



## Original Research Article

## Which functional responses preclude extinction in ecological population-dynamic models?

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## ABSTRACT

The growth and loss terms of interacting populations, called functional responses, are known to have a significant impact on the extinction dynamics of ecological models. We are able to construct models that preclude extinction for any parameter value, simply through the use of particular combinations of functional responses. These structural coexistence (SC) models have functional responses where the *per capita* growth terms remain positive (non-vanishing), while the *per capita* loss terms tend to zero (vanishing) as the relevant population tends to zero. Any of the commonly used functional responses, such as Holling Types I, II, and III, lead to non-vanishing growth terms for nutrient uptake, while any type of nonlinearity such as Ivlev or density dependent mortality of the population leads to vanishing loss terms. In order for herbivore/carnivore feeding terms to simultaneously be a vanishing loss term for the prey and a non-vanishing growth term for the predator, the exponent on the predator population must be exactly one, whilst the exponent on the prey population must be greater than one (such as a Holling Type III response). Any SC system with at least one autotroph and (possibly many) heterotrophs will always possess an internal equilibrium point. We show that the inclusion of linear mortality terms are, however, sufficient to restore the possibility of population extinctions. This allows for the formulation of ‘mixed’ systems, where some populations are guaranteed to coexist, whilst others are subject to the possibility of extinction. SC models have use in studies of, for example, biogeochemical cycling or the plankton base of fisheries models, where extinction is not desirable or relevant.

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## 1. Introduction

Biological systems play a fundamental role in climate dynamics and geochemical cycling (Anderson, 2005). The ecological models used to describe the population dynamics of these systems are typically complex, replete with nonlinear dynamics, and solved numerically. Coexistence in plankton ecosystems has been a contentious topic in theoretical ecology for quite some time. Using the results of laboratory experiments Gause (1934) posited the “principle of competitive exclusion”, which says that the number of populations that can coexist in an environment is equal to the number of ecological niches in the system. Observations of nature, where coexistence of competitors is common, contradict this classical theory leading to Hutchinson’s “paradox of the plankton” (Hutchinson, 1961). The advent of modern computing means that

it is possible to solve mathematical ecosystem models that are far more complex than is possible using traditional analytic techniques (Anderson, 2010). Three dimensional ecosystem models coupled to chemical/physical ocean models, commonly referred to as dynamic green ocean models (DGOMs), are becoming an increasingly important tool in the study of global biogeochemical cycling (Hood et al., 2006; Hashioka et al., 2013; Sailley et al., 2013). The solutions of DGOMs (and other similarly formulated models) are very sensitive to the mathematical form of their nonlinear equations and are prone to instability which, in combination with often poorly constrained parameters, means that inordinate amounts of time and resources are often spent calibrating and validating parameter values (Denman, 2003; Fulton et al., 2003; Anderson et al., 2010). One of the difficulties facing model developers is the *in silico* realisation of competitive exclusion – many simulated planktonic groups experience spurious extinction.

Ecosystem models that use a currency of limiting nutrient and respect local mass balance (which many, if not most, computer

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models of marine ecosystems do) have been constructed to show that in many cases competing populations go extinct (Armstrong and McGehee, 1980), or to ensure *a priori* that no populations go extinct, regardless of the parameter values chosen (Cropp and Norbury, 2012b; Bates et al., 2015). Models that ensure coexistence through their choice of functional response have been dubbed structural coexistence (SC) models. Specifically, SC models have vanishing *per capita* loss terms (i.e. the *per capita* loss term goes to zero as the population goes to zero) and non-vanishing *per capita* growth terms (i.e. the *per capita* growth term remains positive as the population goes to zero). This property ensures that no boundary equilibrium points of an SC model are stable, which then prevents any populations from going extinct. The ease and efficacy of using this approach to construct complex ecosystem models was recently demonstrated by Bates et al. (2015) who developed an SC model with 21 populations to simulate a near shore Antarctic ecosystem and used its boundary equilibrium properties to accelerate the convergence of the parameter calibration.

SC models are useful in studies that require stable populations to recycle various nutrients and chemicals, and for which extinction or invasion events are not relevant. For instance, the model developed by Bates et al. (2015) was used to study the partitioning and recycling of persistent organic pollutants in Antarctic marine environments (Bates et al., submitted to *Environmental Chemistry*). Vallina and Le Quéré (2011) used an SC model to calculate resilience, resistance and interaction strength in six population food-webs. Whilst SC models are useful in the aforementioned types of applications, they are not appropriate in studies where extinction is an important factor.

The aim of this study is to clearly articulate the properties of SC models, what mathematical mechanisms give rise to these properties, and to examine the component functional responses that lead to SC models. In addition, we outline how to construct SC models (including “mixed” models where not all populations have the SC property). To achieve all of this, we examine a number of relatively straightforward (two and three population) illustrative examples. The understanding obtained from these heuristic models gives insight into the properties of more complex models, such as fisheries models or DGOMs. We begin in Section 2 by showing *per capita* population interactions that satisfy local mass balance lead to global mass conservation. The satisfaction of local mass balance means there must be symmetry in the functional responses that describe the interactions of consumers and resources. Familiar mathematical forms, such as Holling Types I, II, and III conform to these requirements. Assuming a closed system (i.e. a constant total amount of limiting nutrient) facilitates mathematical analysis, allowing us to gain insight not otherwise possible in more complex systems.

We then find the small population limit of functional responses that yield SC models. There are a number of studies that have found that Holling Type III grazing (Haydon, 1994; Gentleman et al., 2003; Anderson et al., 2010) and quadratic mortality (Steele and Henderson, 1992; Edwards and Brindley, 1996, 1999) functional responses have a stabilising effect on ecosystem models, leading to a greater probability of population coexistence. In Section 3 we derive the most general forms that ensure coexistence of populations, even when parameters vary greatly.

We also examine the location and properties of equilibrium points in SC models, which is a key question in theoretical ecosystem modelling. By focusing on the boundary equilibrium points (i.e. where one or more populations are zero), we show how to classify the (local) stability of these boundary points in terms of the model parameters. In Section 4 we use this information to ascertain the location and orientation of null surfaces, which we then use to infer the existence of internal equilibrium point(s). This

analysis shows that for systems of autotrophs and heterotrophs (so long as there is at least one autotroph to uptake inorganic nutrient), there is always an internal equilibrium point in these SC models. We also show that ‘mixed’ systems, where some populations are SC and others are not, can be constructed relatively simply, and give an example of that in Section 4.5. These mixed systems are particularly useful for fisheries models where it is important to ensure the existence of the plankton base, but, extinction is an important property to capture for higher trophic populations.

## 2. Model formulation

We utilise the conservative normal (CN) framework (Cropp and Norbury, 2009, 2012a, 2013) in the formulation and analysis of SC models. Formulating our models in the CN framework simplifies the analysis of our models and as such, its utilisation is a matter of analytic convenience. In analogy with mesocosms, which are simpler to control and observe than the natural world, the results we derive here qualitatively apply to more complex models that do not strictly adhere to the CN framework. In this section, we first describe the elements of the CN framework that are most pertinent to our study. Much of what is contained in this section is a summary of existing work, and a more complete description of the CN framework can be found in the aforementioned references.

In many models it is common to use a limiting nutrient (such as nitrogen) as the ‘model currency’ (Denman, 2003). Populations are measured in terms of the total organismal nutrient, rather than biomass or abundance. The *per capita* growth and loss of a population  $j \in 1, 2, \dots, n$  is given by

$$\frac{1}{\tilde{x}_j} \frac{d\tilde{x}_j}{dt} = \hat{f}_j(\tilde{x}_1, \tilde{x}_2, \dots, \tilde{x}_n, \tilde{N}) \quad (1)$$

where  $\tilde{x}_j$  is the total organismal nutrient of the population,  $\tilde{N}$  is the amount of abiotic nutrient, and  $n$  is the number of interacting populations in the ecosystem. The ‘life function’,  $\hat{f}_j$ , describes the various *per capita* growth and loss processes. Whilst the term ‘*per capita*’ typically means per individual, here we take it to mean any of per unit mass, density, or concentration of nutrient.

The life function, which has units of inverse time, can be divided into four parts: (1) growth from inorganic nutrient uptake ( $\hat{h}_j$ ), (2) growth from feeding ( $\hat{g}_{ij}$ ), (3) loss from being fed upon ( $\hat{p}_{jk}$ ), and (4) other losses ( $\hat{m}_j$ ), such as natural mortality,

$$\begin{aligned} \hat{f}_j(\tilde{x}_1, \tilde{x}_2, \dots, \tilde{x}_n, \tilde{N}) = & \hat{h}_j(\tilde{x}_1, \tilde{x}_2, \dots, \tilde{x}_n, \tilde{N}) \\ & + \sum_{i \in \mathbf{i}_j} \hat{g}_{ij}(\tilde{x}_1, \tilde{x}_2, \dots, \tilde{x}_n) - \sum_{k \in \mathbf{k}_j} \hat{p}_{jk}(\tilde{x}_1, \tilde{x}_2, \dots, \tilde{x}_n) \\ & - \hat{m}_j(\tilde{x}_j), \end{aligned} \quad (2)$$

where  $\mathbf{i}_j$  is a list of populations that  $j$  feeds upon, and  $\mathbf{k}_j$  is a list of populations that feed upon  $j$ . Conventionally subscripts are ordered in ascending trophic level, usually leading to  $\mathbf{i}_j \subset \{1, 2, \dots, j-1\}$  and  $\mathbf{k}_j \subset \{j+1, j+2, \dots, n\}$ . All of the functions  $\hat{h}_j$ ,  $\hat{g}_{ij}$ ,  $\hat{p}_{jk}$ , and  $\hat{m}_j$  must be positive for sensible values of  $\tilde{x}_1, \tilde{x}_2, \dots, \tilde{x}_n$  [see Eq. (11) and surrounding discussion for what we mean by ‘sensible values’].

Any model whose currency is nutrient should respect local mass balance, that is, nutrient cannot be created, destroyed, or lost when it is transferred between the various populations or between a population and the abiotic nutrient pool. A corollary of local mass balance is that losses from one population must be precisely balanced by growth in another population and/or the abiotic nutrient pool. As a consequence there must be some symmetry in the equations describing the rate of change of the various

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