**The mechanisms of coexistence and competitive exclusion in complex
plankton ecosystem models.**

SHORT TITLE: Competition and coexistence in ecosystem models

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ABSTRACT

The biodiversity of plankton ecosystems may no longer be a paradox, but the mechanisms that determine coexistence of explicit competitors in ecosystems remain a mystery. This is particularly so in ecosystem models, where competitive exclusion remains the dominant process. Climate and fisheries models require plankton ecosystem sub-models that maintain competing plankton functional types extant, but coexistence can be reproduced in only a few ‘just so’ theoretical models. This limits our ability to predict the impacts of climate change and fisheries on ocean biota. We consider ecosystems of Kolmogorov form that conserve mass (CK systems). These systems describe a general class of ecosystem models that includes many theoretical and applied models. We develop heuristics that illuminate the key mechanisms that allow the coexistence of explicit competitors in these systems. These heuristics facilitate the identification of a large class of models with the structural property that all species coexist for all time. Our approach unifies many theoretical and applied models in a common biogeochemical framework, providing a powerful tool with the potential to generate new insights into the properties of complex ecosystems.

KEYWORDS: Competitive exclusion

 Coexistence

 Plankton functional type model

 Long-term low-density growth rate

Keystone species

Trophic cascade

Introduction

The principle of competitive exclusion (Gause, 1934; Hardin, 1960) states that the number of species in an ecosystem cannot exceed the number of resources. The apparent exception to the principle obvious in plankton ecosystems led Hutchinson to pose the ‘paradox of the plankton’ (Hutchinson, 1961). While perhaps no longer paradoxical, in theoretical and applied plankton ecosystem models competitive exclusion remains the dominant outcome of explicit competition for resources (Tilman, 2007; Cropp and Norbury, 2009a). These models have contributed little to understanding of competition. The mechanisms that allow explicit competitors to coexist on limited resources in the constant, homogeneous environments found in much of the upper ocean hence remain a mystery (Tilman, 2007).

A changing climate presents major theoretical and social challenges to predict the response of plankton ecosystems to changes in ocean stratification, acidity, nutrient regimes and other anthropogenic pressures that may have important implications (Montes-Hugo et al., 2009; Boyce et al., 2010). The robust plankton functional type (PFT) models needed to simulate the role of plankton ecosystems in gas exchange between the ocean and atmosphere (Le Quéré et al., 2005), and to facilitate whole-of-ecosystem approaches to fisheries management (Rose et al., 2010), still labour under the constraint of competitive exclusion. The theoretical coexistence of competitors has been demonstrated for special cases that include internal chaotic dynamics (Huisman and Weissing, 1999), external forcing (Ebenhoh, 1988), spatiotemporal effects (Petrovskii et al., 2003) and interaction effects such as prey-switching

by predators (Krivan, 2003). However, these solutions can be delicate (Schippers et al., 2001), and have failed to provide robust heuristics for constructing complex PFT models.

Consequently, the current generation of PFT models commonly maintain species alive in computer simulations by not allowing populations to fall below prescribed levels (Cropp and Norbury, 2009a).

Here, we analyse a broad class of ecosystem models to demonstrate the mechanisms of coexistence in these models. We consider Kolmogorov systems (Kolmogorov, 1936), that is systems of equations that can be written in the form $\dot{u}_i = f_i u_i$, and we impose the additional property that they conserve mass. Many theoretical ecosystem models are two-component Kolmogorov systems (Huang and Zhu, 2005), and many applied simulation models of plankton ecosystems, that typically have many more than two components (Spitz et al., 2001; Franks, 2002; Vallina et al., 2008), are also Kolmogorov systems. These latter systems also commonly conserve the mass of the limiting nutrients as marine plankton ecosystems tightly cycle nutrients within the upper ocean. The key properties of mass-conserving Kolmogorov systems (which we shall hereafter denote as *CK* systems) are that the species populations in the model are measured in the same currency (often the mass of limiting nutrient) and that the model conserves that currency.

We use the properties of *CK* systems to develop a unifying framework that allows the factors controlling competition and coexistence in theoretical and applied ecosystem models to be explicitly articulated regardless of model complexity. We derive analytic expressions that describe the potential for species to successfully compete and show that these are easily obtained for even the most complex ecosystem model. These expressions exactly describe the ‘long-term low-density growth rates’ central to invasion theory (Law and Morton, 1996;

Chesson, 2000) and may provide general insights into competition properties of many ecosystems.

Conservative Kolmogorov (CK) systems

CK systems are dynamical systems of coupled ordinary differential equations in which each equation that describes the change in the population of a species may be written in the Kolmogorov form:

$$\dot{u}_i = f_i(u_1, u_2, \dots, u_n)u_i \quad i = 1, 2, \dots, n, \quad (1)$$

where each species is represented by a state variable $u_i(t)$, defined for $t > 0$, and where

$\dot{u}_i \equiv \frac{du_i}{dt}$. The equations are written in a currency of mass of limiting inorganic nutrient and

explicitly resolve competition for the limiting nutrient. Together, the state variables completely describe the state of the system at any time. The total nutrient (N_T) contained in the system is constant, which implies the redundant state variable (N) that describes the quantity of inorganic nutrient available for autotroph growth at any time:

$$N = N_T - u_1 - u_2 - \dots - u_n \Leftrightarrow \dot{N} = -\dot{u}_1 - \dot{u}_2 - \dots - \dot{u}_n. \quad (2)$$

These two key properties, Kolmogorov form (equation (1)) and conservation of mass (equation (2)), provide definitive criteria according to which any ecological model may be classified independently of the specific form of the right-hand sides of the equations. For any CK system we may then derive analytic expressions that describe the mechanisms of competition and allow us to predict the outcomes of explicit competition in these models. We can then develop heuristics that allow us to construct complex ecosystem models in which the outcomes of competition are determined *a priori*. We will show that these heuristics depend

explicitly on the forms of the terms that make up the right-hand sides of the model equations. Prior to articulating these heuristics, we must discuss some of the basic properties of *CK* systems.

Ecological state space

We consider non-dimensionalised systems in which each species population is represented as a proportion of the total nutrient pool, which has been scaled so that $N_T = 1$. An ecological state space with all species $0 \leq u_1, u_2, \dots, u_n \leq 1$, that contains all possible states of the system, including extinction of some or all species, is consequently defined. Since N must satisfy $0 \leq N \leq N_T = 1$, we see that there is a ‘lid’ $u_1 + u_2 + \dots + u_n = 1$ to our state space in the positive region $u_i \geq 0$ for all i . This lid defines an “ecospace” within the state space as it constrains population sizes to ecologically realistic levels and represents a whole-of-ecosystem carrying capacity. Time is measured relative to a typical dominant autotroph growth rate, so in our non-dimensional *CK* systems the biomass of the species, the parameters and time do not have units.

The per capita change over time of each species population ($\frac{1}{u_i} \dot{u}_i$) is represented by a life function (f_i) that describes the per capita growth and the losses to predation, respiration and natural mortality of each species. The life functions are comprised of the state variables $u_1, u_2, \dots, u_n$, and parameters that describe the attributes of the species and how they interact.

Equilibrium Points and Stability of *CK* systems

Equilibrium points $\{u_i^*\}$ in ecosystem models (also variously called critical or steady state points) are points where the state of the system does not change in time (i.e. $\dot{u}_i = 0$ for all i).

A *CK* system with n species has 2^n sets of n equations that describe its equilibrium points

$\{u_i^*\}$, $i = 1, 2, \dots, n$, that could exist in the n -dimension ecospace. This large number of sets arises because there are two ways in which the right-hand side of each of the n equations may equal zero: if $u_i = 0$ or if $f_i = 0$. Each of these sets of equations may define single or multiple points within the ecospace, single or multiple points outside the ecospace, or single or multiple points that collapse to the same physical location as points defined by other sets of equations.

All n -species *CK* systems have at least $2^n - 1$ extinction equilibrium points where one or more species are extinct (i.e. $\{u_i^* = 0\}$ for some i) including the origin of the ecospace, defined by $\{u_i^* = 0\}$ for all i where all species are extinct. They also have one coexistence equilibrium point, defined by $\{u_i^* \neq 0\}$ for all i , where all species coexist, although this does not necessarily reside within the ecospace. The number, location and stabilities of the equilibrium points that exist in the ecospace depends on both the formulations of the life functions (f_i) and the values assigned to their parameters. The stabilities of the equilibrium points are crucial to our analysis of the mechanisms of coexistence; we therefore define stability carefully to be the Lyapunov (local) stability of an equilibrium point. Lyapunov stability is determined by the eigenvalues of the Jacobian (or community) matrix (J) of the system evaluated at the equilibrium point (May, 1973; Kot, 2001).

Equilibrium points, which may have complex eigenvalues, are stable in the Lyapunov sense if the real parts of all the eigenvalues are negative. Unstable equilibrium points have at least one eigenvalue with a positive real part. The state of a system is attracted to a stable equilibrium point from nearby states, and hence returns to a stable point if perturbed away from it. An unstable equilibrium point may initially attract the state of the system, but will always ultimately repel it in experiments, mathematically and computationally, provided that very

small species populations are treated sufficiently accurately in computations. Unstable equilibrium points may possess nearby stable limit cycles, where the system stably orbits near the equilibrium point but never converges to it. These stable limit cycles arise from complex eigenvalues with positive real parts, but these, and other possibilities such as eigenvalues with zero real parts, do not affect our analysis.

Extinction in ecosystem models

Extinction in mathematical models of ecosystems occurs if a model has an extinction point (an equilibrium point at which a variable u_i representing a species equals zero) that is stable. Generally, analytic expressions for the eigenvalues (λ_i) of the Jacobian matrix of a system, that determine the stability of equilibrium points, are available only for very simple ecosystem models. However, *CK* systems have the property that we can always find an analytic expression for the eigenvalue λ_j associated with a species u_j at an extinction point, where $u_j^* = 0$. This is given by the value of its life function evaluated at the extinction point, that is $\lambda_j = f_j^*|_{u_j=0}$.

These competition eigenvalues determine the potential for a species to compete successfully with established species and grow from very low population levels. If the competition eigenvalue of a species is positive it can survive in or invade an established system; if negative, any invasion attempt will fail and the species will go extinct. Extinction will not occur in an ecosystem model if all the extinction points of the model have at least one positive competition eigenvalue. Analytic expressions for competition eigenvalues are uniquely identified and easily determined for a *CK* system of any size and complexity, and this is the key attribute that makes *CK* systems ideal for investigating competition in complex ecosystem models.

A spectrum of *CK* systems

We first identify two fundamental types of *CK* systems that are the end members of a spectrum of *CK* systems that have the property that all species remain extant. We define *sCK* systems to have the *structural* property that all competition eigenvalues are positive at every extinction point, and *pCK* systems to be systems that are *parameterized* so that at least one competition eigenvalue is positive at every extinction point. We will show that coexistence is a robust property of *sCK* systems that holds for any reasonable parameter set, but is conditional in *pCK* systems and holds only for carefully chosen parameter sets.

To succinctly articulate the key attribute of the function forms that determines whether a system will have structural or contingent coexistence, we must distinguish between functional forms in the life function f_i that tend to zero as u_i tends to zero from those that do not. We shall use “vanishing” to describe a functional form that describes a process in the life function f_i if the value of the functional form tends to zero as the population $u_i \rightarrow 0$. Similarly, we shall use “non-vanishing” to describe terms that do not have this property. Clearly, a functional form in f_i will be vanishing if u_i can be factored out, and will be non-vanishing if it cannot.

The structural properties of *sCK* systems are ensured if every species has non-vanishing growth processes coupled with vanishing loss processes. Non-vanishing growth processes include Droop, Michalis-Menten, Holling Type II and Lotka-Volterra growth while vanishing loss processes include Holling Type III grazing and nonlinear mortality (Holling, 1965; Steele and Henderson, 1992; Edwards and Bees, 2001; Gross et al., 2009). All these forms are commonly used in both theoretical and applied ecosystem models, and we note that species with non-vanishing growth and vanishing loss processes have been reported in real ecosystems (Ohman and Hirche, 2001).

pCK systems are composed of species that have at least one non-vanishing loss term, for example Holling type I or II grazing, or linear mortality. We shall demonstrate that *pCK* systems have the potential for much more varied properties than *sCK* systems, but note they are more difficult to construct, as they require the locations of all boundary and interior equilibrium points in the ecospace to be known so that the sign of every competition eigenvalue at every extinction point may be evaluated. Therefore, while it is possible that a *pCK* system could be parameterised to have the same properties as the equivalent *sCK* system, in practice this would be quite difficult for anything other than simple models. We demonstrate some properties of *pCK* and *sCK* systems by considering exemplar end-members of the spectrum of *CK* systems.

Example *pCK* and *sCK* models

We consider *CK* models of four plankton functional types (PFTs) belonging to two trophic levels in a stable, homogeneous environment with a single limiting nutrient. We stipulate that u_1 is a phytoplankton functional type (pPFT) and allow u_2 , u_3 and u_4 to be either pPFTs or zooplankton functional types (zPFTs). We allow mixotrophy and omnivory so that the food web is potentially fully connected (Figure 1).

The example models (equations (9) - (12)) are constructed from process formulations common to both theoretical and applied ecosystem models. Definitions of all parameters and ranges for their non-dimensional values are given in Table 1. The growth of autotrophs is represented in the autotroph life functions in both *pCK* and *sCK* models by non-vanishing Michaelis-Menten nutrient uptake kinetics:

$$g_i(u_1, u_2, u_3, u_4) = \frac{\mu_i N}{N + \kappa_i}, \quad (3)$$

where μ_i is the maximum growth rate of i , κ_i is the nutrient uptake half-saturation coefficient and we recall that $N = 1 - u_1 - u_2 - u_3 - u_4$. Predation terms, which include mixotrophy and omnivory, on all prey in the pCK models are represented by Lotka-Volterra interactions, where for predation of u_j on u_i these appear in the prey equations as non-vanishing loss terms:

$$p_{ij}(u_j) = \varphi_{ij} u_j, \quad (4)$$

where φ_{ij} is the maximum rate of predation of u_j on u_i , and in the corresponding predator equation as non-vanishing growth terms:

$$g_{ij}(u_i) = \varphi_{ij} (1 - \psi_{ij}) u_i, \quad (5)$$

where ψ_{ij} is an assimilation efficiency for consumption of u_i by u_j .

Predation terms are described in the sCK systems by Holling Type III interactions; for predation of u_j on u_i these appear in the prey life functions as vanishing loss terms:

$$p_{ij}(u_1, u_2, u_3, u_4) u_i = \frac{\varphi_{ij} u_j}{u_i^2 + \kappa_{ij}} u_i, \quad (6)$$

where κ_{ij} is the half-saturation constant for predation of u_j on u_i , and in the corresponding predator life function as non-vanishing growth terms:

$$g_{ij}(u_1, u_2, u_3, u_4) = \frac{\varphi_{ij} (1 - \psi_{ij}) u_i^2}{u_i^2 + \kappa_{ij}}. \quad (7)$$

Natural mortality/respiration for all functional types in all models is formulated as:

$$m_i(u_i) = \sigma_i u_i^\gamma. \quad (8)$$

where σ_i is the mortality rate of u_i . $\gamma = 0$ results in non-vanishing mortality in the *pCK* models, while $\gamma = 1$ represents vanishing mortality in the *sCK* models.

The *sCK* models are then composed of equations of the form:

$$\frac{dP_i}{dt} = \left(\frac{\mu_i N}{N + \kappa_i} + \sum_{h=1}^{i-1} \frac{\hat{\phi}_{hi} (1 - \psi_{hi}) P_h^2}{P_h^2 + \hat{\kappa}_{hi}} - \sum_{j=i+1}^x \frac{\hat{\phi}_{ij} P_i P_j}{P_i^2 + \hat{\kappa}_{ij}} - \sum_{k=1}^y \frac{\phi_{ik} P_i Z_k}{P_i^2 + \kappa_{ik}} - \sigma_i P_i \right) P_i, \quad (9)$$

$$\frac{dZ_k}{dt} = \left(\sum_{i=1}^x \frac{\phi_{ik} (1 - \psi_{ik}) P_i^2}{P_i^2 + \kappa_{ik}} + \sum_{p=1}^{k-1} \frac{\tilde{\phi}_{pk} (1 - \tilde{\psi}_{pk}) Z_p^2}{Z_p^2 + \tilde{\kappa}_{pk}} - \sum_{q=k+1}^y \frac{\tilde{\phi}_{kq} Z_k Z_q}{Z_k^2 + \tilde{\kappa}_{kq}} - \tilde{\sigma}_k Z_k \right) Z_k, \quad (10)$$

where pPFTs are represented by P_i , and zPFTs are represented by Z_k .

The *pCK* models are composed of equations of the form:

$$\frac{dP_i}{dt} = \left(\frac{\mu_i N}{N + \kappa_i} + \sum_{h=1}^{i-1} \hat{\phi}_{hi} (1 - \hat{\psi}_{hi}) P_h - \sum_{j=i+1}^x \hat{\phi}_{ij} P_j - \sum_{k=1}^y \phi_{ik} Z_k - \sigma_i \right) P_i, \quad (11)$$

$$\frac{dZ_k}{dt} = \left(\sum_{i=1}^x \phi_{ik} (1 - \psi_{ik}) P_i + \sum_{p=1}^{k-1} \tilde{\phi}_{pk} (1 - \tilde{\psi}_{pk}) Z_p - \sum_{q=k+1}^y \tilde{\phi}_{kq} Z_q - \tilde{\sigma}_k \right) Z_k, \quad (12)$$

where in both models x is the number of pPFTs, y is the number of zPFTs, $h, i, j \in [1, 2, \dots, x]$,

$k, p, q \in [0, 1, \dots, y]$, $x \in [1, 2, 3, 4]$, $y \in [0, 1, 2, 3]$ and $x + y = 4$.

We consider four cases each of both *sCK* and *pCK* models: a *PPPP* model

$(u_1, u_2, u_3, u_4 \equiv P_1, P_2, P_3, P_4)$; a *PPPZ* model $(u_1, u_2, u_3, u_4 \equiv P_1, P_2, P_3, Z_1)$; a *PPZZ* model

$(u_1, u_2, u_3, u_4 \equiv P_1, P_2, Z_1, Z_2)$ and a *PZZZ* model $(u_1, u_2, u_3, u_4 \equiv P_1, Z_1, Z_2, Z_3)$. We also consider

a special case of the *PPPP* model, a *PPPP** model $(u_1, u_2, u_3, u_4 \equiv P_1, P_2, P_3, P_4)$ in which

mixotrophy is not permitted as this allows comparison of the properties of a classic

phytoplankton competition model, upon which R^* theory is based (Tilman, 2007), with its CK equivalent.

Parameter Space

A large parameter space, based on measured values (Cropp and Norbury, 2009a), is defined so that all models may search the same space (Table 1). As such an “oversize” parameter space can generate unrealistic parameter combinations, we restrict our analysis to the valid (ecologically realistic) parameter sets for each model (see below). The valid parameter sets for pCK models are assessed for the eigenvalue sign structures that we dictate (see Pinball Dynamics below), so that coexistence solutions for the pCK models are a subset of the valid parameter sets. The structural properties of the sCK models dictate that all valid parameter sets produce a model in which all species coexist. Example parameter sets are arbitrarily drawn from the results of the parameter space searches to demonstrate the dynamics of the systems. The parameter values used in the dynamic simulations are provided in the Appendix.

Ecological Realism

We ensure the ecological realism of the models by examining only valid parameter sets. We define ecological realism analogously to Kolmogorov (1936), requiring that a minimum set of boundary equilibrium points exist in the ecospace ($0 \leq u_1^*, u_2^*, u_3^*, u_4^* \leq 1$). For models with no predators we require that every autotroph (pPFT) has an equilibrium point where it alone exists ($\{u_i^*, 0, 0, 0\}$, defined by $\{f_i = 0, u_{j \neq i} = 0\}$). For predator-prey (autotroph-grazer) systems we require that in addition to a boundary equilibrium point for each autotroph (pPFT) that each predator-prey pair (pPFT-zPFT) has a boundary equilibrium point where only they exist ($\{u_i^*, u_j^*, 0, 0\}$, defined by $\{f_i = 0, f_j = 0, u_{k \neq i, j} = 0\}$). We refer to these sub-system points collectively as ‘boundary’ equilibrium points since they reside on the boundaries of the

higher-dimension ecospace. A randomly chosen parameter set is defined to be ecologically realistic if every required boundary equilibrium point of the model exists within the ecospace.

Secondary Properties

The primary focus of this work is on the coexistence properties of ecosystem models, but in constructing models to have particular coexistence properties it is possible to prescribe the models to have secondary properties. Here we demonstrate that *pCK* models may be constructed to have keystone species, and hence extinction cascades that are predictable *a priori*. We also observe that *sCK* models cannot have keystone species. We further show that the models may be constructed to have equilibrium or non-equilibrium dynamical properties. *sCK* models typically have equilibrium dynamics, and we may also construct *pCK* models to have similar dynamics, but also so that they have special non-equilibrium dynamics that we call ‘pinball dynamics’, that are not possible in *sCK* models. Dynamics that might be called pinball dynamics have previously been observed as heteroclinic cycles in three species competition systems (May and Leonard, 1975) and as limit cycles in four species predation/competition models (Cropp and Norbury, 2009b).

Keystone species

We stipulate particular sign relationships on the competition eigenvalues of the boundary equilibrium points of the *pCK* models to ensure that they do not have any interior equilibrium points (Figure 2). The requirement for smooth internal vector fields implies that in such arrangements equilibrium points other than the boundary equilibrium points generally do not exist (but see note in Appendix). This produces models in which every PFT is crucial for the maintenance of the ecosystem and hence is a ‘keystone’ species (Power et al., 1996).

Removal of any PFT by setting $u_i = 0$ then causes a predictable cascade of extinction as the system collapses to a boundary equilibrium point.

Generally, keystone species are not possible in *sCK* models, as the positive competition eigenvalues at each equilibrium point imply the existence of progressively higher-dimension equilibrium points (Figure 3). The removal of any PFT from an *sCK* model merely causes the system to find a new stable equilibrium point that does not include the removed PFT. The exception to this is if the sole autotroph is removed from a system (for example, if *P* is removed from the *PZZZ* model). In this case, the requirement for a complete set of boundary equilibrium points for ecological realism is not satisfied, and the system collapses completely and all PFTs go extinct.

Pinball Dynamics

The rules for constructing *pCK* models with keystone species also allow us to generate extreme non-equilibrium dynamics that we call pinball dynamics. These are a special form of non-equilibrium dynamics in which the state of the system ‘bounces’ between the boundary equilibrium points (May and Leonard, 1975; Cropp and Norbury, 2009b). The direction of the dynamics is controlled very tightly by the competition eigenvalues which act as signposts at each equilibrium point, drawing the state of the system in from the previous equilibrium point and shooting it out towards the next equilibrium point. The order in which different species bloom in these dynamics may be predicted from the rules used to construct the system (Figure 2).

Several dynamical solutions are possible for each of the scenarios in Figure 2. The *PPPZ* and *PZZZ* models have two possible dynamics – ‘clockwise’ as shown in Figure 2 (b and d) and ‘anticlockwise’, where the signs of the eigenvalues are reversed, and the dynamics shown by the solid arrows are consequently also reversed. The *PPPP* and *PPZZ* models have six possible dynamics, comprised of clockwise and anticlockwise dynamics of three basic sequences of visitation of the equilibrium points. For the *PPPP* model these are:

- $\{P_1^*\} \rightarrow \{P_2^*\} \rightarrow \{P_3^*\} \rightarrow \{P_4^*\}$ clockwise (Figure 2(a)) and anticlockwise (signs of the eigenvalues on the solid arrows reversed from Figure 2(a)),
- $\{P_1^*\} \rightarrow \{P_2^*\} \rightarrow \{P_4^*\} \rightarrow \{P_3^*\}$ clockwise and anticlockwise, and
- $\{P_1^*\} \rightarrow \{P_3^*\} \rightarrow \{P_2^*\} \rightarrow \{P_4^*\}$ clockwise and anticlockwise,

where the combinations of signs of the eigenvalues determine the directions of visitation. The *PPZZ* model also has six possible dynamics, given by:

- $\{P_1^*, Z_1^*\} \rightarrow \{P_2^*, Z_1^*\} \rightarrow \{P_2^*, Z_2^*\} \rightarrow \{P_1^*, Z_2^*\}$ clockwise (Figure 2(c)) and anticlockwise (signs of the eigenvalues on the solid arrows reversed from Figure 2(c)),
- $\{P_1^*, Z_1^*\} \rightarrow \{P_2^*, Z_1^*\} \rightarrow \{P_1^*, Z_2^*\} \rightarrow \{P_2^*, Z_2^*\}$ clockwise and anticlockwise, and
- $\{P_1^*, Z_1^*\} \rightarrow \{P_1^*, Z_2^*\} \rightarrow \{P_2^*, Z_1^*\} \rightarrow \{P_2^*, Z_2^*\}$ clockwise and anticlockwise.

Equilibrium Dynamics

sCK models typically have equilibrium dynamics, but the exact nature of these dynamics is not prescribed by the *sCK* construction rules as it is for *pCK* models. Associated with each positive competition eigenvalue at an extinction point of an *sCK* system is an eigenvector that directs the dynamics of the system into the interior of the state space (Figure 3). In *sCK* models with smooth vector fields, the competition eigenvectors associated with a pair of competing species (for example P_1 and P_2 of equilibrium points $\{P_1^*, Z_1^*\}$ and $\{P_2^*, Z_1^*\}$ in Figure 3) imply the existence of the internal equilibrium point ($\{P_1^*, P_2^*, Z_1^*\}$ in Figure 3). Similarly, the competition eigenvectors of these points then imply the existence of higher dimension points such as the coexistence point $\{P_1^*, P_2^*, Z_1^*, Z_2^*\}$ in Figure 3. The competition

eigenvectors always have real and positive eigenvalues at their origin at the extinction point, but the coexistence equilibrium point that they infer does not necessarily have real eigenvalues, and may therefore have stable equilibrium or limit cycle dynamics.

Numerical Simulations

Ubiquity of Parameter Sets

The results of the search of the parameter space (Table 2) for the *sCK* models confirm the accuracy of our algorithm. The structural properties of *sCK* models ensure that all valid parameter sets provide a coexistence solution and our numerical results are consistent with this. In this case, the parameter space needs only to be searched for valid parameter sets.

We did not find any parameter sets that allow coexistence in the *PPPP*^{*} *pCK* model. This result is consistent with the properties of a classical phytoplankton competition model (Tilman, 2007) and provides a continuum of properties from the classical models to the *CK* framework. However, every parameter set randomly generated for the *PPPP*^{*} *sCK* model provides a valid parameter set, which also allows coexistence of all PFTs in the model. Equation (9) reveals that for the *PPPP* and *PPPP*^{*} *sCK* models every parameter set must deliver a valid equilibrium point as $f_i > 0$ whenever $P_i = 0$ and $f_i < 0$ whenever $P_i = 1$, so that there always exists a $0 < P_i^* < 1$ defined by $f_i = 0$. The dichotomy between the *pCK* *PPPP*^{*} model (0% solutions) and the *sCK* *PPPP*^{*} model (100% solutions) suggests that neither model is realistic as a model of this type should allow some species to coexist and some species to go extinct. Gross et al (2009) considered similar models and suggested that a hybrid model with both vanishing and non-vanishing mortality processes may be more appropriate. They demonstrated that including both linear and nonlinear mortality terms allowed the model to produce all realistic outcomes of competition.

Generally, coexistence solutions for *sCK* models are more common than for *pCK* models: 80-100% of sampled parameter sets result in valid sets for *sCK* models, of which all are coexistence solutions, whereas only 45-65% of sampled parameter sets result in valid sets for *pCK* models, of which 1-2% are coexistence solutions. Where our results for the *PPPP*^(*) models confirm the well-known effect of the density-dependence of mortality terms in phytoplankton competition models (Ruan et al., 2007; Gross et al., 2009), our results for the *PPPZ*, *PPZZ* and *PZZZ* models suggest that the density-dependence of grazing interactions may also be an important facilitator of coexistence in complex ecosystem models (McCann and Hastings, 1997; Emmerson and Yearsley, 2004).

Dynamical Properties

We extracted parameter sets from the solutions found in Table 1 to demonstrate typical dynamics of the models (Appendix Table 1). To demonstrate the predictability of the models to extinction we impose extinction on u_3 (P_3 in panels A and B, Z_1 in panel C and Z_2 in panel D of Figures 4 and 5) two-thirds of the way through each simulation.

The *pCK* models all exhibit pinball dynamics (Figure 4) consistent with the dynamical cycles that we prescribed (Figure 2), where the arrangements of the signs of the competition eigenvalues control the sequence of plankton blooms. Similarly, all *sCK* models exhibit stable equilibrium dynamics (Figure 5), a likely property of these systems. Extreme pinball dynamics are evident for the first two-thirds of the simulation for the *PPPP* *pCK* model (Figure 4(A)), where the system visits the $\{P_1^*\}$, $\{P_2^*\}$, $\{P_3^*\}$ and $\{P_4^*\}$ equilibrium points in sequence. As the pPFT boundary equilibrium points are near the vertices of the ecospace, the dynamics of this system traverses almost the entire state space as it moves between points. The *PPPZ*, *PPZZ* and *PZZZ* models have less extreme pinball dynamics as predator-prey equilibrium points are more centrally located in the ecospace (Figure 4 (B - D)).

The imposition of extinction on u_3 two-thirds of the way through each simulation demonstrates it is possible to prescribe keystone species *a priori* in *pCK* models, and to predict the effect of their removal on the other species in the model. The extinction of u_3 in the *pCK* models (Figure 4) in each case causes at least one other PFT to go extinct, and hence triggers a cascade of extinction. This cascade is pre-determined by choices made in the construction of the *pCK* models, and may be predicted from Figure 2. Removal of u_3 from each of the systems in Figure 2 results in the removal of its destabilising competition eigenvalue from one of the boundary equilibrium points: from $\{P_2^*\}$ in (A), indicating that removal of P_3 will cause the extinction of P_1 and P_4 ; from $\{P_2^*, Z^*\}$ in (B), indicating that P_1 will also go extinct; from $\{P_1^*, Z_2^*\}$ in (C), indicating that P_2 will also go extinct; and from $\{P^*, Z_3^*\}$ in (D), indicating that Z_1 will also go extinct. However, the removal of u_3 in the *sCK* models (Figure 5) confirms that removing u_3 does not affect the existence of the other PFTs. The state of these systems merely moves to an equilibrium solution that does not include u_3 that is predictable from Figure 3, and confirms that *sCK* models cannot have keystone species.

Discussion

We have described a new framework for the analysis of competition in ecosystem models. The framework, based on the criterion of mass-conservative Kolmogorov systems, unifies many theoretical and applied ecosystem models. It provides a continuum of analytical solutions between very simple theoretical models and very complex applied models. As a consequence, we have been able to describe the fundamental mechanisms that determine the

outcomes of competition in a broad class of models. As *CK* systems unify many theoretical and applied models of explicit competition for a limiting resource our theoretical approach can identify unifying principles that explain the mechanisms of biodiversity in many ecosystem models.

The mechanisms underpinning plankton biodiversity that we have described have broad implications for applied models of marine ecosystems in particular. For example, the PFT models currently being developed for climate and fisheries simulation include multiple functional types to perform specific biogeochemical or ecosystem roles. These models face the immediate challenge to maintain competing species extant in computer simulations. Our results show that this may be achieved without resorting to setting artificial minimum population levels if the current models are modified to have *sCK* form. However, the next generation of models will be required to predict invasions, extinctions and ecosystem change in response to climate change (Montes-Hugo et al., 2009; Boyce et al., 2010), and this will require the development of *pCK* models.

The analytic framework we describe may also be applied more generally to practical ecosystem modelling. Ecosystem models are generally built from the “bottom up”, that is, the developer considers each of the ecosystem processes involved and represents each of the processes in the model using functional forms according to their understanding of how the processes operate. They do not make any assumptions about the overall properties of the ecosystem model, but in fact determine these by the choices that they make for the functional forms although in many cases there is not convincing evidence to support choosing one functional form over another. Our work reveals that choosing a Holling Type II functional form for a grazing interaction rather than a Holling Type III, a choice for which the empirical justification appears equivocal (Sarnelle and Wilson, 2008), can have profound effects on the

properties of a model. While some modellers will therefore select functional forms to ensure that their models have specific properties, others will be able to construct their models according to their understanding of the processes, but can now do so fully cognizant of the implications of the choices that they make for the functional forms that they use to represent those processes. The different coexistence and dynamical properties of the *sCK* and *pCK* systems emphasise the profound impacts that choices of vanishing or non-vanishing terms for loss processes can have for many properties of ecosystem models.

The mechanisms we have described also have broad implications for theoretical models of terrestrial, aquatic and marine ecosystems. A central point of our results is that it is the vanishing functional forms of the loss terms that ensure structural coexistence. We have therefore identified in *sCK* systems a previously unknown class of models for which the classical theory of the mechanisms of coexistence (for example Tilman (2007)) is not useful.

However, our analysis confirms that classical concepts of the features that facilitate coexistence are important in *pCK* systems, because they have non-vanishing grazing terms. These include concepts suggested to be central to the coexistence of explicit competitors, that intra-specific effects must outweigh inter-specific effects and that interaction links must be weak (McCann et al., 1998; Emmerson and Yearsley, 2004; Namba et al., 2008). A key point of our results in this context is that all loss terms are critical when parameterising coexistence in *pCK* systems. It is the sign of the competition eigenvector at the extinction point that is critical; the analytic expressions for these eigenvalues in *pCK* systems always include all loss processes, and the key attribute for survival is that the eigenvalue is positive. The relative importance of the loss terms in making the eigenvalue positive will depend on the functional forms and parameters used in a particular model, and therefore we would expect the analysis of different models to emphasise the importance of different terms.

The models we use to demonstrate typical properties of *CK* systems are the end-members of a spectrum of models. At one end of the spectrum, the structural properties of *sCK* systems reliably ensure the coexistence of all competitors in models with any number of species and trophic levels. These systems generally have equilibrium dynamics, and are immune to cascades of extinction. At the other end of the spectrum *pCK* systems may have non-equilibrium dynamics, and can simulate keystone species and cascades of extinction. However, *pCK* systems are difficult to develop, as the parameter sets that confer coexistence are rare in parameter space. Real ecosystems probably occupy positions within this spectrum with intermediate properties – a key question remaining is where do real ecosystems fit within this spectrum? There are many more ways in which a functional form may be vanishing than there are for it to be non-vanishing, for example, exactly linear mortality is the only non-vanishing form for mortality, whereas there are an infinite number of nonlinear mortality terms that are vanishing. There appears then to be greater potential for real ecosystems to reside nearer the *sCK* end of the spectrum than the *pCK* end.

We only consider the mechanisms controlling competition in ecosystem models in this work, but the very general nature of the properties of ecosystem models that we have identified as determining competitive outcomes provide useful heuristics for the consideration of the mechanisms of competition in real ecosystems. Our simple criteria; Kolmogorov form, which requires that a per capita life function may be written for each population; conservation of mass, which many ecosystems approximate; and density dependence or independence of process functions; are commonly found in both theoretical and applied ecosystem models, suggesting that they are central to understanding of how real ecosystems function. The modelling results we present here may therefore contribute a theoretical basis for the study of competition in real ecosystems.

Our results also reflect on the diversity-stability debate and the mechanisms that contribute to stability in ecosystems (Ives and Carpenter, 2007). The existence of *sCK* systems, that may be infinitely diverse yet appear generally to be stable (points or limit cycles), suggest that for a large class of systems there may be no simple or general relationship between food web structure and stability. Similarly, weak interaction strengths, a mechanism commonly suggested to be crucial to coexistence (McCann, 2000), make no contribution to the potential for coexistence in *sCK* systems. Against this robustness of *sCK* systems we contrast *pCK* systems, in which weak interaction strengths may be crucial, as they increase the likelihood that the loser in the interaction will have a positive competition eigenvalue at their extinction point. This is consistent with the first “certain conclusion” of the ESA Report (Hooper et al., 2005) that species’ functional characteristics strongly influence ecosystem properties.

Models that have contingent coexistence become increasingly difficult to construct as their complexity increases, which suggests an inverse relationship between complexity and the likelihood of stability in these systems. We won’t speculate on whether the practical difficulties associated with constructing complex *pCK* models reflects the properties of real ecosystems. However, we do note that there are many more ways in which species may have the vanishing loss functions central to structural coexistence than the non-vanishing functions that constrain them to parameterised coexistence.

Conclusions

We conclude by reiterating that many of the models studied in theoretical ecology and applied in predictive ecosystem modelling are conservative Kolmogorov systems. One of the very useful properties of this very general class of models is that analytic expressions for the key eigenvalues that determine coexistence in these models may be easily obtained. These eigenvalues do not necessarily describe the stability properties of the systems, but do

explicitly describe the mechanisms that control extinction in the models. They thus provide a means of differentiating fundamental ways in which coexistence may occur in models (structural vs conditional). They provide tools that permit the coexistence properties of complex models to be understood, and allow some secondary properties to be predicted.

The theory and heuristics we have described in this work provide practical, powerful tools for the construction and analysis of ecosystem models for many applications including climate change and fisheries modelling. These rules may be used to construct models with specific properties such as coexistence of competing species or functional types. We have demonstrated how to design models that variously have equilibrium and non-equilibrium coexistence states, keystone species and pinball dynamics. The rules may also be used to understand the properties of models that are constructed from the “ground up”, and the implications of making choices between process functional forms.

Our approach provides a unifying framework for understanding theoretical models that spans the divide between population dynamics and ecosystems. We present this work in the context of plankton ecosystems, as these are the source of many of the classical paradoxes in ecology, but note that the work has broad application across many systems, including terrestrial ecosystems.

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Table Legends

Table 1. Parameters and parameter space used in the parameter searches for the example *sCK* and *pCK* models.

Table 2. The result of searches for parameter sets for each of the model types. 1×10^6 random parameter sets were evaluated in each case.

Tables

Table 1. Parameters and parameter space used in the parameter searches for the example *sCK* and *pCK* models.

Par	Description	Min	Max
μ_i	Maximum rate of uptake of inorganic nutrient for P_i	0.01	3
κ_i	Half-saturation constant for uptake of inorganic nutrient for P_i	0.01	2
$\phi_{ij}, \hat{\phi}_{ij}, \tilde{\phi}_{ij}$	Maximum predation rates of P_j or Z_j on P_i or Z_i	1	10
$\kappa_{ij}, \hat{\kappa}_{ij}, \tilde{\kappa}_{ij}$	Half-saturation constants for predation of P_j or Z_j on P_i or Z_i	0.01	2
$\psi_{ij}, \hat{\psi}_{ij}, \tilde{\psi}_{ij}$	Assimilation efficiency for predation of P_j or Z_j on P_i or Z_i	0.01	0.99
$\sigma_i, \tilde{\sigma}_j$	Natural mortality rates of P_i or Z_j	0.01	0.50

Table 2. The result of searches for parameter sets for each of the model types. 1×10^6 random parameter sets were evaluated in each case.

Model	Number of Parameter Sets ¹			
	<i>sCK</i> models		<i>pCK</i> models	
	Valid Sets	Solutions	Valid Sets	Solutions ²
<i>PPPP</i> *	1,000,000	1,000,000	479, 866	0
<i>PPPP</i>	1,000,000	1,000,000	479,644	1
<i>PPPZ</i>	831,192	831,192	438,466	4,525
<i>PPZZ</i>	813,145	813,145	484,568	9,095
<i>PZZZ</i>	872,716	872,716	639,578	9,803

¹ These values will vary for different models, process formulations and/or parameter spaces, but are indicative of the relative frequencies.

² All possible solutions for the *pCK* models are combined into a total number of solutions. 97% of solutions for the *PPPZ pCK* model had the sequence shown in Figure 1 (B) and 98% of solutions for the *PZZZ pCK* model had the sequence shown in Figure 1 (D). 70% of solutions for the *PPZZ pCK* model had dynamics that visited the equilibrium points in the order ($\{P_1^*, Z_1^*\} - \{P_2^*, Z_1^*\} - \{P_1^*, Z_2^*\} - \{P_2^*, Z_2^*\}$) and 15% visited in the order shown in Figure 1 (C). 1.5% of *PZZZ* solutions were equilibrium solutions, as were 0.6% of *PPPZ* and 0.02% of *PPZZ* solutions.

Figure Legends

Figure 1. Schematic of generic food web structure. Arrows indicate the direction of flow of mass, or “who eats whom”. Mortality and respiration lead to re-mineralization and re-absorption into the inorganic nutrient pool, upon which at least u_1 grows.

Figure 2. Eigenvalue sign structures required at the boundary equilibrium points for coexistence in the pCK models for (A): $P_1P_2P_3P_4$, and $P_1P_2P_3P_4^*$, (B) $P_1P_2P_3Z$, (C) $P_1P_2Z_1Z_2$ and (D) $PZ_1Z_2Z_3$ models. Shaded boxes represent the boundary equilibrium points identified by their non-zero state variables; boxes with dotted borders represent the sign requirements of the competition eigenvalues at the equilibrium point they are near. The eigenvalues are identified by the appropriate life function, i.e. the competition eigenvalue associated with P_1 is denoted by f_{P1} . Solid arrows indicate the sequence in which the equilibrium points are visited and reveal the sequence of blooms for the arrangement of competition eigenvalues shown. Dotted arrows in (A) indicate potential alternate dynamics but we have precluded these by requiring the corresponding competition eigenvalues to be negative. Other combinations of signs (for example $f_{P1} > 0$, $f_{P2} < 0$, $f_{P3} < 0$, $f_{P4} < 0$) would potentially allow more complicated dynamics.

Figure 3. Eigenvalue sign structures for the $P_1P_2Z_1Z_2$ sCK model. Shaded boxes represent the boundary, extinction and coexistence equilibrium points identified by their non-zero state variables; boxes with dotted borders represent the signs of the competition eigenvalues at the

equilibrium point they are near. The eigenvalues are identified by the appropriate life function, i.e. the competition eigenvalue associated with P_I is denoted by f_{P_I} . Solid arrows indicate that the competition eigenvalues imply the existence of the equilibrium point that they point to, assuming smooth vector fields. Dotted arrows show competition between PFTs. Equivalent figures may be constructed for each of the other *sCK* models discussed in the paper.

Figure 4. Time series of PFT dynamics for the *pCK* models: (A): $P_1P_2P_3P_4$, (B) $P_1P_2P_3Z$, (C) $P_1P_2Z_1Z_2$ and (D) $PZ_1Z_2Z_3$. In all panels PFTs are coloured dash-dot, dotted, dashed or solid lines in the order of the name of each model. Extinction of u_3 ($u_3 = 0$, dashed line) is imposed at $t = 2,000$ in panel A and at $t = 400$ in panels B - D. u_3 is P_3 in panels (A) and (B), Z_1 in panel (C) and Z_2 in panel (D). PFT populations are shown as proportions of the total nutrient mass and time is scaled by the maximum P_I growth rate. Both are dimensionless.

Figure 5. Time series of PFT dynamics for the *sCK* models. Lines and panels as for Figure 4. Extinction of u_3 ($u_3 = 0$, dashed line) is imposed at $t = 100$ in all panels.

Figures

Figure 1

Figure 2:

Figure 3:

Figure 4:

Figure 5:

Appendix

Keystone species

We note that this result is not certain, as a smooth (but perhaps distorted or buckled) internal vector field may be achieved by the existence of a stable and an unstable equilibrium point pair, such as might exist after a blue-sky bifurcation (Strogatz, 1994). This would not affect the coexistence properties of the model, but may mean that changes in parameter values may switch it between having keystone species and not having them. Therefore, in contrast to the robustness of *sCK* systems, where multiple extinction equilibrium points may exist without affecting the co-existence property of the model, *pCK* systems may not always result from a ‘correct’ eigenvalue sign relationship. However, such cases appear rare in practice.

Appendix Table 1. Parameters values used in the simulations for the example *sCK* and *pCK* models.

PAR	<i>sCK</i> models				<i>pCK</i> models			
	<i>PPPP</i>	<i>PPPZ</i>	<i>PPZZ</i>	<i>PZZZ</i>	<i>PPPP</i>	<i>PPPZ</i>	<i>PPZZ</i>	<i>PZZZ</i>
μ_1	1.800	0.433	1.086	1.059	2.554	2.170	2.734	2.271
μ_2	0.339	1.021	0.982	-	2.674	1.310	1.917	-
μ_3	0.966	0.464	-	-	2.480	2.480	-	-
μ_4	0.257	-	-	-	1.685	-	-	-
κ_1	1.250	0.496	1.833	1.649	0.064	0.866	1.403	1.850
κ_2	1.380	0.301	1.471	-	1.784	1.577	1.330	-
κ_3	1.440	0.745	-	-	0.126	0.790	-	-
κ_4	1.220	-	-	-	1.290	-	-	-

σ_1	0.422	0.039	0.379	0.336	0.207	0.308	0.224	0.389
σ_2	0.277	0.210	0.174	-	0.025	0.117	0.441	-
σ_3	0.317	0.170	-	-	0.492	0.277	-	-
σ_4	0.402	-	-	-	0.216	-	-	-
$\tilde{\sigma}_1$	-	0.138	0.373	0.492	-	0.464	0.186	0.109
$\tilde{\sigma}_2$	-	-	0.091	0.444	-	-	0.319	0.346
$\tilde{\sigma}_3$	-	-	-	0.160	-	-	-	0.245
$\hat{\phi}_{12}$	4.300	3.535	9.384	-	7.842	9.937	2.761	-
$\hat{\phi}_{13}$	2.960	3.472	-	-	6.428	1.426	-	-
$\hat{\phi}_{14}$	1.110	-	-	-	1.039	-	-	-
$\hat{\phi}_{23}$	8.580	2.835	-	-	4.293	9.420	-	-
$\hat{\phi}_{24}$	6.120	-	-	-	4.862	-	-	-
$\hat{\phi}_{34}$	1.220	-	-	-	7.063	-	-	-
$\hat{\kappa}_{12}$	1.530	0.537	1.400	-	-	-	-	-
$\hat{\kappa}_{13}$	1.360	0.879	-	-	-	-	-	-
$\hat{\kappa}_{14}$	0.267	-	-	-	-	-	-	-
$\hat{\kappa}_{23}$	1.900	0.434	-	-	-	-	-	-
$\hat{\kappa}_{24}$	0.908	-	-	-	-	-	-	-
$\hat{\kappa}_{34}$	0.430	-	-	-	-	-	-	-
$\hat{\psi}_{12}$	0.437	0.971	0.088	-	0.212	0.671	0.719	-
$\hat{\psi}_{13}$	0.157	0.253	-	-	0.953	0.872	-	-
$\hat{\psi}_{14}$	0.258	-	-	-	0.979	-	-	-
$\hat{\psi}_{23}$	0.290	0.047	-	-	0.744	0.814	-	-
$\hat{\psi}_{24}$	0.055	-	-	-	0.967	-	-	-

$\hat{\psi}_{34}$	0.922	-	-	-	0.528	-	-	-
φ_{11}	-	4.320	5.630	4.889	-	2.106	8.503	8.121
φ_{12}	-	-	1.388	7.745	-	-	1.231	5.611
φ_{13}	-	-	-	6.966	-	-	-	5.079
φ_{21}	-	1.970	2.611	-	-	7.006	1.425	-
φ_{22}	-	-	1.083	-	-	-	8.763	-
φ_{31}	-	9.375	-	-	-	8.189	-	-
$\tilde{\varphi}_{12}$		-	2.835	7.658	-	-	2.054	9.661
$\tilde{\varphi}_{13}$	-	-	-	8.538	-	-	-	3.326
$\tilde{\varphi}_{23}$		-	-	7.363	-	-	-	3.676
κ_{11}	-	0.328	1.466	0.073	-	-	-	-
κ_{12}	-	-	1.920	0.584	-	-	-	-
κ_{13}	-	-	-	1.862	-	-	-	-
κ_{21}	-	0.522	0.464	-	-	-	-	-
κ_{22}	-	-	0.161	-	-	-	-	-
κ_{31}	-	0.880	-	-	-	-	-	-
$\tilde{\kappa}_{12}$	-	-	1.408	0.598	-	-	-	-
$\tilde{\kappa}_{13}$		-	-	1.915	-	-	-	-
$\tilde{\kappa}_{23}$		-	-	0.883	-	-	-	-
ψ_{11}	-	0.917	0.129	0.872	-	0.707	0.820	0.342
ψ_{12}	-	-	0.447	0.560	-	-	0.425	0.325
ψ_{13}	-	-	-	0.974	-	-	-	0.383
ψ_{21}	-	0.837	0.257	-	-	0.371	0.658	-
ψ_{22}	-	-	0.607	-	-	-	0.519	-

ψ_{31}	-	0.887	-	-	-	0.553	-	-
$\tilde{\psi}_{12}$	-	-	0.088	0.391	-	-	0.371	0.073
$\tilde{\psi}_{13}$	-	-	-	0.589	-	-	-	0.368
$\tilde{\psi}_{23}$	-	-	-	0.409	-	-	-	0.082