

Modelling plankton ecosystems and the Library of Lotka.

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ABSTRACT

Predicting how change will impact ecosystems requires the development of complex models. The complexity of ecosystem models often defies the power of analytical mathematical techniques so they are commonly solved using computers. A problem with this approach is the difficulty in assessing the credibility of model simulation results.

We apply ecological axioms to the construction of complex model ecologies. The axioms ensure realistic ecological properties and internal consistency of a broad class of models that encompass many theoretical and applied models. A key new analytical result for our dynamical systems in ecospace is that extinctions can be studied without knowledge of either interior equilibrium points or their stability. By looking only at boundary extinction points we can immediately comment on the extinction behaviour without solving for any of the dynamics. This is a striking simplification, and even holds when the dynamics are chaotic.

We demonstrate the approach by constructing three plankton ecosystem models that we design to have specific properties and show that the effect of change on plankton blooms and/or extinctions depends on the properties of the model chosen for the simulation.

KEYWORDS: Library of Lotka; ecosystem model; dynamical system; consistent normal ecologies; emergent properties; climate change

1. Introduction

A demand for construction of computer ecosystem models of increasing complexity is emerging from the need to predict the impacts of anthropogenic activities on natural systems.

In the marine field, these may include the impacts of climate change on resources such as fisheries, or on processes such as the exchange of gases between the ocean and the atmosphere (Moore et al., 2002; Le Quéré et al., 2005; Kishi et al., 2007). A fundamental constraint on the development of such models, and in particular their application to predict ecosystem responses to changing environments, has been the analytic intractability of complex dynamical systems. Analytic solutions to even simple nonlinear systems are rare, and geometric approaches to understanding what the solutions look like also become difficult for systems with more than three interacting populations as local stability analysis requires finding the roots of high-order polynomials (Kot, 2001). Predictions of ecosystem responses to external changes are generally obtained by calculating numerical solutions to computer models of the ecosystems. A vast number of solutions may be calculated from a model of a complex ecosystem by varying the complexity of the modelled food web, the process formulations and parameter values. A key challenge for the computer simulation approach is how to determine which of these solutions are useful.

1.1 The Library of Lotka

The solutions of complex ecosystem models define an ecological equivalent to the Library of Babel (Borges, 1941) that we name the Library of Lotka. The Library of Babel contains every possible version of a book of 410 pages, each page of 40 lines, each line of 80 characters. Borges allowed only 25 characters, but the Library of Babel contains at least $25^{1,312,000} \approx 10^{1,834,097}$ books (Bloch, 2011). The library contains all useful information on all topics, past present and future. It contains, for example, an accurate biography of every reader of this manuscript. However, the Library of Babel also contains all incorrect information and all variants in-between. So in addition to one accurate biography of the reader, it also contains many biographies with one error, two errors, etc. up to all possible completely incorrect biographies. Consequently the Library of Babel, although it is known to contain all correct

1 information, is a useless repository of knowledge because true information is
2 indistinguishable from false information.

3 We define the Library of Lotka as containing the solutions to a climate change
4 scenario produced by an ocean plankton ecosystem model. We define the library in terms of a
5 model of similar complexity to the PlankTOM10 model being developed to model
6 biogeochemical cycles in the oceans (Le Quéré et al., 2005). This model contains 10 plankton
7 populations: 6 autotrophs and 4 heterotrophs. We simplify the food web structure of this
8 model considerably to facilitate a succinct discussion and assume that all heterotrophs graze
9 all autotrophs and that there is no predation within either trophic level.

10 Three processes determine the change in any population: growth, grazing and
11 respiration/mortality, and we further simplify the consideration of these processes. We shall
12 assume that all autotrophs grow on inorganic nutrient according to Michalis-Menten kinetics
13 (equivalent to the Droop cell quota form). We shall use three generic functional forms to
14 represent grazing interactions: linear, hyperbolic and sigmoidal (Holling Types I, II and III).
15 Further, we shall consider mortality/respiration simply in terms of whether it is linear or
16 nonlinear. The shape of each functional form may be described by two parameters. We
17 assume that we know the real parameter values to $\pm 10\%$ accuracy, and that we estimate
18 parameters with a precision of 1%, resulting in 21 values that may be used for each parameter
19 (PlankTOM10 and similar models generally nominate parameter values to two or three
20 significant figures, and on occasion to four).

21 The six autotroph equations each contain six terms; one growth, four grazing, one
22 mortality. Each of the grazing terms may have one of three forms, and the mortality term one
23 of two forms, so there are 162 structurally different forms for each autotroph equation. The
24 heterotroph equations each contain seven terms (six growth and one mortality), but the six

growth terms have been defined by the grazing terms in the autotroph equations, so there are only the two options for the mortality term, and hence only two possible forms for each of these equations. We may therefore construct $162^6 \times 2^4 \approx 10^{14}$ structurally different models within this template.

Each autotroph equation has twelve parameters and each heterotroph equation has eight (two for mortality and we add one assimilation efficiency parameter to the grazing uptake from each autotroph) so each model requires 104 parameters, each of which may have 21 values. Each model structure therefore has 21^{104} different parameterisations, and each parameterisation of each model structure will produce a different prediction of the ecosystem response to climate change. For a single climate change scenario, the Library of Lotka for this model then contains $162^6 \times 2^4 \times 21^{104} \approx 10^{151}$ different predictions. This is a lower bound on the size of the library as it is well known that complex nonlinear models typically have some chaotic parameterisations and may have alternate states, and therefore including uncertainty in the model initial conditions could substantially increase the number of different predictions.

The Library of Lotka will contain the correct response of the ecosystem to the climate change scenario, and many responses that look very similar to the correct response. However, it will also contain many more completely incorrect responses, and as with the Library of Babel, there is no way of distinguishing correct predictions from incorrect predictions. This presents a formidable challenge to the computer experiment approach to predicting the response of marine ecosystems to changing environments. The common practice of using complex computer models that reproduce existing ecosystems ‘reasonably well’ to predict impacts of climate change does little to address the issue of how we differentiate true information from false information in the Library of Lotka.

We should abandon all hope that browsing the shelves of the Library of Lotka, as the computer simulation approach does, will produce any useful predictions of how ecosystems might respond to climate change. We suggest that understanding the properties of complex ecosystem models and why they produce the solutions they do is the first step to extracting useful information from the Library of Lotka, and is the topic of this paper.

1.2 Cataloguing the Library of Lotka

Recent theoretical work (Cropp and Norbury, 2012a, b) has shown that there exists a very general class of complex ecosystem models that are both ecologically realistic and somewhat amenable to mathematical analysis. We argue that the construction of computer ecosystem models should commence with the application of ecological axioms that ensure the populations in the models have ecologically realistic and consistent properties. These consistent normal ecologies have properties that allow certain attributes to be predicted and also facilitate the design of models to have particular attributes. These predictable attributes include whether:

- a species will coexist with other species and persist in an environment,
- a species can invade an established ecosystem,
- a species will go extinct if the environment changes,
- the extinction of one species will cause a cascade of extinction in other species,
- and
- in some cases whether a model will have equilibrium dynamics, or even an extreme non-equilibrium dynamical behaviour called pinball dynamics (May, 1973; Cropp and Norbury, 2012b).

Knowledge of these attributes *a priori* means that some attributes that might currently be described as ‘emergent’ properties of simulation models can now be cast in their correct context as resulting from assumptions and choices made during the construction of the model. This understanding of the basic properties of complex models provides a much more robust basis for prediction of the impacts of climate and other change on natural living systems.

1.3 Generic Climate Change Scenarios

Here we apply the rules for normal ecologies to nutrient – phytoplankton – zooplankton ($NP_1P_2Z_1Z_2$) ecosystem models in generic climate change scenarios. These models are designed to demonstrate the different outcomes that can arise from different choices made in model construction, but do not simulate a particular ecosystem or climate scenario. We do not investigate the influence of changes in parameter values other than a ‘climate change induced’ increase in mortality rate.

We use models that are sufficiently complex to defy the usual analytical dynamical systems analysis, but are sufficiently simple to succinctly demonstrate the efficacy of our approach. We allow mixotrophy and omnivory so that the models may represent any food web connectance but note that the presence or absence of these processes has no effect on the model properties we consider here.

We show that some attributes of the responses of complex models to changes in their environment may be pre-determined during their construction. We construct three models with different properties to demonstrate the importance that choices in process formulations have in determining the responses of the models to change: structural coexistence with equilibrium dynamics; conditional coexistence with equilibrium dynamics; and conditional coexistence with pinball dynamics. We simulate the effects of climate change by modifying

the mortality rate of one phytoplankton population and demonstrate the (predictable) responses of the different models.

2. Theoretical Basis

We first articulate the rules for construction of ecosystem models. These rules impose on the models ecological constraints that have neat mathematical descriptions, which allow them to be easily applied to existing models or used to construct models that have particular properties.

2.1 Rules for Normal Ecologies

Normal ecologies comply with the following rules:

2.1.1 Rule 0: Population variables:

Measurements $\hat{x}_i(t)$ of the populations $i = 1, 2, \dots, n$ are taken at time t in terms of a limiting resource, say the limiting nutrient \hat{N} , which has the total amount \hat{N}_T available to and being used in the ecology under study. Then our population variables in this marine ecology are the fractions $x_i(t) = \frac{\hat{x}_i(t)}{\hat{N}_T}$ of limiting nutrient in each population, and the remaining (mineral) available nutrient fraction is $N(t) = \frac{\hat{N}(t)}{\hat{N}_T}$, so that the initial (measured) values satisfy $x_1(0) + x_2(0) + \dots + x_n(0) + N(0) = 1$.

Note that we will only consider (see later rules) $0 \leq x_i(t), N(t) \leq 1$, and that the per capita growth rates of the active variables $\frac{1}{x_i} \dot{x}_i := \frac{1}{x_i(t)} \frac{dx_i(t)}{dt}$ are measurement scale invariant at any given time.

2.1.2 Rule 1: Per Capita Growth Function:

Each population interacts with the others and the available nutrient according to the growth function \hat{f}_i as follows:

$$\frac{1}{x_i} \dot{x}_i(t) = \hat{f}_i(x_1, x_2, \dots, x_n; N) \quad \text{for } t > 0. \quad (1)$$

Here each growth function \hat{f}_i is continuously differentiable in its arguments $x_i, N \geq 0$. Each solution $x_i(t) > 0$ is a population life history starting at $x_i(0) > 0$.

The growth functions \hat{f}_i are usually estimated from laboratory or shipboard experiments or observed in the field, and are often known only approximately. There is seldom compelling empirical or theoretical evidence to choose one functional form over another, for example Holling Type II grazing over Holling Type III. A key point of this paper is to demonstrate that such uncertainties in the exact nature of the growth functions can lead to fundamentally different model outcomes. Note that the dependence of \hat{f}_i on parameters, on other quantities such as salinity, oxygen content, sunlight and temperature, and on micro-nutrients such as iron, vitamin B and so on, is ignored when applying the rules for conservative normal ecologies.

2.1.3 Rule 2: Limiting Nutrient Mass Conservation:

As the life histories unfold according to (1), the total amount of limiting resource, or nutrient, is conserved in the ecology. That is,

$$\begin{aligned} x_1(t) + \dots + x_n(t) + N(t) &= 1 \quad \text{for all } t > 0 \\ \Leftrightarrow \dot{x}_1 + \dots + \dot{x}_n &= -\dot{N} \quad \text{with initial condition.} \end{aligned} \quad (2)$$

Then the dynamical system (1) becomes, on using

$$f_i(x_1, x_2, \dots, x_n) := \hat{f}_i\left(x_1, x_2, \dots, x_n; 1 - \sum_{j=1}^n x_j\right),$$

for $i = 1, 2, \dots, n$:

$$\frac{1}{x_i} \frac{dx_i}{dt} = f_i(x_1, x_2, \dots, x_n) \quad \text{for } t > 0 \quad (3)$$

where $x_i(t) > 0$ for $t > 0$.

2.1.4 Rule 3: Lid Condition:

To ensure $N(t) \geq 0$ for $t > 0$ we impose the Lid Condition:

$$\dot{N} \geq 0 \quad \text{whenever} \quad N(t) = 1 - \sum_{j=1}^n x_j(t) = 0 \quad \text{for } t \geq 0. \quad (4)$$

Then $x_1(t) + x_2(t) + \dots + x_n(t) = 1 - N(t) \leq 1$ for $t \geq 0$. So we define an ecospace E by the positive simplex

$$E = \{x_1, x_2, \dots, x_n : 0 < x_i, 0 < x_1 + x_2 + \dots + x_n \leq 1\}$$

1 since all life histories of (3) that satisfy (4) will lie in E . Rules 1 and 2 ensure that $x_i(t) > 0$
 2 for all $t > 0$ given $x_i(0) > 0$. Rule 3 ensures that these solutions lie in E , and that the
 3 (hidden) variable $N(t)$ is physically reasonable.

4 **2.1.5 Rule 4: Resource Dependence:**

5 Let each population x_i , $i \geq 1$, consume resource R_i that is either another population
 6 x_j , with $j < i$, or is the available nutrient N , which we label x_0 for this discussion. (When
 7 x_i has resource $N = x_0$ it is known as an autotroph.) Note that $0 \leq R_i \leq 1$. We define normal
 8 ecologies as those in which each population x_i :

9 a) Requires resource $R_i > 0$ to thrive, so that $f_i|_{R_i=1} > 0 > f_i|_{R_i=0}$; and

10 b) Grows better when there is more resource R_i available. That is, when we move
 11 directly through E from the vertex where $R_i = x_j = 1$ to the face where
 12 $R_i = x_j = 0$, the corresponding growth function f_i decreases monotonically.

13 This condition 4(b) can be checked using the following ray condition: for each f_i , we check
 14 that the derivative of f_i in the ray direction is negative, where the rays have the resource
 15 vertex ($R_i = x_j = 1$) as origin, and extend through E to the face $R_i = x_j = 0$ for some $j < i$.

16 So checking for all $(x_1, x_2, \dots, x_n) \in E$, that, for each $i \geq 1$:

$$17 \quad x_1 \frac{\partial f_i}{\partial x_1} + \dots + x_{j-1} \frac{\partial f_i}{\partial x_{j-1}} - (1 - x_j) \frac{\partial f_i}{\partial x_j} + x_{j+1} \frac{\partial f_i}{\partial x_{j+1}} + \dots + x_n \frac{\partial f_i}{\partial x_n} \leq 0 \quad (5)$$

18 where the resource R_i vertex is at $(x_j = 1, x_k = 0 \text{ for all } k \neq j)$, gives 4(b).

2.2 Properties of Normal Ecologies

Normal ecologies have several properties that improve their analytical tractability. All n -species normal ecologies have at least $2^n - 1$ sets of equations that describe potential extinction equilibrium points where one or more species are extinct (i.e. $\{x_i^* = 0\}$ for some i) including the origin of the ecospace, defined by $\{x_i^* = 0\}$ for all i where all species are extinct. They also have one set of equations, defined by $\{x_i^* \neq 0 = f_i\}$ for all i , that may describe a coexistence equilibrium point, where all species coexist. 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. Normal ecologies do not guarantee that all possible equilibrium points reside in the ecospace E , but as noted above we will require that a specific set of boundary equilibrium points must exist in E for a particular parameterisation to be considered valid.

The stabilities of the extinction equilibrium points are crucial to coexistence, where we define the stability of an equilibrium point to be the Lyapunov stability. This is determined by the eigenvalues of the Jacobian (or community) matrix (J) of the system evaluated at the equilibrium point (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.

Extinction in mathematical models of ecosystems occurs if a model has an extinction point 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, normal ecologies have the property that we can always find an analytic expression for the eigenvalue λ_j associated with a population x_j at

an extinction point, where $x_j^* = 0$. This “competition eigenvalue” is given by the value of its life function evaluated at the extinction point, that is $\lambda_j = f_j^*|_{x_j^*=0}$. The condition for coexistence or persistence in normal ecologies is therefore that no extinction equilibrium point is stable, i.e. that an eigenvalue there satisfies $\lambda_j = f_j^*|_{x_j^*=0} > 0$.

Normal ecologies may have *structural coexistence*, where all equations have the property that $\lambda_j = f_j^*|_{x_j^*=0} > 0$ for all reasonable parameter choices (i.e. such that Rule 4 above is satisfied), or they may have *conditional coexistence*, where parameter values are carefully chosen so that at least one competition eigenvalue is positive at each extinction point. Structural coexistence occurs if all life functions (f_i) have vanishing loss terms, that is, terms that tend to zero as the population $x_i \rightarrow 0$. (In general, ecosystem models have non-vanishing per capita growth terms that do not tend to zero as $x_i \rightarrow 0$.) Conditional coexistence occurs when the equations have one or more non-vanishing loss terms, and relies on values being chosen for the parameters that ensure that the competition eigenvalue condition is met. In practice, it can be quite difficult to find parameter sets for conditional coexistence models with the property that all populations remain extant (Cropp and Norbury, 2012b).

2.3 Coexistence in the Library of Lotka

Of the approximately 10^{14} structural forms in the Library of Lotka as we have defined it above, only one form has the property of structural coexistence, and only approximately 10^{137} of the 10^{151} predictions in the Library will be produced by models with this property. However, we need to interpret these figures with care. For example, we distinguished only between linear and nonlinear mortality terms when constructing the library, but note that there

is only one way in which a mortality term can be exactly linear, but an infinite number of ways in which it could be nonlinear.

We also don't know what fraction of the other models in the Library have the property of conditional coexistence as this depends on their parameter values, but we gain some insight into their rarity for our example models in §3.4 below. This paucity of coexistence solutions in the Library of Lotka places into clear relief the 'Paradox of the Plankton' articulated by Hutchinson (1961) in response to the difficulty of finding models that could reproduce the coexistence of multiple species on the few resources obvious in real plankton ecosystems. It would appear that Hutchinson and those that followed were browsing the Library of Lotka looking for a solution, and we see now that their probability of success was extremely low.

3. Simulation Methods

3.1 Example Ecosystem Models

We use a simple $NP_1P_2Z_1Z_2$ ecosystem as a basis to construct examples of plankton models commonly used in climate change and fisheries applications. These example models are sufficiently complex that the usual geometric techniques used to understand the solutions (Kot, 2001) are of little practical use. We design two versions of the $NP_1P_2Z_1Z_2$ model to have different properties using different process representations as described by Cropp and Norbury (2012b). One version has the property of structural coexistence, where all populations coexist for all time for any parameter set that complies with our rules. This model is constructed using non-vanishing growth terms and vanishing loss terms when the model is written in consistent normal form:

$$\frac{dx_i}{dt} = x_i (growth_{NV} - grazing_V - mortality_V). \quad (6)$$

Here, $growth_{NV}$ indicates any non-vanishing growth formulation such as Michalis-Menten or Droop, $grazing_V$ indicates any vanishing grazing formulation such as Holling Type III, and $mortality_V$ indicates a vanishing mortality/respiration formulation such as any nonlinear mortality.

The alternate model also complies with the consistent normal criteria but has the property of conditional coexistence, where all populations coexist only for particular carefully chosen parameter sets. This model is constructed using non-vanishing growth terms and non-vanishing loss terms:

$$\frac{dx_i}{dt} = x_i (growth_{NV} - grazing_{NV} - mortality_{NV}). \quad (7)$$

Here, $grazing_{NV}$ indicates any non-vanishing grazing formulation such as Holling Type I or II, and $mortality_{NV}$ indicates a non-vanishing mortality/respiration formulation such as linear mortality.

3.2 Structural Coexistence Model

The example Structural Coexistence model is defined by equations (8) - (11):

$$\frac{dP_1}{dt} = P_1 \left(\frac{\mu_1 N}{N + \kappa_1} - \frac{\hat{\phi}_{12} P_1 P_2}{P_1^2 + \hat{\kappa}_{12}} - \frac{\phi_{11} P_1 Z_1}{P_1^2 + \kappa_{11}} - \frac{\phi_{12} P_1 Z_2}{P_1^2 + \kappa_{12}} - \sigma_{P1} P_1 - \sigma_{P1}^* \right), \quad (8)$$

$$\frac{dP_2}{dt} = P_2 \left(\frac{\mu_2 N}{N + \kappa_2} + \frac{\hat{\phi}_{12} (1 - \hat{\psi}_{12}) P_1^2}{P_1^2 + \hat{\kappa}_{12}} - \frac{\phi_{21} P_2 Z_1}{P_2^2 + \kappa_{21}} - \frac{\phi_{22} P_2 Z_2}{P_2^2 + \kappa_{22}} - \sigma_{P2} P_2 \right), \quad (9)$$

$$\frac{dZ_1}{dt} = Z_1 \left(\frac{\phi_{11} (1 - \psi_{11}) P_1^2}{P_1^2 + \kappa_{11}} + \frac{\phi_{21} (1 - \psi_{21}) P_2^2}{P_2^2 + \kappa_{21}} - \frac{\tilde{\phi}_{12} Z_1 Z_2}{Z_1^2 + \tilde{\kappa}_{12}} - \sigma_{Z1} Z_1 \right), \quad (10)$$

$$\frac{dZ_2}{dt} = Z_2 \left(\frac{\phi_{12} (1 - \psi_{12}) P_1^2}{P_1^2 + \kappa_{12}} + \frac{\phi_{22} (1 - \psi_{22}) P_2^2}{P_2^2 + \kappa_{22}} + \frac{\tilde{\phi}_{12} (1 - \tilde{\psi}_{12}) Z_1^2}{Z_1^2 + \tilde{\kappa}_{12}} - \sigma_{Z2} Z_2 \right), \quad (11)$$

where $N = 1 - P_1 - P_2 - Z_1 - Z_2$. Note that structural coexistence models cannot include a linear mortality term. The linear mortality term $\sigma_{P_1}^*$ has been added to the P_1 equation in this structural coexistence model solely to facilitate simulation of the effect of climate change, that is $\sigma_{P_1}^*$ increases with ‘global warming’ and the remaining populations P_2 , Z_1 and Z_2 then all respond to this variation through P_1 . The application of the rules for a consistent normal ecology for the structural coexistence model is shown in Appendix One.

3.3 Conditional Coexistence Model

The example Conditional Coexistence model is composed of equations (12) - (15):

$$\frac{dP_1}{dt} = P_1 \left(\frac{\mu_1 N}{N + \kappa_1} - \frac{\hat{\phi}_{12} P_2}{P_1 + \hat{\kappa}_{12}} - \frac{\phi_{11} Z_1}{P_1 + \kappa_{11}} - \frac{\phi_{12} P_1 Z_2}{P_1 + \kappa_{12}} - \sigma_{P_1} \right), \quad (12)$$

$$\frac{dP_2}{dt} = P_2 \left(\frac{\mu_2 N}{N + \kappa_2} + \frac{\hat{\phi}_{12} (1 - \hat{\psi}_{12}) P_1}{P_1 + \hat{\kappa}_{12}} - \frac{\phi_{21} Z_1}{P_2 + \kappa_{21}} - \frac{\phi_{22} Z_2}{P_2 + \kappa_{22}} - \sigma_{P_2} \right), \quad (13)$$

$$\frac{dZ_1}{dt} = Z_1 \left(\frac{\phi_{11} (1 - \psi_{11}) P_1}{P_1 + \kappa_{11}} + \frac{\phi_{21} (1 - \psi_{21}) P_2}{P_2 + \kappa_{21}} - \frac{\tilde{\phi}_{12} Z_2}{Z_1 + \tilde{\kappa}_{12}} - \sigma_{Z_1} \right), \quad (14)$$

$$\frac{dZ_2}{dt} = Z_2 \left(\frac{\phi_{12} (1 - \psi_{12}) P_1}{P_1 + \kappa_{12}} + \frac{\phi_{22} (1 - \psi_{22}) P_2}{P_2 + \kappa_{22}} + \frac{\tilde{\phi}_{12} (1 - \tilde{\psi}_{12}) Z_1}{Z_1 + \tilde{\kappa}_{12}} - \sigma_{Z_2} \right), \quad (15)$$

where again $N = 1 - P_1 - P_2 - Z_1 - Z_2$. The application of the rules for a consistent normal ecology for the conditional coexistence model is shown in Appendix Two.

We apply the axioms for the construction of normal ecological models described in Cropp and Norbury (2012a) to ensure that the models are consistent computer ecologies. We define competition eigenvalues and parameterise the models by randomly sampling a large parameter space using criteria on the signs of the competition eigenvalues.

3.4 Parameters

We chose parameter sets for the models by randomly generating 10^6 sets of parameter values from a parameter space described in Cropp and Norbury (2012b). For all models, the parameter sets were required to comply with the criteria that the set of boundary equilibrium points, $\{P_1^*, 0, 0, 0\}$, $\{0, P_2^*, 0, 0\}$, $\{P_1^*, 0, Z_1^*, 0\}$, $\{0, P_2^*, Z_1^*, 0\}$, $\{P_1^*, 0, 0, Z_2^*\}$ and $\{0, P_2^*, 0, Z_2^*\}$, existed within the ecospace $E \equiv \{0 < P_1 + P_2 + Z_1 + Z_2 < 1; 0 \leq P_1, P_2, Z_1, Z_2 \leq 1\}$. We refer to parameter sets that comply with this condition as reasonable.

The properties of normal ecologies mean that any reasonable parameter set for a model with structural coexistence typically results in the model having equilibrium dynamics, where the coexistence equilibrium point is locally stable. The parameter search for the structural coexistence model found 813,145 reasonable parameter sets, each with the property that the competition eigenvalues ($\lambda_i = f_i \big|_{x_i^*=0}$) at each extinction equilibrium point $x_i^* = 0$ for some $i = 1, \dots, 4$ are all positive. One parameter set was arbitrarily chosen from the reasonable parameter sets for the structural coexistence model for use in the simulations (Table 1, Structural Coexistence). We will refer to this parameterisation of the Structural Coexistence model as the SCE model.

Reasonable parameter sets for the conditional coexistence model do not necessarily result in coexistence solutions, and further conditions must be applied to find these solutions. We searched the reasonable parameter sets to obtain conditional coexistence models with different dynamical properties. We first required that all the competition eigenvalues of all the required boundary equilibrium points were positive; this parameterises the conditional coexistence model to have equilibrium dynamics similar to the structural coexistence model (Table 1, Conditional Equilibrium). We then searched for a parameter set that produced

pinball dynamics in the conditional coexistence equations by stipulating that each of the required boundary equilibrium points had one positive and one negative competition eigenvalue (Table 1, Conditional Pinball).

The parameter search for the conditional coexistence model found 484,568 valid parameter sets of which 9,095 parameter sets complied with our coexistence criteria. Reasonable parameter sets with all competition eigenvalues positive, that endow the conditional coexistence model with equilibrium dynamics, comprised 0.02% of valid coexistence parameter sets; one of these that provided a solution similar to the parameter set chosen for the structural coexistence model was selected for the numerical simulations (Table 1, Conditional Equilibrium). We will refer to this parameterisation of the Conditional Coexistence model as the CCE model.

The remainder of the valid coexistence parameter sets produced pinball dynamics. We chose a parameter set with a competition eigenvalue structure such that the dynamics of the system will visit the vicinity of each boundary equilibrium point in the sequence $\{P_1^*, 0, Z_1^*, 0\} \rightarrow \{P_1^*, 0, 0, Z_2^*\} \rightarrow \{0, P_2^*, 0, Z_2^*\} \rightarrow \{0, P_2^*, Z_1^*, 0\} \rightarrow \{P_1^*, 0, Z_1^*, 0\}$ (Table 1, Conditional Pinball). We will refer to this parameterisation of the Conditional Coexistence model as the CCP model.

3.3 Seasonal Forcing and Climate Change

A forcing, which notionally simulates seasonal variations in light, was applied to demonstrate that models with the same properties can exhibit different dynamic outcomes when subjected to environmental forcing of different amplitudes. The seasonal forcing was represented by a simple sine function ($R = 1 + A \sin\left(\frac{2\pi t}{100}\right)$) operating on the phytoplankton

growth rates (μ_1 and μ_2). This function had a period of 100 time units and amplitude of $A = 0.10$ to represent weak amplitude seasonal light forcings typical of the tropics or $A = 0.50$ to represent the larger amplitude seasonal light forcings typical of temperate and polar regions.

Climate-induced mortality was applied only to one phytoplankton (P_1) as an increase in the coefficient of the linear mortality term. The change in mortality due to the changing climate was modelled as a simple linear increase with temperature ($M_i(t) = c_i + m_i t$) where t is time and the change in temperature over time is implicit. As the models used random parameter values we tuned the mortality functions to produce extinctions at approximately two-thirds of the way through the simulation in all models. For the SCE model $c_i = 0$ and $m_i = 0.05$; for the CCE model $c_i = 1$ and $m_i = 0.001$, and for the CCP model $c_i = 1$ and $m_i = 0.002$.

4. Results and Discussion

The simulation results with no seasonal forcing or mortality change (Figure 1) show the endogenous dynamics of the three models. Figure 1 shows the constant population levels of the SCE and CCE models that are typical of the endogenous dynamics of these models. In contrast the CCP model has an endogenous cycle of approximately 450 time units, with extended periods when the system is in the vicinity of the boundary equilibrium point $\{P_1^*, 0, 0, Z_2^*\}$ interspersed with shorter periods when the system visits the other points in turn as described above.

When a weak forcing is applied to the growth rates of P_1 and P_2 to simulate small seasonal variations in irradiance (Figure 2), the SCE model responds with all populations showing low amplitude oscillations with a period approximately the same as the forcing. The CCE model similarly responds with population oscillations of 100 time units, the same as the forcing, but with much larger amplitude oscillations. In contrast, the dynamics of the weakly forced CCP model are almost identical to that of the unforced model, with the amplitude of the oscillation reducing slightly and the period reducing (for P_1 from about 450 to 320 time units).

The dynamics of the CCP model do respond to the application of a stronger seasonal forcing (Figure 3), with the endogenous dynamics now becoming entrained into the 100 time unit period of the exogenous forcing. The responses of the SCE and CCE models to the stronger exogenous forcing are just to increase the amplitude of the population oscillations, which remain with the same 100 time unit period of the forcing. As for the weak forcing, the amplitude of the oscillations in the CCE model is much larger than in the SCE model.

The application of ‘climate change’ dependence to the mortality rate of P_1 is calculated to result in extinction of P_1 ($\lambda_{P_1} = f_{P_1} \Big|_{P_1^*=0} < 0$ at one or more boundary equilibrium point where $P_1^* = 0$) at about time unit 500 in the simulations for each model (Figures 4-6). The impact of these extinctions is known from the properties of the models (Cropp and Norbury, 2012b). The SCE and CCE models both initially had the property that the competition eigenvalues were all positive at every boundary equilibrium point. This means that when P_1 goes extinct, when λ_{P_1} becomes negative, the only impact is that the models will become attracted to a new coexistence equilibrium solution $\{0, P_2^*, Z_1^*, Z_2^*\}$ where $P_1^* = 0$. In contrast, only one competition eigenvalue is positive at each boundary equilibrium point in

the CCP model, and the extinction of P_1 will cause the system to attract to one of the boundary equilibrium points (Cropp and Norbury, 2012b). For the parameterisation of the CCP used in this case, this will result in the $\{0, P_2^*, Z_1^*, 0\}$ point becoming the new, and in this case equilibrium, solution to the CCP model. This means that the extinction of P_1 as a result of climate change will also lead to the extinction of Z_2 in the CCP model, that is, a cascade of extinctions will occur.

While the changes to the food web structure as a result of the increasing mortality of P_1 may be predicted precisely from knowledge of the model properties, and may in fact be designed for where the model is constructed as we have done here, the dynamical responses to the changing climate are not so explicitly known or as explicitly defined by the model properties. Figures 4 and 5 show that the gradual reduction, and eventual change in sign, of λ_{P_1} produces quite different dynamical responses in the three models. The most gradual and predictable response occurs in the SCE model in both the weak (Figure 4) and strong (Figure 5) seasonal forcing scenarios. Here, the P_1 population gradually reduces in size until it eventually reaches zero at about time unit 500. At this point a trans-critical bifurcation occurs where the stable $\{P_1^*, P_2^*, Z_1^*, Z_2^*\}$ interior equilibrium point collides and exchanges stability with the previously unstable $\{0, P_2^*, Z_1^*, Z_2^*\}$ equilibrium point. The CCE model behaves similarly to the SCE model, as expected, because they have identical competition eigenvalue structures. The major difference between these models is their sensitivity to the external seasonal forcing, and in both cases the amplitudes of the CCE population oscillations are greater than those of the equivalent SCE populations.

The dynamical response of the CCP model is quite different to those of the SCE and CCE models in both the weak and strong seasonal forcing cases. In the weak case (Figure 4) the P_1 population responds to the changing climate by dominating the system until it precipitously goes extinct at about 450 time units. At this point the $\{0, P_2^*, Z_1^*, 0\}$ boundary equilibrium point attracts the dynamics and Z_2 goes extinct as a result of P_1 's extinction. The same process occurs in the strong seasonal forcing (Figure 5), but in this case the dynamics are quite different. Here, the seasonal cycle forces a series of P_1 blooms that increase in size until the population fails to recover and manages only a small bloom at about time 420 before it goes extinct shortly after. Although the new system has a stable equilibrium point at $\{0, P_2^*, Z_1^*, 0\}$ on the boundary, as it does for the weak forcing case, the system does not settle down quickly to an equilibrium solution as in the weak case. Instead, a series of short blooms and busts ("breathers") are observed with both the P_2 and Z_1 populations reducing to very low levels between blooms.

The differing scenarios presented in Figures 1-5 might variously be viewed as 'plausible' outcomes of a modelling exercise by different observers. Our point is not whether these outcomes are realistic or not, but that the outcomes are determined by decisions made during the construction and parameterisation of the computer model. In particular, the 'climate change' simulations of Figures 4 and 5 reveal significant differences in 'predictions' due to differences in the model equations (SCE vs. CCE), different parameterisations of the same equations (CCE vs. CCP), and different environments for the same model, most obvious in the CCP model for weak and strong forcings. These differences can determine whether a system has a predictable route to extinction (SCE, weak and strong) or a catastrophic collapse (CCP, weak); an equilibrium post-extinction state (CCP, weak) or apparent chaos (CCP, strong).

We know that the SCE model will respond to climate change by moving from its original equilibrium state to a new equilibrium that does not include the extinguished population because this is a structural property of the equations, and will occur for any parameter set. We know that the CCE model will exhibit the same behaviour, despite it being composed of different equations, because we have parameterised the equations to have the same competition eigenvalue structure as the SCE model. And we know that the CCP model, despite having the same equations as the CCE model, will exhibit a cascade of extinctions in response to climate change because we have parameterised it to have a competition eigenvalue structure that leads to this outcome. In this case, we know that the outcome of extinction of P_1 will be an ecosystem composed only of P_2 and Z_1 , but the competition eigenvalues give us no information on the dynamics of this new state.

5. Conclusions

Complex ecosystem models are generally constructed from the “bottom-up”, that is, from a best (but imperfect) understanding of the important interactions between populations. Choices must be made between the different functional forms used to represent interactions between populations, often with little theoretical or empirical justification. In such circumstances we argue that modellers should consider very carefully what formulation they choose, and be aware of the impact that such choices can have on the properties of the model. A key new analytical result for our dynamical systems in ecospace is that extinctions can be studied without knowledge of either interior equilibrium points or their stability. By looking only at boundary extinction points, and the sign of the relevant life function there, we can immediately comment on the extinction behaviour without solving for any of the dynamics. This is a striking simplification, and even holds when the dynamics can become chaotic.

1 We have shown that this is especially important when making choices between non-
 2 vanishing and vanishing loss terms, such as Holling Type II and III grazing interactions and
 3 linear and nonlinear mortality. The latter distinction has received substantial attention from
 4 marine ecosystem modellers (Steele and Henderson, 1992; Edwards and Brindley, 1999;
 5 Morozov, 2010), but we have shown (Cropp and Norbury, 2012b) that the full implications of
 6 this choice only become evident when considered in conjunction with the form of the other
 7 loss terms.

8 It is sometimes assumed, when faced with significant uncertainty in experimental
 9 measurements of per capita mortality rates that the “least biased assumption” is to calculate
 10 the average per capita mortality and apply it in a linear term. We suggest that in fact linear
 11 mortality should be considered a special case, and propose that a better modelling practice is
 12 to include both a linear and a nonlinear mortality term. This suggests that experimental per
 13 capita mortality data should be fitted with a regression line with nonzero slope and intercept.
 14 We note that Gross et al (2009) also argue for a combination of linear and nonlinear mortality
 15 coefficients, although from a different perspective.

16 The key message that we wish to convey in this manuscript is that the ‘answer’ to how
 17 ecosystems will respond to climate, or any other, change that will be obtained from complex
 18 simulation models will depend on the known properties of the ecosystem model, and that
 19 these properties are determined when the model is constructed and parameterised. The
 20 choices available to modellers for food web complexity, process functional forms and
 21 parameter values mean that the interpretation of model predictions must recognise the Library
 22 of Lotka and the intrinsic difficulty of ascribing credibility to model predictions without *a*
 23 *priori* information. We argue that the first step to winnowing incorrect predictions from the

Library of Lotka is to utilise the rules for consistent normal ecologies to construct models with at least some known properties.

This should not be interpreted to mean that we recommend that ecosystem models should be constructed from the “top-down” as we have done in this manuscript. (However, we observe that this is a better pragmatic solution to the problems of population extinctions in simulations than the common practice of setting artificial minimum population levels.) Ecosystem models should continue to be constructed from the “bottom-up” by considering the nature of the process interactions between populations, but this should be done in cognizance of the ecological axioms and analysis techniques that we summarise here and provide in more detail in Cropp and Norbury (2012a, b).

The analysis techniques demonstrated here provide a powerful tool that helps us to understand the properties of ecosystem models of any complexity, and hence the basic characteristics of their predictions of ecosystem responses to a changing world. A key new analytical result for our dynamical systems in ecospace is that extinctions can be studied without knowledge of either interior equilibrium points or their stability. By looking only at boundary extinction points, and the sign of the relevant life function there, we can immediately comment on the extinction behaviour without solving for any of the dynamics. This is a striking simplification, and even holds when the dynamics can become chaotic. We have presented this work in the context of plankton ecosystems, partly to justify ignoring spatial inhomogeneity, but we note that the theoretical basis for this work is applicable to any ecosystem.

6. Final Comment

1 The Library of Lotka provides a useful metaphor within which to evaluate the
 2 meaning of the results of simulation models of ecosystems. When constructing the library we
 3 have used a reasonable model structure (essentially that of PlankTOM10), used a few widely
 4 accepted functional forms to represent the processes that control the dynamics of the
 5 populations (Holling Type I, II and III grazing; linear and nonlinear mortality), and used a
 6 very small range of uncertainty ($\pm 10\%$) around known parameter values with a reasonable
 7 precision (1%). The Library of Lotka for this model contains at least 10^{151} model predictions,
 8 only one of which is correct, but all of which are plausible.

9 We all know that 10^{151} is a large number, but it is useful to consider whether this
 10 presents a fundamental constraint on browsing the Library of Lotka or just a temporary
 11 impediment that will soon be overcome by the apparently inexorable increase in computing
 12 power. Imagine that we construct a very large parallel computer, and that it requires one
 13 kilogram of matter to construct each processor, its memory and its amortised power supply.
 14 Assume we construct 'state of the art' processors that can calculate one model solution every
 15 second. To put 10^{151} in context, if we used all the matter in the universe we could construct a
 16 computer with 10^{54} processors. If we used that computer to compute solutions for as long as
 17 the universe has existed (approximately 10^{17} seconds) we could compute about 10^{71} solutions.
 18 Our universal metaphor turns out to be serendipitous because there are approximately 10^{80}
 19 atoms in the universe. Hence, if we build a computer the size of the universe and use it to
 20 calculate solutions for as long as the universe has existed we can compute a fraction of the
 21 possible solutions equivalent to only one atom in the entire universe. It is safe to assume that
 22 we will never find a correct solution by browsing the Library of Lotka.

23 We suggest that chiseled into the portico of the Library of Lotka should be the
 24 warning to those intending to browse the shelves: "Abandon all hope ye who enter here". The

1 correct solution to a climate, or any other, change scenario cannot be found by naively
2 browsing the Library of Lotka looking for sensible predictions – we must instead create a
3 catalogue to the library that will direct us to the correct solutions. This catalogue can only be
4 created from better information about the functional forms of, in particular, grazing
5 interactions and mortality processes; from more accurate and complete measurements of
6 parameters; and from a better analytic understanding of the properties of complex ecological
7 models.

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Tables

Table 1. Parameters values used in the simulations for the structural coexistence model and the conditional coexistence models with equilibrium and pinball dynamics.

R	PA	Structural	Conditional	Conditional
		Coexistence	Equilibrium	Pinball
	μ_1	1.086	1.6684	1.8255
	μ_2	0.982	2.0227	1.9068
	κ_1	1.833	0.2037	1.5008
	κ_2	1.471	0.9215	1.6399
	σ_{P1}	0.379	0.4748	0.3468
	σ_{P2}	0.174	0.1576	0.4011
	σ_{Z1}	0.3726	0.0055	0.1918
	σ_{Z2}	0.0091	0.2471	0.4487
	σ_{P1}^*	0.01	-	-
	$\hat{\phi}_{12}$	9.384	3.3076	2.6684
	$\hat{\kappa}_{12}$	1.400	1.3999	1.3999
	$\hat{\psi}_{12}$	0.088	0.1949	0.6084
	ϕ_{11}	5.630	8.1719	2.6386
	ϕ_{12}	1.388	4.2469	7.2484
	ϕ_{21}	2.611	8.1293	9.7025
	ϕ_{22}	1.083	6.9113	9.7548

$\tilde{\phi}_{12}$	2.835	3.4365	4.0366
κ_{11}	1.466	1.4656	1.4656
κ_{12}	1.920	0.4636	0.4636
κ_{21}	0.464	1.9197	1.9197
κ_{22}	0.161	0.1608	0.1608
$\tilde{\kappa}_{12}$	1.408	1.4077	1.4077
ψ_{11}	0.129	0.7508	0.5448
ψ_{12}	0.447	0.8324	0.7581
ψ_{21}	0.257	0.2662	0.4713
ψ_{22}	0.607	0.5965	0.5926
$\tilde{\psi}_{12}$	0.088	0.1275	0.4025

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Figure Legends

Figure 1. Solutions to models with no external forcings. Ecology with structural coexistence (top panel) and ecologies with conditional coexistence with equilibrium dynamics (centre panel), and pinball dynamics (bottom panel). Thick solid line is P_1 , thin solid line is P_2 , dotted line is Z_1 , and dashed line is Z_2 .

Figure 2. Solutions to models with weak external forcings (10% annual variation in light). Panels and lines as for Figure 1.

Figure 3. Solutions to models with strong external forcings (50% annual variation in light). Panels and lines as for Figure 1.

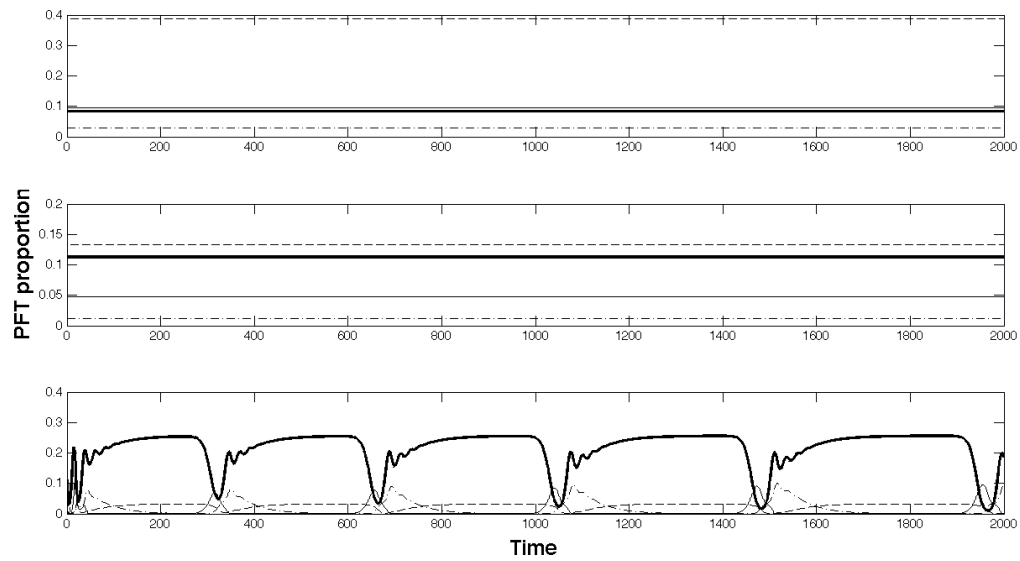
Figure 4. Solutions to models with weak external forcings and increasing temperature dependent mortality on P_1 . Panels and lines as for Figure 1.

Figure 5. Solutions to models with strong external forcings and increasing temperature dependent mortality on P_1 . Panels and lines as for Figure 1.

1

2 Figures

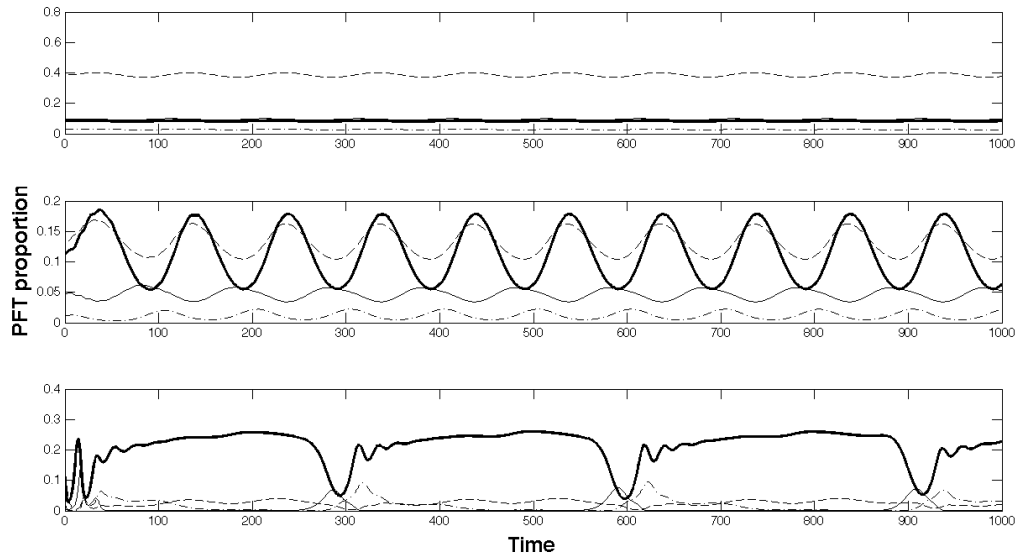
3 Figure 1.



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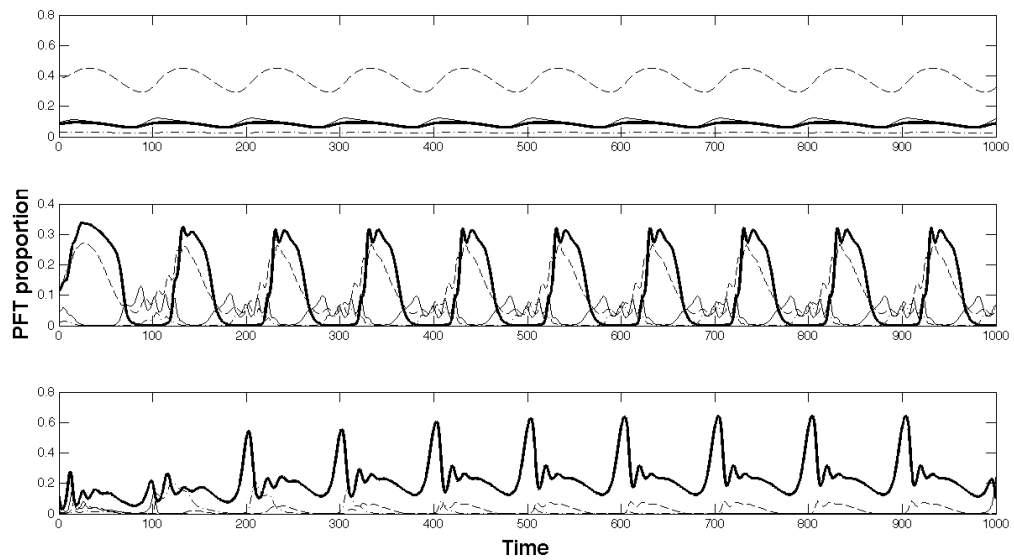
6 Figure 2.



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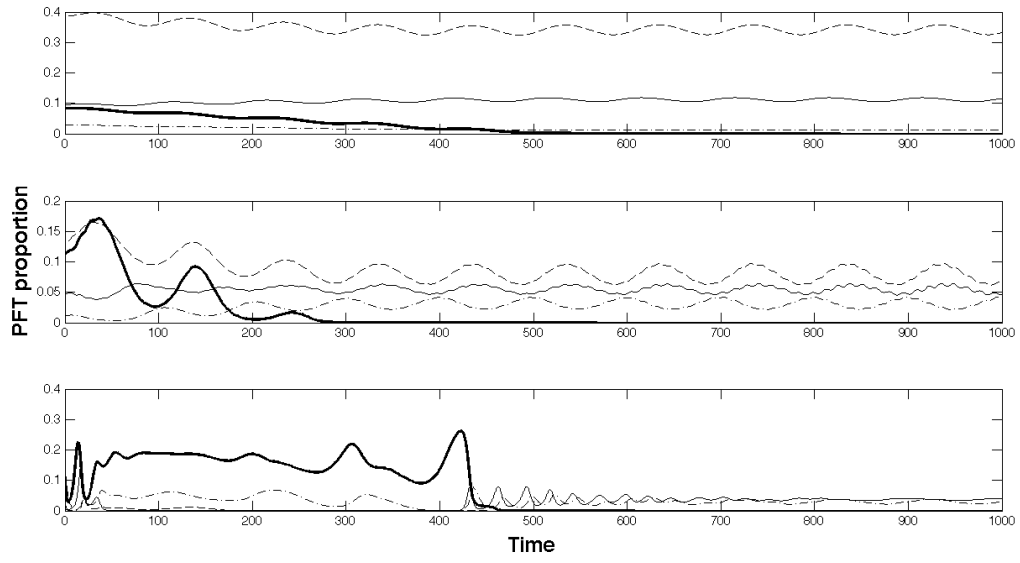
3 Figure 3.



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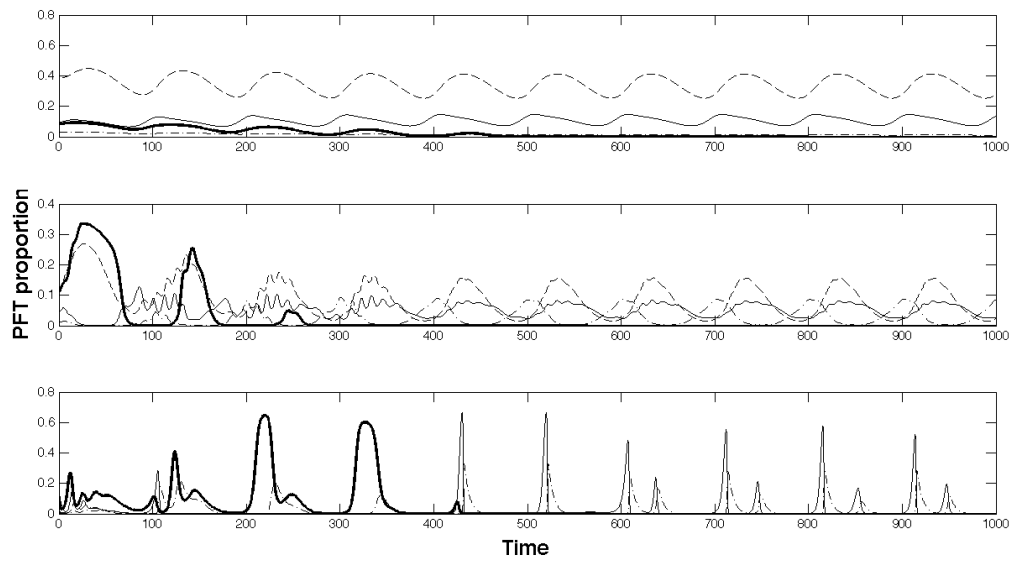
6 Figure 4.



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2 **Appendix One: Checking the Rules for Structural Coexistence**3 **Rule 0:** equations (8) - (11) are measurement independent as $\frac{1}{x_i} \dot{x}_i$ is defined and $N_T = 1$,

4 then populations are fractions of the limiting nutrient.

5 **Rule 1:** the per capita growth function derivatives $\frac{\partial f_i}{\partial x_j}$ exist smoothly for all $x_i \geq 0$ with the6 initial condition $x_i(t) > 0$.7 **Rule 2:** $\sum_i x_i = 1 - N$ defines $N(t)$, hence we may eliminate N . (In practice, we retain N in

8 the notation for parsimony of expression.)

9 **Rule 3:** $\dot{N} \geq 0$ on $N = 0$ and the initial condition ensures that $N(t) \geq 0$ where,

$$\begin{aligned}
\frac{dN}{dt} = & -\frac{\mu_1 N P_1}{N + \kappa_1} - \frac{\mu_2 N P_2}{N + \kappa_2} + \sigma_{P_1} P_1^2 + \sigma_{P_2} P_2^2 + \sigma_{Z_1} Z_1^2 + \sigma_{Z_2} Z_2^2 \\
& + \frac{\hat{\phi}_{12} \hat{\psi}_{12} P_1^2 P_2}{P_1^2 + \hat{\kappa}_{12}} + \frac{\phi_{11} \psi_{11} P_1^2 Z_1}{P_1^2 + \kappa_{11}} + \frac{\phi_{12} \psi_{12} P_1^2 Z_2}{P_1^2 + \kappa_{12}} + \frac{\phi_{21} \psi_{21} P_2^2 Z_1}{P_2^2 + \kappa_{21}}, \\
& + \frac{\phi_{22} \psi_{22} P_2^2 Z_2}{P_2^2 + \kappa_{22}} + \frac{\phi_{11} \psi_{11} P_1^2 Z_1}{P_1^2 + \kappa_{11}} + \frac{\tilde{\phi}_{12} \tilde{\psi}_{12} Z_1^2 Z_2}{Z_1^2 + \tilde{\kappa}_{12}}
\end{aligned} \tag{16}$$

11 and $N = 0 \Rightarrow \sum_i x_i = 1$ and $\frac{dN}{dt} > 0$ (i.e. the Lid exists).12 **Rule 4:** we consider the resources R_i independently to properly define the system. The13 resource for P_1 is $R_1 = x_0 = N$; then $f_1|_{R_1=1} = \frac{\mu_1}{1 + \kappa_1} > 0$, and

1 $f_1|_{R_1=0} = -\frac{\hat{\phi}_{12}P_1P_2}{P_1^2 + \hat{\kappa}_{12}} - \frac{\phi_{11}P_1Z_1}{P_1^2 + \kappa_{11}} - \frac{\phi_{12}P_1Z_2}{P_1^2 + \kappa_{12}} - \sigma_{P_1}P_1 < 0$, so the f_1 resource ray sign conditions are

2 satisfied when N is the resource. The directional derivative (5) for f_1 is

$$3 \quad \begin{aligned} & P_1 \left(-\frac{\mu_1\kappa_1}{(N + \kappa_1)^2} - \sigma_{P_1} \right) + P_2 \left(-\frac{\mu_1\kappa_1}{(N + \kappa_1)^2} - \frac{2\hat{\phi}_{12}\hat{\kappa}_{12}P_1}{(P_1^2 + \hat{\kappa}_{12})^2} \right) \\ & + Z_1 \left(-\frac{\mu_1\kappa_1}{(N + \kappa_1)^2} - \frac{2\phi_{11}\kappa_{11}P_1}{(P_1^2 + \kappa_{11})^2} \right) + Z_2 \left(-\frac{\mu_1\kappa_1}{(N + \kappa_1)^2} - \frac{2\phi_{12}\kappa_{12}P_1}{(P_1^2 + \kappa_{12})^2} \right) < 0 \end{aligned} \quad (17)$$

4 This ray derivative is always negative and f_1 satisfies rule 4.

5 As P_2 is allowed to be a mixotroph, and hence has multiple resources, its resource
6 conditions must be checked on each resource independently after setting the other resource to
7 zero. When acting as an autotroph the resource for P_2 is $R_2^1 = x_0 = N$; then

8 $f_2|_{R_2^1=1} = \frac{\mu_2}{1 + \kappa_2} > 0$, and $f_2|_{R_2^1=0} = -\frac{\phi_{21}P_2Z_1}{P_2^2 + \kappa_{21}} - \frac{\phi_{22}P_2Z_2}{P_2^2 + \kappa_{22}} - \sigma_{P_2}P_2$. When acting as a mixotroph

9 the resource for P_2 is $R_2^2 = x_1 = P_1$; then $P_1 = 1$ $f_2|_{R_2^2=1} = \frac{\hat{\phi}_{12}(1 - \hat{\psi}_{12})}{1 + \hat{\kappa}_{12}} > 0$, and at $P_1 = 0$, after

10 setting the alternate resource N to zero, $f_2|_{R_2^2=0} = -\frac{\phi_{21}P_2Z_1}{P_2^2 + \kappa_{21}} - \frac{\phi_{22}P_2Z_2}{P_2^2 + \kappa_{22}} - \sigma_{P_2}P_2 < 0$. The

11 directional derivative (5) in the $R_2^1 = x_0 = N$ resource space, after setting the alternate

12 resource $P_1 = 0$, is

$$13 \quad \begin{aligned} & P_1 \left(-\frac{\mu_2\kappa_2}{(N + \kappa_2)^2} \right) + P_2 \left(-\frac{\mu_2\kappa_2}{(N + \kappa_2)^2} - \frac{\phi_{21}\kappa_{21}Z_1}{(P_2^2 + \kappa_{21})^2} - \frac{\phi_{22}\kappa_{22}Z_2}{(P_2^2 + \kappa_{22})^2} - \sigma_{P_2} \right) \\ & + Z_1 \left(-\frac{\mu_2\kappa_2}{(N + \kappa_2)^2} - \frac{\phi_{21}\kappa_{21}P_2}{(P_2^2 + \kappa_{21})^2} \right) + Z_2 \left(-\frac{\mu_2\kappa_2}{(N + \kappa_2)^2} - \frac{\phi_{22}\kappa_{22}P_2}{(P_2^2 + \kappa_{22})^2} \right) < 0 \end{aligned} \quad (18)$$

1 and in the $R_2^2 = x_1 = P_1$ resource space, after setting the alternate resource $N = 0$, is

$$\begin{aligned}
 & (1-P)_1 \left(-\frac{\hat{\phi}_{12}\hat{\kappa}_{12}(1-\hat{\psi}_{12})P_1}{(P_1^2 + \hat{\kappa}_{12})^2} \right) + P_2 \left(-\frac{\phi_{21}\kappa_{21}Z_1}{(P_2^2 + \kappa_{21})^2} - \frac{\phi_{22}\kappa_{22}Z_2}{(P_2^2 + \kappa_{22})^2} - \sigma_{P_2} \right) \\
 & + Z_1 \left(-\frac{\phi_{21}\kappa_{21}P_2}{(P_2^2 + \kappa_{21})^2} \right) + Z_2 \left(-\frac{\phi_{22}\kappa_{22}P_2}{(P_2^2 + \kappa_{22})^2} \right) < 0
 \end{aligned} \quad (19)$$

3 Both these ray derivatives are always negative and f_2 satisfies rule 4.

4 Z_1 also has two resources, $R_3^1 = x_1 = P_1$ and $R_3^2 = x_2 = P_2$. When feeding on P_1 , at

$$P_1 = 1 \quad f_3 \Big|_{R_3^1=1} = \frac{\phi_{11}(1-\psi_{11})}{1+\kappa_{11}} > 0 \quad \text{and at } P_1 = 0, \text{ with } P_2 = 0, \quad f_3 \Big|_{R_3^1=0} = -\frac{\tilde{\phi}_{12}Z_1Z_2}{Z_1^2 + \tilde{\kappa}_{12}} - \sigma_{Z_1}Z_1 < 0.$$

6 When feeding on P_2 , at $P_2 = 1 \quad f_3 \Big|_{R_3^2=1} = \frac{\phi_{21}(1-\psi_{21})}{1+\kappa_{21}} > 0$ and at $P_2 = 0$, with $P_1 = 0$,

$$f_3 \Big|_{R_3^2=0} = -\frac{\tilde{\phi}_{12}Z_1Z_2}{Z_1^2 + \tilde{\kappa}_{12}} - \sigma_{Z_1}Z_1 < 0. \quad \text{The directional derivative (5) in the } R_3^1 = x_1 = P_1 \text{ resource}$$

8 space, with $P_2 = 0$, is

$$(1-P_1) \left(-\frac{2\phi_{11}\kappa_{11}(1-\psi_{11})P_1}{(P_1^2 + \kappa_{11})^2} \right) + Z_1 \left(-\frac{\tilde{\phi}_{12}\tilde{\kappa}_{12}Z_2}{(Z_1^2 + \tilde{\kappa}_{12})^2} - \sigma_{Z_1} \right) + Z_2 \left(-\frac{\tilde{\phi}_{12}\tilde{\kappa}_{12}Z_1}{(Z_1^2 + \tilde{\kappa}_{12})^2} \right) < 0, \quad (20)$$

10 and the directional derivative (5) in the $R_3^2 = x_2 = P_2$ resource space, with $P_1 = 0$, is

$$(1-P_2) \left(-\frac{2\phi_{21}\kappa_{21}(1-\psi_{21})P_2}{(P_2^2 + \kappa_{21})^2} \right) + Z_1 \left(-\frac{\tilde{\phi}_{12}(\tilde{\kappa}_{12} - Z_1^2)Z_2}{(Z_1^2 + \tilde{\kappa}_{12})^2} - \sigma_{Z_1} \right) + Z_2 \left(-\frac{\tilde{\phi}_{12}Z_1}{Z_1^2 + \tilde{\kappa}_{12}} \right), \quad (21)$$

12 Both these ray derivatives are unequivocally negative, so rule 4 holds for f_3 .

- 1 Z_2 is an omnivore, and has three resources, $R_4^1 = x_1 = P_1$, $R_4^2 = x_2 = P_2$ and
- 2 $R_4^3 = x_3 = Z_1$. When feeding on P_1 , at $P_1 = 1$ $f_4 \Big|_{R_4^1=1} = \frac{\varphi_{12}(1-\psi_{12})}{1+\kappa_{12}} > 0$ and at $P_1 = 0$, with
- 3 $P_2 = 0$ and $Z_1 = 0$, $f_4 \Big|_{R_4^1=0} = -\sigma_{Z2}Z_2 < 0$. Similarly, when feeding on P_2 , at $P_2 = 1$
- 4 $f_4 \Big|_{R_4^2=1} = \frac{\varphi_{22}(1-\psi_{22})}{1+\kappa_{22}} > 0$ and at $P_2 = 0$, with $P_1 = 0$ and $Z_1 = 0$, $f_4 \Big|_{R_4^2=0} = -\sigma_{QZ2}Z_2 < 0$.
- 5 Finally, when feeding on Z_1 , at $Z_1 = 1$ $f_4 \Big|_{R_4^3=1} = \frac{\tilde{\varphi}_{12}(1-\tilde{\psi}_{12})}{1+\tilde{\kappa}_{12}} > 0$, while at $Z_1 = 0$, with $P_1 = 0$
- 6 and $P_2 = 0$, $f_4 \Big|_{R_4^3=0} = -\sigma_{Z2}Z_2 < 0$.

- 7 The directional derivative (5) in the $R_4^1 = x_1 = P_1$ resource space, with $P_2 = 0$ and
- 8 $Z_1 = 0$, is

$$9 \quad (1-P_1) \left(-\frac{\varphi_{12}\kappa_{12}(1-\psi_{12})P_1}{(P_1^2 + \kappa_{12})^2} \right) + Z_2(-\sigma_{Z2}) < 0, \quad (22)$$

- 10 in the $R_4^2 = x_2 = P_2$ resource space, with $P_1 = 0$ and $Z_1 = 0$, is

$$11 \quad (1-P_2) \left(-\frac{2\varphi_{22}\kappa_{22}(1-\psi_{22})P_2}{(P_2^2 + \kappa_{22})^2} \right) + Z_2(-\sigma_{Z2}) < 0, \quad (23)$$

- 12 and in the $R_4^3 = x_3 = Z_1$ resource space, with $P_1 = 0$ and $P_2 = 0$, is

$$13 \quad (1-Z_1) \left(-\frac{2\tilde{\varphi}_{12}(1-\tilde{\psi}_{12})Z_2}{(Z_1^2 + \tilde{\kappa}_{12})^2} \right) + Z_2(-\sigma_{Z2}) < 0. \quad (24)$$

- 14 All of these ray derivatives are unequivocally negative, so rule 4 is always satisfied for f_4 .

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2 **Appendix Two: Checking the Rules for Conditional Coexistence**

3 This model similarly complies with our rules, but differs from the structural
 4 coexistence model in that the sign restrictions of Rule 4 place constraints on the magnitude of
 5 the mortality terms of each PFT:

6 • for $P_1 \left. f_1 \right|_{R_1=1} > 0$ requires that $\sigma_{P1} < \frac{\mu_1}{1+\kappa_1}$;

7 • for $P_2 \left. f_2 \right|_{R_2^1=1} > 0$ requires that $\sigma_{P2} < \frac{\mu_2}{1+\kappa_2}$ and $\left. f_2 \right|_{R_2^2=1} > 0$ requires that

8
$$\sigma_{P2} < \frac{\hat{\phi}_{12}(1-\hat{\psi}_{12})}{1+\hat{\kappa}_{12}} ;$$

9 • for $Z_1 \left. f_3 \right|_{R_3^1=1} > 0$ requires that $\sigma_{Z1} < \frac{\phi_{11}(1-\psi_{11})}{1+\kappa_{11}}$ and $\left. f_3 \right|_{R_3^2=1} > 0$ requires that

10
$$\sigma_{Z1} < \frac{\phi_{21}(1-\psi_{21})}{1+\kappa_{21}} ; \text{ and}$$

11 • for $Z_2 \left. f_4 \right|_{R_4^1=1} > 0$ requires that $\sigma_{Z2} < \frac{\phi_{12}(1-\psi_{12})}{1+\kappa_{12}}$, $\left. f_4 \right|_{R_4^2=1} > 0$ requires that

12
$$\sigma_{Z2} < \frac{\phi_{22}(1-\psi_{22})}{1+\kappa_{22}} \text{ and } \left. f_4 \right|_{R_4^3=1} > 0 \text{ requires that } \sigma_{Z2} < \frac{\tilde{\phi}_{12}(1-\tilde{\psi}_{12})}{1+\tilde{\kappa}_{12}} .$$

13 Where Rule 4 imposes more than one criterion on the mortality term at least one of these
 14 conditions must be satisfied for the ecology to be consistent.

15 The directional derivative for f_1 is

$$\begin{aligned}
& P_1 \left(-\frac{\mu_1 \kappa_1}{(N + \kappa_1)^2} \right) + P_2 \left(-\frac{\mu_1 \kappa_1}{(N + \kappa_1)^2} - \frac{\hat{\phi}_{12} \hat{\kappa}_{12}}{(P_1 + \hat{\kappa}_{12})^2} \right) \\
& + Z_1 \left(-\frac{\mu_1 \kappa_1}{(N + \kappa_1)^2} - \frac{\phi_{11} \kappa_{11}}{(P_1 + \kappa_{11})^2} \right) + Z_2 \left(-\frac{\mu_1 \kappa_1}{(N + \kappa_1)^2} - \frac{\phi_{12} \kappa_{12}}{(P_1 + \kappa_{12})^2} \right) < 0
\end{aligned} \quad (25)$$

which is unequivocally negative.

P_2 is again a mixotrophy with multiple resources and its resource conditions must be checked on each resource independently after setting the other resource to zero. When acting as an autotroph the directional derivative in the $R_2^1 = x_0 = N$ resource space, after setting the alternate resource $P_1 = 0$, is

$$\begin{aligned}
& P_1 \left(-\frac{\mu_2 \kappa_2}{(N + \kappa_2)^2} \right) + P_2 \left(-\frac{\mu_2 \kappa_2}{(N + \kappa_2)^2} \right) + Z_1 \left(-\frac{\mu_2 \kappa_2}{(N + \kappa_2)^2} - \frac{\phi_{21} \kappa_{21}}{(P_2 + \kappa_{21})^2} \right) \\
& + Z_2 \left(-\frac{\mu_2 \kappa_2}{(N + \kappa_2)^2} - \frac{\phi_{22} \kappa_{22}}{(P_2 + \kappa_{22})^2} \right) < 0
\end{aligned} \quad (26)$$

and in the $R_2^2 = x_1 = P_1$ resource space, after setting the alternate resource $N = 0$, is

$$(1 - P)_1 \left(-\frac{\hat{\phi}_{12} \hat{\kappa}_{12} (1 - \hat{\psi}_{12})}{(P_1 + \hat{\kappa}_{12})^2} \right) + Z_1 \left(-\frac{\phi_{21} \kappa_{21}}{(P_2 + \kappa_{21})^2} \right) + Z_2 \left(-\frac{\phi_{22} \kappa_{22}}{(P_2 + \kappa_{22})^2} \right) < 0. \quad (27)$$

Both ray derivatives are unequivocally negative and therefore rule 4 is satisfied for f_2 .

Z_1 has two resources, $R_3^1 = x_1 = P_1$ and $R_3^2 = x_2 = P_2$. The directional derivative in the

$R_3^1 = x_1 = P_1$ resource space, with $P_2 = 0$, is

$$(1-P_1) \left(-\frac{2\varphi_{11}\kappa_{11}(1-\psi_{11})}{(P_1 + \kappa_{11})^2} \right) + Z_2 \left(-\frac{\tilde{\varphi}_{12}\tilde{\kappa}_{12}}{(Z_1 + \tilde{\kappa}_{12})^2} \right) < 0, \quad (28)$$

and the directional derivative (5) in the $R_3^2 = x_2 = P_2$ resource space, with $P_1 = 0$, is

$$(1-P_2) \left(-\frac{\varphi_{21}\kappa_{21}(1-\psi_{21})}{(P_2 + \kappa_{21})^2} \right) + Z_2 \left(-\frac{\tilde{\varphi}_{12}\tilde{\kappa}_{12}}{(Z_1 + \tilde{\kappa}_{12})^2} \right) < 0, \quad (29)$$

Both these ray derivatives are unequivocally negative, so rule 4 holds for f_3 .

Z_2 is an omnivore, and has three resources, $R_4^1 = x_1 = P_1$, $R_4^2 = x_2 = P_2$ and

$R_4^3 = x_3 = Z_1$. The directional derivative in the $R_4^1 = x_1 = P_1$ resource space, with $P_2 = 0$ and

$Z_1 = 0$, is

$$(1-P_1) \left(-\frac{\varphi_{12}\kappa_{12}(1-\psi_{12})}{(P_1 + \kappa_{12})^2} \right) < 0, \quad (30)$$

in the $R_4^2 = x_2 = P_2$ resource space, with $P_1 = 0$ and $Z_1 = 0$, is

$$(1-P_2) \left(-\frac{\varphi_{22}\kappa_{22}(1-\psi_{22})}{(P_2 + \kappa_{22})^2} \right) < 0, \quad (31)$$

and in the $R_4^3 = x_3 = Z_1$ resource space, with $P_1 = 0$ and $P_2 = 0$, is

$$(1-Z_1) \left(-\frac{\tilde{\varphi}_{12}(1-\tilde{\psi}_{12})Z_2}{(Z_1 + \tilde{\kappa}_{12})^2} \right) < 0. \quad (32)$$

All of these ray derivatives are unequivocally negative, so rule 4 is always satisfied for f_4 .

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