C(K) < 1$. The equilibrium $(R_*, C_*, 0)$, is an attractor in the dynamics without apex predator. The dynamics of these points are summarized in **Figure 1** and for more details see **Supplementary Material**.

Let us note that concerning the existence of an equilibrium of coexistence, i.e., a triad (R^*, C^*, P^*), such that $R^* \cdot C^* \cdot P^* \neq 0$, this depends on whether an apex predator can on average replicate itself by finding the abundance of consumers in its equilibrium, that is, $\mathcal{R}_P(C_*) > 1$. With this consideration, the unique possibility, adding the condition $\mathcal{R}_C(K) > 1$ is:

$$(R^*, C^*, P^*) = \left(K \cdot \left\{1 - \frac{\mathcal{R}_C(K) - 1}{\mathcal{R}_C(K)\mathcal{R}_P(C_*)}\right\}, \frac{K}{\mathcal{R}_P(K)}, \frac{\{R^* - R_*\}\,\Theta}{R_*}\right), \tag{7}$$

where $\Theta = \delta_C d(m_C) f_{\oplus}^{-1} / \phi(m_P, m_C)$. Note that under the condition $\mathcal{R}_C(K) > 1$, the assumption $\mathcal{R}_C(R^*) > 1$ is equivalent to $\mathcal{R}_P(C_*) > 1$. It is important to note that these net reproductive rates, $\mathcal{R}_C(K)$ and $\mathcal{R}_P(C_*)$, do not monotonically concerning the m_C/m_R and m_P/m_C ratios respectively.

4. INVASION CRITERIA AND TROPHIC CASCADE

4.1. Invasion Criteria

Weitz and Levin (2006) to answer the question: What is the optimal size ratio? propose and study an invasion criterion in a two-trophic level system. This criterion makes it possible to establish that size is linked to an evolutionarily stable strategy (Geritz et al., 1997) in which a predator with specific body size cannot be replaced by any other with different body size. Consider an invasive species with abundance L, of mass m_L that consumes the same resource of abundance C. So, we have the system formed by Equations (1, 3), and

$$\frac{dC}{dt} = \left\{G_C - f_{LC} \cdot \phi(m_L, m_C) \cdot L\right\} \cdot C \quad \text{and} \quad \frac{dL}{dt} = G_L \cdot L, \tag{8}$$

with $(R, C, P, L)(0) = (R^*, C^*, P^*, L_0)$, where, with equivalent meanings of the parameters, $G_L := e_L \cdot \{m_C/m_L\} \cdot f_{LC} \cdot \phi(m_L, m_C) \cdot C - \delta_L \cdot d(m_L)$ and $L_0 > 0$.

The invasion does not occur when $L'(0) = G_L[C(0)] \cdot L_0 < 0$, this is, $G_L[C^*] < 0$. What implies $C^* < 1/\mathcal{R}_L(1)$, if we extend definition (5) to $Y = L$. This is a condition equivalent to write $\mathcal{R}_L(1) < \mathcal{R}_P(1) = 1/C^*$. Thus, the number of native predators left by a predator during its average lifetime must be greater than those left by the invading predator. This number $\mathcal{R}_P(1)$ is greater when C^* is less. Nevertheless, considering $\alpha := \alpha_r = \alpha_d$ and the notation $\nu := m_P/m_C$, we have:

$$C^* = \frac{1}{\mathcal{R}_P(1)} = \frac{\delta_C}{e_C} \cdot m_C^{-(\beta - \alpha + 1)} \cdot \frac{1}{\Gamma(\nu)},$$

where $\Gamma(\nu) = \nu^{\beta - \alpha} \cdot F(\nu) \cdot \Pi(\nu)$ defines the *invasion criteria*. Notice that $\Gamma(\cdot)$ as a function of ν is a positive and unimodal, therefore it reaches a single maximum at a certain ν denoted by ν^*. From an ecological point of view, this maximum corresponds to an evolutionarily stable strategy for which other predators of equal body size cannot invade (Weitz and Levin, 2006).

4.2. Trophic Cascade

Trophic Cascade allows an understanding of the structure and functions of the ecosystem (Terborgh et al., 2010). The study of the intensity of trophic cascades is linked to the regulation of basal resource production through top-down control. For example, trophic cascade intensities can reduce pest abundance and increase agricultural yields, among other benefits that contribute to the well-being of ecosystems (Costamagna and Landis, 2007; Strickland et al., 2013). Trophic cascade intensity T_C is defined as the ratio of the equilibrium abundance of the basal resource R^* (when it occurs with its consumer and a predator) to the equilibrium R_* abundance of the resource (when it occurs only with its consumer); this is, $T_C := R^*/R_*$. As a consequence of the system parameterization, the intensity of the cascade will depend on the net reproductive rates. As expected, in a chain of exclusive consumers, notice that coexistence implies trophic cascade intensity bigger than one. Indeed, from coexistence condition $\mathcal{R}_C > 1$ and $\mathcal{R}_P(C_*) > 1$, we have $R_* < R^*$, more precisely $T_C = 1 + (\mathcal{R}_C(K) - 1)(\mathcal{R}_P(C_*) - 1)/\mathcal{R}_P(C_*)$. Moreover, this top-down forcing correlates positively with both net reproductive rates, $\mathcal{R}_C(K)$ and $\mathcal{R}_P(C_*)$. Then, it is imperative to consider (**Table 3**) when consumer or predator body masses are big.

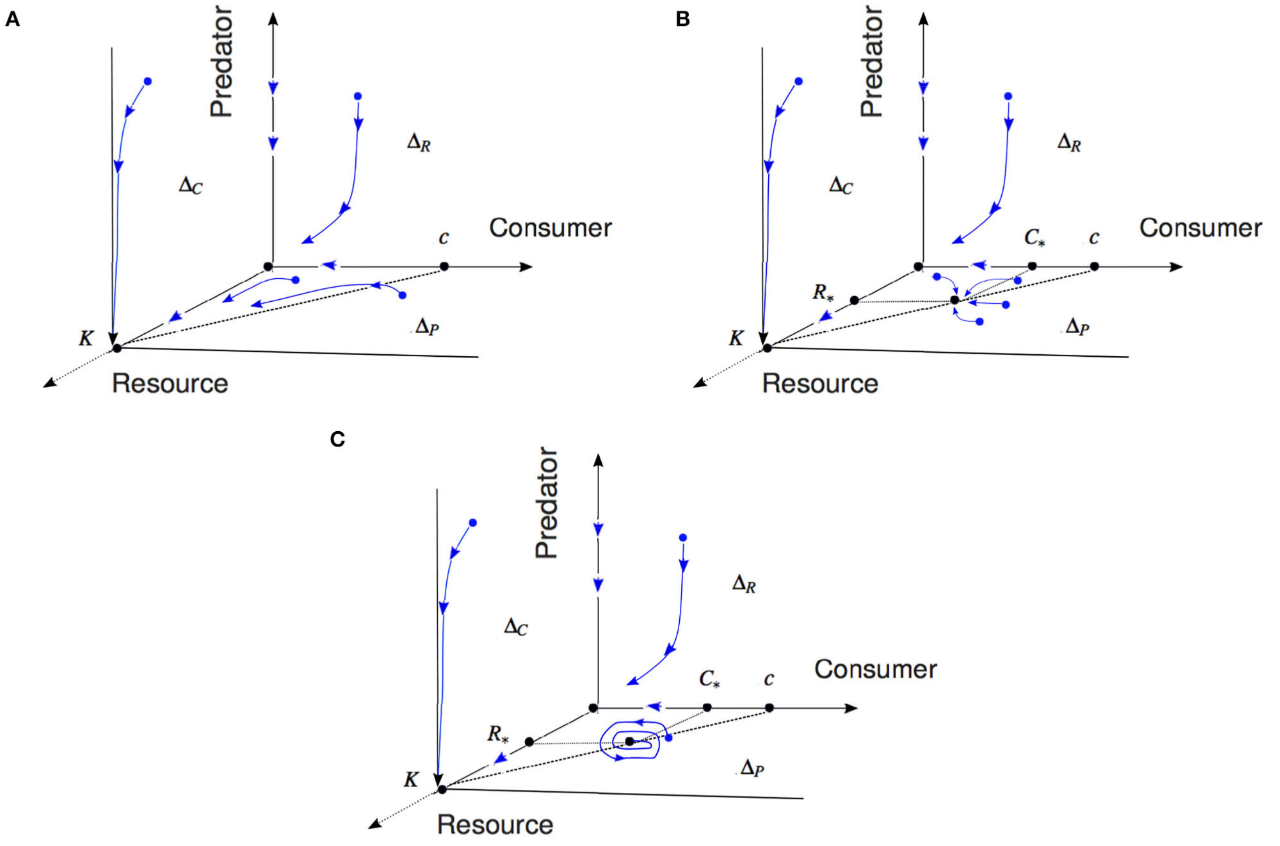

FIGURE 1 | Qualitative analysis of dynamic system. In **(A)**, case $\mathcal{R}_C(K) \leq 1$, the equilibrium $(K, 0, 0)$ attracts all trajectories starting within the $R - C$ plane . When $\mathcal{R}_C(K) > 1$, cases **(B)** or **(C)**, an equilibrium $(R_*, C_*, 0)$ appears on the diagonal line $1 = R/K + C/c$, with $c = r/(f_{CR}\phi)$, which is a global attractor inside the $R - C$ plane. In case **(B)**, defined by $T^2 > 4 \cdot D$ (where T is the trace and D is the determinant of the Jacobian matrix) this equilibrium is a node. In case **(C)**, when $T^2 < 4 \cdot D$, the singularity $(R_*, C_*, 0)$ is a focus (spiral point). For more details see **Supplementary Material**.

TABLE 3 | Limits values of the reproductive numbers (determinants of coexistence) for big body sizes of consumers and predators.

If	$\alpha_r < \beta$	$\alpha_r = \beta$	$\alpha_r > \beta$
$m_C \to \infty$	$\mathcal{R}_C(K) \to \infty$	$\mathcal{R}_C(K) \propto m_R^{-\gamma+1}$	$\mathcal{R}_C(K) \to 0$
$m_P \to \infty$	$\mathcal{R}_P(C_*) \to \infty$	$\mathcal{R}_P(C_*) \propto m_C \cdot C_*$	$\mathcal{R}_P(C_*) \to 0$

5. RESULTS

5.1. Coexistence

According to the system parameters it turns out that the conditions of coexistence and global stability, $\mathcal{R}_C(K) > 1$ and $\mathcal{R}_P(C_*) > 1$, depend on the body size of the species. To highlight the dependence of the body masses (fixing the other parameters), assuming the case $\alpha_r = \alpha_d$, we obtain the results of **Table 3**.

In the case where $\alpha_r < \beta$, fixing the body sizes of the resources and assuming that the predator sizes are extremely large, extremely large reproductive numbers are obtained. That is, giant predators are replaced at an incredible rate, which is not ecologically viable. Moreover, we rule out this case, since this condition implies that there are no body size-optimal predators (Weitz and Levin, 2006). In the second case, $\alpha_r = \beta$. If the body size of consumers is extremely large, the number of secondary predators a predator leaves alive depends on the body size of the consuming species. Although it makes sense, this case makes the mathematical representation difficult. Whereas, under the condition $\alpha_r > \beta$, if the body size of consumers is extremely large, the basic reproduction number is extremely small (close to zero). This situation is of ecological interest and we represent in the **Figure 2**, the space of body sizes that determine the coexistence conditions.

5.1.1. Effects of Predator on Community: Size-Density Scaling

A demographic pattern recorded in empirical research is the "size-density relationship," which indicates a negative relationship between density, D, and average body size value, m (kg). This can be expressed as: $D \propto m^{-3/4}$ (Damuth, 1987, 1993, 2007; Marquet et al., 1990). In our model, the equilibrium abundances of the consumed species correspond to the macroecological pattern that negatively relates density and body size (Kleiber, 1932; Damuth, 1981; Hatton et al., 2019).

Denoting $a_Y = \delta_Y/(e_Y f_{YX})$ for $Y \in \{C, P\}$, and $\eta = (1 + \beta) - \alpha > 0$, we have that

$$R_* = a_C \cdot m_R^{-\eta} / \Gamma(m_C/m_R) \quad \text{and} \quad C^* = a_C \cdot m_C^{-\eta} / \Gamma(m_P/m_C).$$

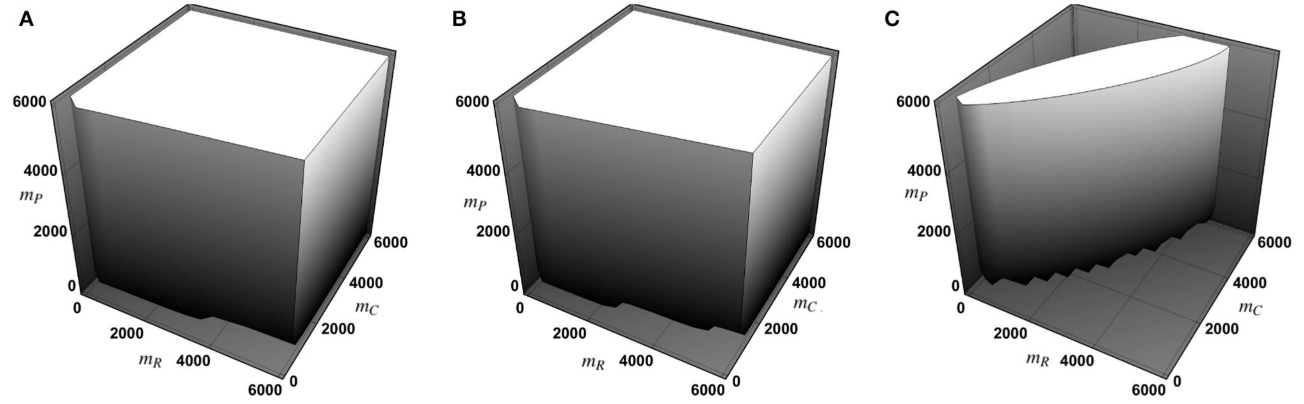

FIGURE 2 | Conditions of coexistence and global stability $\mathcal{R}_C(K) > 1$ and $\mathcal{R}_P(C_*) > 1$ in terms of body sizes m_R, m_C and m_P. **(A)** With allometric exponent $\alpha_r = 2/3$ (surface law), $\gamma = 3/4$ and $\beta = 1/2$. **(B)** With allometric exponent $\alpha_r = 3/4$ (Kleiber's law), $\gamma = 3/4$ and $\beta = 1/2$. **(C)** With allometric exponent $\alpha_r = 1$ (isometry), $\gamma = 3/4$ and $\beta = 1/2$. The other parameter values are: $r_0 = 0.5$, $K_0 = 5$, $e_C = 0.5$, $e_P = 0.5$, $d_C = 0.74$, $d_P = 0.74$, $f_{CR} = 5$, $f_{PC} = 7$, $f_0 = 0.5$ and, $f_\infty = 0.25$.

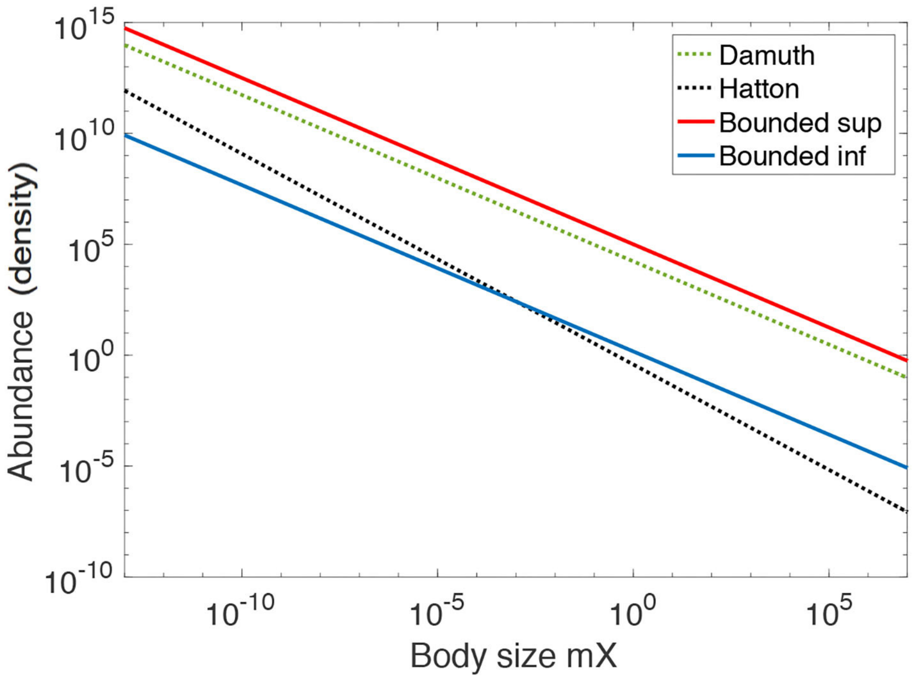

FIGURE 3 | Scaling of density with body size. The green dotted color represents Damuth's rule and the black dotted color represents the adjustment for a large group of species (mammals, plants and ectotherms) made by Hatton et al. (2019). The solid lines red and blue represent the upper and lower bounds of the basal resource used in the inequality 9. The parameter values used are: $\alpha = 3/4$, $\beta = 1/2$, $K_0 = 5$, $\delta_C = 0.74$, $e_C = 10$, $f_{CR} = 0.3$, and $\Gamma(\nu^*) = 1.45$.

Let us note that this is our case for link $X \quad Y$, when $\eta = 3/4$ (i.e., $\alpha_r = 3/4$ and $\beta = 1/2$) and $\Gamma(\nu^*)$ is the maximum value of the regulation factor, reached in the optimal proportion ν^*. This is, $R_* = [a_C/\,\Gamma(\nu^*)] \cdot m_R^{-3/4}$ and $C^* = [a_P/\,\Gamma(\nu^*)] \cdot m_C^{-3/4}$.

This corresponds to the direct effect that apex predators leave on the abundance of their prey. Regarding, the indirect effect of predators on the basal resource, it can be seen in the condition of coexistence in the region Δ, given by $\min\{\mathcal{R}_C(K),\, \mathcal{R}_P(C_*)\} > 1$, which is equivalent to $R_* < R^* < K$, represented in the following inequality: $m_R^{-\eta} \cdot [\Gamma(m_C/m_R)/a_C]^{-1} < R^* < m_R^{-\alpha} \cdot K_0$, which in terms of logarithms can be rewritten as

$$\Lambda_\eta(m_R) - \log(K_0\, \Gamma(m_C/m_R)/a_C) < \log(R^*) < \Lambda_\alpha(m_R), \quad (9)$$

where $\Lambda_z(m_R) = -z \cdot \log(m_R) + \log(K_0)$ and $z \in \{\eta, \alpha\}$.

In the case $\alpha_r = \alpha_d = \gamma = 3/4$ and $\beta = 1/2$, we have $\eta = \alpha$, so it is obtained (in the log-log plane) a band for the estimation of $\log(R^*)$. This is depicted in **Figure 3**. Invasion criteria Γ will determine the band's width. So that, the mass of the population of intermediate consumers, at its optimum, will

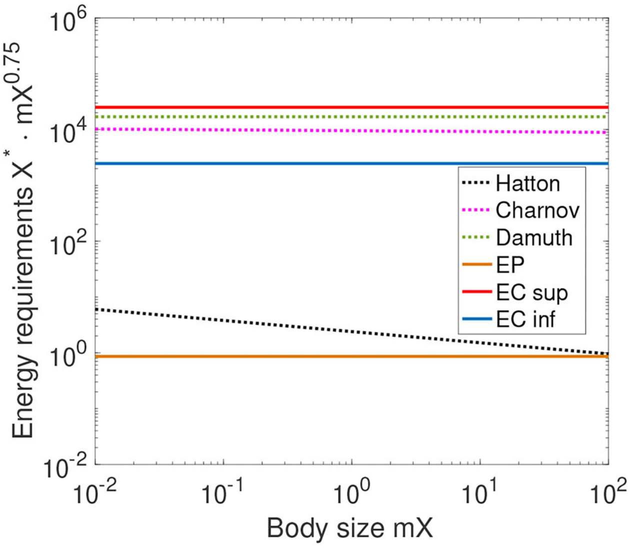

FIGURE 4 | Energy requirements. The green dotted color represents Damuth's rule, the black dotted color represents the adjustment for a large group of species made by Hatton et al. (2019) and the purple dotted represents (Charnov et al., 2001). The solid lines orange, red and blue energy requiriments of apex predator and the upper and lower bounds for consumer. The parameter values used are: $\alpha = 3/4$, $\beta = 1/2$, $K_0 = 5$, $\delta_C = 0.74$, $e_C = 10$, $f_{CR} = 0.3$, $m_R = 1$, $m_C = 2$, $m_P = 8$, $\rho_C = 1.1$, and $\rho_R = 10^{3.7}$. Note that the equilibrium abundance of the consumer is between the upper and lower bounds as well as that of the apex predators.

affect the abundance of the base resource. These results suggest that small variations in basal metabolic requirements α_r, α_d, intensity of predation (β), and demographic changes (γ) change the universal pattern 3/4.

5.2. Energy Requirements

The positive relationship between metabolic rate (B) and body size (m) is presented through the allometric expression $B \propto m^{3/4}$ (Kleiber, 1932; Hatton et al., 2019). The value 3/4, has been widely discussed for its possible universality (Marquet et al., 1995; Medel et al., 1995; Loeuille and Loreau, 2005; Hatton et al., 2019). In addition, considering the above relationships, energy resources are independent of body size if they are estimated as the product of density and metabolic rate. In other words, species of different body sizes use approximately equal amounts of energy (Damuth, 1981). This phenomenon is called the energy equivalence rule (Damuth, 1981, 1987; Isaac et al., 2013; Sewall et al., 2013). However, this notion has been criticized from at least three points of view: (i) empirical data supporting the size-density relationship (Nee et al., 1991; Marquet et al., 1995; Cohen et al., 2003; Russo et al., 2003); (ii) methodological techniques (Medel et al., 1995); and (iii) theoretical foundations (Marquet et al., 1995). In the model, having a prey-predator link $X \quad Y$, usually the energy requirements of a local population of the species Y, denoted by E_Y, can be estimated by the equality $E_Y = X^* \cdot B_X$, with B_X the individual metabolic rate and X^* the equilibrium of the preys. Note that, $B_X = \rho_X \cdot m_X^{\alpha}$, where ρ_X is a constant that depends on the species and α the allometric exponent, commonly associated with the value 3/4, due to the Kleiber rule (Kleiber, 1932; Brown, 1995; Brown et al., 2004). Therefore, the energy requirements of predators, $E_P = C^* \cdot B_C = C^* \cdot \rho_C \cdot m_C^{\alpha}$, for $\alpha := \alpha_r = \alpha_d$, can be expressed through the equation: $E_P = \left[\rho_C \cdot a_P / \Gamma(m_P/m_C)\right] \cdot m_C^{-(\beta-2\alpha+1)}$, showing that the energy requirements explicitly depends on the invasion criteria and therefore of the body size of the predator.

Now, considering that $E_C = R^* \cdot \rho_R \cdot m_R^{\alpha}$, we get the inequality: $\mathcal{E}_C < E_C < \rho_R \cdot K_0$, with $\mathcal{E}_C := \left[\rho_R \cdot a_C / \Gamma(m_C/m_R)\right] \cdot m_R^{-(\beta-2\alpha+1)}$. Then, the regulation factor regulates the lower bound of the energy requirements.

If we consider $\alpha = 3/4$ and $\beta = 1/2$, we have $E_P = \rho_C \cdot a_P / \Gamma(m_P/m_C)$ and $\left[\rho_R \cdot a_C / \Gamma(m_C/m_R)\right] < E_C < \rho_R \cdot K_0$.

The graphical representation of energy requirement quantities is presented in **Figure 4** and is in accordance with field research (Damuth, 1981; Charnov et al., 2001; Hatton et al., 2019). According to these expressions, the energy requirements for intermediate consumers depends on the regulation factor, which is independent of the body size of intermediate consumers. While the energy requirements for intermediate consumers is limited by an expression that is independent of the body size of the species. However, the lower limit depends on the invasion criterion and then on the mass m_C. In the literature, the energy equivalence rule is called the case in which the availability of resources is independent of the body size of the species (Damuth, 1981, 1987, 1993, 2007).

5.3. Trophic Cascade Intensity

We consider the trophic cascade intensity model $T_C := R^*/R_*$ proposed by Borer et al. (2005) and we have $T_C > 1$. Moreover, we obtain that: $T_C = \mathcal{R}_C(K)\left\{1 - f_{CR} \cdot \phi(m_C, m_R) \cdot C^*/r(m_R)\right\}$, that makes ecological sense when $r(m_R) > f_{CR} \cdot \phi(m_C, m_R) \cdot C^*$. Expression equivalent to $f_{CR} \cdot \Gamma(m_C/m_R) \cdot \rho_C \cdot m_C^{\alpha} \cdot C^* \cdot m_R^{1-2\cdot\alpha+\beta} < \rho_C \cdot r_0$. This last condition in terms of the body sizes of the species and energy requirements of apex predators, E_P, is: $E_P < r_0 \cdot \{\rho_C/\rho_R\} \cdot \{e_C/\delta_C\} \cdot \mathcal{E}_C$ or equivalently $E_P < \rho_C \cdot r_0 \cdot m_R^{2\alpha-\beta-1} \cdot f_{CR}^{-1} / \Gamma(m_C/m_R)$. Therefore, for the particular values $\alpha = 3/4$, $\beta = 1/2$ and $\nu^* = m_C/m_R$ it follows that

$$E_P < \rho_C \cdot r_0 \cdot f_{CR}^{-1} / \Gamma(\nu^*). \tag{10}$$

In terms of Equation (10), it is established that the energy requirements of the superior predators are superiorly limited. It is known that the predator determines the architecture of food chains (Brose et al., 2019), thus this upper bound for energy resources may eventually become a biological indicator to quantify how well ecosystems are functioning (Carbone and Gittleman, 2002).

The **Figure 5** corresponds to the T_C function by setting the body size of the intermediate consumers. The left surface is obtained with $m_C = 10$. The right image corresponds to the contour lines of the surface. In this one, the $\mathcal{A}$ region of body sizes is distinguished from the predators and resources that generate the highest intensity of trophic cascade. This result is consistent with empirical research suggesting that food chains with larger predators may experience stronger trophic cascade intensities than food chains with smaller predators (Brose et al., 2006b; DeLong et al., 2015).

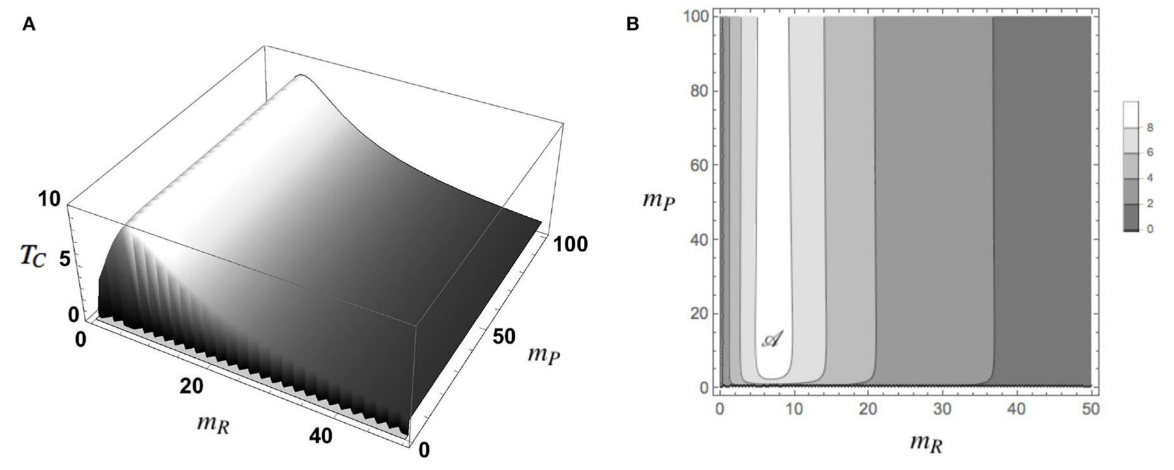

FIGURE 5 | Trophic cascade model with fixed body size of intermediate consumers $m_C = 10$ (*kg*). **(A)** Graph of the trophic cascade intensity considering the body size of fixed intermediate consumers. **(B)** Graph of the level curves of (a). The other parameter values are: $r_0 = 0.5$, $K_0 = 5$, $e_C = 0.5$, $e_P = 0.5$, $d_C = 0.74$, $d_P = 0.74$, $f_{CR} = 5$, $f_{PC} = 700$, $f_0 = 0.5$, and $f_\infty = 0.25$.

6. DISCUSSION

Our model is a straightforward representation of the community dynamics. However, it allowed us to investigate the conditions of coexistence characterized by the net reproductive rates, to study the energy requirements and the intensity of the trophic cascade. The empirical values of the allometric exponents play an essential role in our analysis. As in the existing literature, we assume that $\alpha_r = \alpha_d = \gamma$ equals to 3/4 (Weitz and Levin, 2006; DeLong and Vasseur, 2012; Hatton et al., 2019) and β equal to 1/2 (Weitz and Levin, 2006). In our approach, we used the epidemiological notion of the basic reproductive number (Garrione and Rebelo, 2016) in the context of a three-level food chain. This notion, called net reproductive rate, represents the number of predators that a predator of average body size leaves during its lifetime. Coexistence and overall stability of the system are obtained by considering: $\mathcal{R}_C(K) > 1$ and $\mathcal{R}_P(C_*) > 1$. These rates are not monotonic concerning the m_C/m_R and m_P/m_C ratios respectively. As a consequence, this morphological constraint is associated with the existence of feeding hierarchies (Arim et al., 2007). Moreover, as argued by Weitz and Levin (2006) using the invasion criterion (see Section 4.1), the process of substitution by invading predators of different body sizes through the mechanism of natural selection will converge to an optimal mass size (stable convergent strategy). Thus, we deduce that an invading predator cannot survive in the chain where the native predator settles with the same body size (stable evolutionarily strategy).

Under the condition $\alpha_r > \beta$, our research proposes a space of species body sizes that can be explored in current or past natural environments as indicated in **Figure 2** (Marshall et al., 2021). In this three dimensional space, the value of the allometric exponent α_r represents (a) $\alpha_r = 2/3$, the surface law indicating the surface-volume constraints on heat dissipation over the surface of geometrically similar body planes, (b) $\alpha_r = 3/4$, this value is known as Kleiber's law (Kleiber, 1932) and (c) $\alpha_r = 1$, this value indicates a constant energy flux per unit of tissue mass and is called isometry. In this way, in **Figures 2A,B**, the mass space is similar to a parallelepiped. This space guarantees a variety of body sizes, indicating a greater diversity of species. Whereas in **Figure 2C**, it is observed that a more limited region of body masses is obtained for the first two trophic levels. Under these energetic assumptions, the coexistence region admits apex predators that exceed the size of one of the largest predators that have existed (average body size of Tyrannosaurus rex: 5,200 kilograms, Farlow, 1993). Therefore, our approach may serve to explore current trophic interactions and interactions of species that lived in other geological times.

In relation to demographic patterns, our model allows us to establish that the equilibrium density of intermediate consumers, C^*, is linked to body mass m_C with allometric exponent $-[\beta - \alpha_r + 1]$ (In the absence of apex predators, a similar result is established for R_*). An analysis of a dataset reported by Damuth (1987) reveals that it is appropriate to consider the values of the allometric exponents $\alpha_r = 3/4$ and $\beta = 1/2$ resulting in a negative relationship between density and body size at the second trophic level (herbivorous mammals) with allometric exponent –3/4 (Damuth, 1981). As a result, we obtain that the equilibrium abundance R^* is bounded below and above by body mass-dependent amounts (Damuth, 2001). It should be added that several studies have shown that densities of some species are not proportional to body size in $-3/4$ and even positive relationships between density and body size have been observed (Russo et al., 2003; Maxwell and Jennings, 2006; van Langevelde et al., 2020). Moreover, these relationships can be generated in a non-linear and polygonal fashion (Leaper and Raffaelli, 1999; Andrew and Hughes, 2008). However, **Figure 3** shows that to keep the apex predator population in equilibrium, consumer (C) and resource (R) densities fall between a band that corresponds to a wide number of species.

The demographic patterns analyzed above, multiplied by the individual metabolic rate (Kleiber, 1932) allow estimating the energetic requirements, which represent the resources needed to maintain a population of a given density as proposed in macroecological theory (Brown, 1995). In the model, considering the prey-predator link $X \quad Y$, the energetic requirements of a local population of species Y, denoted by E_Y, are mathematically presented by the product between the prey density X^* and individual metabolic rate B_X ($E_Y = X^* \cdot B_X$). Setting the parameter values: $\alpha_r = \alpha_d = \gamma = 3/4$ and $\beta = 1/2$, it is possible to estimate the energy requirements of the predators, E_P, as shown in **Figure 4**. In the same way as Damuth (1981) has recorded, in our model and with the parameter values specified in the beginning, E_P is set to be independent of the body size of intermediate consumers (Damuth, 1981). This phenomenon is called the energy equivalence rule (Isaac et al., 2013). This implies that body size does not confer advantages in competition for energy use among populations (Isaac et al., 2013; Sewall et al., 2013). Recently, Hatton et al. (2019) have made it clear that the energy equivalence rule persists over a wide taxonomic and body size range. Furthermore, in our model it is possible to estimate the energy requirements of intermediate consumers. As shown in the **Figure 4**, we obtain that E_C is bounded by a lower and upper level of energy resources that does not depend on the body sizes of the basal resource (Damuth, 1987; Marquet et al., 1995; Charnov et al., 2001). The limiting of basal resource densities is linked to alternative assumptions to the energy equivalence rule that energy requirements will increase with body size, decrease with body size or reach a maximum level for a given body size (Sewall et al., 2013). This is consistent with Silva et al. (1997) who argue that species from different trophic groups exhibit different allometric exponents. The mathematical expressions that have been used to perform the analysis of the demographic patterns and energy requirements ($Y = b \cdot m^{\alpha}$), are also called Power Laws (Marquet, 2000; Schneider, 2001). These mathematical relationships describe the behavior of nonlinear interactions, where one dependent variable is expressed as the power of an independent variable and where the exponent value determine the scaling relationship. Power laws are scale invariant, a property that contribute to the understanding of general principles of ecological systems across different levels of organization (Marquet et al., 2005).

On the other hand, predators affect directly the abundance of their prey but this effect can also extend to lower trophic levels indirectly. Considering a three-level chain, the apex predator reduces the abundance of the second level, which in turn allows higher abundances at the lower trophic level. The strength of this indirect interaction measured in terms of abundance differences at equilibrium is called trophic cascade intensity. Piovia-Scott et al. (2017) argue that trophic cascade intensity depends on several species and ecosystem factors. Moreover, multiple models and metrics are used to quantify the intensity of trophic cascades (Leroux and Loreau, 2008). However, it is reasonable to assume that intensity depends on the species' body size (Delong et al., 2015). Our mathematical representation of trophic cascade intensity corresponds to a positive function with varying species body sizes. In agreement, with the coexistence conditions, we require that $R_* < R^*$ so that T_C is greater than 1. In addition, the condition that the energy requirements of apex predators (E_P) are limited is necessary for this model to make ecological sense (i.e., that it is a positive function). This is because the model specifies that consumers are specialists and does not incorporate external food flows. These factors are fundamental to determining the intensity of the cascade and can be modified by incorporating food subsidies at the different trophic levels (Leroux and Loreau, 2008). On the other hand, by setting the mass of intermediate consumers at $m_C = 10$, we hypothesize that in communities larger predators can generate stronger trophic cascade intensities than smaller predators, shown in **Figure 5**. Our results are consistent with empirical research (Brose et al., 2006a; Terborgh et al., 2010) and is reported in Delong et al. (2015). Furthermore, our theoretical contribution by characterizing trophic cascade intensity with the net reproductive rates may eventually support current research on possible mechanisms to explain variation in trophic cascade intensity.

Our research is not without limitations, as our models do not incorporate spatial and/or environmental factors that may contribute to maintaining or modifying demographic patterns. Despite this, we propose that body sizes influence the strength, distribution, and characteristics of interactions: delimit species body size ranges, which determine coexistence, demographic patterns, energetic requirements and the intensity of the trophic cascade inherent to the three-species food chain. It should also be mentioned that body size is a climate-sensitive trait (Binzer et al., 2012; Ohlberger, 2013; McLean et al., 2020). Challenging these complications, we would like to integrate the knowledge of how different types of organisms function in their physical, chemical, and biological environments into these types of ecological-mathematical models, to understand how global changes will affect organisms and biodiversity. Potentially, our research could be used to guide future empirical studies from a macroecological point of view.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

WC-L carried out both the mathematical model and analysis of this and wrote the first draft of the manuscript. All authors contributed to the conceptualization of the study, wrote, reviewed, and edited the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.821176/full#supplementary-material

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