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Transient phenomena in ecology

Alan Hastings
University of California, Davis

Karen C. Abbott
Case Western Reserve University

Kim Cuddington
University of Waterloo

Tessa Francis
University of Washington, Tacoma

Gabriel Gellner
Colorado State University

See next page for additional authors

REVIEW SUMM RY

ECOLOGY

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BACKGROUND: Much of ecological theory and the understanding of ecological systems has been based on the idea that the observed states and dynamics of ecological systems can be represented by stable asymptotic behavior of models describing these systems. Beginning with early work by Lotka and Volterra through the seminal work of May in the 1970s, this view has dominated much of ecological thinking, although concepts such as the idea of tipping points in ecological systems have played an increasingly important role. In contrast to the implied long time scales of asymptotic behavior in mathematical models, both observations of ecological systems and questions related to the management of ecological systems are typically focused on relatively short time scales.

A number of models and observations demonstrate possible transient behavior that may persist over very long time periods, followed by rapid changes in dynamics. In these examples, focusing solely on the long-term behavior of systems would be misleading. A long transient is a persistent dynamical regime—including near-constant dynamics, cyclic dynamics, or even apparently chaotic dynamics—that persists for more than a few and as many as tens of generations, but which is not the stable long-term dynamic that would eventually occur. These examples have demonstrated the potential importance of transients but have often appeared to be a set of idiosyncratic cases. What is needed is an organized approach that describes when a transient behavior is likely to appear, predicts what factors enhance long transients, and describes the characteristics of this transient behavior. A theory of long ecological transients is a counterpart to the related question of tipping points, where previous work based on an analysis of simple bifurcations has provided broad insights.

ADVANCES: Just as ideas based on the saddle-node bifurcation provide a basis for understanding tipping points, a suite of ideas from dynamical systems provides a way to organize a systematic study of transient dynamics in ecological systems. As illustrated in the figure, a relatively small number of ideas from dynamical systems are used to categorize the different ways that transients can arise. Translating these abstract results from dynamical systems into observations about both ecological models and ecological system dynamics, it is possible to understand when transients are likely to occur and the various properties of these transients, with implications for ecosystem management and basic ecological theory. Transients can provide an explanation for observed regime shifts that does not depend on underlying environmental changes. Systems that continually change rapidly between different long-lasting dynamics, such as insect outbreaks, may most usefully be viewed using the framework of long transients.

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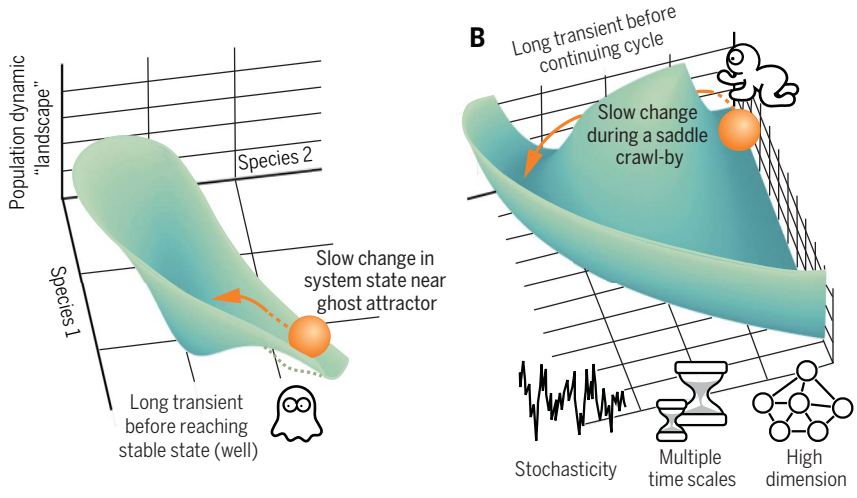
An initial focus on conceptual systems, such as two-species systems, establishes the ubiquity of transients and an understanding of what ecological aspects can lead to transients, including the presence of multiple time scales and particular nonlinear interactions. The influences of stochasticity and more realistic higher-dimensional dynamics are shown to increase the likelihood, and possibly the temporal extent, of transient dynamics.

OUTLOOK: The development of such a framework for organizing the study of transients in ecological systems opens up a number of avenues for future research and application. The approach we describe also raises important questions for further development in dynamical systems. We have not, for example, emphasized nonautonomous systems, which may be required to understand the implications of a changing environment for transients. Systems with explicit time dependence as well as stochastic nonlinear systems still present great mathematical challenges.

Implications for management and basic ecological understanding depend on both the results we describe and future developments. A recognition of the difficulty of prediction caused by long transients, and of the corresponding need to match dynamics to transient behaviors of models, shows that basing either management or interpretation of ecological observations only on long-term dynamics can be seriously flawed.



Two ways that long transients arise in ecology, illustrated as a ball rolling downhill. A) Slow transition away from a ghost attractor: a state that is not an equilibrium, but would be under slightly different conditions. **B**) Lingering near a saddle: a state that is attracting from some directions but repelling from others. Additional factors such as stochasticity, multiple time scales, and high system dimension can extend transients.

The list of author affiliations is available in the full article online.
*Corresponding author. Email: amhastings@ucdavis.edu
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REVIEW

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Alan Hastings[1]* Karen C. Abbott[2] Kim Cuddington[3] Tessa Francis[4] Gabriel Gellner[5] Ying-Cheng Lai[6] Andrew Morozov[7 8] Sergei Petrovskii[7] Katherine Scranton[9] Mary Lou Zeeman[10]

The importance of transient dynamics in ecological systems and in the models that describe them has become increasingly recognized. However previous work has typically treated each instance of these dynamics separately. We review both empirical examples and model systems and outline a classification of transient dynamics based on ideas and concepts from dynamical systems theory. This classification provides ways to understand the likelihood of transients for particular systems and to guide investigations to determine the timing of sudden switches in dynamics and other characteristics of transients. Implications for both management and underlying ecological theories emerge.

nderstanding ecological dynamics over relevant time scales underpins almost all major questions in ecology, such as explanations for observed distributions and abundances of species, population changes through time, and management of ecological systems. There is a growing recognition that dynamics on ecological time scales, called transients, may be different from asymptotic dynamics. The inherent impermanence of transients means that an ecological system in a transient state can change abruptly, even without any underlying change in environmental conditions parameters). Conversely, the possibility of long transients implies that an ecological system may remain far from its asymptotic behavior for a long time. Insect outbreaks *1*) such as that of the spruce budworm *2*), where dynamics shift markedly over relatively short time scales, provide an important class of examples.

Thus, understanding the implications of transients for ecology depends on understanding potential rapid transitions between two kinds of dynamics, the behavior of systems far from their final dynamics, and the underlying time scales for these transitions. However, with the current lack of a systematic framework to facilitate understanding of transient dynamics, each example appears novel and idiosyncratic. Concepts from dynamical systems Table 1) can provide tools for a more systematic approach to the incorporation of transient dynamics in ecological models and theories, as well as guide applications to natural and managed systems. Tools will emerge for understanding which ecological factors produce long transients, and for identifying appropriate responses to the possibility of sudden system changes in management and in experimental and observational studies.

A major ecological question is how to relate observations of changes in dynamics to underlying causes. With transients there may be no underlying proximal cause of a sudden change in dynamics. There may have been no underlying environmental change, or the change may have occurred quite far in the past. In contrast, identification of the proximal factors responsible for regime shifts has been a major focus of attention over the past two decades *3*, *4*). Regime shifts may occur as a result of slow, directional change in ecological parameters, especially when such a change leads to a "bifurcation" of the ecosystem properties e.g., a disappearance of a stable steady state) *3*, *4*), also known as a "tipping point." In turn, the directional change in parameter values is often assumed to result from an exogenous process such as, for instance, global climate change. Intense study of one kind of exogenously triggered regime shift those caused by saddle-node bifurcations) has provided important insights *3*, *5*, *6*) across a range of ecological systems. There is, however, a growing body of evidence that we review here, from both empirical and modeling studies, suggesting alternative underlying mechanisms for some regime shifts.

The approach for understanding regime shifts can be extended to a much broader range of phenomena and systems by focusing on transients in ecological systems, where once again ideas from dynamical systems can organize what may at first appear to be a disparate set of observations and explanations. In the cases we focus on here, the ecological dynamics are essentially transient *7*–*12*) and shifts occur in the absence of any clear trend in the environmental properties. Ecological transients can arise for a number of reasons, including responses to environmental fluctuation as well as a variety of human interventions. Some transients are short; others can last for a very long time. An ecosystem exhibiting long transient behavior would typically show an apparently stable dynamic e.g., periodic oscillations, as in Fig. 1, A, D, and E) over time that may span dozens or even hundreds of generations before experiencing a sudden transition to another state e.g., extinction) or another regime e.g., oscillations with a very different mean value). Therefore, long transients may provide

[1]Department of Environmental Science and Policy, University of California, Davis, CA 95616, USA. [2]Department of Biology, Case Western Reserve University, Cleveland, OH 44106, USA. [3]Department of Biology, University of Waterloo, Waterloo, Ontario N2L 3G1, Canada. [4]Puget Sound Institute, University of Washington, Tacoma, WA 98421, USA. [5]Department of Biology, Colorado State University, Fort Collins, CO 80523, USA. [6]School of Electrical, Computer and Energy Engineering, Arizona State University, Tempe, AZ 85287, USA. [7]Department of Mathematics, University of Leicester, Leicester LE1 7RH, UK. [8]Shirshov Institute of Oceanology, Moscow 117851, Russia. [9]Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095, USA. [10]Department of Mathematics, Bowdoin College, Brunswick, ME 04011, USA.
*Corresponding author. Email: amhastings@ucdavis.edu

Table 1. Key concepts used in this paper. See *70*, *71*) for further elaboration of ideas from dynamical systems.

Term	Definition
Asymptotic dynamics	The behavior that a system will eventually exhibit and then retain indefinitely if unperturbed i.e., dynamics that are not transient). Examples would include equilibria or limit cycles of predator-prey systems.
Bifurcation	A qualitative change in a system s asymptotic dynamics as a parameter is varied, caused by gain, loss, or change in stability of an invariant set. Examples are crises, Hopf bifurcations, and saddle-node bifurcations.
Regime shift	A qualitative change in a system s dynamics after a long period of apparent stasis. Can occur at tipping points where a bifurcation is crossed, or at a transition from transient dynamics to asymptotic dynamics or from one transient to another).
Tipping point	The conditions or value of a changing parameter) at which a bifurcation occurs, producing qualitatively different asymptotic behavior.
Transient	Nonasymptotic dynamics.
Long transient	Nonasymptotic dynamics that persist over ecologically relevant time scales of roughly dozens of generations or longer).

an alternative explanation of ecological regime shifts.

Transients are not an isolated phenomenon but are related to other aspects of the dynamics of ecological systems that provide challenges for long-term prediction. With transient dynamics, the difficulty of predicting the timing of the shift between dynamic behaviors is compounded by the difficulty of determining asymptotic behavior from observations of short-term behavior or the converse). Chaotic dynamics limit the time over which accurate predictions are possible *13–15*). The permanent influence of external and internal noise on population dynamics also substantially reduces ecological predictability in a number of ways *16*, *17*). Ecological predictions are further complicated by regime shifts *5*, *6*) that occur as underlying environmental conditions slowly change. As a result, any conclusions or estimates made on the basis of observations preceding the regime shift simply become irrelevant after the shift. Regime shifts can often result in catastrophic changes in the ecosystem structure and function, in particular leading to species extinction and biodiversity loss.

Although long transients are often observed in ecological data Table 2) and have been seen in many different models in ecology *7*, *18*, *19*) as well as in neuroscience *2* , *21*) and other natural sciences *22*), a systematic consideration of this highly relevant phenomenon has been missing so far. Additionally, there has been some confusion about the relationship between regime shifts and long transients. We begin with an overview of ideas from dynamical systems that show why transients are a universal feature of ecological systems. We propose a simple classification scheme that shows that the mechanisms producing transients can be put into a small number of classes. This classification thus provides a new unified framework for incorporating transients into interpretations of ecological dynamics as well as into management responses. We emphasize that we can view a system as moving between transients, especially if we change the time scale we are focusing on. Additionally, we provide a road map for future investigations based on open challenges in the study of transient dynamics.

Classification and mechanisms

The unifying principle underlying past studies of long transients is a focus on multiple time scales *23*). One example is regime shifts where slow parameter changes eventually lead to relatively rapid shifts in the state of an ecosystem. We extend this view in two critically important ways: We ask about the dynamics on both of these time scales, and we include other ways in which transients arise. Beyond this emphasis on multiple scales, we emphasize that the ecologically relevant time scales are typically not the asymptotic time scales that have been the focus of many ecological modeling studies and that form the basis of theory on which many empirical studies rest. Nor are very short time scales the appropriate focus.

The tools of dynamical systems provide the means for a systematic approach to long transients. Thus, we first review concepts from dynamical systems *23*) that underlie the more traditional view of ecological systems representing and being represented by the asymptotic behavior of mathematical models. The simplest long-term, or asymptotic, behavior would be a stable equilibrium; a slightly more complex possibility would be a stable limit cycle. A cycle or an equilibrium are both examples of invariant sets: If the system is at an equilibrium or on a cycle, it will remain there forever in the absence of any perturbation or change in parameter values. There are also more complex invariant sets, including chaotic ones. Under the traditional view of ecological systems, on time scales that are relevant for understanding these systems, the focus should not only be on invariant sets; it should also be limited to stable invariant sets that are approached through time. A major limitation of this view is that the relevant time scale for important ecological questions may be short enough that the asymptotic behavior is not an appropriate description. We can, however, still use ideas from dynamical systems to understand and classify the behavior of ecological systems on these shorter but not very short) time scales.

There is a broad range of transient patterns in real ecological systems, likely caused by a range of mechanisms Table 2). We can classify these mechanisms into two general categories: those that occur in the vicinity of an invariant set, and those that do not. Within this broad classification we also can identify properties that make

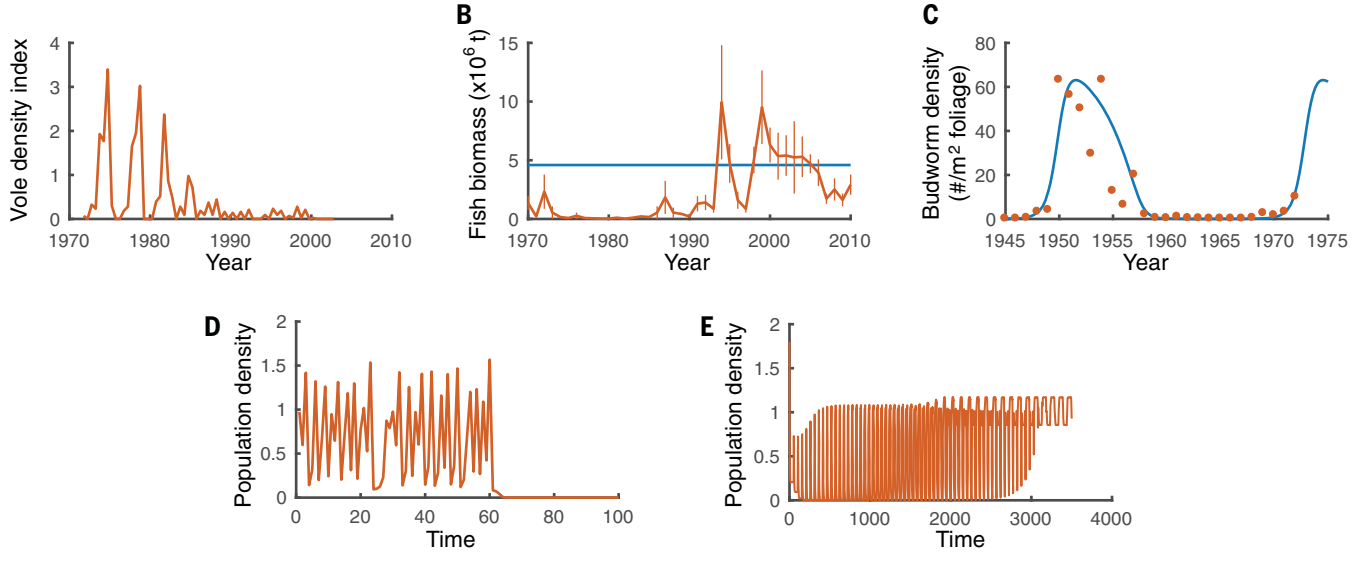

Fig. 1. Examples of transient dynamics. **A** to **C**) Empirical examples of regime shifts occurring after long transient dynamics. A) Population abundance of voles in northern Sweden, showing a transition from large-amplitude periodic oscillations to nearly steady-state dynamics [redrawn from *67*)]. B) Biomass of forage fishes in the eastern Scotian Shelf ecosystem; a low-density steady state changes to a dynamical regime with a much higher average density [blue line is the estimated carrying capacity; error bars are SEM; redrawn from *27*)]. C) Spruce budworm [dots; data from *68*)] has a much faster generation time than its host tree, resulting in extended periods of low budworm density interrupted by outbreaks. A model blue line) with fast budworm dynamics and slow foliage dynamics shows qualitative agreement with the data *2*). **D** and **E**) Examples of long transients on population dynamics models: D) apparently sustainable chaotic oscillation suddenly results in species extinction *18*); E) large-amplitude periodic oscillations that persist over hundreds of generations suddenly transition to oscillations with a much smaller amplitude and a very different mean *19*).

Table 2. Empirical evidence for long ecological transients.

Population s)	Observed pattern	Duration	
		Generations	Years
Laboratory population of beetles *Tribolium* spp.) *25*)	Switch from a regime with an almost constant density to large-amplitude oscillations	15	~1.5 70 weeks)
Growth of macrophytes in shallow eutrophic lakes in the Netherlands *46*)	Switch from a macrophyte-dominated state to a turbid water state	1 to 5	1 to 5
Population of large-bodied benthic fishes on the Scotian Shelf of Canada s east coast *27*)	Switch from a forage fish and macroinvertebrate)–dominated state to a benthic fish–dominated state	5 to 8	20
Coral and microalgae in the Caribbean *47*, *48*)	Shifts from coral to macroalgal dominance on coral reefs	20 to 25 corals); 50 to 100 macroalgae)	10
Voles, grouse in Europe *59*)	Switch between cyclic and noncyclic regimes, or between cyclic regimes with different periodicity	60 voles); 20 to 30 lemmings); 5 grouse)	~30
Dungeness crab *Cancer magister*) *53*)	Large-amplitude transient oscillations with further relaxation to equilibrium	10 to 15	45
Zooplankton-algal interactions in temperate lakes in Germany *26*)	Variation of amplitude and period of predator-prey oscillations across the season	80 to 100 algae); 5 to 8 zooplankton)	1
Planktonic species in chemostat and temperate lakes *72*)	Long-term variation of species densities, with extinction of some species	40 to 100	~0.05 to 0.15 3 to 8 weeks)
Laboratory microbial communities *56*)	Slow switch between alternative stable states	20 to 40	0.11 to 0.21 6 to 12 weeks)
Grass community in abandoned agricultural fields in the Netherlands *57*)	Long-term existence of a large number of alternative transient states	10	9
Extinction debt phenomena as a consequence of habitat loss [plants, birds, fish, lichens, and others *60*)]	Long-term extinction of populations, occurring either steadily or via oscillations	20 to 100 or more)	1 to 100
Fish and invertebrates in watersheds in western North Carolina, USA *49*)	Influence of past habitat structure on present biodiversity patterns after restoration	10 to 20 fish); 40 invertebrates)	40
Modeled spruce budworm outbreaks in balsam fir forests *2*)	Budworm outbreaks driven by slow changes in condition of fir foliage	5 refoliation); 50+ budworm)	50

a system particularly prone to long transients, such as the presence of multiple time scales, high dimensionality, and stochasticity.

We call a dynamical regime e.g., a nearly constant state or persistent cycles) a long transient if it exhibits the following two properties:

1) The dynamical regime persists for a sufficiently long time and is quasi-stable approached over shorter time scales), rather than actually stable. Thus, if the dynamics are observed for a sufficiently long time in appropriate time units, e.g., generations of a relevant species), a clearly seen transition eventually occurs to another equilibrium or dynamic regime.

2) The transition between the regimes occurs on a time scale much shorter than the time of existence of the quasi-stable regime. In other words, the dynamics both before and after the transition last much longer than the time of transition.

Below, we consider a few simple models that exhibit long transients with somewhat different properties. We use these to formalize our classification and describe the mechanisms underlying the long transients.

Ghosts and crawl-bys

One class of long transients arises when a system is near a bifurcation. If we imagine a system s dynamics represented as a ball rolling on an uneven surface, wells correspond to stable equilibria and peaks to unstable ones. If placed into a well, the ball will roll to a stable equilibrium Fig. 2A). Consider now the situation where the surface is

being gradually deformed in such a way that one of the wells becomes more and more shallow. Eventually the system passes the tipping point at which the stable equilibrium at the bottom of this well and the adjacent unstable equilibrium both disappear, and the ball starts rolling down the slope Fig. 2B). However, how fast it starts moving away—or, in other words, how much time it remains in the vicinity of the location where the stable equilibrium was before the bifurcation—depends on the flatness of the slope. The flatter the surface is, the longer the ball stays close to its original location before moving away: The long transient emerges. Although beyond the tipping point the system does not possess an equilibrium at this long-lasting state, for a considerable time its dynamics mimic the dynamics of the system with an attractor here Fig. 2, C and D). We call this situation a ghost attractor *24*) or simply a ghost.

The origin of a ghost attractor and an example of the long transients it can cause are shown in Fig. 2, A to D. To understand the importance of this effect, imagine, for instance, that competitor 1 in Fig. 2, B and D, is a native species competing with an invader. At the early stages of invasion, we expect the native species to be abundant and the invader rare. From these initial conditions, the system can spend considerable time in this state, even if the ultimate asymptotic result is that the invader excludes the native species as in Fig. 2B). This occurs because the invaded system has conditions that are close to, but distinct from, those that would have allowed the invader and the native species to coexist Fig. 2, A and C). Correspondingly, if the system is only monitored on an intermediate time scale, this long transient dynamic may give an impression that both species will coexist indefinitely—a conclusion that would obviously be erroneous on a longer time scale Fig. 2D).

The long transient dynamics in Fig. 2 occur because of a bifurcation that results in the disappearance of a stable equilibrium. Beyond the bifurcation, there is no longer an equilibrium in the vicinity of what is now a ghost, but the system may still spend a long time in this vicinity. In other words, the long transient occurs without an invariant set. In contrast, the second class of transients we define requires the existence of an unstable equilibrium more specifically, the existence of a saddle). The system approaches the saddle along a stable direction and spends a long time near the saddle. We call this transient a crawl-by.

We find examples of this type of long transient in predator-prey systems Fig. 3). Note that dynamics with similar properties are observed in more realistic and more complicated models *25*, *26*) and are corroborated by some field and laboratory data *25*–*27*) see also Fig. 1B), which points at the generality of the suggested mechanism.

Note that crawl-bys and ghosts appear to be similar: Having spent some considerable time in the vicinity of its original position, the system e.g., the ball) eventually moves away. However,

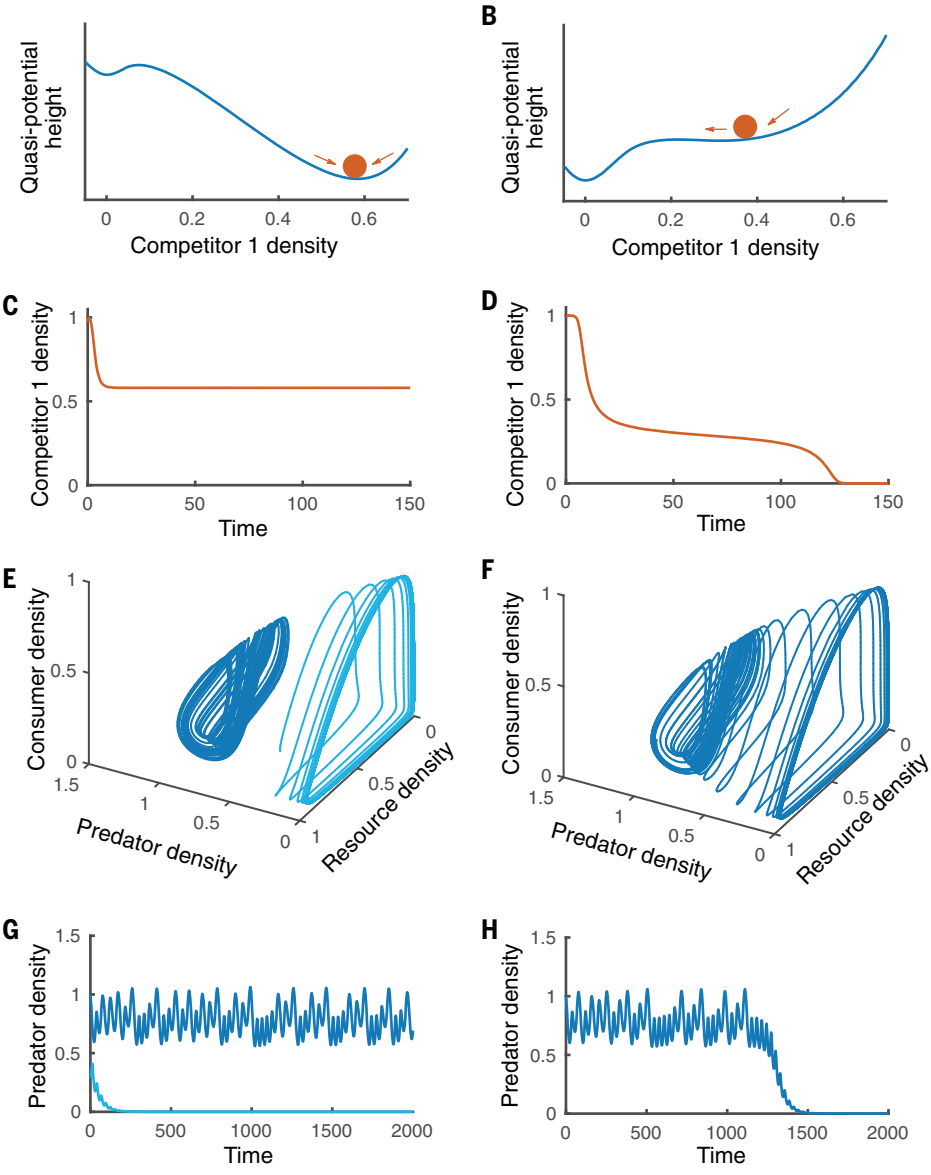

Fig. 2. Ghost attractors. Illustration of ghost attractors in a two-species competition model **A** to **D**) and a resource-consumer-predator model **E** to **H**). In the left column [A), C), E), and G)], there are two stable invariant sets and no ghost attractors. In the right column [B), D), F), and H)], there is a single stable invariant set, plus a ghost attractor that causes long transients. A bifurcation tipping point) occurs for parameter values intermediate to these two cases; at this bifurcation, one stable state is lost and a ghost attractor takes its place. [A) and B)] Dynamics of one of the competitors depicted as a ball on a quasi-potential surface. In A), a ball to the right of the hump at 0.07 will tend to roll toward the stable equilibrium well) at 0.58, as in time series C). In B), the surface is relatively flat, rather than containing a well, to the right of ~0.1; a ball to the right will eventually roll to the stable equilibrium at 0 but will roll very slowly on the flat part of the surface, generating a long transient. There is a ghost attractor at a density around 0.3, which is visible in time series D). [E) to H)] The same phenomenon with more complex invariant sets: [E) and G)] The system shows bistability where a chaotic three-species attractor dark blue) coexists with a stable consumer-resource limit cycle with no predators light blue); dark and light trajectories differ only in their initial conditions. [F) and H)] For parameter values on the other side of a bifurcation that turns the chaotic attractor into a chaotic saddle, any trajectory will eventually converge to the stable limit cycle, which is now the global attractor. However, convergence can be slow, as seen in H), because the chaotic set is now a ghost. Models are as follows: [A) to D)] Competitor 1 is v and competes with species u: $du\ dt = u\ 1-u) - a_{12}u^n v$, $dv\ dt = \gamma[v\ 1-v) - a_{21}u^n v]$ with $a_{12} = 0.9$, $a_{21} = 1.1$, $\gamma = 10$, and $n = 3$ [A) and C)] or $n = 1.55$ [B) and D)]; [E) to H)] from *28*, *29*), where the resource is R, consumer C, and predator P: $dR\ dt = R[1-\ R\ K)] - x_c y_c CR\ \ R + R_0)$, $dC\ dt = x_c C\{[y_c R\ \ R + R_0)] - 1\} - x_p y_p PC\ \ C + C_0)$, $dP\ dt = x_p P\{[y_p C\ \ C + C_0)] - 1\}$ with $x_c = 0.4$, $y_c = 2.009$, $x_p = 0.08$, $y_p = 2.876$, $R_0 = 0.16129$, $C_0 = 0.5$, and $K = 0.99$ [E) and G)] or $K = 1$ [F) and H)]. Quasi-potentials in A) and B) were computed using *69*).

a distinction appears when the history of the system is taken into account. For a system to be influenced by a ghost, its initial state must be near the ghost as in Fig. 2B) or more extreme, such that it passes by the ghost en route to another state as in Fig. 2D). One reason a system s history might place it near a ghost is if that system recently underwent a change in conditions that caused the ghost attractor to appear. Individual crawl-bys can also occur if the history of the system places it on track to closely approach a saddle, but crawl-bys may also repeat in perpetuity, as in Fig. 2, C and D. This occurs because the saddles that give rise to crawl-bys are always attracting from some directions, whereas ghosts may or may not have attracting directions.

The mechanisms described above that cause long transients are not restricted to simple dynamics such as steady states or limit cycles. Similar effects can be seen in cases of chaotic dynamics. An illuminating example is given by a resource-consumer-predator system 28, 29). In a certain parameter range, this system exhibits chaotic dynamics [see the chaotic attractor dark blue) in Fig. 2, E and G]. However, a change in parameter values e.g., an increase in the resource species carrying capacity) can bring the system to a bifurcation at which the strange attractor disappears 29). Beyond this tipping point, the chaotic dynamic is not sustainable any more; it becomes transient and eventually converges to a periodic oscillation with a stable limit cycle Fig. 2, F and H). However, this convergence is slow, so that the dynamics remain essentially chaotic over a long time. Similar dynamics are observed in time-discrete systems 2). This behavior is apparently similar to the crawl-by near a saddle point, and indeed the term "chaotic saddle" is used in the physics literature to refer to a nonattracting dynamical invariant set responsible for transient chaos 3 , 31) in dynamical systems theory, it is also called a chaotic supertransient). More generally, a common dynamical mechanism for transient chaos is crisis 3), a type of global bifurcation that changes the nature of the underlying chaotic invariant set.

An important point is that one property common to long transients caused by ghost attractors and chaotic crawl-bys is that the system is just beyond the tipping point. Thus, if a parameter controlling a system has pushed the system just past a tipping point, there may not be a sudden change; instead, a long transient may result.

Slow-fast systems

Much of the literature on tipping points considers multiple time scales: fast intrinsic dynamics affected by a slow-changing external factor. However, some systems have multiple time scales within their intrinsic dynamics. This can also lead to transients, as in a prey-predator system written in its general form:

$$\frac{dN(t}{dt} = f(N\ P\ \varepsilon$$

$$\frac{dP(t}{dt} = \varepsilon g(N\ P\ \varepsilon \qquad (1$$

where $\varepsilon << 1$ is a non-negative dimensionless parameter that quantifies the difference between orders of magnitude for the time scales of prey N) and predator P) 32), and f and g are the growth rate of the prey population on the natural time scale for the prey and the growth rate of the predator population on the natural time scale for the predator, respectively. Such a difference is common in resource-consumer interactions. For example, univoltine insect herbivores that feed on trees have much faster population dynamics than their hosts. Reproduction and mortality rates of zooplankton are typically lower by one to two orders of magnitude than the corresponding rates of phytoplankton on which the zooplankton feed. Similar differences exist for birds and insects, foxes and voles, etc. 33).

Viewed on the slow time scale, the prey population evolves quickly and is always at its equilibrium, with the predator population acting essentially as a slowly changing parameter with dynamics determined by the predator equation. The net result is alternation between long periods of relative stasis and periods of rapid change. An almost steady-state dynamic of prey at a very low density accompanied by a gradual decrease in the predator density as shown by the left side of the cycle in Fig. 3E and each trough in Fig. 3F) can go on for hundreds of generations of prey before suddenly changing to an outbreak in the prey population. The next phase is a slow, gradual decrease in the prey population along with a slow increase in the predator population the right side of the cycle, and peaks in the prey time series) before accelerating to a fast drop in the prey density. The difference between this dynamic and the transients described above, in which there is only

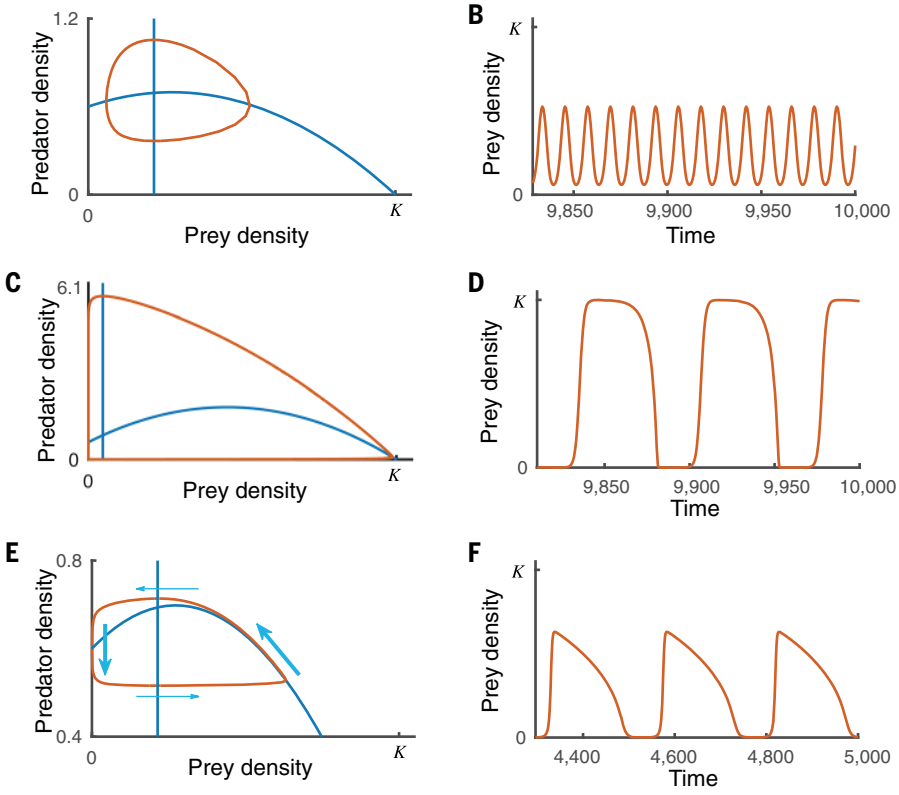

Fig. 3. Predator-prey dynamics with and without transients. Predator-prey dynamics without long transients **A** and **B**), with long transients due to crawl-bys **C** and **D**), and with long transients due to slow-fast dynamics **E** and **F**). In A), C), and E), the intersection of the predator s and prey s isoclines blue lines) produces a coexistence equilibrium. When the prey s predator-free carrying capacity K is beyond a threshold Hopf bifurcation), the system exhibits limit cycles around this equilibrium. [A) and B)] For K just beyond this threshold, relatively small limit cycles occur and there are no long transients. [C) and D)] With an increase in K, the cycle grows in size and closely approaches the two saddle points at 0,0) and K,0). In D), crawl-bys are visible at 0 and K. E) When predator slow) and prey fast) dynamics occur on very different time scales, the shape of the cycle changes, and more horizontal parts of the cycle thin arrows) proceed much more quickly than more vertical parts thick arrows). F) The corresponding time series for the prey shows long transients at 0 and higher prey density. The difference between F) and B) is entirely due to the slower predator dynamics in F). In all panels, for prey species N and predator P, $dN\ dt = N[1 - N\ K)] - \gamma NP\ N + H)$, $dP\ dt = \varepsilon\{[\nu\gamma NP\ N + h)] - mP\}$ with $\gamma = 2.5$, $h = 1$, $\nu = 0.5$, $m = 0.4$. In A), B), E), and F), $= 1.5$, $K = 2.2$; in C), $= 1.5$, $K = 10$; in D), $= 0.8$, $K = 15$; in A) to D), $\varepsilon = 1$; in E) and F), $\varepsilon = 0.01$.

one intrinsic time scale, is whether the slowly changing variable is viewed as internal or external to the system. This is important because slowly changing variables are often considered the result of human actions or a changing environment; they could alternatively be viewed as part of the system itself. These systems with inherent multiple time scales lead to the view that whether we think of a system as having transients may depend on the time scale of ecological interest relative to the time scales embodied in the system.

Transients in high-dimensional systems

Most systems outside a laboratory or experimental environment are very high-dimensional because of the presence of space or time delays that greatly increase the potential for transients, including very long transients. In the examples considered so far, all the processes or forces shaping the dynamics are instantaneous and local in space. In real-world systems, it is not always so.

Time delays are a common property in ecological dynamics resulting from processes and mechanisms such as nutrient recycling *34*, *35*), maternal effects *36*, *37*), or development in stage-structured populations. Time delays were shown to lead to the emergence of long transients in a few modeling studies *19*, *38*), and there is a certain similarity between delay-caused long transients and those caused by ghost attractors. Systems with time delay are different from instantaneous systems not only because of different processes taken into account, but also from the viewpoint of dynamical systems theory as the phase-space argument and the corresponding analysis become irrelevant. In a general case, even a low-dimensional e.g., two-species) system with delay is equivalent to an infinite-dimensional instantaneous system *39*, *4*). These findings suggest that time delay is a separate mechanism that can result in long transient dynamics.

Spatiotemporal dynamical systems are necessarily high-dimensional, and the transient time can greatly increase with the system size. An early study *7*) reported extremely long transients in such systems Fig. 4A). In systems described by a coupled map lattice, the transient time can increase exponentially with the system size or faster *41*), leading to supertransients *42*).

Effect of noise

Until now, we have considered long transient dynamics in deterministic settings, absent noise or stochasticity. In natural systems, noise and random disturbances are inevitable and may create or extend transients. In other cases, stochasticity may essentially eliminate transient dynamics; as we have emphasized, the practical impact of stochasticity once again will depend on the time scale of ecological interest relative to the time scales of the system dynamics.

Noise may affect a system with existing long transient dynamics caused, for example, by a ghost or crawl-by. In transient dynamics caused by a crawl-by, such as the limit cycles of a predator-prey system Fig. 3, C and D), small

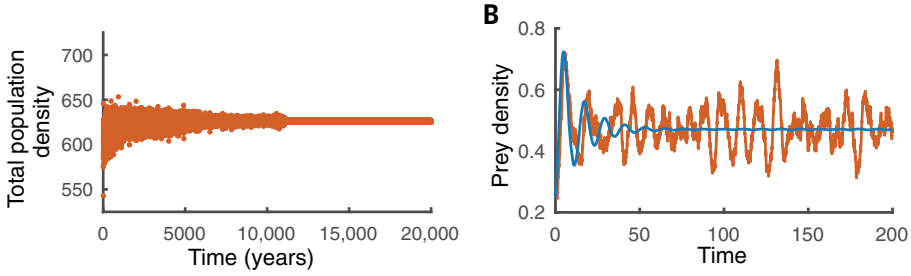

Fig. 4. Examples of additional mechanisms leading to long transients. **A**) Spatial structure in a simple population model leads to very long transients when the local population growth rate is high [from *7*); local dynamics are governed by $N_{t+1} = N_t \exp[r\ 1 - N_t)]$ with $r = 3.5$; the total population density summed across all localities is plotted here]. **B**) For these parameter values = 1.5, $K = 1.5$, $\gamma = 2.5$, $h = 1$, $\nu = 0.5$, $m = 0.4$, $\varepsilon = 1$), the deterministic predator-prey model from Fig. 3 exhibits short transient cycles, then converges to a stable equilibrium point blue curve). However, when stochasticity is added, the same model will exhibit sustained cycles with approximately the same period red line; here, stochasticity was incorporated by representing the prey s intrinsic growth rate, , as a random variable with mean 1.5).

populations very close to the saddle at 0,0) are vulnerable to stochastic extinctions, where random events may move the system to one of the saddle points, causing either the prey or predator population or both) to go extinct. Stochasticity in the system near the saddle also has the potential to alter the length of the transient period, widening the distribution of resulting durations of the transient period or times to convergence *43*). Stochasticity in the system near a ghost attractor also widens the distribution of transient periods, depending on the steepness of the surface around the ghost. Noise that is skewed "uphill" will lengthen the transient, dooming the ball to repeatedly roll nearer the ghost Fig. 2B). Noise can also induce sustained transients or oscillations in a system that would exhibit damped oscillations to an equilibrium in the absence of noise *44*, *45*) Fig. 4B). Noise can also provide a mechanism for transient dynamics of a system to become long-lived Fig. 4B). For systems with transient chaos, the interaction with stochasticity can be even more complex *42*).

Transients in the real world

The systematic classification of long transient types and mechanisms conducted here provides a framework for recognizing and understanding these dynamics in observed natural systems Tables 1 to 3). Note that our classification does not include nonautonomous systems, not because long transients do not occur in nonautonomous systems, but because their classification and discussion warrants treatment beyond the scope of the present review. In this section we describe how empirically observed behavior may be the result of long transients in a wide variety of situations; through examples, we emphasize implications for management.

An empirical example of long transients due to a ghost attractor similar to that presented in Fig. 2) is the well-documented switch from a macrophyte-dominated state to a turbid water state in freshwater lakes in the Netherlands *46*). The study tracked about 70 shallow lakes after a water drawdown that stimulated macrophyte growth, temporarily creating a macrophyte-dominated, clear water attracting state. When water levels subsequently rose, some of the lakes returned immediately to a turbid state, while others lingered for more than 4 years in the clear water state that was no longer stable. In other words, the physical modification to the system caused by the changes in water level resulted in the formation of a clear water ghost attractor that slowed movement toward the turbid water attractor, sometimes quite substantially. A similar mechanism of long transients due to ghost attractors may underlie the transition from coral to macroalgal dominance reported for Caribbean coral reefs *47*, *48*), the shift from a forage fish state to a state dominated by large-bodied benthic fish species in the Scotian Shelf of Canada s east coast *27*), and the shifts between populations of fish and invertebrates in watersheds in western North Carolina after habitat restoration *49*).

Long transients due to crawling past a saddle are often observed in planktonic ecosystems—in particular, in the interactions between phytoplankton and zooplankton—creating oscillations in which periods of high population density alternate with long periods of low density *26*). Other examples of crawl-bys are given by patterns of cyclic succession reported in a number of ecosystems, including competition in communities of side-blotched lizards *5*), coral reef invertebrates *51*), and heather-moss-bearberry succession *52*). In each of these systems, a long dominance of one species is observed before its displacement by the next competitor in the cycle.

Empirical examples of long transients related to slow-fast systems include a number of observations of univoltine insect herbivores that feed on trees *2*) Fig. 1C). At short time scales of a few insect generations, the tree density is approximately constant. However, on longer time scales, the impact of the growing insect population may become high enough to cause a sudden collapse in the quantity or quality of foliage, resulting in a regime shift.

Real ecosystems are often disturbed by noise that can trigger patterns of long transients. A notable example includes the population dynamics

Table 3. Overview of long transient LT) classification and mechanisms.

Type of LT	Relationship to invariant set	Relationship to bifurcation	Dynamics mimicked by LT	Possibility of recurrent LTs?	Biological example
Ghost Fig. 2)	No invariant set	Occurs past a bifurcation where stable equilibrium is lost	Equilibrium, cycles, chaos	No	Forage fish *27*) Fig. 3B)
Crawl-by Fig. 3, C and D)	Caused by saddle-type invariant set	None necessary	Equilibrium, cycles, chaos	Yes	Phytoplankton-grazer models *26*)
Slow-fast systems Fig. 3, E and F)	None necessary	Multiple time scales	Periodic or aperiodic cycles	Yes, if invariant set s) present	Univoltine insects *2*) Fig. 3C)
High dimension e.g., time delays, space) Fig. 4A)	None necessary	None necessary	Equilibrium, cycles, chaos	Yes	Chemostat microbial communities *57*)
Stochasticity Fig. 4B)	If invariant set present:	None necessary	Aperiodic cycles, chaos	Yes	*Cancer* crabs *53*)
	If invariant set absent:	Past a bifurcation where cycles/chaos are lost	Quasi-periodic cycles		

of Dungeness crab, *Cancer magister*, in eight West Coast ports of the United States *53*). By combining data analysis with modeling fitted to data, large-amplitude transient oscillations followed by relaxation to an equilibrium were shown to occur as a result of stochastic perturbations of a deterministic system with a stable state. Another example is given by an empirical study on *Tribolium* *54*) in which random perturbations of cyclic population dynamics result in chaotic-like behavior. Seasonal dynamics create a particular structure of environmental stochasticity. For example, in plankton communities in temperate lakes, each cold season "resets" the initial conditions for the warm, growing season. This prevents the system from reaching equilibrium and thereby allows for high biodiversity transients to be the norm *26*, *55*).

High-dimensional systems may be likely to possess long transients. For example, slow succession of patterns of biodiversity is found in experimental microbial communities in a chemostat *56*). The precise mechanism of these observed long transients is still unclear because of the high complexity of systems containing dozens of interacting species and the existence of several time scales. Similarly, long-term existence of a large number of alternative transient states is seen in the restoration of agricultural fields *57*), which is also characterized by a high degree of complexity.

Implications for management

The existence, identification, and forecasting of long transient dynamics in ecosystems have substantial implications for the management of ecosystems. Broadly speaking, management is aimed at maintaining or creating a desirable state of the ecosystem. The challenge is in predicting system behavior given dynamical regime uncertainty. If a system transition is detected, the important questions are what has caused it and how long it can be expected to last. What a study of long transients reveals is that a system may shift in ways that are not simply tracking underlying conditions, so a focus on asymptotic behavior without considering transients may give misleading answers.

In some cases, mechanistic mathematical models that are constructed from first principles, fitted to empirical data, and explored within realistic parameter ranges can help to 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 United Kingdom *58*). In other cases, when it is difficult to distinguish whether observed dynamics are transient or at equilibrium, models of both possibilities can be developed to test the sensitivity of proposed management strategies to the model assumptions.

Incorporating considerations of transient system behavior into management also requires shifting perspectives about the relevant time scale. A fundamental issue is a mismatch between relevant ecological transient) time scales and management time scales. Implementation of management plans where long transients are at play will require adjustments to accommodate the transient changes in dynamical regime.

Acknowledging transient system behavior affects management assumptions, practices, and interventions. In addition, detecting long transients, and incorporating risk analysis for long transients, requires the development and application of new tools to reflect this change in thinking. A full treatment of the management consequences and opportunities presented by long transients requires further attention beyond the present review.

Implications and future directions

Sudden changes in ecological dynamics through time represent both great challenges and opportunities for unraveling the forces that regulate ecosystem functioning. Much recent work in this vein has focused on the concept of regime shifts as a rapid response of dynamics to slow changes in environmental conditions such as climate change, habitat destruction, resource exploitation, etc.). However, there are many examples of situations and systems that do not fit into this classical framework; in particular, a shift can suddenly occur in a seemingly constant environment. The existence of long transients explains how this may happen: As we have shown here, the ecosystem dynamics past a tipping point can be very slow, sometimes indistinguishable from the steady state for hundreds of generations "ghosts"). Long transient dynamics can also be responsible for regime shifts in the absence of any associated tipping point, thus significantly broadening the regime shift paradigm. Finally, the dynamics of some systems with multiple time scales may best be viewed as a succession of transients.

The traditional approaches in ecological sciences are usually based on asymptotic dynamics. Here we have shown that this focus is often insufficient and sometimes irrelevant, and needs to be reconsidered in a systematic way. Long transients provide a new dimension in our understanding of observed changes in ecological dynamics. Although the existence of long transients has been previously acknowledged both in theoretical and empirical studies, any systematic approach to this phenomenon has been lacking. We bridge this gap by developing a simple classification of different types of long transient dynamics and linking empirical observations to simple prototypical models. As one important result of our investigation, we have arrived at the conclusion that both identifying long transients and understanding their implications e.g., for ecosystem management) requires coupling across several ecologically relevant time scales.

Identifying from observations whether a natural ecosystem is close to an equilibrium or is experiencing long transient behavior constitutes a major challenge. Perhaps the easiest case is a situation where the population density shows a clear disappearance of periodic cycles of voles, lemmings, and grouse in Europe *59*) Fig. 1A), or the slow steady population decline in extinction debt phenomena *6*). Less evident is the situation where the dynamics do not show a pronounced trend. In this case, one can compare characteristics of the observed community with those thought to represent equilibrium systems, such as a relatively undisturbed community of a similar type or the same community in the past. These ideas have been implemented to reveal an extinction debt caused by habitat fragmentation, by comparing the current species-area relation to historical records *6*) and by verifying whether the species-area relation holds *61*). As an alternative approach, recently developed techniques make it possible to build an ecological model directly from a time series by reconstructing model equations from data. A particularly promising new approach is based on compressive sensing using a powerful sparse optimization framework *62*–*65*). Once a model is available, its properties can be analyzed, in particular to reveal long transients. However, we argue that any essential progress in this area is only likely to be achieved by combining various methods borrowed from data mining, stochastic modeling, and bifurcation theory. Another important aspect will be the exchange of ideas with other areas of biology such as neuroscience, where transients are considered important and have been studied with both data and models *2* , *21*). Existing methods to identify transients in empirical data are not always reliable and can result in either overlooking the approaching regime shift or in false alarms, which can be very costly. This poses substantial new challenges for ecologists, mathematicians, and data analysts.

Acknowledging long-term transient behavior drastically affects our perception of ecological dynamics. First, sudden shifts in dynamics may occur in the absence of underlying parameter changes i.e., in the absence of the tipping point). Second, analysis of ecological processes must be done across a few relevant time scales rather than focusing only on asymptotic behavior. In particular, one should take into account both fast and slow variables and feedbacks. Third, stochasticity may play a key role in generating long transients, in particular by bringing an ecosystem to the vicinity of an unstable equilibrium causing a crawl-by) or a ghost. Finally, in the context of ecosystem management practices, it is well known that sometimes long transients may offer a window of response time that would not be available for systems with rapid switches between stable states *66*). On the other hand, transients can add more uncertainty to the anticipation of regime shifts, because such a shift can occur without a noticeable change of parameters.

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Transient phenomena in ecology

Alan Hastings, Karen C. Abbott, Kim Cuddington, Tessa Francis, Gabriel Gellner, Ying-Cheng Lai, Andrew Morozov, Sergei Petrovskii, Katherine Scranton, and Mary Lou Zeeman

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Making sense of transient dynamics

Ecological systems can switch between alternative dynamic states. For example, the species composition of the community can change or nutrient dynamics can shift, even if there is little or no change in underlying environmental conditions. Such switches can be abrupt or more gradual, and a growing number of studies examine the transient dynamics between one state and another—particularly in the context of anthropogenic global change. Hastings *et al.* review current knowledge of transient dynamics, showing that hitherto idiosyncratic and individual patterns can be classified into a coherent framework, with important general lessons and directions for future study.

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