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Effects of predator body size on community dynamics

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Resumen

Understanding the current dynamics and mechanisms that impact the structure of wildlife communities within aquatic or terrestrial environments, are the challenges that ecological science needs to address. The group of species that directly or indirectly interact with other in a given geographical location is called a community. The biological structure of the community is defined as all the species that exist in a given ecosystem and their relative abundance.

Scientific studies have acknowledged the importance of predation within such structure as a function of the various communities that interact. Nowadays, species such as large carnivores are threatened and have experienced a massive worldwide decline in their population sizes and geographical location ranges. If, within a hypothetical scenario, predators become extinct, a chaotic scenario will appear with dramatic consequences such as: the diversity of native species will immediately decrease; the functioning of the natural nutrient cycle will be altered; rivers will seek new channels; and new contagious diseases will emerge even for the human population.

An scientific approach to study such communities is based on trophic chain that can be characterizad by a dynamic system using differential equations. Such a modelling approach allows us a better understanding of the ecological phenomena based on species coexistence, demographic stability and trophic cascade.

This research project aims to analyze the predator mass effect over the conditions and processes that support the stability of natural coexistence amongst species; the demographic stability and the cascade intensity within a three-level trophic chain. The methodology that we intend to use will consider a mathematical modelling tool based on the bifurcation theory. We expect 1) Create three-dimensional representations of the coexistence ranges determined by the body sizes of the species in a three-level trophic chain. 2) Explain the effects of the predator mass on the stable coexistence of the species and demographic stability within a three-level trophic chain. In addition, the study of those phenomena will take into account that predator consume the basal resources. 3) Based on body size of predator, be able to describe the indirect effects over the basal resource, by converting the trophic cascade into a three-level trophic chain. In addition, the study of those phenomena taking into account that predators consume basal resources.

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1. Introduction

Understanding the properties and processes that impact the structure of communities in aquatic and terrestrial environments are current challenges in ecology (Lima 2002; De Mazancourt, 2013; Tilman 2014; Bideault, 2019). The complex relationships between biotic and abiotic factors in a given area occur in an ecosystem. The group of species that interact directly or indirectly is called a community (Smith, 2009). The biological structure of the community is given by all the species present and their relative abundances (Ives, 1999).

Empirical studies have registered the importance of predation in the structure and function of various ecosystems (Atkins, 2019). Currently, species such as large carnivores are threatened and have experienced massive declines in their populations and geographic ranges worldwide (Ripple et al, 2014). If predators become extinct, the diversity of native species will decrease, the functioning of the nutrient cycle will be altered, river flows will change, contagious diseases will proliferate among other consequences (Schmitz, 2010).

An approach to the study of a community is through an object called trophic network (Elton, 1927), which consists of the interconnection of trophic chains. A trophic chain, like the one depicted in Fig. 1, is an abstract description of the nutrient transfer process in which each species feeds on the preceding one and is consumed by the following (Fretwell 1987; Dunne, 2012).

Trophic networks and in particular trophic chains are characterized by a set of structural, functional and dynamically connected properties. Despite this, these properties have been investigated separately, configuring in the literature the energy paradigm and the dynamic paradigm (Barbier et al, 2018). The energy paradigm focuses on static patterns in order to study how energy is distributed across different trophic levels (Lindeman, 1942). While the dynamic paradigm emphasizes temporal patterns and species characteristics, the main focus of interest is stability, cycles, chaos, collapse, the impact of disturbances and behavior. (Saéz y González-Olivares 1999; González-Olivares y Ramos-Jiliberto, 2003; Ramos-Jiliberto, 2003; González-Olivares et al, 2011; Vilches et al, 2018; Rivera-Estay et al, 2020). From a dynamic perspective, there is a wide variety of mathematical models, represented by differential equations, which allow us to understand ecological phenomena such as species coexistence, demographic stability, and trophic cascade.

Coexistence results when populations of several species that use the same limited resources manage to persist in the same location (Smith, 2009). The phenomenon of demographic stability consists of the stability of the patterns of temporal change in population size, its definition can be classified into two categories (Levin et al, 2012), the first based on the stability of a dynamic system (May, 1973) and the second in definitions based on the ability of a system to challenge change, resilience, and resistance (McCann, 2000). The trophic cascade phenomenon (Borer et al, 2005; Wotton et al, 2005; Terborgh y Estes, 2010; Piovia-Scott, 2017) it refers to the indirect effects of a superior

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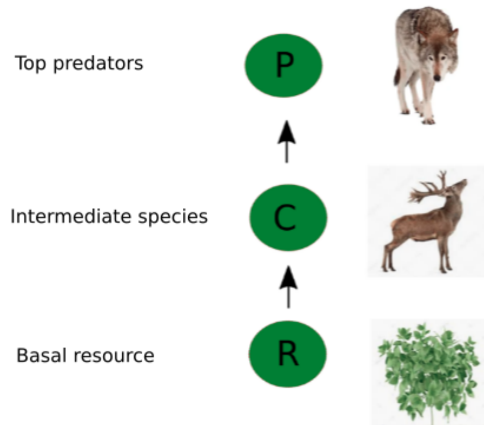

Figura 1: Conceptual diagram showing a trophic chain of three trophic levels. The links are described with arrows that begin in primary producers towards consumers. Species that do not need others to acquire energy are called basal species or basal resources, while species that are not consumed by others are called top predators or higher consumers. The species that are consumers and resources are called intermediate species.

predator on the basal resource, through interaction with some intermediate species, a schematic representation is presented in Fig. 2. The biological control of agricultural pests is an example of an application of trophic cascades to solve practical problems. These issues have been central to the development of current ecological theory, but little has been studied how these phenomena emerge from energetic, evolutionary and physiological restrictions of the species that interact in biological systems (Pawar et al, 2015; Momo, 2017).

These three phenomena depend fundamentally on the forces, distributions and characteristics of the interactions that connect the species in a trophic chain (Kalinkat, 2013). Traditionally, interactions have been classified according to the relationship between the rate of predation and the abundance of resources. This relationship is called a functional response (Holling, 1959) and describes how feeding rates vary according to resources (Williams y Martinez, 2004; Rall et al, 2012). It has also been recorded that one of the drivers of the interaction forces is body size, because this determines the energy requirements and influences the space occupied by the species, the detection of prey, among other aspects (Peter, 1983). Therefore, it is pertinent to include it in the functional responses associated with different dynamics (Yodzis e Innes, 1992; Weitz y Levin, 2006; Otto et al, 2007; Delong y Vaseseur, 2012; Pawar, 2015). This feature is considered an element of the phenotype that has great significance for fitness modifications (Brown et al, 1993). It is also known to determine basal metabolism, growth rate, mortality rate, stationary density of prey in the absence of predators and conversion efficiency (Kleiber, 1932; Calder, 1984; Damuth, 1993; West et al, 2001; Savage et al 2004; Loeuille y Loreau 2005). To articulate the relationship between body size and interactions in a trophic chain, the models used in the dynamic paradigm allow us to study and understand the three phenomena presented.

Weitz and Levin (2006) present a dynamic model of the type Rosenzweig-MacArthur (Rosenzweig y MacArthur, 1963; Turchin, 2003; Sierralta, 1992). This formulation describes that the rate of change of the population of prey dR/dt it is equal to the logistic growth in the absence of predators, less the term of interaction between the species using a linear functional response (Holling type I, 1959) where his inclination ϕ it depends on both the mass of the prey and of the predator, which at the

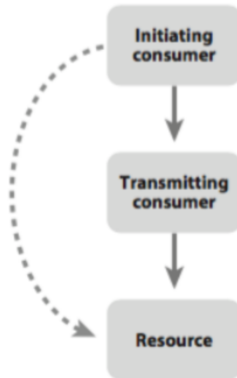

Figura 2: Trophic cascade where solid arrows represent direct negative effects of consumers and the dashed arrow represents a positive indirect effect of the consumer towards the resource.From Piovia-Scott et al. (2017).

same time decomposes in two terms, $\Pi(m_C/m_R)$ which is the probability of successfully killing a prey and $I(m_R, m_C)$ is the interaction rate per unit of density of the predator while the predator population change rate dC/dt is equal to the consumption of prey converted with efficiency ϵ in growth, minus the mortality of predators. This is expressed in the following system of differential equations (1)

$$\begin{cases} \dfrac{dR}{dt} &= r(m_R) \cdot R \cdot \left(1 - \dfrac{R}{K(m_R)}\right) - g(R, m_R, m_C) \cdot C, \\ \\ \dfrac{dC}{dt} &= \epsilon_C \cdot g(R, m_R, m_C) \cdot C - d_C \cdot C. \end{cases} \tag{1}$$

The body size of prey and predators is represented by m_R and m_C respectively. All model parameters are expressed in terms of the body sizes of the species, as detailed in the following table

Table 1. Model parameters. Modified from Weitz and Levin. (2006).

Parameter	Scaling	Meaning
r	$m_R^{\alpha-1}$	Population growth rate.
K	$m_R^{-\alpha}$	Damuth's Rule
d	$m_C^{\alpha-1}$	Mortality rate.
ϕ	$I(m_R, m_C) \cdot \Pi(m_C/m_R)$	Predation rate per unit of prey.
ϵ_C	m_R/m_C	Efficiency of conversion.

In this study, regions are established for coexistence in the mass plane of the prey v / s mass of the predator, determining two-dimensional displays for certain parameter values. For example, in the Fig. 3, for $\alpha = 0{,}75$ and $\beta = 0{,}4$ the red curve encloses a region of coexistence.

Mathematical developments suggest that dynamic models involving only two species may overlook important ecological behaviors (May, 1973; Rosenzweig, 1973; Wollkind, 1976; Hasting, y Powell 1991, Saéz et al, 2015). When adding a trophic level to these systems, the study of coexistence and

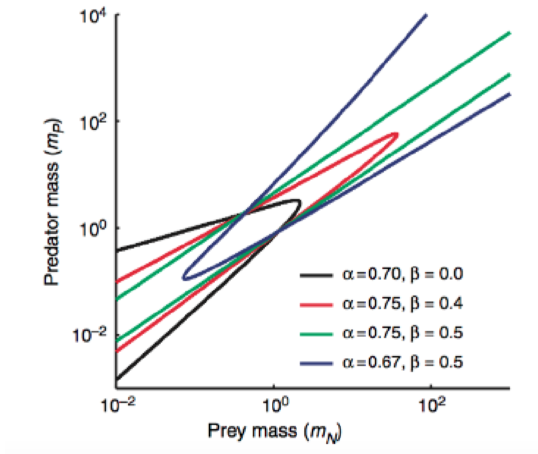

Figura 3: Examples of the size range of predators capable of successfully coexisting with prey. In the figure α is the marginal metabolic rate and β is related to the intensity of the interaction. From Weitz and Levin (2006).

stability requires modern mathematical tools. Using a three-level trophic chain, completely parameterized by the body sizes of the species, Delong et al (2015) characterize the strength of a trophic cascade explicitly in terms of the body size of the predator. The model used is represented by the system of differential equations (2) of continuous time, where each trophic level is represented by an equation, as follows

$$\begin{cases} \dfrac{dR}{dt} = r(m_R) \cdot R \cdot \left(1 - \dfrac{R}{K(m_R)}\right) - a_C \cdot R \cdot C, \\ \\ \dfrac{dC}{dt} = \epsilon_C \cdot a_C \cdot R \cdot C - a_P \cdot C \cdot P - m_C \cdot C, \\ \\ \dfrac{dP}{dt} = \epsilon_P \cdot a_P \cdot C \cdot P - m_P \cdot P. \end{cases} \tag{2}$$

In the model it is presented a basal resource (R) consumed by an intermediate species (C, parameters with subscript c), which is consumed by a predator (P, parameters with subscript p). The growth rate of the basal resource is represented by r and the support capacity by K (Chapman and Byron, 2018). The area of capture or attack efficiency is represented by a, the conversion of prey into new consumers is carried out with efficiency ϵ, and the species die at an intrinsic mortality rate m. This research supports empirical studies that suggest that the loss of larger predators will have greater consequences on the trophic control and structure of the trophic chain than the loss of smaller predators (Elser et al, 1998; Meserve et al, 2003; Brose et al, 2006; Laws y Joern, 2013). In addition, this research provides an important mechanical explanation of trophic cascades on the potential of top-down control that is established by the force of interaction between the first and second trophic levels (van Veen y Sanders 2013), and the magnitude of this effect that depends on the strength of interaction between the second and third trophic levels (Delong, 2015). This type of model allows us to understand and anticipate the consequences of the variation in body size of predators on the ecosystem.

Our goal is to test the following hypothesis: The body size of the predator, by influencing the strength, distributions and characteristics of the interactions, delimits the mass ranges of the species that determine the coexistence, demographic stability and intensity of the cascade inherent in the three-level trophic chain.

2. Mathematical model and methodology

The hypothesis will be validated in an environment modeled by the system of differential equations (3) of continuous time, that represents a three-level trophic chain and incorporates a functional response in both consuming species [1] [5]. The techniques to carry out this study are typical of the bifurcation theory [2] [3] [4], which will be used to detail the local behavior of the equilibrium states, the global flow and stability in order to obtain a qualitative idea of the behavior of the system. The abundance of the basal resource is represented by R that is consumed by an intermediate species C, consumed by a predator P. The trophic chain that this system models is schematically illustrated in Fig. 1.

$$\begin{cases} \dfrac{dR}{dt} &= r(m_R)\cdot R\cdot\left(1-\dfrac{R}{K(m_R)}\right)-\Phi_1(m_R,m_C,R)\cdot C-\Phi_2(m_R,m_P,R)\cdot P, \\ \dfrac{dC}{dt} &= \epsilon_C\cdot\Phi_1(m_R,m_C,R)\cdot C-d_C\cdot C-\Phi_3(m_C,m_P,C)\cdot P, \\ \dfrac{dP}{dt} &= \bar{\epsilon}_P\cdot\Phi_2(m_R,m_P,R)\cdot P+\epsilon_P\cdot\Phi_3(m_C,m_P,C)\cdot P-d_P\cdot P. \end{cases} \tag{3}$$

This system will be studied in three stages. The first stage aims to extend the results of Weitz and Levin (2006) to a system of three species, in this case it is considered $\Phi_2 = 0$. The second stage consists in studying the dynamics using bifurcation theory for the case in which $\Phi_2(\mathrm{i} = 1.3)$ are defined as in the research developed by Delong et al (2015). In this stage, $\Phi_2 = 0$ is considered. The third stage consists of a detailed study of the model, using analytical and computational techniques to determine the conditions of coexistence, local stability, global stability, phase diagram and present bifurcation scenarios using MATCONT (Sahoo and Poria, 2014; Rivera and Aguirre 2019; Sadowski and Grosholz, 2019). These systems can present a chaotic behavior, a phenomenon that has been intensely studied (Schaffer, 1985) and can be controlled with impulse differential equation techniques (Robledo et al 2012, Huang, 2013; Stamova, 2016).

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