

# Transients: the key to long-term ecological understanding?

Alan Hastings

Department of Environmental Science and Policy, University of California, Davis, CA 95616, USA

**Ecological theory has been dominated by a focus on long-term or asymptotic behavior as a way to understand natural systems. Yet experiments are done on much shorter timescales, and the relevant timescales for ecological systems can also be relatively short. Thus, there is a mismatch between the timescales of most experiments and the timescales of many theoretical investigations. However, recent work has emphasized the importance of transient dynamics rather than long-term behavior in ecological systems, enabling the examination of forces that allow coexistence on ecological timescales. Through an examination of what leads to transients in ecological systems, a deeper appreciation of the forces leading to persistence or coexistence in ecological systems emerges, as well as a general understanding of how population levels can change through time.**

Many of the traditional approaches in ecological theory are based on a paradigm that the ecological systems that we observe in nature correspond in some way to stable equilibria of relatively simple ecological models. This is a view embodied in many classic approaches to ecological problems, ranging from the use of models to look at the coexistence of species to the interpretation of short-term ecological experiments [1]. This approach, however, has been questioned. As ecologists emphasize that long-term experiments yield different results compared with short-term experiments [2], theory must take the role of timescales into account and look beyond an emphasis on determining stable equilibria. Applications, such as adaptive management of renewable resources, require an understanding of short-term responses rather than long-term behavior.

One natural extension to looking at equilibrium behavior is to look at long-term, or ASYMPTOTIC BEHAVIOR (see Glossary) of systems, but including final dynamics that are more complicated than an equilibrium, such as LIMIT CYCLE dynamics, or even chaos [3]. Moreover, stochastic influences can play a role in asymptotic behavior [4]. In particular, explanations for variability in ecological populations (and in the dynamics of childhood diseases) have led to questions such as whether observed variability is due to external (exogenous) forces or internal (endogenous) forces [4]. Recent approaches for understanding variability have focused on the idea that both

kinds of force interact to produce the dynamics observed in natural systems [4].

Yet, many answers to this central question of the cause of variability have still focused on the long-term (or asymptotic) behavior of the models in question. My goal here is to look instead at the importance and role of TRANSIENT dynamics as an essential explanatory aspect of understanding ecological systems. I define transient dynamics as behavior that is different from the long-term behavior. Transient dynamics has been the subject of numerous recent investigations [5–24]. However, the ideas underlying the concept are not new and, indeed, studies of epidemics [25] have essentially focused on

## Glossary

The definitions given here are heuristic, rather than mathematically rigorous.

**Asymptotic behavior** : the eventual dynamics of a system (see Figure 1).

**Basin boundaries** : divisions between the sets of initial conditions that lead to different asymptotic behaviors.

**Chaotic attractor** : a solution that is chaotic (exhibiting sensitive dependence to initial conditions) and is approached by all nearby solutions.

**Chaotic saddle** : a solution that is chaotic (exhibiting sensitive dependence to initial conditions), and is also a saddle, so that it is approached by some solutions, but not by all 'nearby' solutions.

**Fast timescale dynamics** : dynamics that occur within short times, when the slow timescale variables can be assumed to be unchanging (Figure 1 and Box 1).

**Integro-difference model** : a model that is discrete in time and continuous in space where the distribution of organisms the following year is calculated from an integral of a function of the population distribution the current year that includes population growth and movement.

**Limit cycle** : behavior of a system where exactly the same state is reached at fixed time intervals, typical of exploiter–victim systems.

**Oscillators** : systems that can produce limit cycle behavior.

**Overcompensatory density dependence** : typified by the Ricker model [44], this is a case where the total number of individuals produced declines as the standing stock is increased, as opposed to the case where only the per capita number of individuals produced declines as the standing stock is increased, as in the Beverton-Holt model [45].

**Phase plane techniques** : analysis of time-dependent systems that depends on the fact that there are two dependent variables (e.g. exploiter and victim) and that ultimately relies heavily on the result that, with two variables, the only asymptotic behavior is either a limit cycle or an equilibrium.

**Saddle** : an unstable equilibrium (or other asymptotic state) that is approached by some solutions.

**Slow timescale dynamics** : dynamics that occur over long time periods, when the fast timescale variables can either be assumed to be at an equilibrium, or can be viewed as their average values (Figure 1 and Box 1).

**Stable manifold** : the set of initial conditions from which an asymptotic solution is approached; is of most interest in the case of a saddle.

**Transient (or transient dynamics)** : behavior of a dynamical system that is not the final behavior (Figure 1).

**Unstable manifold** : the set of initial conditions from which an asymptotic solution is approached, if time is run backwards. Thus, for 'typical' parameter values where there is no center manifold, all initial conditions can be decomposed into the sum of a point in the stable manifold and a point in the unstable manifold.

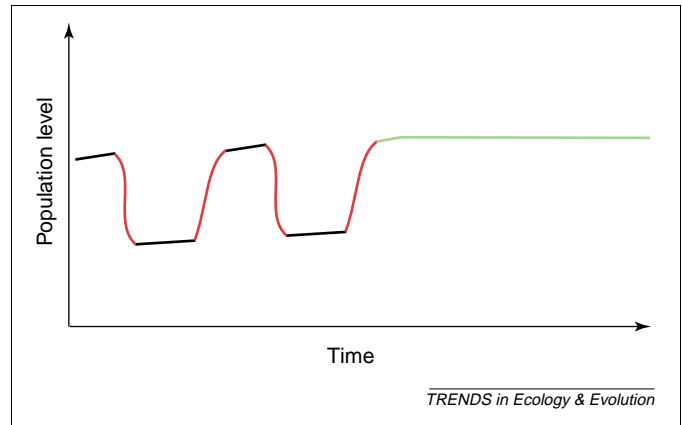
transient dynamics. A reexamination of these concepts provides further insight into more general ecological questions of persistence and coexistence.

My goal here is not to provide an exhaustive review of ecological dynamics, but to emphasize the underlying principles that can be used to understand transient dynamics. Mathematical concepts of SADDLES and the role of processes operating on different timescales [26] will play a central role. Ecologists all appreciate that different organisms operate on different timescales because of different generation times, ranging from microorganisms that reproduce hourly to univoltine insects with one year generation times to trees with generation times in the tens or hundreds of years. What is not appreciated enough is how these different underlying timescales and ecological interactions play a role in generating dynamics that appear at different timescales.

Yet, the concept and importance of studying transients, rather than asymptotics, has a long history in population biology, going back to the seminal studies of epidemic dynamics by Kermack and McKendrick [25]. This example provides insight into both the concepts underlying the importance of transients and the more recent examples of transients in ecological models. The key to the formulation and analysis of the initial epidemic models was the recognition that the appropriate timescale was one where the host population was not affected by births and deaths (other than those resulting from the epidemic), and that the question of interest was the time course of the epidemic, rather than the final state, which is always one where the disease dies out. In the simplest models of an epidemic, the SIR (susceptible–infective–removed) models, the analysis can be quite complete. Using PHASE PLANE TECHNIQUES, which involve graphing the two variables S and I with time viewed implicitly, a complete approximate description of numbers of infectives through time can be obtained. Thus, the relevant values, such as the maximum number of infectives and the maximum rate of infection can be determined as well as information about the final state (the number of susceptibles in the population after the epidemic has run its course). With demographic considerations added, such as births and periodicity of infections arising from the school calendar, more recent investigations have used the SIR model as the basis for understanding the periodic epidemics of childhood diseases [27].

### Timescales and transients

For epidemics, the relevant timescale can be the scale of a single epidemic, or longer, if the question of interest is the timing between epidemics [27]. This same issue of timescales (Figure 1) arises in many areas of ecology. Whatever the question, it is important to match the timescale of observation with the analysis of the models. Another way of viewing what is essentially a mismatch between ecological models and theories on the one hand, and the systems that these models are attempting to explain on the other, is that the ecological experiments are often on a short timescale relative to the asymptotic behavior of the models. In this vein, a recent overview of ecological experiments [2] has emphasized the importance of looking



**Figure 1.** Concepts of slow and fast timescales, and transient and asymptotic dynamics. The black and red parts of the curve of population dynamics through time represent the transient dynamics, which is roughly cyclic; the green part of the curve represents the long time, or asymptotic, dynamics, which is an approach to an equilibrium. During the transient phase, the black portion corresponds to slow timescale changes, whereas the red parts are changes on a fast timescale. The relatively rapid switch from the transient phase to the asymptotic phase is not unrealistic, and occurs in this example when the fast timescale dynamics bring the population level to a high enough point that the asymptotic equilibrium state is approached.

at longer term experiments to match better the timescale of ecological dynamics. Another aspect of timescales underlies attempts to explain the coexistence of species in plankton [13], especially in temperate lakes, where seasonality effectively reduces the relevant timescale to less than one year. Consequently, any attempt theoretically to explain coexistence in temperate lakes must only consider the behavior of models within a single season and then restart of the models the next season, rather than looking at the long-term outcome of the models. The models in [13,14] show that the time until species go extinct in a model of competition can be much longer than the single year timescale before the resetting of the system that occurs each winter.

The key to understanding transient dynamics is to understand that transients are an aspect of timescales (Figure 1), another area that has also been recently emphasized [26,28]. Ecological systems typically have different timescales, as in interactions between long-lived trees with generation times of decades and forest insects with generation times of one year (Box 1). If there are dynamics on multiple timescales, then transients are likely to appear. The transients will be of great ecological importance if the dynamics on the multiple timescales are different and the 'FAST-TIMESCALE' DYNAMICS are on a scale that is ecologically relevant, and if the 'SLOW-TIMESCALE' DYNAMICS are still fast enough so that they are also ecologically relevant, albeit perhaps on much longer timescales. Then the transients can cause apparently inexplicable changes in dynamics. A classic example is the work of Ludwig *et al.* [29] on the outbreak of the spruce budworm. This also illustrates the importance of the transient concept: high population values for the spruce budworm occur not as the result of long-term dynamics, but as the result of what is essentially a transient (Box 1). Here, the fast timescale is one where the insect population changes from outbreak level to low level or vice versa. On a longer timescale, the system changes levels of insect

### Box 1. Multiple timescales and spruce budworm dynamics

Interactions between forest insects and trees provide a striking example of the importance of timescales in ecological systems, and the presence of different timescales underlies the concept of transient dynamics. The classic example of the spruce budworm studied by Ludwig *et al.* [29] provides a specific example of this phenomenon. Insect dynamics occur on a very short timescale, with significant population changes within a single year or over several years. However, the number of forest trees only changes significantly over a period of decades. Thus, as used by Ludwig *et al.* in their analysis, this interaction can be understood if you first assume that the number of trees is constant, and consider the dynamics of the insects. Then, take the average insect population

density, and consider the population dynamics of the trees in response to the average population density of the insects rather than the density within a single year.

The analysis can become more complex if the dynamics of the fast system (the insects) changes as the numbers of the slow variable (the trees) change. Then, the dynamics of the trees can change through a feedback mechanism as the average insect population level responds to a change in the number of trees. This kind of dynamics can be analyzed using geometric methods [26,28,42] and the presence of cycles, which depend, in part, on the presence of the different timescales can be demonstrated.

abundance owing to changes in the slower variables representing other aspects of the dynamics, such as the dynamics of the trees. Recent work has [26,28] shown how to explore mathematically dynamics on different timescales in ecological models.

#### Role of saddles in understanding transients

Saddles, equilibria that are unstable but approached by some solutions, arise in even the simplest two-species ecological models of predation or competition (Box 2). Yet, saddles provide one of the major mathematical concepts for understanding how ecological models produce transient dynamics. A transient analysis of models is essential when the timescale of the transients is of ecological relevance, even when the long-term dynamics are not approached on the ecological timescale. For example, the asymptotic dynamics could lead to the elimination of a species, whereas the transient dynamics could explain coexistence (Box 1). Some recent attempt to understand plankton communities have shown in models how coexistence is found in the short term, but not in the long term, because of CHAOTIC SADDLES (see below) [13,14].

A deeper appreciation of the importance and generality of transients depends on an analysis of ecological models from a dynamical systems point of view. If we are to understand what kind of ecological conditions leads to transient dynamics, a first step will be to focus on the simplest class of dynamics that can lead to multiple timescales. The concept of saddles (Box 2) as appearing in linear systems also extends to more complex systems and is a key factor that can lead to multiple timescales in solutions. In a study of the dynamics of laboratory populations of flour beetles [6], both from an experimental and theoretical standpoint, saddles were used as way to understand changes in the dynamical behavior of the population numbers through time (Box 3). More general aspects of ecological models that can lead to multiple timescales are discussed below.

#### Classes of ecological system leading to transients

If ecologists are to understand and appreciate the role that transient dynamics can play, a heuristic understanding of the kinds of feature in models that have been found to produce transients is essential. Features that lead to transients are ubiquitous in ecological systems. As noted previously, many of these features reduce to the concept of saddles. However, the different ways (mathematically)

that these saddles can arise and produce transients can have very different ecological implications.

#### Chaotic saddles

The dynamics of food chains and food webs have exhibited potentially long transients (many tens to hundreds of generations) in model studies, which is another manifestation of the saddle phenomena. In this case, a CHAOTIC ATTRACTOR becomes unstable as a parameter is varied, and the attractor loses stability and becomes a saddle. So, over a short time, a solution to the system looks chaotic, but, eventually, the solution approaches an attractor. In this case, the complexity of the chaotic dynamics can mean that the time the system spends in the vicinity of the saddle can be very long [30,31]. However, for these systems, a deeper understanding can be obtained. There appears to be a scaling law that relates the time spent in the transient to the difference in the value of a parameter from the parameter value at which the system becomes unstable. Thus, for example, as the carrying capacity for the lowest trophic level in a three-species model is increased, the population dynamics change from a stable equilibrium to a limit cycle and eventually to chaotic dynamics. As the carrying capacity is increased further, the chaotic solution becomes unstable, leading to long chaotic transients that become shorter chaotic transients as the carrying capacity is increased [32].

#### Spatial systems

Spatial systems, such as an INTEGRO-DIFFERENCE MODEL [10] with alternating reproduction and dispersal, are one of the best investigated, and most dramatic kinds of system in which transients occur. They also illustrate the concept that transients are intimately connected with aspects of both spatial and temporal scales.

The simplest kind of spatial system that exhibits these dynamics is one where there are a large number of populations whose behavior is described by a discrete time model, with OVERCOMPENSATORY DENSITY DEPENDENCE. Here, it was first shown that, with a wide range of different coupling, very long (thousands or more generation) transients could result, provided that the density dependence was strong enough, [10]. This behavior has since been shown to occur in systems with two components, and in a wide range of other systems. The underlying mathematical mechanisms leading to these transients are still not fully understood, but it has been demonstrated in some specific cases, and strongly conjectured to be more

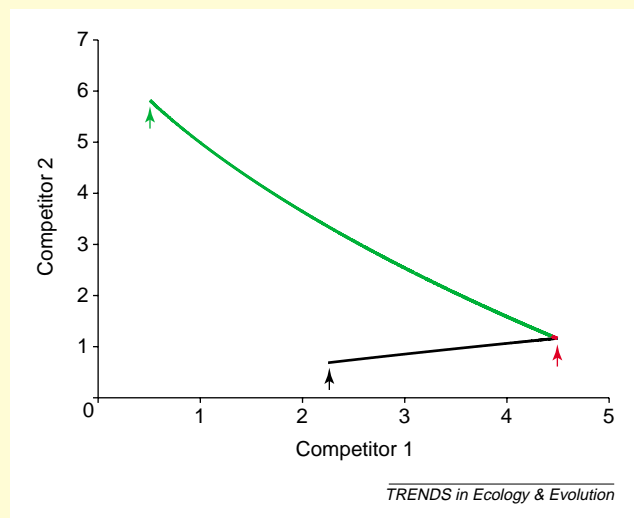
## Box 2. Saddles and dynamical phenomena leading to multiple scales

The concepts underlying transients can be best understood on the basis of simple ideas from dynamical systems. These ideas, in turn, can be understood in the context of examples familiar to ecologists and evolutionary biologists.

One key idea in the generation of transients is saddles, which are present in many ecological models, including the simplest two-species predator–prey models and competition models with interference competition. The simplest version of a saddle would be an equilibrium point that is approached from some directions and not others. When the system approaches the equilibrium point, it slows down (Figure 1), and the system can spend such a long time near the saddle, that even the unstable equilibrium can have great biological relevance. Such behavior is found near the point at which both predator and prey are absent in a simple predator–prey system [26]. Here, it makes sense that the system slows down, because population changes in either species will be slow as both populations are so small.

The nonlinear extension of the direction in which the saddle is approached is called the stable manifold, and the direction in which the saddle is left from is called the unstable manifold. These manifolds can provide further insight into the dynamics.

Saddles occur when an equilibrium point is approached in some directions, but left in other directions. The phenomena of multiple timescales can also arise when the equilibrium point is approached in all directions, but much more quickly in some than in others. A biological example of this is selection for an intermediate optimum in quantitative genetics, where the mean of the trait quickly attains the optimum value, whereas the variance is reduced much more slowly [43]. Thus, on a relevant timescale, variability will be maintained if there is variability initially. This phenomenon of differing rates of approach to an equilibrium from different directions is simply another way of looking at transient dynamics.



**Figure 1.** Transient dynamics owing to a saddle in a two-species Lotka–Volterra model of competition. The plot depicts part of the dynamics of a single solution in the phase plane that starts at the end of the black portion (black arrow) and ends at the end of the green portion (green arrow), where the different colors are used to highlight the time. The black portion is a plot of the solution for a scaled time between 0 and 2, the red portion is a plot of the solution for time between 2 and 12, and the green portion is a plot of the solution for time between 12 and 25. This is a case where there is contingent competition owing to interference, so this model has a saddle, which is located at the red portion of the plot. Thus, for this initial condition, the system spends so much time near the unstable equilibrium that the equilibrium is relevant for ecological understanding. Although the eventual outcome in this case is the elimination of species 1, the system exhibits coexistence on an ecologically relevant timescale, so the transient dynamics before the eventual outcome are ecologically important. The solution initially (the black portion) follows along the stable manifold of the saddle, then (the red portion) is near the saddle, and finally (the green portion) follows along the unstable manifold of the saddle.

general, that saddles are at the heart of the behavior [17–19,33]. A further consequence and related aspect is unpredictability owing to complex BASIN BOUNDARIES [23], which appears to be related to transient dynamics [31].

### Linear systems with varying timescales

Saddles are one way in which different timescales can happen, but there can be different timescales even in the approach to an equilibrium (Box 1). Another way that transients can arise is if a system has different timescales, which occurs even in linear systems. One of the most striking examples of this is ‘extinction debt’, which occurred in simple models incorporating a colonization competition tradeoff [34]. Here, after habitat is removed, the effect on species diversity through extinctions is not immediate. Although the model is nonlinear, essentially, it is the presence of very different dynamic rates in the response of the species near the equilibrium that explains why the time until equilibrium is reached is so long that the consequences of current human actions on the long-term diversity of ecosystems will not be apparent until a long time has elapsed.

### Coupled oscillators

The consequences of first approaching a ‘slow manifold’ (Box 1) can also arise in nonlinear ecological models. Many ecological systems can oscillate and, in particular predator–prey and other exploiter–victim systems can produce oscillations. Coupling OSCILLATORS, either spatially or in some other fashion (as parts of a food web) can lead to transient dynamics because of the presence of two different timescales. One timescale is the fast one, corresponding to the dynamics of the exploiter–victim interaction. On a slower timescale, the phase of the two oscillators changes. Coupled predator–prey models have been shown to exhibit transients in modeling studies [11], because there are two timescales. On the shorter, faster timescale, the numbers of exploiters and victims oscillate, whereas, on the longer timescale, the difference in time between the peak populations in the different patches changes. As the coupled systems get into phase, the amplitude of the oscillations increases, increasing the likelihood of extinction resulting from low population levels. This is a phenomenon that can have a dramatic effect on the characterization of the conditions leading to coexistence.

### Role of stochasticity

The role of stochasticity can greatly change both the dynamics of a system and the transient dynamics. In many cases, the lifetime of a transient can be greatly extended by stochasticity. The simplest kind of setting in which this can occur is in the neighborhood of a stable spiral point where, in the absence of stochasticity, the system would approach the equilibrium. Rather than appear as a stable equilibrium, the addition of stochastic influences will make the system appear as though it has a stable limit cycle [35], as has been observed in metapopulation models. This effect can be much more dramatic [12], leading to dynamics that are complex when the deterministic model produces an equilibrium or a simple limit cycle, as has been shown in

### Box 3. Transients in a laboratory population of *Tribolium*

The explicit demonstration of the importance of the dynamics of saddles (other than the role played by the equilibrium with both species absent in an exploiter–victim system) is a difficult endeavor, and recent work with laboratory populations of the flour beetle *Tribolium* provides one of the best examples. The analysis used an underlying model phrased in terms of the number of larvae, pupae and adults that was analyzed in discrete time corresponding to the experimental protocol used [6]. Here, there is an equilibrium with constant numbers that is unstable, but is a saddle. Thus, for appropriate initial conditions for the model (when the system starts near the stable manifold of the saddle, as defined in the glossary), the system will approach the saddle, whereas, for other initial conditions, the system never gets near the saddle. The final, stable, asymptotic behavior is a two-point limit cycle.

This kind of transient behavior can be seen not just in the model, but in laboratory experiments. Because the laboratory system includes variability, as expected, for some replicates of the system (Figure 2, main text), the saddle is approached, whereas, for others it is not. When the saddle is approached, the numbers first approach the equilibrium (constant population levels) and then finally exhibit the two-point cycle, whilst for other replicates, the system just approaches the two-point cycle, with no apparent behavior that resembles a stable equilibrium. This experiment and analysis emphasizes that transient behavior depends strongly on the starting conditions for the system. Transients might only arise for certain initial conditions and, if the basin boundaries are complex, it might not be obvious how small changes in initial conditions lead to the presence or absence of saddles.

studies of models for the dynamics of childhood diseases [36,37]. Stochastic influences also can lead to jumps between different attractors, which would appear as transient behavior [38].

#### Evidence for and importance of transients in ecology

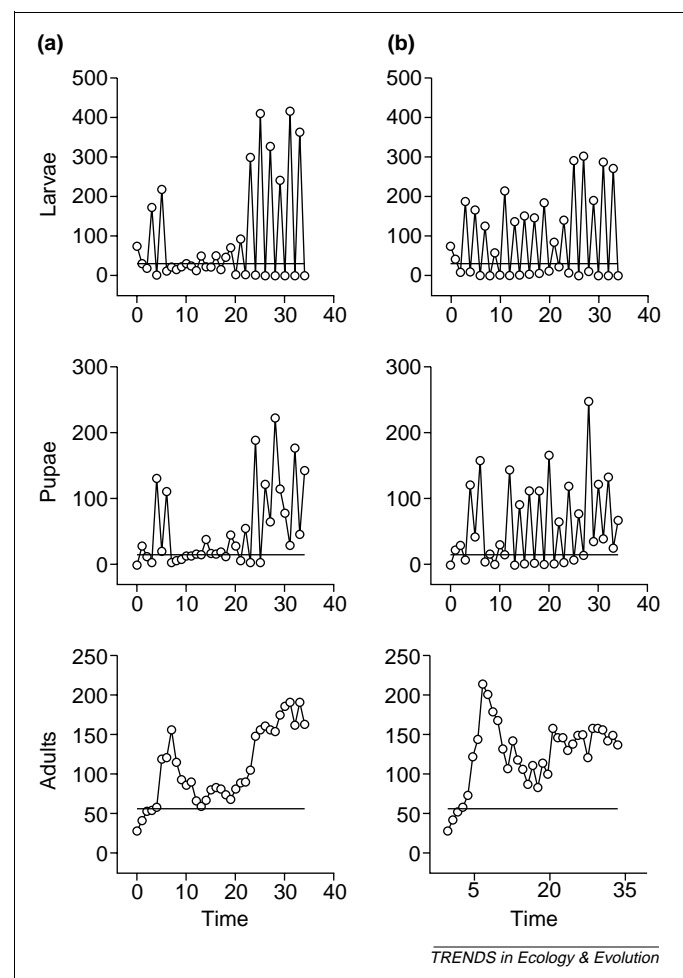
The importance of transients comes not only from the recognition that endogenous dynamics can be an explanation for sudden changes in ecosystem behavior, but also from the awareness that, in many systems, transient behavior can be an essential part of the explanation for the distribution and abundance of species. Recently, the recognition that transient dynamics can be an important aspect of the coexistence of exploiters and victims, and also of competitors, has received much attention. Any study of outbreaks (insects or diseases) focuses very much on the transient dynamics [9,17–19,24,39–41].

#### Evidence for transients

What is the evidence for transients in either experimental or natural systems? This evidence is best understood in those cases where models describing the dynamics of a population or system have been fitted to the system. The presence of transients can then be demonstrated by considering the model dynamics.

One of the best understood experimental systems exhibiting transients (Box 3) is the laboratory dynamics of *Tribolium* [6]. Here, a carefully developed model based on the simplification of considering three classes (larvae, pupae and adults) has been extensively studied. For some parameter values, this system has a saddle, with a two-dimensional STABLE MANIFOLD and a one-dimensional UNSTABLE MANIFOLD. As argued above, if the system starts very close to the stable manifold, then it would approach the saddle (and, in this case, exhibit approximate equilibrium behavior), and then eventually approach the long-term dynamics (which, in this case, is a two-cycle). However, Cushing *et al.* argue that the occurrence and importance of transients is in fact amplified by the inclusion of stochasticity, which makes it more likely that the system will eventually end up near the stable manifold of the unstable equilibrium, and the saddle would in fact be approached. Using the laboratory populations, the experimenters confirmed the presence of the saddle, showing that the system first approached the saddle, and then approached the two-cycle equilibrium (Figure 2).

A second example suggesting the importance of the interaction between stochasticity and transients is from a study that fitted nonlinear models to data for Dungeness crab *Cancer magister* populations [12], obtained from eight US west coast ports in California, Oregon and Washington. In this study, for the fitted model, the long-term deterministic dynamics approach a stable equilibrium in



**Figure 2.** Transient dynamics are shown for a laboratory population of *Tribolium*, as reproduced with permission from [6]. For one replicate (a), the population numbers (of larvae, pupae and adults) go through a period of approximate constancy, and then the dynamics change so that a two-point cycle is observed. For the other replicate (b), no transient dynamics are observed. This demonstrates that, even in a simple laboratory system, transient dynamics can be observed and that different dynamics are observed on a different timescale.

all but one of the populations, and approach a small amplitude limit cycle in the other. But both the model, with the observed level of environmental stochasticity, and the data showed very large amplitude oscillations. Thus, the observed dynamics were essentially the manifestation of a transient.

#### *Transients are changing our views of ecological systems*

Recent investigations of food-web dynamics [5] have begun to show how transient dynamics can affect the persistence of ecological communities. Researchers argue, on the basis of extensive simulations, that theories of food-web structure based on long-term dynamics near equilibria might be misleading. Those webs that are actually observed to persist in the face of perturbations are the ones whose transient behavior allows persistence. And, because perturbations are features of natural systems, transients must be considered when thinking of those webs that are likely to be observed in natural systems.

Recent investigations of coexistence in planktonic systems [13–16] have focused not only on complex dynamics, but also on the transient behavior of models. Not surprisingly, this is helping to determine what enables species to coexist in lakes, because, with seasonality, long-term solutions can be essentially irrelevant. Also, not surprisingly, recent approaches to understanding the dynamics of epidemics have continued to rely on transient dynamics [27].

#### Prospects

Ecologists have just begun to appreciate the importance of transients, and future work will clearly help to elucidate that importance. Additionally, further advances in dynamical systems theory have helped provide an underpinning for such study. Further progress will be spurred in part by advances in computational resources, as exemplified by the recent emphases on nonlinear time series that have begun to provide insights into complex dynamics, and provide the tools to analyze transient responses. Only through this quantitative match between theory and data will a deeper understanding of the forces shaping natural communities emerge.

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#### 5–7 April 2004

BES/EEF Annual Symposium: Ecology Without Frontiers: Environmental Challenges across Europe, Exeter University, UK (<http://www.britishecologicalsociety.org/articles/meetings/current/2004/annualsymposium/>)

#### 19–23 April 2004

The 4th International Conference on Applications of Stable Isotope Techniques to Ecological Studies, Wellington, New Zealand (<http://207.195.94.13/isoecol/>)

#### 28–29 April 2004

Cetacean Systematics: Meeting the Needs of Conservation and Management, Scripps Institute of Oceanography, La Jolla, CA, USA (<http://cmbc.ucsd.edu/about/cetaceanconf.cfm>)

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Seed Ecology 2004: An International Meeting on Seeds and the Environment, Rhodes Island, Greece (<http://www.biology.uoa.gr/SeedEcology2004.htm>)

#### 3–5 June 2004

International Conference on *Rhododendron ponticum*, Sheffield, UK (<http://www.shu.ac.uk/sybionet/confer/rhody>)

#### 6–10 June 2004

52nd Annual Meeting of the North American Benthological Society, University of British Columbia, Canada. (<http://www.benthos.org/Meeting/index.htm>)

#### 14–16 June 2004

Second International Conference on Prevention, Assessment, Rehabilitation and Development of Brownfield Sites, Siena, Italy (<http://www.wessex.ac.uk/conferences/2004/index.html>)

#### 25–29 June 2004

Annual meeting of the Society for the Study of Evolution, Colorado State University, Fort Collins, CO, USA (<http://lsvl.la.asu.edu/evolution/symp04.html>)

#### 10–15 July 2004

10th Jubilee Congress of the International Society for Behavioral Ecology, Jyväskylä, Finland (<http://www.isbe2004.com>)

#### 25–30 July 2004

7th INTECOL International Wetlands Conference, Utrecht, the Netherlands (<http://www.bio.uu.nl/INTECOL>)

#### 30 July–2 August 2004

The 18th Annual meeting of the Society for Conservation Biology, Columbia University, NY, USA (<http://cerc.columbia.edu/scb2004/>)

#### 1–6 August 2004

Ecological Society of America Annual Meeting, Portland, OR, USA (<http://www.esa.org/portland/>)

#### 22–27 August 2004

10th International Symposium on Microbial Ecology, Cancun Mexico (<http://www.kenes.com/isme/>)

#### 4–8 September 2004

Jacques Monod Conference on the Evolutionary Ecology of Host-Parasite Relationships, Roscoff, France (<http://www.cnrs.fr/SDV/cjm.html>)

#### 7–9 September 2004

British Ecological Society 2004 Annual Meeting, University of Lancaster, UK (<http://www.britishecologicalsociety.org/articles/meetings/current/>)

