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Long Transients in Ecology

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1 Abstract

The underlying biological processes that govern many ecological systems can create very long periods of transient dynamics in mathematical models, followed in some cases by sudden transitions to stable, long term states. It is often difficult or impossible to distinguish transient dynamics from similar dynamics that would persist indefinitely. The period of time over which the dynamics appear to be stable, but are in fact transient, is under appreciated in management. Recognizing the possibility that the state of an ecosystem may be less stable than it appears will be crucial to the long term success of management strategies in systems with long transient periods. In some cases, the shift from the transient dynamics to the long-term, stable dynamics may occur in an otherwise stable, unchanging system. In other cases, cycles that do not settle into a stable state may appear to be stable owing to the cycle length. Here we demonstrate the consequences of ignoring the potential of transient system behavior for management actions across a range of ecosystem organizational scales and natural system types. We demonstrate the value of developing mechanistic models that capture critical system dynamics for increasing opportunities to support system resilience and avoid system collapses.

2 Introduction

A major challenge facing the management of ecosystems worldwide is the fluctuation and variability in the production of ecosystem services and benefits upon which humans rely. Invading species dominate landscapes and displace important native species. Shifting species distributions produce novel communities and interactions. Changes in the abiotic environment alter species composition and relative dominance in existing communities.

Unlike these systems that may change through time in some predictable way, other ecosystems can dramatically switch between types of dynamics, posing a new challenge in the management of ecological systems. Current dynamics may not be the asymptotic (long term) state, even though observations appear to show a steady pattern such as noise around an equilibrium or regular oscillations. Many systems are in transient states, exhibiting apparently stable dynamics, often over dozens to hundreds of generations, but will ultimately experience a regime shift into a new, stable state. Importantly, some state shifts may occur in the absence of influence by exogenous factors.

Such long transients are surprisingly common and have been shown to exist across a range of species and systems (cite paper 1). Their occurrence has been documented and a framework developed for mathematical classification of the underlying analytical causes of the long transient phenomena. Still, we lack an understanding about how to accommodate the potential for long transients in management. This is particularly challenging because quite often, the existence of transient behavior is not apparent in observations of the system until after the regime shift has occurred. While this is similar to the challenge posed by tipping points, a key difference is that transients occur in the absence of any change or trend in environmental conditions, such as nutrient loads or temperature, and the transient period is long. Common approaches to predicting critical thresholds or tipping points are therefore not helpful here, leaving a gap in our ability to manage ecosystems that may be in a transient period.

The challenge of long transients is of particular importance in an adaptive management framework, where management strategies are informed by predicted and observed system responses to management actions. The main challenge is that transient behaviour in one mathematical system may be identical to asymptotic behaviour in another system. However, management is often based upon the assumption of the asymptotic state. With notable exceptions (fisheries management, disease control), common efforts to predict impacts of management action on natural systems are based upon asymptotic assumptions. Analytical efforts can be used to avoid actions that create areas of rapid change in nonlinear dynamics (Samhouri et al. 2010), representing abrupt system changes. However, the presence of "ghost" system attractors or non-linearities in the system landscape can shape system responses to perturbation in unexpected ways or over longer than expected time horizons. Currently there lacks a framework for distinguishing between thresholds separating alternate stable states, or tipping points (Samhouri et al., 2017), and the sudden shift from transient to asymptotic dynamics that is not precipitated by any recent management action (Hastings, 2004).

In some cases, mechanistic models of true system dynamics can describe dynamical behavior, identify "ghost" attractors, and other key transient features. **However, beyond the cases where system dynamics can be described by one of the family of mechanistic models that can reproduce transient dynamics, we will not be able to clearly identify long transient states. If we cannot distinguish between transient and asymptotic states how can we manage for the future? What are the consequences of failing to recognize a long transient? What are the relative costs of acting early versus late when system attractors erode and the system enters a transient?**

Here we explore the consequences for management of transient systems, using simulated examples of long transients under potential management strategies. We illustrate the challenges facing management when we may not know either how long the transient will last or the eventual asymptotic state. We review a series of examples of long transient behavior, and for each we associate an underlying mechanistic model with the case, use the model to replicate the long transient, identify key features of the dynamical landscape that have implications for management, and evaluate management strategies under assumptions of transient versus asymptotic behavior. We create models that realistically represent the system and are capable of exhibiting long transient dynamics. A biologically realistic range of values for model parameters spans regions of long transient behaviour as well as regions of relatively quick approaches to an asymptotic state. We analyze the model, comparing predictions of future system states in both parameter regions. We include management interventions in our model, exploring the consequences of not identifying the transient behavior. We then apply some typical statistical approaches to evaluating system stability and dynamics and evaluate their performance in the case of long transients. Lastly, we offer some general rules of thumb for managing ecosystems that accommodate ubiquity of transient behavior.

3 Long transient model explorations

Models that capture the underlying system dynamics can be helpful in elucidating implications of long transients for managing ecosystems, because they can be structured or parameterized to reveal a transient. Here we use examples of these models to illustrate some of the consequences of management actions for dynamical systems under transient dynamics.

3.0.1 Lake eutrophication

We imagine the scenario where management actions have been taken to reduce phosphorus loading in a freshwater lake, in an effort to reduce eutrophication. If phosphorus levels have been sufficiently reduced, phytoplankton densities will drop and submerged macrophytes will absorb even more phosphorus, allowing the system to enter a stable clear water state. However, if the phosphorus reduction has been too small, we may remain near the eutrophic stable state in a bistable regime (Fig 1c). It is also possible that we have indeed sufficiently reduced the nutrient loading in this system enough to destablize the eutrophic state, but there is a long transient from this former to the stable oligotrophic system.

Scheffer et al. (2001) provide a simple model for the change in turbidity that is caused by high nutrient loads consumed by phytoplankton. In this case we can describe the lake turbidity as the change in phosphorus suspended in phytoplankton, X:

$$\frac{dX}{dt} = \left(\frac{rX^p}{(X^p + h^p)} - bX + a\right) + \varepsilon \tag{1}$$

where r is the internal recycling rate , b is the removal rate, a is the rate of external loading and ε gives additive white noise. For fixed p, b and r, this equation has a single attracting equilibrium until a crosses a threshold value above which there are two stable states: one oligotrophic and one eutrophic separated by a saddle (Fig 1). Further increases in a move the system to a regime where there is a single attracting eutrophic state.

(a) (b)

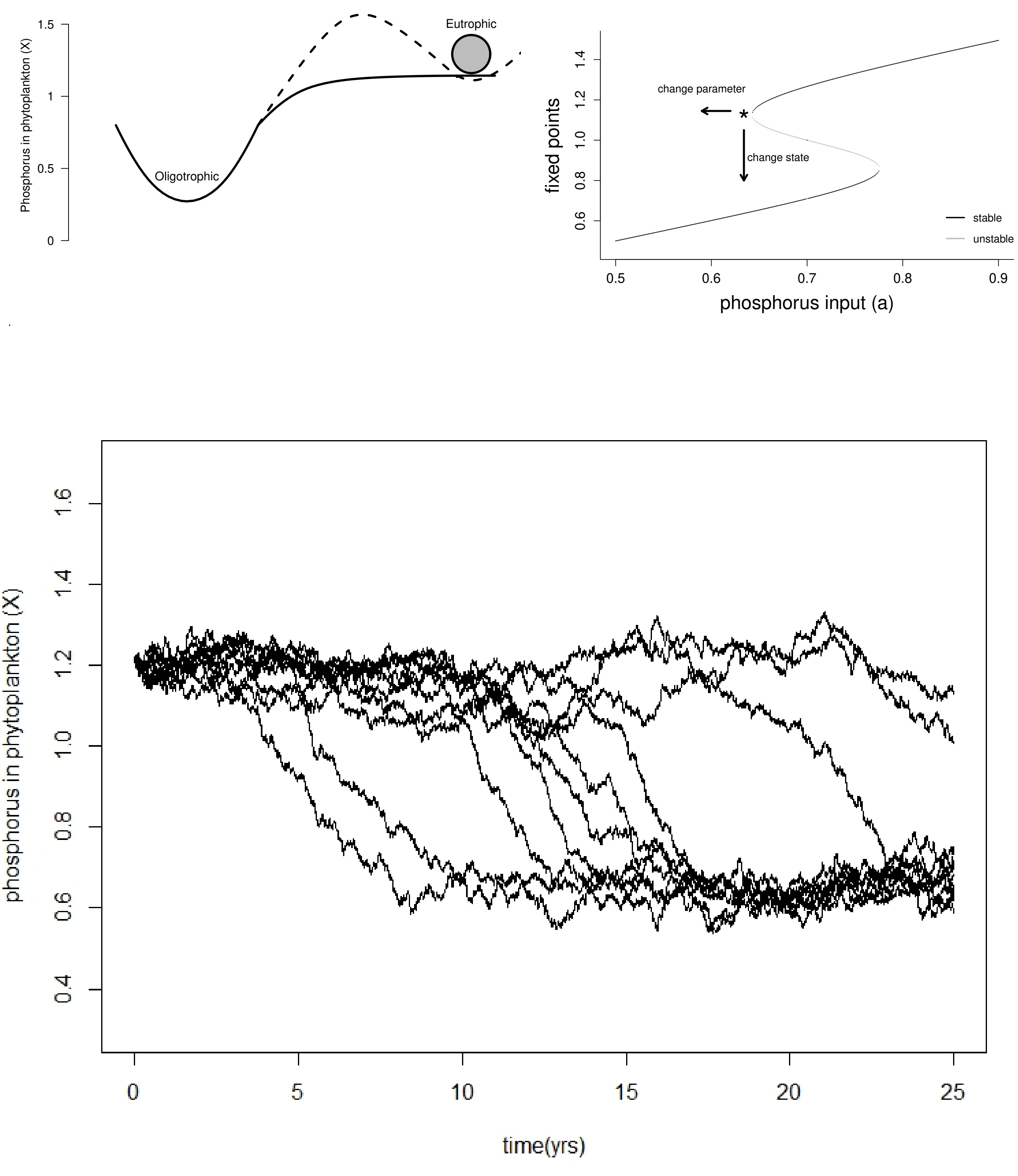

Figure 1: (a) Schematic representation of the stability of the oligotrophic state and the position of the current system state where the previous state (dashed line), leaves a ghost attractor in the new state (solid line) (b) bifurcation diagram showing the current state of the system (*) and the value of the the stable eq'm (c) Example times series from a realization of eqn (1).

We assume that the efforts to reduce external phosphorus loading have been successful, and the lake has now entered a regime where there is a single attracting oligotrophic state. We now expect phytoplankton densities will drop and submerged macrophytes will absorb even more phosphorus, allowing the system to enter a regime where there is a single attracting oligotrophic state.

Following implementation of the management action, the lake is observed for a 10 year period to determine the success. In some cases, the system may linger near the former attracting state (i.e., ghost attractor, see Hastings et al. 2019) for long periods. Depending on how close the new value of the phosphorus loading parameter, a, is to the to the bifurcation threshold between the single stable oligotrophic state and the bistable regime, there is a significant probability that there may be an extremely long transient to the oligotrophic condition (Fig 1 and appendix). The long transient to the stable state may lead observers to conclude that the management action has been unsuccessful.

We assume that an adaptive management strategy is adopted, whereby the lake state is assessed periodically and further actions are attempted to shift the system to an oligotrophic state either because the managers have missclassified the dynamic regime because of a long transient, or because, even if managers are aware that they may be in a transient, it is taking too long to reach the desired oligotrophic state. The mangers evaluate the lake state every 5 years to determine if it has reached the oligotrophic state. If the lake is not in the desired state, we provide added controls on phosphorus loading such that the parameter a is decreased by either 0.01 (Fig 2a), or 0.1 (Fig 2b). We find shorter transients where there is larger reduction in the phosphorus input, but long transients are not uncommon for smaller reductions.

From a management point of view, given the length of transients as a function of the external loading (e.g., Fig 2 and appendix), it is clear that we can certainly ensure a very high probability of a fast switch to an oligotrophic state by increasing the magnitude of the the nutrient reduction. For larger nutrient loads below the bifurcation threshold, the sequential application of more stringent nutrient reductions can speed the attainment of an oligotrophic state when the system is in a long transient, with a faster transition for a larger nutrient reduction (Fig 4 and 3). We can also manage the state of the lake, perhaps by planting macrophytes, and in that way reduce probable transient length (Fig 3). However, the concern here regarding long transients may be the continued cost of management efforts towards achieving an oligotrophic state, when in fact, that state will be attained without any further management action.

References

4 Methods

4.1 Lake eutrophication

We fit the simulation model $dX_t = \left(\frac{0.6X_t^{12}}{(X_t^{12}+1.0^{12})} - 1.0X_t + a\right)dt + 0.05dW_t$ to the timeseries using a L-BFGS-B optimization algorithm and the Ozaki estimator of pseudo-likelihood. Where the paramter a is close to the bifurcation boundary there are long transients (some longer than 20 years) to the stable oligotrophic state (Fig 4)

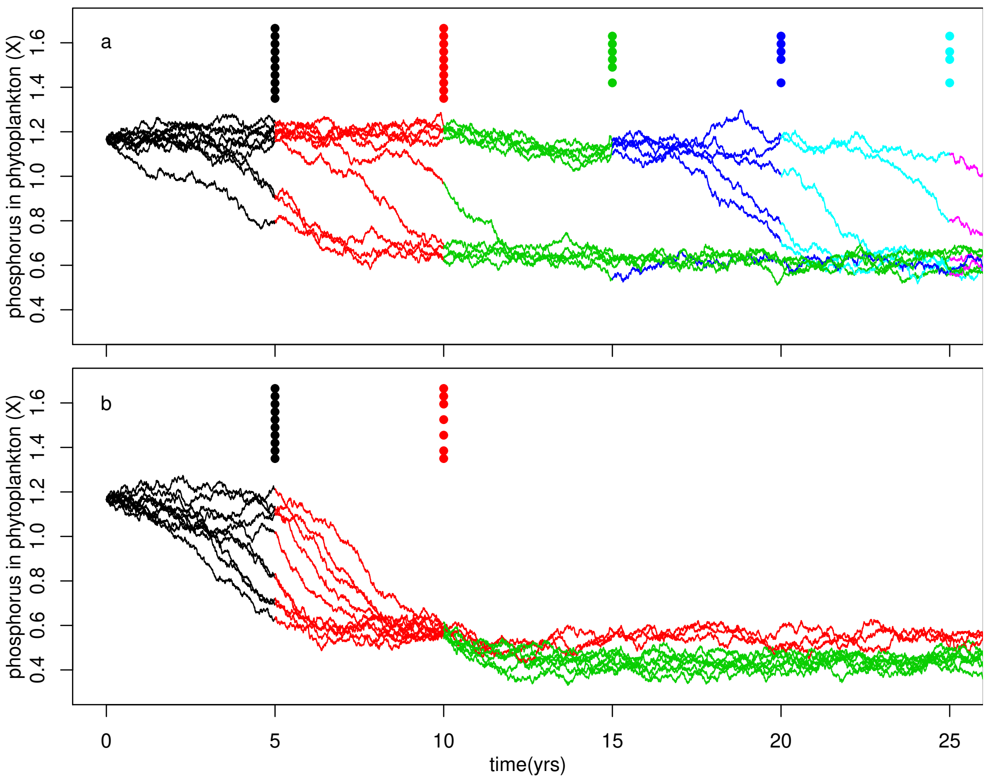

Figure 2: Trajectories of lake turbidity from eutrophic conditions in the vicinity of a former attractor, to a stable oligotrophic state where the lake is managed by re-evaluating every 5 years and, if not within 20% of desired state, the phosphorus loading, a is reduced by 0.01 (a) or 0.1 (b) for each management event. Colour of the trajectory and dots above indicate whether a management action was undertaken in that year

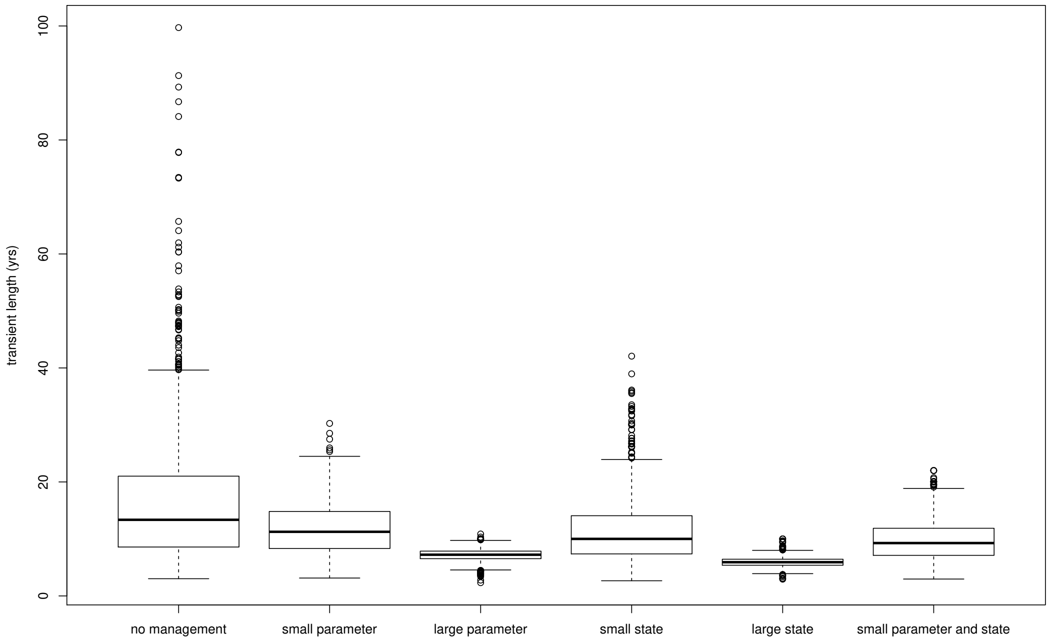

Figure 3: Boxplots of time to reach the stable oligotrophic equilibrium for 1000 replicate simulations where a close to the bifurcation boundary where either the system is managed by evaluating lake state every 5 years and adjusting a down by 0.01 (small parameter), 0.1 (large parameter), or where system state is adjusted down by 0.05 (small state), or 0.25 (large state), or where both a and system state are adjusted down by 0.01 and 0.05 respectively

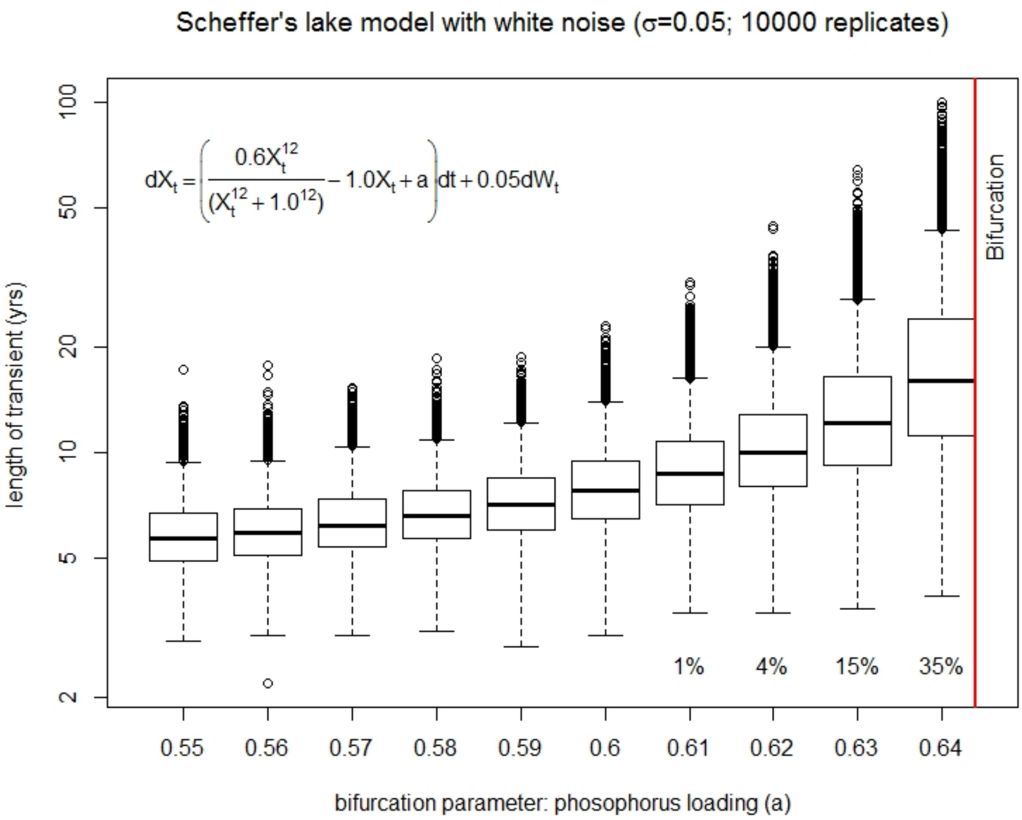

Figure 4: Boxplot of time to reach the stable oligotrophic equilibrium for different values of the bifurcation parameter *a*. Percentages under some boxes give the fraction of simulations where the transient was longer than 20 years.