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An inverse ecosystem model of year-to-year variations with first order approximation to the annual mean fluxes

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Abstract

Ecosystems exhibit nonlinear dynamics that are often difficult to capture in models. Consequently, linearization is commonly applied to remove some of the uncertainties associated with the nonlinear terms. However, since the true model is unknown and the operating point to linearize the model about is uncertain, developing linear ecosystems models is non-trivial. To develop a linear ecosystem model, we assume that the annual mean state of an ecosystem is a minor bias from the long-term mean state. A first order approximation inverse model to govern the year-to-year dynamics of ecosystems whose characteristic time scales are less than 1 year is developed, through theoretically formulation, on the basis of steady state analysis, time scale separation and nondimensionalization. The approach is adept at predicting year-to-year variations and to tracking system response to changes in environmental drivers when compared to data generated with a standard nonlinear *NPZD* model.

Keywords: Inverse model; Ecosystem modeling; First order approximation; Flux analysis; Time scale separation

1. Introduction

One of the primary goals of ecology is to understand the response of an ecosystem to changes in environmental drivers. The realization of this goal is that one can predict the ecosystem's variation to environmental drivers once an appropriate model has been developed. The basis of model development is mathematically approximating the instantaneous and/or short-term response of the organism to its environment. For example, the temperature–photosynthesis relationship, $Q_{10}^{(T-10)/10}$ (Eppley, 1972), the light–photosynthesis relationship, $(I/I_o)\exp(1-(I/I_o))$ (Steel, 1962), the Michaelis–Menten function, $N/(N+K)$, are all instantaneous functions with respect to environmental variables of temperature T, light intensity I, and limiting nutrient concentration N, respectively. However, the practical concern in environmental ecology is often the year-to-year variations and/or long-term variations rather than short-term ones. For example, annual yield in fishery ecology is the scale of interest, not instantaneous or daily yield.

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There are two major challenges to develop a model based on the rules governing the instantaneous biology-environment interactions. First, one needs to supply information that describes the short-term changes in environmental drivers; however, it is difficult to obtain accurate predictions on the dynamics of environmental drivers very far into the future, which is necessary for daily/seasonal ecological model simulations. Generally, long-term trends are less difficult to obtain, such as annual average temperature 50 years into the future. Second, short-term tends are more difficult to understand and explain than long-term trends. Consider fishery yield. A daily yield hardly makes sense. Daily variation has a far larger range than that of the annual mean daily yield. Models used to describe short-term dynamics require more state variables and more parameters for each state equation than models used to describe annual mean variations.

If instead, the modeling focus is placed on long-term trends, then the above two challenges can be mitigated. However, the rules that govern the long-term mean response cannot be derived from the rules that govern short-term dynamics. For instance, it has been shown that calculating long-term expected values of temperature dependent functions can seldom be achieved by applying the functions to mean temperature (Lischke et al., 1997), because temperature dependencies are often nonlinear. Short-term rules are developed through short-term experiments and/or observations. It is possible to do the same for long-term rules provided long-term experiments and/or observations are available. If data are available, inverse methods can be used to estimate flows between compartments (Vézina and Platt, 1988); however, flow analysis models cannot be used for prediction. Although standard state space models can be used for prediction, almost all of the models developed thus far focus on short-term dynamics and are not applicable to long-term behavior. The main contribution of this manuscript is to combine flow analysis with first order approximations of process rates to predict ecosystem annual dynamics. Consequently, our approach allows the long-term response of an ecosystem to be predictable from the long-term mean environmental drivers.

In brief, steady state analysis, linearization, time scale separation, and dimensional analysis are employed to formulate a first order approximation model to describe the year-to-year dynamics of an ecosystem in which nutrient and organismal concentrations are annual averaged. An inverse method is used to estimate model parameters. A typical *NPZD* compartment model is used to generate simulated observations and test the first order approximation model. A forecast experiment is carried out to test the predictive capability of this model.

2. Model formulation

2.1. A steady state analysis

Although steady state analysis applied to ecosystems has an extensive and controversial history (Nilsson and Grelsson, 1995), the qualitative concepts will be useful for our model development and should not be interpreted in a strict mathematical sense. A mature ecosystem can be thought of as being in a steady state or, if inherently chaotic, in low amplitude oscillations about an attractor. This steady state allows for diel and annual fluctuations, but the ecosystem's description necessarily takes place at some averaged level. Given a permanent alteration of the ecosystem drivers, it will settle on a new steady state, again in some spatially and temporally averaged sense (van den Berg, 1998). What do we consider a mature ecosystem? What alterations may be considered as permanent? We tentatively assume that an ecosystem remains at steady state, once the environmental drivers are constant with respect to a given temporal scale. When the surroundings change to a new value, the ecosystem will transfer to a new steady state after a certain transient time. The transient time required to reach a new steady state is on the order of the doubling time of the slowest growing organism. For example, in a planktonic ecosystem, the response time is less than 1 month.

For model development purposes, we will consider a plankton ecosystem composed of four compartments: nutrient *N*, phytoplankton *P*, zooplankton *Z* and detritus *D* with mass flow connectivity as illustrated in Fig. 1. We assume that under the long-term averaged surroundings of temperature $\bar{T}$ and light $\bar{L}$, this system attains a steady state (SS) with stocks $\bar{N}$, $\bar{P}$, $\bar{Z}$, $\bar{D}$, and fluxes $\bar{f}_1$, $\bar{f}_2$, $\bar{f}_3$, $\bar{f}_4$ and $\bar{f}_5$. According to the mass flow connectivity (Fig. 1), the following conservation