Management implications of long transients in ecological systems

Short Title: Managing Long Transients

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Abstract

The underlying biological processes that govern many ecological systems can create very long periods of transient dynamics. It is often difficult or impossible to distinguish this transient behaviour from similar dynamics that would persist indefinitely. In some cases, a shift from the transient to the long-term, stable dynamics may occur in the absence of any exogenous forces. Recognizing the possibility that the state of an ecosystem may be less stable than it appears is crucial to the long-term success of management strategies in systems with long transient periods. Here we demonstrate the importance of considering the potential of transient system behavior for management actions across a range of ecosystem organizational scales and natural system types. Developing mechanistic models that capture essential system dynamics will be crucial for promoting system resilience and avoiding system collapses.

1. 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[1], shifting species distributions[2], and environmental changes that alter both community composition[3,4] and functional traits[5] are expected to be increasingly important in ecosystems globally[6]. An additional challenge in the management of ecological systems is that the current dynamics may not be the asymptotic (long term) state, even though observations appear to show a steady pattern that resembles noise around an equilibrium or regular oscillations. Many systems are in long transient states, exhibiting apparently stable dynamics, often over dozens to hundreds of generations, but will ultimately experience a shift into a new, stable state[7–11]. Importantly, some state shifts within long transients may occur in the absence of influence by exogenous factors, such as underlying environmental change.

Such long transients are surprisingly common across a range of species and systems, and the importance of the long view for understanding ecological processes has long been recognized[12]. Transient dynamics over a long period of time are common and their appreciation is evidenced in part by the extended network of Long Term Ecological Research (LTER) sites. Systems with slow variables or interactions between slow (e.g. soil development, erosion) and fast (e.g. plant-herbivore interactions) variables[13] that often lead to system behavior such as tipping points[14] can undergo long transients. High dimensional systems are also more likely to experience transient behavior, such as systems with large spatial complexity (e.g., metapopulations), or high food web dimensionality[7]. Quite often, the existence of transient behavior is not apparent in observations of the system until after a shift in behavior has occurred. While this is similar to the challenge posed by tipping points, an important observation is that shifts caused by transients can occur in the absence of any underlying change in environmental conditions, such as nutrient loads or temperature. Therefore, approaches to predicting regime shifts or tipping points developed around identifying critical thresholds in environmental drivers will not apply to long transients, leaving a gap in our ability to manage ecosystems that may be in a transient period. Recent classification of the underlying causes of long transients[15,16] creates an opportunity to look more closely at the implications of these phenomena for managing ecosystems, and to expand our understanding of the impacts of management interventions vis-à-vis transient behavior.

Adaptive management inherently acknowledges uncertainties and nonstationarity in the responses of complex systems to human intervention[17–20]. This often includes an understanding that ecosystem responses to management actions can be slow. Underappreciated is the fact that long transients can occur even in the absence of human intervention or changes in exogenous drivers, and that observations of transient behavior in one system may appear as identical to asymptotic behavior in another system. 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 when typical management interventions interact with transient (versus asymptotic) dynamics? Here, we offer formal explorations of the intersection between transient dynamics and ecosystem management, with the aim of supporting adaptive management approaches and programs, and recommend that the adaptive management framework incorporate assumptions about long transients (see Fig. 1).

Models that capture underlying system dynamics can be helpful in elucidating implications of long transients for managing ecosystems. Closing the gap between theoretical studies and management applications is an ongoing challenge, as summarized for the control of invasive species by Funk et al.[21]. As they note, and as is backed up by a survey on incorporating climate change into management[22], managers are often eager to be able to incorporate results from ecological theory, but there are substantial barriers. Here we use several models to illustrate some of the consequences of management actions for different ecological systems with transient dynamics. Finally, we offer some general rules of thumb for managing ecosystems, revealed by the case studies, that accommodate the ubiquity of transient behavior in ecological systems.

2. Exploring management with long transients

We explore the consequences for management of long transients in ecological systems, using simulated examples of long transients under potential management strategies. We use these models as a way to develop a general understanding of how to manage in the face of transients. This both provides a guide to cases where not enough is known to justify a detailed model and highlights how to develop approaches when more detailed modeling efforts are justified[23]. For each example, we associate an underlying mechanistic model with the case, use the model to replicate the long transient, identify key features of the dynamical landscape (e.g., saddles and ghost attractors) that have implications for management, and evaluate management strategies under assumptions of transient versus asymptotic behavior.

2.1 Marine Protected Areas: Managing transient responses in long-generation species

Fisheries related to marine protected areas (MPAs) illustrate the importance of considering transients, which may be long from a management standpoint, even if not in number of generations. From a single species perspective, establishment of a marine protected area should change both the equilibrium population level and the equilibrium age distribution of harvested fish species with relatively sedentary adults by removing an age-specific mortality source, namely harvesting. A potential challenge in the evaluation of the effectiveness of the marine protected area arises from not considering the transient nature of the response and instead comparing the state of populations after too short a time to a new expected equilibrium distribution. The arguments can be made more precise, but intuitively starting from the idea that multiple generations would be required to approach a new equilibrium means that fish with a high age-to-maturity, which implies long generation times, will take many decades reach a new stable state. More details describing the general theory are given in several analyses of single population models with age structure[24].

From a management standpoint, these issues become important in evaluating MPAs that have been recently established, such as those created under the auspices of the California Marine Life Protection Act.

Here, a first challenge is that management evaluations regarding success or failure of MPAs to increase previously-fished populations may be made on a relatively short time frame. Understanding the time frame of the response, i.e., the length of the transient, is key[25]. So even an examination of the simple conservation implications of protection depends on an understanding of transients.

The goals of MPA establishment are much broader than increasing biomass inside the protected area. After implementation of a marine protected area, one goal is to increase and stabilize yield from a fishery that will be now be restricted to the part of the habitat where fishing is allowed. Such a scenario has been analyzed using a two-patch metapopulation model with one fished area and one reserve area[26]. Understanding the transient response in yield is key to understanding how long-term goals for yield can be met, even though yield may be reduced over the short term. If the results are extended beyond the linear effects of age structure to include density dependence and interactions between species, as in the following examples, the importance of transients for understanding the response of the system to management actions becomes even more evident.

2.2 Invasion dynamics: Managing to stay on a low impact transient

Suppose a non-native species arrives where a native competitor population is growing. If this low-invader state is a transient due to a saddle crawl-by, versus a stable equilibrium (see Box 1 for definitions and Fig. S1 for an illustration), preserving the system near this state may require perpetual, repeated manipulations to move populations toward the stable manifold of the saddle. Manipulations that get closer to the stable manifold will be most effective because the subsequent crawl-by is expected to be slower. If we mistake the low-invader state for an equilibrium, our decision for how to manage could have disastrous outcomes.

To illustrate this, we use a stochastic Lotka-Volterra competition model, which has an equilibrium at $(N_1, N_2) = (K_1, 0)$ (N_1 is the density of the native with carrying capacity K_1, and N_2 is invader density).

Our stochastic term allows immigration to re-establish populations after local extinction (Supplementary Information), reflecting the fact that complete eradication is often unrealistic. Because invaders are initially rare, $(K_1, 0)$ appears to be an attractor early on (Fig. 2A). However, if $(K_1, 0)$ is a saddle as in this simulation, the dynamics will eventually crawl by this state as the invader establishes (Fig. 2B). In this simulation, active management that promotes repeated crawl-bys of the saddle at $(K_1, 0)$ are required to avoid establishment of the invader. Examples of such actions include invader removal (orange arrow, Fig. 2C), removal of both species i.e., to maximize the chance of reducing the invader to 0 (light blue), and invader removal with native addition (red), because each of these moves the populations toward the stable manifold of $(K_1, 0)$. Native addition alone (dark blue arrow) will not promote crawl-bys and is therefore not predicted to be effective for managing this invasion. To confirm, we simulated the same model applying one of these actions whenever the invasive population crossed a threshold value ($N_2 > 0.02$), provided the last management action was at least a year ago (Fig. 2D). Indeed, native addition alone (dark blue trajectory) requires much more frequent management and is much worse at controlling invader density than the other strategies (Figs. 2D, S2-S3). Removal of both species (because we assume this makes it possible to get the invader density closer to 0) is the most effective (Figs. S2-S3).

If we did not know $(K_1, 0)$ to be a saddle, we might reasonably conclude from data such as simulated in Fig. 2A that it is actually a stable node. To understand the implications of this mistake, we fit the Lotka-Volterra equations to simulated time series, assuming that $(K_1, 0)$ is a stable node. Evaluating management options using this model would lead us to conclude that all strategies perform comparably (Fig. 2E). If N_1 addition were the least labor-intensive (e.g. seed addition or stocking), it would likely be chosen – a costly mistake (Fig. 2D). If we instead fit the Lotka-Volterra equations with $(K_1, 0)$ as a saddle, we regain the insight that native addition is an inferior strategy, although due to parameter uncertainty, we may underestimate how much so (Figs. 2F, S2-S3). At a more basic level, if a monitoring program was directed solely at detecting the invasive species, i.e., the primary system component of interest, and not also its competitor, i.e., a secondary system component, management strategies would be inadequate. We also found that standard statistical time series approaches misspecify the dynamical landscape in this case (Supplementary Information), making it easy, for example, to mistake a saddle for a stable equilibrium. This illustrates that management interventions based on time series analyses that do not account for transient dynamics can be at high risk of failure. An understanding of ecological dynamics can provide the basis for invasive species management[27], as demonstrated for forest insect pests, and these lessons provide a framework for other management problems.

2.3 Grassland restoration: Managing to escape an undesirable persistent transient

In long-term ecological research experiments at the Cedar Creek Ecosystem Science Reserve in Minnesota, the competition between a biodiverse collection of native grasses and a duo of exotic European species was studied before, during, and after several years of nitrogen deposition (representing increases in atmospheric and/or agricultural nitrogen). The native grasses are only able to resist invasion by exotics in a low nitrogen environment; therefore, during the years of nitrogen deposition, the system flips from a native-dominated state to a less biodiverse, exotic-dominated state. More surprisingly, following cessation of nitrogen deposition, the exotic-dominated state persists for decades, even after soil nitrogen levels have returned to their original low state[28]. In a case where biodiversity is a management objective, and the identified major stressor is nutrient inputs, the lack of system response to manipulating the stressor is a management challenge.

The observations suggest that in a low nitrogen environment the native-dominated state is stable, and in a high nitrogen environment the exotic-dominated state is stable. Two possible hypotheses exist for the persistence of the exotics after cessation of the nitrogen deposition: Hypothesis 1, where both the exotic-dominated state and native-dominated state are stable in a low nitrogen environment (in other words, the system is bistable), so cessation of nitrogen deposition does not return the system to the native-dominated state; and Hypothesis 2, where in a low nitrogen environment the exotic-dominated state is a saddle point, and because the system was brought close to the saddle by the years of nitrogen deposition, after cessation of that deposition it exhibits a long transient, slowly crawling by the saddle before eventually recovering to the biodiverse native state.

From a management point of view, if the goal is to restore biodiversity, Hypothesis 1 suggests that management is definitely needed to escape the basin of attraction of the exotic-dominated state. Hypothesis 2 is more encouraging; the biodiverse state is expected to eventually recover on its own. But a delay of decades before this recovery occurs may be undesirable, so management may be needed to speed the recovery. One mechanism that has been proposed for what holds the system close to the exotic-dominated state, causing stability (Hypothesis 1) or a long transient (Hypothesis 2), relates to the differing rate of accumulation of leaf litters of the exotics versus native plants[29]. In similar Park Grass experiments in England, where the experimental plots were hayed twice yearly (mowed and leaf litter removed[30]), the biodiverse state recovered quickly.

In Brettin et al.[31] and Meyer et al. (in prep.), a model of the Cedar Creek system is developed, tracking the amount of nitrogen in the soil and in live and decaying plant tissue as the native and exotic plants compete. Inspired by the Park Grass experiments, the model system can be hayed regularly using a "flow-kick" approach, where the system is "kicked" by removing organic matter sources, then "flows" to a new state on the dynamical landscape[32]. Biodiversity in the model system can be recovered by haying in both low and high nitrogen environments, with differing levels of haying effort needed depending on model hypotheses and parameters. This model approach could be used to explore trade-offs in management regimes that combine some balance of nitrogen reduction vs haying in grassland maintenance and restoration. Management intervention can speed the system towards recovery of the biodiverse state in both the transient and asymptotic systems, but an additional option of low or no investment exists only if the system is in a long transient.

2.4 Lake eutrophication: Managing to escape a ghost attractor

Reduction of phosphorus loading to freshwater lakes is a widely-used best-practice strategy to reduce eutrophication[33,22]. Simple heuristic models of a bistable regime can be used to illustrate that if phosphorus reduction has been too limited, a lake may remain in a eutrophic stable state or in a bistable regime (Fig. 3A, B). An alternative framing can be used to show that it is also possible for the system to linger near a former attracting eutrophic state (Fig. 3C, i.e., ghost attractor, see Box 1 for definition) for very long periods in a long transient.

This can be further illustrated using a general mathematical model of a system with alternative stable states, applied to the case of eutrophication. Turbidity caused by high phosphorus loads consumed by phytoplankton can be modeled[35] (Supplementary Information) to reveal the effects of the external phosphorus input rate, a. A single attracting oligotrophic (clear water) equilibrium exists until a crosses a threshold value, above which there are two stable states: one oligotrophic and one eutrophic, separated by an unstable equilibrium (Fig. 3B). Further increases in a result in a single stable eutrophic state.

If there is a long transient, managers may impose a management action, monitor for decades and see no change, then conclude the intervention has been unsuccessful. Instead, an adaptive management strategy could be adopted, where the lake state is assessed periodically and further actions are taken to shift the system to the desired oligotrophic state. We simulate these alternative management strategies and assume a monitoring program returns lake state data every five years. If the lake is not in the desired state after a 5-year observation period, phosphorus loading is further reduced (the parameter a is decreased by either 0.01 or 0.1 (Fig. 4A, B). The model predicts that larger reductions in phosphorus inputs result in shorter transients, while long transients are not uncommon for smaller reductions.

These simulations illustrate the tradeoffs between the magnitude and number of the management actions and the time to reach the desired system state (Fig. 4C). For larger phosphorus 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 (Fig. 4B). An alternative approach is to manage a state variable such as the internal phosphorus pool, for example by adding alum to lock phosphorus in the sediments of deep lakes, and in that way reduce probable transient length (Fig. 4C). The challenge facing managers is that restricting assessment to the period immediately following intervention can have either catastrophic[36] or cost-prohibitive[37] effects. Management could take a longer view and weigh the costs and benefits of additional intervention, novel intervention (i.e., changing state variable versus parameter), and waiting. In a review of eight European and US lakes, Fastner et al.[38] noted that in all cases phosphorus reduction was highly successful, although the response times varied from 5 to 30 years. When there is a failure of phytoplankton to respond to management in a given timespan, other explanatory mechanisms such as low water exchange rate, internal phosphorus release from sediments, or changes in community structure[39–41] are sought, but long transients is another possibility, and one which could alter our management response.

2.5 Social-Ecological System: Managing to avoid a transient induced by slow and fast time scales

Here, as an illustration of management of a system with long transients owing to the interaction of slow and fast variables[15], we consider a model of a simple social-ecological system, based on a typical midwestern United States lake with a sport fishery and lake residential development[42] (Fig. 5). In this system, there are two primary management objectives: a resilient fish population, and a human population of visiting anglers and lake residents. The "fast" dynamics are trophic interactions among harvested (target), predatory, and juvenile fish[43]. Survival of the juvenile fish is governed by lake habitat, in the form of woody debris (dead and downed trees)[44,45]. Local and visiting anglers harvest adults of the target fish species. Management occurs via harvest rules governing the per-angler catch in the sport fishery. Stock status and harvest rules feed back to human angling effort and lakeshore development. Increased residential development on the lake reduces woody debris, via removal of logs (to clear beaches for swimming, for example) and deforestation of riparian trees, the source of woody debris[46,47]. Reduced residential development allows forest regeneration and woody debris accumulation, the "slow" variable that occurs at the pace of tree growth and senescence, which can take decades. In this model, there are two equilibria in the trophic dynamics, where harvest and fish recruitment rates balance: one is stable, and one is unstable. Movements of the system away from the unstable equilibrium, for example in the case of lower recruitment, can lead to depensatory dynamics and collapse of the target fish population. Changes in habitat can increase or decrease the basin of the stable state.

Harvest rules can either be fixed, with a constant harvest rate, or adaptive, with harvest rate adjusted based on information about the target fish stock status. Because of the feedbacks between habitat, fish populations, harvest, and residential development, and the combination of slow (coarse woody debris recruitment) and fast (harvest and trophic dynamics) variables in the system, long transient periods between collapse and rebuilding can occur under fixed management rules (Fig. 6 A,C). Knowledge of the impact of the slow variable, coarse woody debris supply, informs an adaptive management approach. During these long transients, the model predicts both human participation and fish are lost from the system. Under no harvest of the target fish, human participation is lost from the system (Fig. 6C). However, under adaptive management rules, where harvest rates are adjusted in response to stock assessments of fish while accounting for both slow and fast variables in the system, i.e., primary and secondary system components, the system can remain in the desirable state, avoiding the long transient recovery phase after a collapse and meeting both the social and ecological objectives (Fig. 6 B,D).

2.6 Three species food chain: Managing to maintain chaotic transient persistence

Transient dynamics can also have special implications for species extinction. In particular, model explorations show that when population dynamics exhibit transient chaos[48–50], population densities change chaotically for a finite period of time before suddenly converging to a stable equilibrium that may represent asymptotic extinction of some species. Therefore the population dynamics of some species can appear to be chaotic and apparently sustainable for a long time, and then move to extinction in a relatively short period of time[10,51]. This is associated with a chaotic ghost or a chaotic saddle[16]. If species extinction is caused by the end of transient chaos, how can we intervene to prevent extinction[52–55]?

A potential management strategy that maintains this transient chaos, and avoids extinction, can be illustrated with a three-species food chain model[51] (Supplementary Information). The resource and consumer alone (without the top predator) can exhibit consumer-resource cycles, and so can the consumer and predator, if the resource level is fixed. When the three species are together, the interaction of these coupled nonlinear oscillators in the food chain can give rise to transient chaos.

For particular parameter settings (see Supplementary Information), the species can undergo chaotic oscillations for a long, but finite, amount of time before converging on a consumer-resource limit cycle at which the top predator is extinct. Predator extinction can be prevented by continually pushing the system toward the chaotic saddle – in which all three species persist – indefinitely via small feedback control[56–58]. In general, the perturbations need to be applied only rarely, although they will be required in perpetuity because the desired state is a transient. Because of the presence of a long chaotic transient, the magnitude of the applied management perturbation can be made arbitrarily small[59]. This suggests that the natural dynamics of the populations need hardly be affected and yet predator extinction can be prevented over long time scales.

3. General guidelines for management

Understanding the potential mechanisms that cause transient behavior leads to several subtle enhancements of adaptive management frameworks to better account for transients (Fig. 1). Understanding ecosystems as dynamical, transient, adaptive systems immediately shifts expectations about management strategies and their impacts. While the resilience approach to managing ecosystems is increasingly well known[60], and while expectations of nonstationary responses to management action underpin adaptive management approaches[61], the potential for long transients in the absence of changing environmental conditions or management intervention is underappreciated in resource management. This tension is reflected in, for example, the existence of two paradigms of rangeland vegetation dynamics: one that assumes continuous and reversible vegetation dynamics versus one that encompasses nonlinear and transient dynamics[62]. Fisheries management systems are often exceptions to this; for example, the Pacific sardine fishery in the Gulf of California has experienced long transient behavior, and managers are now grappling with how to manage the ecosystem under assumptions of transience[63].

We recognize that our work here is a small step towards producing the kind of information that would be directly useful to practitioners, and that application of the ideas we develop here will require further steps. Our contribution here is to indicate important issues that need to be taken into account when developing plans for specific systems. Our work does emphasize the need to consider transients when managing in the face of climate change and does provide the kinds of general principles that are important. Here, we offer some general rules of thumb for accommodating the potential of transient behavior in natural ecosystems.

3.1 Plan

The planning of management strategies should account for potentially lengthy transient dynamics by evaluating the feasibility of management goals, the associated level of intervention required, and the costs and benefits of maintaining a system in a transient state via intervention. This can be achieved in part by confronting inherent assumptions about the system, such as whether the observed behavior is asymptotic or transient. The development of alternative management actions is then informed by framing management objectives according to whether the aim is to remain in the current state or leave it.

In general, the models upon which management actions are based should be subjected to a form of "sensitivity analysis" that accounts for the risk of getting the dynamical regime of the system wrong (equilibrial vs. transient). Mechanistic mathematical models that are constructed from first principles, fitted to empirical data, and explored within realistic parameter ranges can help identify whether an ecosystem is currently experiencing transient dynamics. For example, this was done to predict the long transients in the extinction debt of butterflies in the UK[64]. In addition, correctly identifying the likely transient mechanism, where possible, can inform adaptive management strategies, such as the magnitude, direction, or target of intervention. For example, the grasslands example suggests a flow-kick strategy for crawl-by transients; while the lake eutrophication example suggests the best strategy for a ghost attractor may be a combination of interventions targeting both system parameters and state variables. In some cases, exploitation of transient dynamics, such as episodic booms in growth and reproduction, could be beneficial to management, if properly identified[65].

3.2 Implement Actions

In addition to adjustments in management perspective, the implementation of management plans may require revision to accommodate dynamical regime behavior. For example, in the Puget Sound estuary of Washington State, USA, many recovery targets for a suite of ecosystem health indicators are based on historical baselines, or ecological models that assume asymptotic behavior (https://www.psp.wa.gov/vitalsigns/). In contrast, other management efforts are aimed at maintaining the system in a transient state. For example, fishery harvesting targets may be aimed at maintaining a population at its most productive density rather than the carrying capacity. Vaccination plans may not be able to eliminate a disease (i.e., an asymptotic target), but aim to maintain the incidence rates at a very low, non-equilibrium value and limit the size of any transient outbreaks. Plans that account for possible long transient behavior will inherently be more resilient to unexpected system change.

Mathematical properties of transients may also translate into management rules of thumb. For example, analogous to supporting management strategies that increase resilience by deepening or broadening desirable basins of attraction (e.g., [66]), management strategies that aim to regularly place the system along the stable manifold associated with a desirable saddle equilibrium can avoid settling at unwanted attractors, as in the invasive species example given here. Modeling approaches that highlight the most important state variables and parameters may be useful here, including the use of multiple models[67] and constructing models of intermediate complexity[68,69].

3.3 Monitor

Incorporating considerations of transient system behavior into management requires shifting perspectives about the relevant timescales[8]. Observational data are often of insufficient duration to be inclusive of the true asymptotic behavior of the system (but see [70]). If a change is observed, the inclination is to wait longer (longer experimental runs, more system monitoring) for the system to revert to a stable state; but this approach is ineffective if the system is in a long transient. Predicting how long a transient may last is a particular challenge, as noted in the above lake eutrophication example, and a nominal amount of stochasticity can increase greatly the time a system spends away from stable equilibrium. Furthermore, high dimensionality in any domain – temporal, spatial, biological – can increase the potential for transient behavior and the likelihood of its lingering. Programs that invest resources into monitoring at temporal and spatial scales sufficient to encompass system dynamics, including fast and slow variables and feedbacks, will most effectively accommodate transient behavior. Likewise, expanding monitoring programs to include responses of primary and secondary components of ecosystems to management actions increases the likelihood of appropriately capturing system dynamics.

3.4 Learn

The most effective way to learn about a system is to conduct an experiment, and indeed large-scale experiments have resulted in some of the most powerful ecological lessons. While mathematical models of the type presented here offer insights into the potential behaviors of natural systems, direct observation following controlled manipulation is invaluable. The long-term grassland experiments at Cedar Creek Ecosystem Science Reserve[31] and the Park Grass Experiment[71] allowed for observations about system dynamics that inspired insights into long transient system behaviors. Large-scale and long-term manipulations of lakes are another example where learning through manipulation reveals unexpected system behaviors[72]. Marine protected areas or predator control programs are additional forms of experimentation, albeit one with looser control over experimental boundaries. The network of Long Term Ecological Research (LTER) sites, of which Cedar Creek is one member, have provided a wealth of insights into system behaviors that play out over longer time scales, including tipping points, bistability, and long transients[73–77].

Governance systems that are flexible to timescale mismatches and multiple types of learning will be most successful in managing transient behavior[78,79]. Characterizing uncertainty, as a target of "learning by doing," is an important component of adaptive management[80]. Whether observed dynamics are asymptotic or transient is yet another relevant uncertainty for management. Evaluation of the effectiveness of management actions related to managing regime shifts can be confounded by long transients. For example, removal of planktivorous fish from Lake Christina in Minnesota to reduce eutrophication resulted in persistent clear water states that lasted as long as 10 years after manipulation, but always degraded to a turbid state over time. Long-term data suggest that the clear water state is now a transient and the turbid state the sole stable state in this system due to changes in nutrient loading and the water regime[37]; the clear water state is only maintained through continual management action. Identifying the appropriate adaptation of the management program in this case depends upon conceptualizing the transient system behavior.

4. Conclusion

Adapting to environmental change is one of the greatest challenges facing natural resource management. Adaptive management practices are increasingly favored, enhancing opportunities for learning about system dynamics and successful approaches. Here, we argue that subtle enhancements to adaptive management frameworks and thinking are needed to account for long transients in ecological systems, given their ubiquity and the risks associated with ignoring their potential effects. Understanding that observed dynamics may not be the final dynamics, and considering possible mechanisms driving current patterns, can reduce such risks substantially, leading to better outcomes.

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Figures

Box 1: Dynamical Systems Terminology (see Fig. S1 and [15,81,82] for further explanation)

Asymptotic dynamics	The behavior that a system will eventually exhibit and then retain indefinitely, if unperturbed; i.e. dynamics that are not transient.
Attractor	An invariant set that a dynamical system will naturally approach, unless perturbed away; an asymptotic state of the system.
Bifurcation	A qualitative change in a system's asymptotic dynamics, caused by gain, loss, or change in stability of an invariant set. Some examples that play a role in this review are crises, Hopf bifurcations, and saddle-node bifurcations.
Crawl-by	Dynamics that approach and then move away from a saddle slowly, causing the system to remain near the saddle for a significant time frame; amplified when the saddle is surrounded by a flat spot.
Flat spot	A region of the potential or quasi-potential surface that has very little curvature, so that the dynamics in this region (like the hypothetical ball rolling on this surface) are slow.
Ghost	A state or set of states that is not an invariant set under the current conditions, but was (or would be) an attractor under similar conditions, such as nearby parameter values.
Invariant set	Ecosystem states (like stable or unstable point equilibria or cyclic or chaotic sets) such that, if the ecosystem is precisely in one of these states, it will remain there in perpetuity unless perturbed.
Long transient	Non-asymptotic dynamics that persist over ecologically-relevant time scales of, roughly, dozens of generations or longer.
Node	A point equilibrium that is approached (if attracting) or departed from (if repelling) without oscillations.
Repellor	An invariant set that a dynamical system will naturally diverge away from, unless perturbed toward it.
Saddle	An invariant set that is attracting from some states and repelling from others; the dynamics may approach a saddle before ultimately moving away.
Slow-fast systems	Systems that incorporate processes that act on drastically different timescales, such as interacting species with very different generation times.

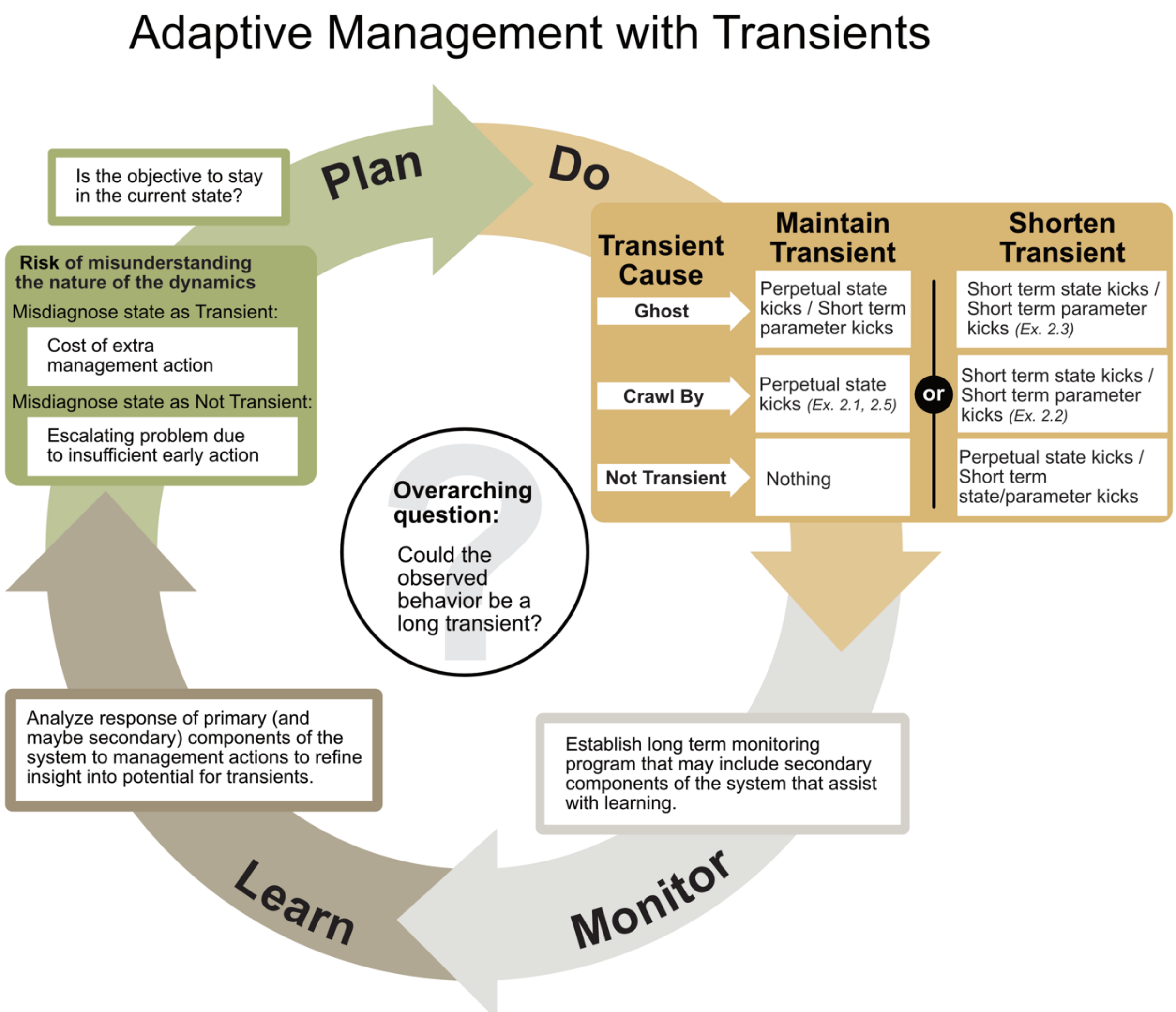

Figure 1: A modified adaptive management cycle that includes consideration of potential long transient system behavior. In general, the question of whether the observed behavior system could be a long transient should inform management. During the planning phase ("Plan:"), managers should consider the potential risks associated with mis-specifying the system dynamics, and categorize management objectives in terms of whether the goal is to remain on or leave the current state. Management actions, or interventions ("Do"), are thus informed by this objective, with implications for the type, duration, and cost of interventions that vary by transient type. Monitoring programs ("Monitor") should be designed as long-term programs to capture multiple life cycles of the primary ecosystem components, and of important secondary ecosystem components whose interactions have strong influence on primary components. Finally, learning from the system responses to management actions ("Learn") should include evaluation of potential transient behavior, and analysis of the secondary components of the ecosystem to refine insight into system dynamics.

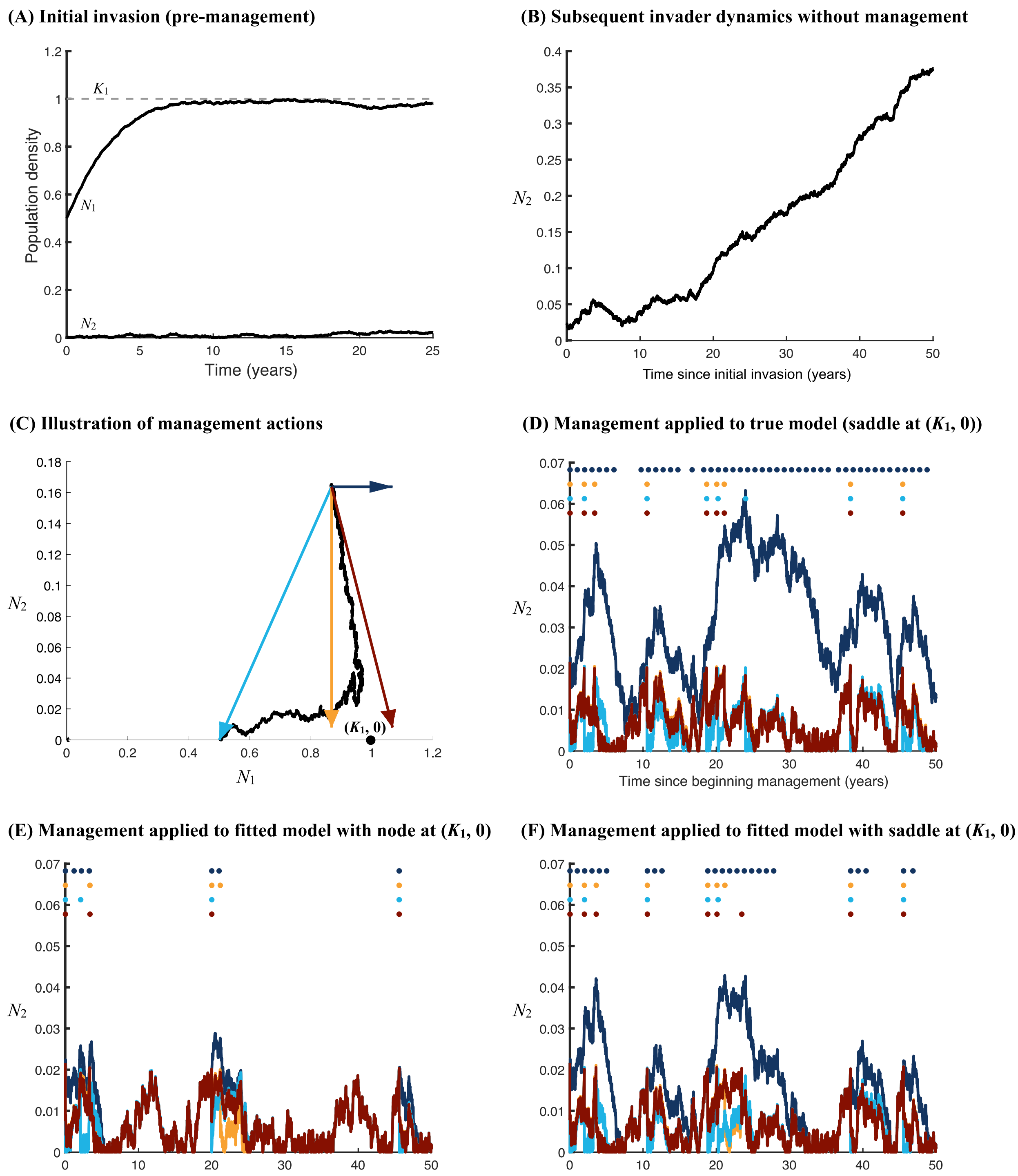

Figure 2: From Example 2.2. (A) Example times series from a realization of the stochastic Lotka-Volterra competition model (see Supplementary Information), where N_1 is the population density of the native species (with carrying capacity K_1) and N_2 is the density of the invader. (B) A simulation of the unmanaged invader population under the same conditions as (D-F), as a baseline. (C) Illustration of relevant features of the state space. The black trajectory shows the

combination of (N_1, N_2) population densities through time, proceeding counterclockwise. Arrows show the effect of each management action (light blue: removal of both species; orange: N_2 removal only; red: N_1 addition with N_2 removal; dark blue: N_1 addition only). The x-axis is the stable manifold of the saddle at (K_1,0); this is the direction along which the saddle is attracting. Management actions that move the system closer to the stable manifold promote additional crawl-bys and sustain the transient (K_1,0) state for longer. (D-F) Time series of abundance under simulated management actions, with colors matching the management strategies illustrated in (C). All four lines (as well as the trajectory in (B)) experienced the same sequence of stochastic perturbations, so differences between the colored lines within a panel are due only to differences in the management strategy. (Differences between panels are also due to differences in the interspecific competition coefficients used in simulation.) Colored dots along the top of the graph mark the times that a management action was triggered (i.e. times at which N_2 exceed 0.02 that were at least 1 year past the previous management action) under each strategy.

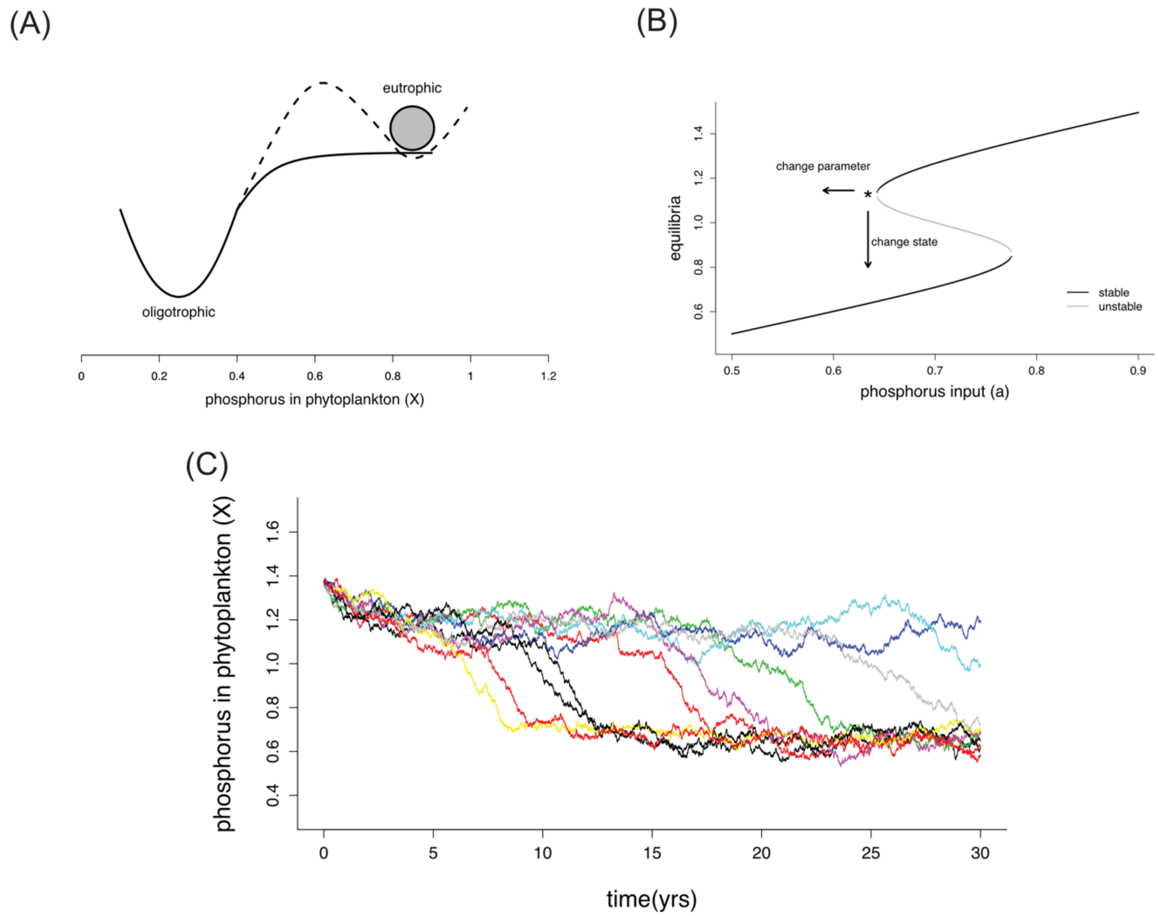

Figure 3: From example 2.4. (A) In this ball in cup representation of the lake system, management actions erode the stability of the eutrophic state (former stability given by the dashed lines), which shifts the landscape to the solid curve. However, the system (ball) remains close to the eutrophic ghost attractor for a long time. (B) Bifurcation diagram showing the current state of the system (*) and the value of the stable and unstable equilibria. (C) Example times series from realizations of the model (see Supplementary Information).

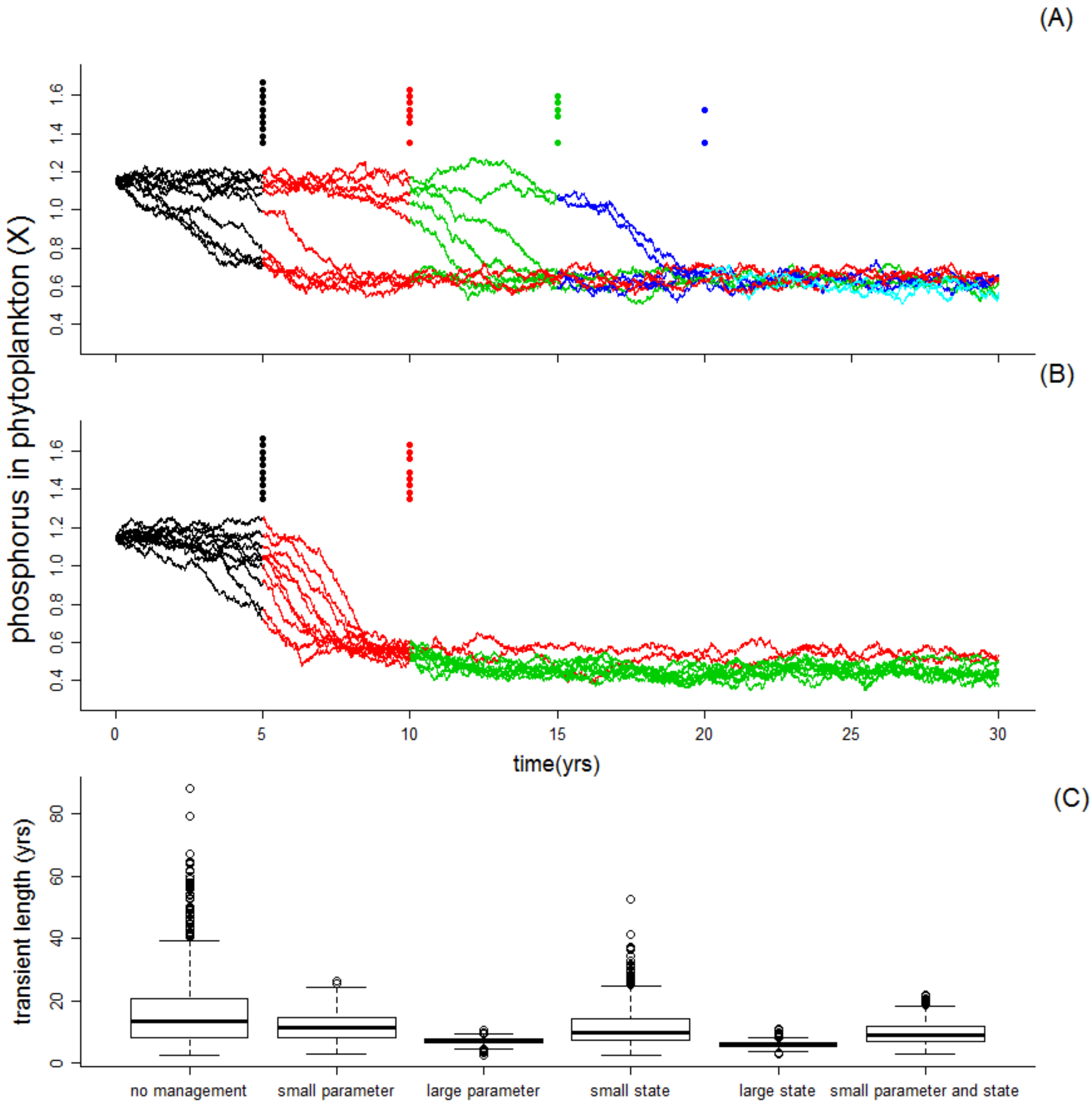

Figure 4: From example 2.4. A-B: Trajectories of lake turbidity moving from eutrophic conditions in the vicinity of a former attractor to a stable oligotrophic state. The lake is managed by re-evaluating every 5 years and, if not within 20% of desired state, the phosphorus loading (a) is reduced by 0.01 (A) or 0.1 (B) for each management event. The colour of the trajectory changes when a management action is taken, and dots above indicate the year of those actions. (C) Boxplots of time to reach the stable oligotrophic state for 1,000 replicate simulations for a close to the bifurcation boundary. The system is managed by evaluating lake state every 5 years and either reducing phosphorus loading, a, by 0.01 (small parameter) or 0.1 (large parameter); adjusting the system state down by 0.05 (small state), or 0.25 (large state); or adjusting both a and the system state by 0.01 and 0.05, respectively.

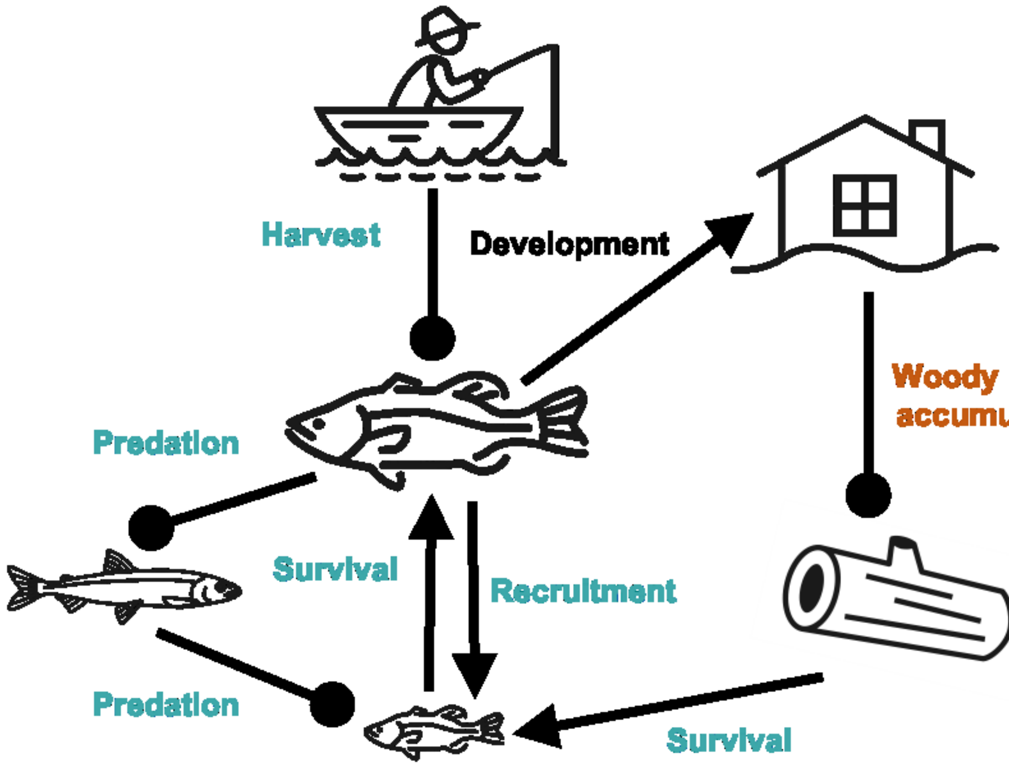

Figure 5. Schematic of a social-ecological system with slow and fast variables that produces long transients under fixed management schemes. Dots are negative effects; arrows are positive effects. Fast variables are in blue; slow variables are in red. See text for additional description. Model adapted from Carpenter and Brock 2004.

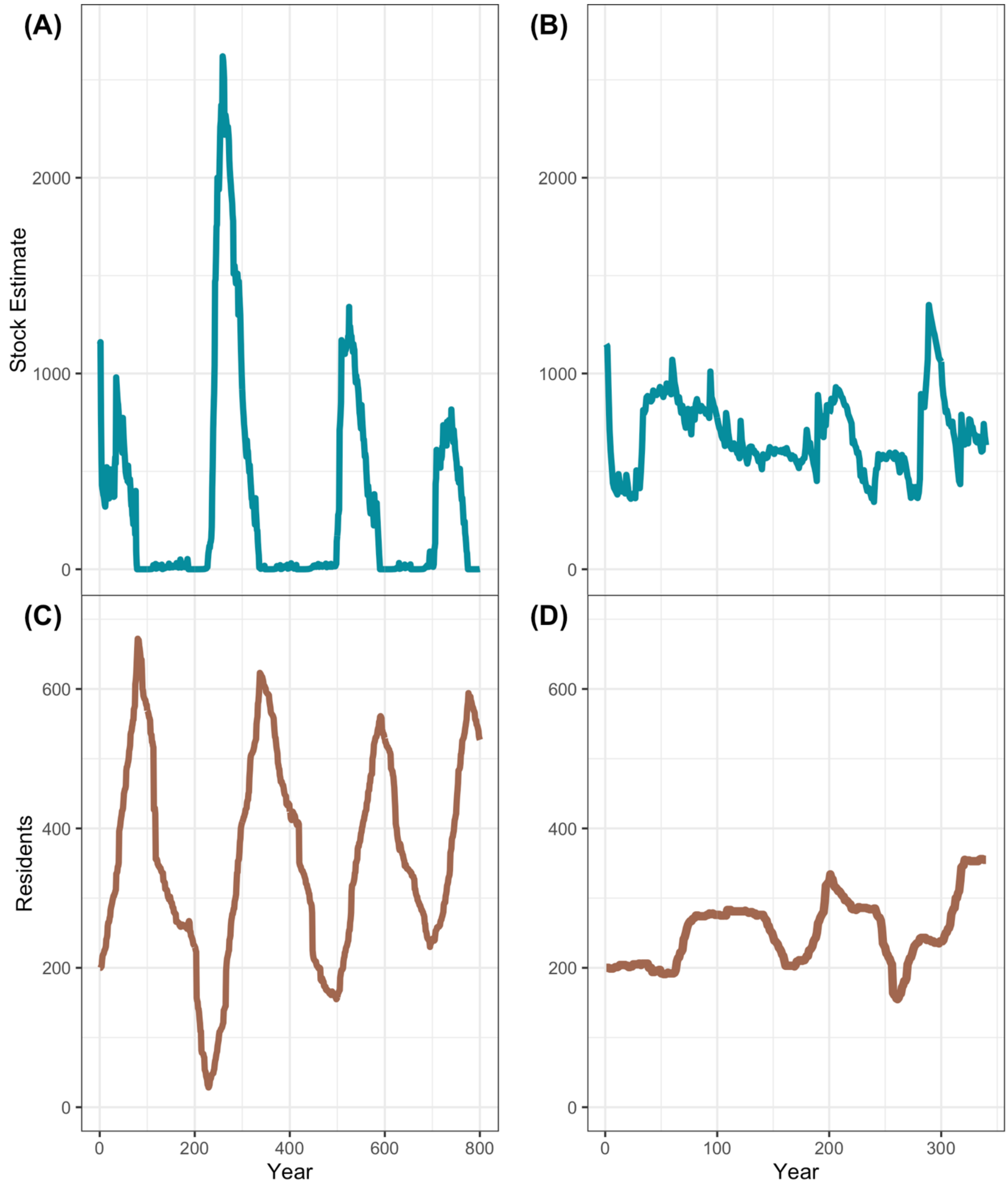

Figure 6: From example 2.5 Results of a fixed (A, C) versus adaptive (B, D) management strategy for a simulated social-ecological system showing target fish stock assessment (A, B) and human use of the lake (C, D). Note different x-axis scales; the longer time scales for the fixed management strategy shows the long-period cycles in the system.