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# Alternative stable states in ecology

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The idea that alternative stable states may exist in communities has been a recurring theme in ecology since the late 1960s, and is now experiencing a resurgence of interest. Since the first papers on the subject appeared, two perspectives have developed to describe how communities shift from one stable state to another. One assumes a constant environment with shifts in variables such as population density, and the other anticipates changes to underlying parameters or environmental “drivers”. We review the theory behind alternative stable states and examine to what extent these perspectives are the same, and in what ways they differ. We discuss the concepts of resilience and hysteresis, and the role of stochasticity within the two formulations. In spite of differences in the two perspectives, the same type of experimental evidence is required to demonstrate the existence of alternative stable states.

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Ecologists are gathering increasing empirical support for the idea, first proposed in the 1960s (Lewontin 1969), that communities can be found in one of several possible alternative stable states (Holling 1973; Sutherland 1974; May 1977; Dublin *et al.* 1990; Laycock 1991; Knowlton 1992; Scheffer *et al.* 1993; Nystrom *et al.* 2000; Scheffer *et al.* 2001; Dent *et al.* 2002). Our purpose here is not to review empirical evidence for or against the existence of alternative stable states. Rather, we aim simply to provide a clearer conceptual basis from which ecologists and managers new to this area of research can evaluate the evidence for themselves. There is some debate among experimentalists regarding what constitutes evidence for alternative stable states, in part because there are two different contexts in which the term “alternative stable states” is used in the ecological literature. One use arises as a direct extension of the analysis of stability in population ecology (Lewontin 1969; Sutherland 1974) and has generated recent attention to community assembly rules (Law and Morton 1993; Drake 1991). Here, the environment is usually regarded as fixed in some sense,

and what is of interest is the number and accessibility of different stable configurations a community may adopt (the “community perspective”). However, another use (May 1977) focuses on effects of environmental change on the state of communities or ecosystems (the “ecosystem perspective”) (Scheffer *et al.* 2001; Dent *et al.* 2002). We will compare and contrast these two uses within a common conceptual framework. By doing so, we hope to facilitate empirical exploration of alternative stable states in real communities.

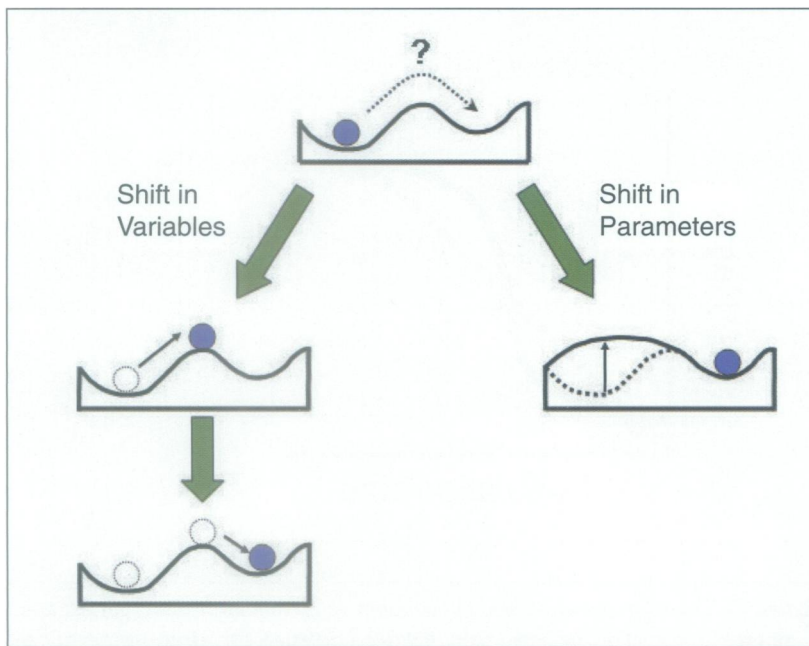
Suppose that the state of a community can be usefully characterized by a set of dynamic state variables, with their relations to each other defined by a set of parameters in a model. The number and choice of variables selected to characterize the community will be determined by what we wish to learn from the model. State variables may be defined in a number of ways, including temporally or spatially averaged abundances of species or guilds, age or stage population components, spatial coverages, and organic or inorganic quantities. Where alternate stable states occur, the selected set of variables will persist in one of a number of different possible configurations, or in other words, at different equilibrium points that are locally stable. The community returns to the same configuration after a small perturbation, but may shift to a different configuration or equilibrium after a large perturbation. Because these shifts can represent catastrophic changes to the community, failure to predict the existence of these alternative states can lead to costly surprises (Carpenter *et al.* 1999; Peterson *et al.* in press). Past examples include the collapse of fishery stocks (Peterman 1977; Walters and Kitchell 2001), outbreaks of disease following inadequate vaccination programs (Haydon *et al.* 1997), effects of invasion by exotic species (Mack *et al.* 2000; With *et al.* 2002), and undesirable vegetation changes in aquatic (Scheffer *et al.* 1993) and terrestrial (Noy-Meir 1975; Dublin *et al.* 1990) ecosystems.

Theoretical ecologists envision two ways in which a

## In a nutshell:

- Empirical studies and discussion of alternative stable states in communities and ecosystems are increasing
- From the modeling perspective, alternative stable states might arise through state variables or parameter shifts
- These different frameworks can be reconciled, allowing the comparison of terms commonly associated with alternative stable states, such as resilience and hysteresis
- Experimental evidence for movement to new alternative stable states involves a demonstration of the stability of a new state in the absence of continued manipulation
- The existence of hysteresis underlies the importance of understanding alternative stable states for management purposes

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**Figure 1.** Two-dimensional ball-in-cup diagrams showing (left) the way in which a shift in state variables causes the ball to move, and (right) the way a shift in parameters causes the landscape itself to change, resulting in movement of the ball.

community can move from one stable state to another. The first requires that different states exist simultaneously under the same set of conditions and that the community be conveyed from one state to another by a sufficiently large perturbation applied directly to the state variables (eg population densities). The second way requires a change in the parameters that determine the behavior of state variables and the ways they interact with each other. For example, this could involve changing parameters such as birth rates, death rates, carrying capacity, migration, or per capita predation. These alterations generally occur because of changes to environmental “drivers” that influence communities. In this second case, the number and location of alternative stable states within the defined system may change.

A useful heuristic device that we will use throughout this article to explain the two ways of thinking about shifting between alternative stable states is the ball-in-cup analogy outlined in Figure 1. All conceivable states of the system can be represented by a surface or landscape, with the actual state of the community as a point or a ball residing on this surface. The movement of the ball can be anticipated from the nature of the landscape. For example, in the absence of external intervention, the ball must always roll downhill. The position of the ball on the landscape represents the actual state of the community (for example, the abundances of all populations). In the simplest representation of alternative stable states, the surface has two basins, with the ball residing in one of them. Valleys or dips in the surface represent domains of attraction for a state (balls always roll into that state once in the “domain”). The question is, how does the ball move from one basin to the other? There are two ways: either move

the ball (Figure 1, left) or alter the landscape upon which it sits (Figure 1, right). The first of these requires substantial perturbation to the variables; this view arises directly from traditional population and community ecology. The latter view envisions a change to the parameters governing interactions within the ecosystem.

### ■ Perturbations to state variables

Altering the populations directly is one way to move communities from one state to another. This formulation requires multiple pre-existing stable equilibrium points at fixed locations in the state space existing simultaneously. To move the community from one stable state to another, a perturbation to the state variables must be large enough to push the community out of the current domain of attraction and into the domain of another stable equilibrium point. Once in a new domain, the community will persist there unless subject to

another large perturbation.

Within this community framework, there are two classes of alternative states. The first considers alternative interior states: “If the system of equations describing the transformation of state is nonlinear...there may be multiple stable points with all species present so that local stability does not imply global stability” (Lewontin 1969). Many cases presented in the community ecology literature represent this type (Sutherland 1974). State shifts have most often been achieved experimentally by predator removal or additions, where predators are considered external to the community of interest and can cause large shifts in prey communities (Paine 1966). Overharvesting a fishery is a classic example by which a new interior community state may arise simply through changes to the size of the fish population. Multiple stable states for a population exist when fish population per capita growth rate is described by a sigmoid curve (eg caused by an Allee effect or depensatory growth) while per capita death rate is a linear function (Figure 2). Each point at which these lines cross represents an equilibrium: the outer two represent stable states and the middle one is unstable. By reducing the fish population to a level below the unstable point in the presence of harvesting (equilibrium X in Figure 2), the population enters the domain of attraction of the lower stable state, where the death rate is higher than the birth rate. Humans are outside of the modeling framework in this example; a change in fishing pressure is therefore represented as a direct change to the state variable, not as a change in the parameters that govern their dynamics.

The second class of alternative stable states in the community framework incorporates boundary states where one or more species is absent (ie its population sits at the zero

boundary). As stated by Lewontin (1969): “If the system of equations governing the species composition of the community is linear, then only one stable composition is possible with all the species represented. However there may be other stable points with some of the species missing.” Two-species Lotka-Volterra competition is a case where the interior coexistence equilibrium may be unstable and alternative states arise through the extinction of one population. When interspecific competition is stronger than intraspecific competition, one population will outcompete the other. Which of these populations persists depends on initial population densities. The introduction of a new species involves moving off a boundary. The order in which species move off boundaries and the different equilibria that result is governed by community assembly rules (Drake 1991; Law and Morton 1993). Dispersal and colonization events affect community assembly and final community states through the order in which population abundances or state variables are altered.

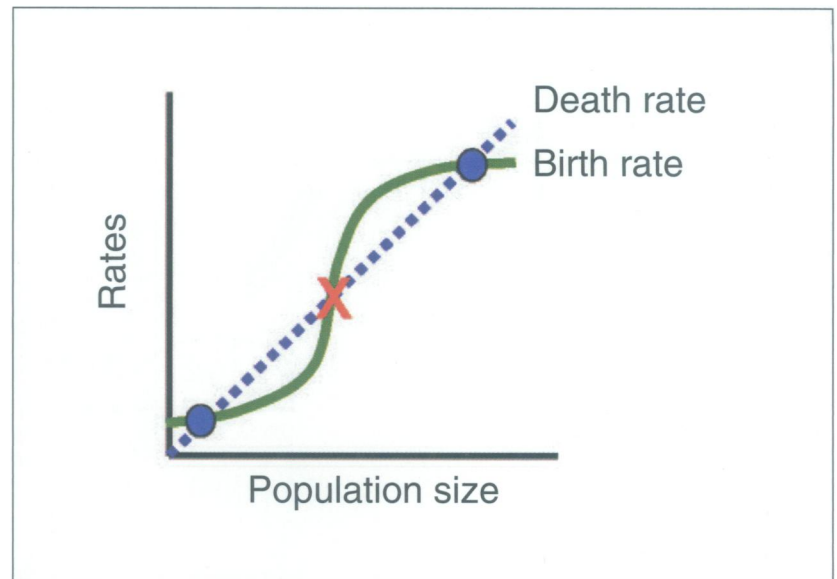
### ■ Changes to parameters

Ecosystem literature on alternative stable states has focused more on the effects of a changing parameter (or environmental driver) within the community. Changes to this parameter cause the community to switch from one state to another (Scheffer et al. 2001; Dent et al. 2002). Each state is stable but, because it corresponds to different parameter values, the associated dynamics (local stability and population fluctuations) are different.

In our heuristic diagrams, the topology of the landscape determines the dynamics of the state variables. In the community perspective, one assumes that the landscape is broadly constant (because the environment is regarded as constant) and only the ball moves. The ecosystem perspective is fundamentally different in that the landscape changes and, as a result, all potential alternative stable states need not be present at all times. Parameter changes may alter the location of a single equilibrium point, or may transiently result in destabilization of the current state, permitting the community to arrive at an alternative, locally stable equilibrium point, which may or may not have existed before the parameter perturbation.

### ■ A common conceptual framework

Ultimately, whether a quantity in a model is treated as a parameter or a variable is a matter of formulation – and therein lies the key to understanding the apparent differences between the community and ecosystem perspectives. In practice, we examine the quantities involved in

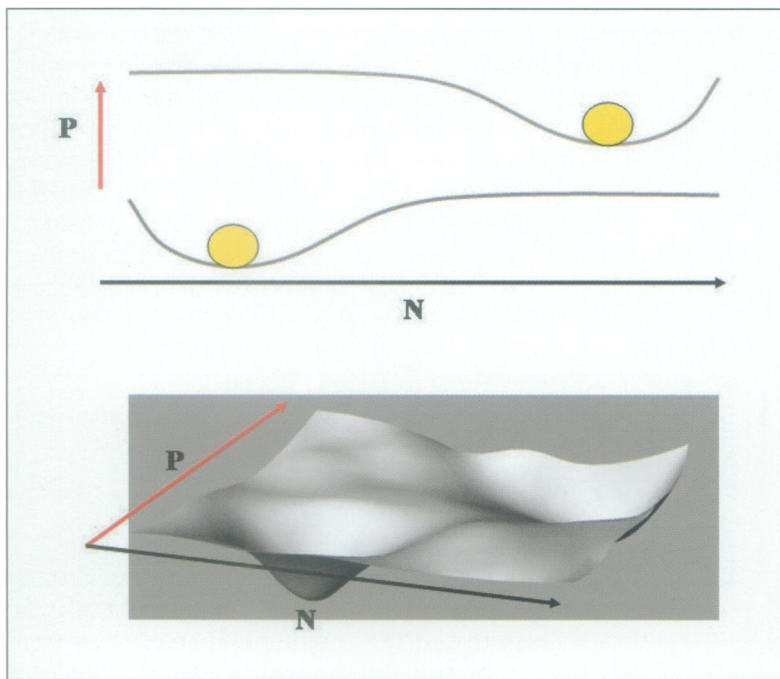


**Figure 2.** The relationship between population death and birth rates that allow for alternative stable states in population size for harvested fish. Intersections of the lines represent possible states, with the circles representing stable ones and the X representing the unstable state.

a dynamic process and identify as variables those quantities that change “quickly” in response to feedback from model dynamics. Parameters are those quantities that are either independent of, or subject only to very slow feedback from state variables within the model. It is differing appreciation or concepts of “quick” and “slow” feedback processes that give rise to the community and ecosystem perspectives. For example, humans often harvest fish at a rate independent of fish population size. If fishing pressure is considered largely independent of feedback from fish stocks, then this pressure may be considered a parameter, and the fishery dynamics examined from an ecosystem perspective. Changing this death rate parameter can drive the fish stocks from one stable state to another (Figure 3, top). However, if fishing pressure is subject to rapid feedback from the state of fish stocks, fishing pressure would best be regarded as a variable within a predator (human)–prey (fish) model, and the fishery dynamics viewed from a community perspective (Figure 3, bottom).

The representation of stochasticity is another key point to consider in discriminating between the community and ecosystem perspectives. Stochasticity may often supply the final impetus for the movement of the ball from one basin to another. Just as there are two ways to cause a community shift between states, environmental stochasticity may be viewed two ways: as variation in parameters omitted from the model, which cause variables to “vibrate” around their deterministic equilibrium points (community perspective); or as variation in parameters that are included in the model, manifesting themselves as “tremors” in the landscape surface (ecosystem perspective), which will be passed on as fluctuations to the state of the community. In either case, environmental and





**Figure 3.** The distinction between the community and ecosystem approaches lies mainly in what one considers a variable and a parameter. In the ecosystem perspective (top), a parameter  $P$  is changed according to the vertical red arrow in response to some external factor. The community equilibrium point moves along the horizontal axis ( $N$ ) driven by the parameter change. There are no feedbacks between the state variable  $N$  and the parameter  $P$ . In the community perspective (bottom), the former parameter  $P$  is now a state variable included in the model, because  $P$  is subject to rapid feedback from the state variables modeled. Perturbations caused by forces external to the variables  $N$  and  $P$  can move the community ball around on the landscape. The landscape is now defined jointly by  $N$  and  $P$  and remains fixed.

demographic stochasticity of sufficient amplitude could cause communities to shift from one basin of attraction to another.

## ■ Resilience

Resilience is an important feature of communities to consider when alternative stable states are discussed. There has been a great deal of confusion about this term because it has been used in different ways by different authors (Peterson *et al.* 1998, Pimm 1991). In our heuristic diagrams, resilience is related to the characteristics of the basin that act to retain the community. When the ball is moved across the landscape, two aspects of the basin affect the ball's subsequent trajectory: the steepness of the slope and the area (or width) of the basin. Steepness of the sides of the basin affects the return time of the ball to the lowest point in the basin. This matters when the perturbation is too small to push the ball out of the basin completely. The ball will roll back towards the lowest point, at a rate determined by the slope. Return time is a measure of local stability (Pimm 1991) and has been called "engineering resilience" by Peterson *et al.* (1998).

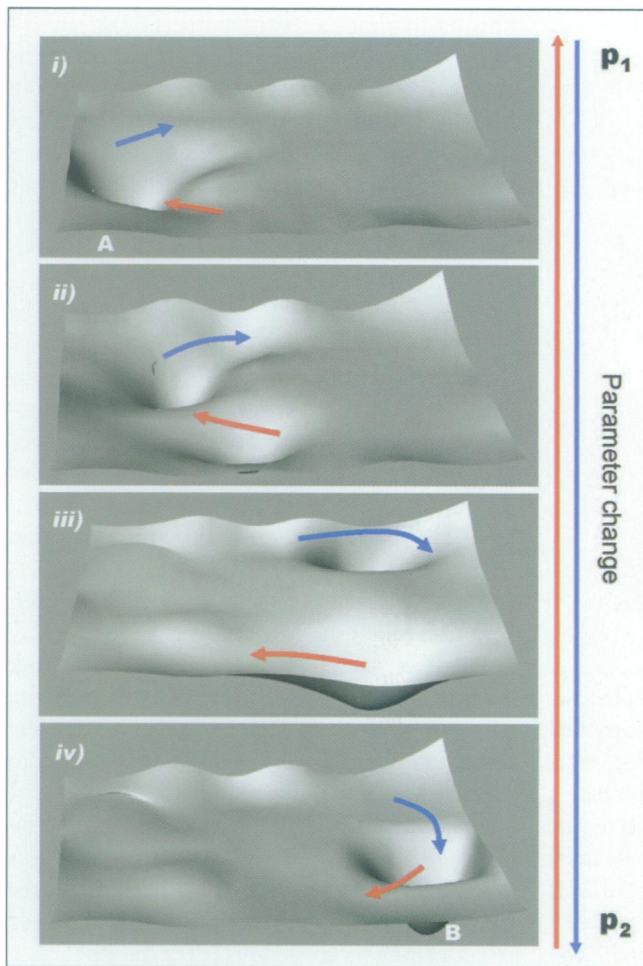
This basin characteristic matters most when a ball is subject to repeated perturbations. The shallower the slope, the slower the ball rolls back following each perturbation and the more likely a smaller subsequent perturbation will push the ball out of that basin altogether. Neubert and Caswell (1997) have characterized this aspect as the "reactivity" of the system. The other basin characteristic that will affect movement of the ball is the width. The ball can only move out of a basin if it experiences a push sufficiently large to escape the basin boundaries. Thus, the size of the perturbation to state variables affects the likelihood of escape from a basin. This has been called "ecological resilience" (Peterson *et al.* 1998).

No change in resilience is possible without modifying the model parameters. In the fishery example (Figures 2, 3, bottom), the size of perturbation required to move between states is always the same. If parameters do change (Figure 3, top), the resilience of the current state can be eroded by reducing the slope, basin width, or both. As this occurs, a new basin may form elsewhere. When the saddle between two basins is low enough, a small stochastic perturbation to state variables can cause the final shift into the new basin. Alternatively, in the absence of stochasticity, the sides of the basin can continue to erode until they disappear and a point within the new basin becomes the lowest point on the landscape close to the ball. Detecting the gradual erosion of the resilience of a particular state is critical to assessing the

vulnerability of a community or ecosystem to stochastic shocks (Scheffer *et al.* 2001). An example is the gradual addition of nutrients to shallow lakes that erodes the resilience of the clear water state (Scheffer *et al.* 1993). This gradual change makes the entire system more prone to catastrophic shifts toward an algae-dominated, turbid water state. Catastrophes arise with slight changes in spring conditions that alter the relative abundances of algae and submerged vascular plants. In both the state variable and the parameter shift cases, the definition of resilience is identical. The fundamental distinction is that from the ecosystem perspective, resilience is seen as a dynamic property of the system, while it is a static property of different states in the community perspective.

## ■ Hysteresis

Hysteresis is commonly invoked as a necessary characteristic of alternative stable states. It is usually defined and described within the context of a parameter perturbation: as a parameter is changed from one value to another, the position of the equilibrium point changes, tracing a particular trajectory across the landscape (Figure 4). When



the perturbation is relaxed and the parameter returned to its original value, hysteresis is revealed if the return trajectory of the equilibrium point differs from that adopted during its “outward” journey (Figures 4 and 5, top). Consequently, there must be multiple possible equilibrium points for some values of the perturbed parameter, and which of these states is adopted depends on the history of past perturbation. However, it is entirely possible that an equilibrium point returns along exactly the same trajectory by which it left, so hysteresis is not a necessary condition for the existence of alternative stable states. Managers and ecologists are interested in the potential for hysteresis because it implies that communities and ecosystems might be easily pushed into some configurations from which it may prove much more difficult for them to recover.

On a static landscape, as envisioned by the community perspective, there is no direct analogue of hysteresis. However, a closely related phenomenon can arise because of asymmetries in the configurations of basins of attraction. For example, it is easy to imagine how stochastic perturbations might force the ball up and over a shallow slope of the basin, whereas return is more likely down a steeper slope. Similarly, topographical asymmetry can result in equal and opposite perturbations to state variables having quite different results, depending on which

**Figure 4.** Hysteresis arises when parameter changes occur and alter the landscape upon which the ball sits. When the dynamics are governed by parameter set  $P_1$ , one stable equilibrium point (A) exists. As the parameter set is changed towards  $P_2$ , the state of the community tracks the route indicated by the blue arrows, until it finally arrives at the equilibrium point (B) indicated in panel (iv). However, if the parameters are then moved back towards  $P_2$ , the community returns via a different route, indicated by the red arrows. In panel (ii) and panel (iii), two equilibria exist, but which is adopted depends on the history of the perturbations

state the community is in when the perturbation is applied (Figure 5, bottom).

### ■ Evidence for alternative stable states

Experimentation usually probes for alternative stable states in two ways: by monitoring events after the cessation of a perturbation or the responses to reversal of a perturbation. If the new state to which the community has been moved is stable, ceasing a perturbation applied to state variables will not result in the return of the community to initial conditions. If the perturbation was too small to cause the community to escape from a locally stable state, or did not sufficiently erode the original basin of attraction, or if there are no alternative states on the global landscape, the community will return to the initial state. If the objective of an experiment is to manipulate a parameter, ceasing that manipulation and allowing the parameter to remain at its new value will result in the system remaining in the last occupied state.

Demonstration of at least two states that are each locally stable is sufficient evidence for alternative stable states. However, reverting to a former state will usually also demonstrate hysteresis; complete reversal of a perturbation will not lead to reversal of community structure because of asymmetry in most ball-in-cup “landscapes”. From a management perspective, it is critical to also demonstrate when, where, and how hysteresis will occur. In this context, it is desirable for empirical work to identify parameter changes that lead to new basins. This could aid identification of potential new states and maintenance of resilience around more desirable ones. Resilience can be augmented by managing for ecosystem characteristics that favor a ball-in-cup landscape with a large basin of attraction for the desired state. Identification of critical parameters and the effects of changing them will often involve a detailed understanding from individual behavior to species interactions in communities, as well as feedbacks to and from the abiotic components of the environment.

Ecologists and philosophers of science have not yet agreed on how different a state must be in order to be deemed truly alternate. Is a statistical difference between abundances sufficient? Alternatively, should more biological or anthropomorphic metrics be used? A pragmatic



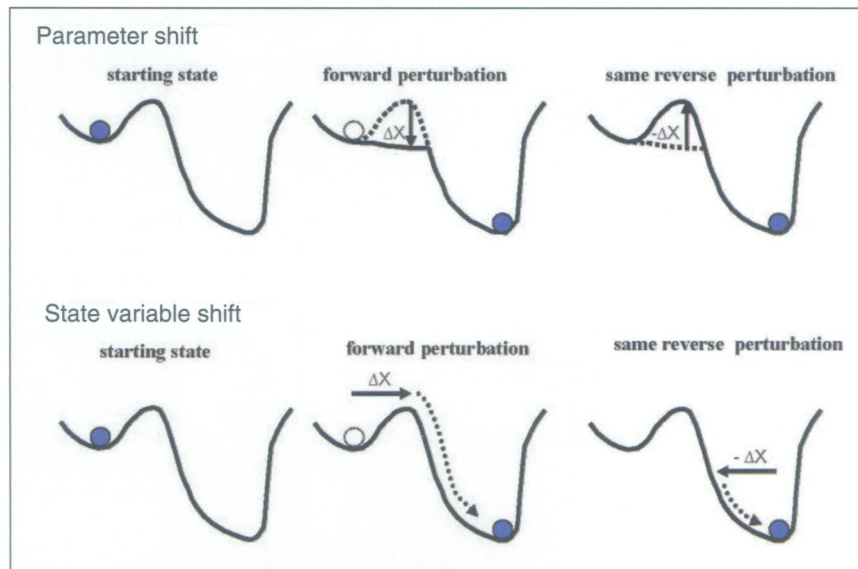
measure might be alterations to ecosystem and community function through changes to flows of energy or resources, especially those that affect humans and our management interests.

## Conclusions

The conceptual frameworks used by ecologists for alternative stable states have different histories. The state variable perturbation approach grew directly out of theoretical population ecology where stability is measured by the ability of populations to withstand direct perturbations. This continues to be the predominant mechanism of concern in community ecology where different “final” configurations of the communities represent different states resulting from community assembly and succession (Usher 1981; Robinson and Dickerson 1987; Drake 1991; Law and Morton 1993). The parameter perturbation framework also evolved from

population ecology, but quickly focused on how environment shifts would affect communities and has been adopted by ecosystem ecologists. The concern here has been with understanding how environmental processes affect parameters that determine the resilience of particular states (May 1977; Scheffer et al. 2001; Dent et al. 2002). To some extent, the current interest in community-wide effects of ecosystem engineers (Jones et al. 1997) may represent a combination of these two approaches, because the focus is on how increasing abundances of particular populations can change parameter values for the rest of the community and change interactions with environmental fluxes.

Because of gradual changes to the explanations of how communities shift from one state to another, it has sometimes become unclear to experimental ecologists how best to gather evidence supporting the existence of alternative stable states. Clearly, for managing alternative states, an understanding of resilience and hysteresis are necessary. In order to define alternative stable states in a way that is useful, and to avoid unexpected changes to the structure and function of communities, ecologists and managers need to work towards defining the boundaries of particular states and understanding the processes that confer resilience around desired states. We need to understand how changes to the environment erode resilience by changing parameters. This information should be combined with knowledge of processes related to changes in population variables, including dispersal (naturally and anthropogenically accelerated) and extinction rates. Both approaches are required to obtain a full understanding of the types of communities that



**Figure 5.** (top) Hysteresis resulting from a parameter perturbation causing landscape changes that force the ball to move to another state, but application of an equal but opposite perturbation fails to return the community to its original state. (bottom) A possible analogous characteristic of state shifts arising from a state variable perturbation. The ball is pushed forward far enough to enter a new basin, but the same size perturbation in the other direction does not return it to its original position.

will emerge with continued human alterations to ecosystems caused by such perturbations as exotic species invasions, global climate change, eutrophication, and other disruptions to the natural patterns of biotic and abiotic fluxes.

## References

- Carpenter SR, Ludwig D, and Brock WA. 1999. Management of eutrophication for lakes subject to potentially irreversible change. *Ecol Appl* 9: 751–71.
- Dent CL, Cumming GS, and Carpenter SR. 2002. Multiple states in river and lake ecosystems. *Philos T Roy Soc B* 357: 635–45.
- Drake JA. 1991. Community-assembly mechanics and the structure of an experimental species ensemble. *Am Nat* 137: 1–26.
- Dublin HT, Sinclair ARE, and McGlade J. 1990. Elephants and fire as causes of multiple stable states in the Serengeti–Mara woodlands. *J Anim Ecol* 59: 1147–64.
- Holling CS 1973. Resilience and stability of ecological systems. *Annu Rev Ecol Syst* 4: 1–24.
- Jones CG, Lawton JH, and Shachak M. 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78: 1946–57.
- Knowlton N. 1992. Thresholds and multiple stable states in coral reef community dynamics. *Am Zool* 32: 674–82.
- Law R and Morton RD. 1993. Alternative permanent states of ecological communities. *Ecology* 74: 1347–61.
- Laycock WA. 1991. Stable states and thresholds of range condition on North American rangelands: a viewpoint. *J Range Manage* 44: 427–33.
- Lewontin RC. 1969. The meaning of stability. *Brookhaven Symp Biol* 22: 13–23.
- Mack RN, Simberloff D, Lonsdale WM, et al. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol Appl* 10: 689–710.
- May RM. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of states. *Nature* 269: 471–77.
- Neubert M and Caswell H. 1997. Alternatives to resilience for

- measuring the response of ecological systems to perturbation. *Ecology* **78**: 653–65.
- Noy-Meir I. 1975. Stability of grazing systems: an application of predator–prey graphs. *J Ecol* **63**: 459–81.
- Nystrom M, Folke C, and Moberg F. 2000. Coral reef disturbance and resilience in a human-dominated environment. *Trends Ecol Evol* **15**: 413–17.
- Paine RT. 1966. Food web complexity and species diversity. *Am Nat* **100**: 65–75.
- Peterman R. 1977. A simple mechanism that causes collapsing stability regions in exploited salmonid populations. *J Fish Res Bd Can* **34**: 1130–42.
- Peterson GD, Carpenter S, and Brock WA. 2003. Model uncertainty and the management of multi-state ecosystems: a rational route to collapse. *Ecology*. In press.
- Peterson G, Allen CR, and Holling CS. 1998. Ecological resilience, biodiversity and scale. *Ecosystems* **1**: 6–18.
- Pimm SL. 1991. *The balance of nature?* Chicago: University of Chicago Press.
- Robinson JV and Dickerson JE. 1987. Does invasion sequence affect community structure? *Ecology* **68**: 587–95.
- Scheffer M, Hosper SH, Meijer ML, *et al.* 1993. Alternative equilibria in shallow lakes. *Trends Ecol Evol* **8**: 275–79.
- Scheffer M, Carpenter SR, Foley JA, *et al.* 2001. Catastrophic shifts in ecosystems. *Nature* **413**: 591–96.
- Sutherland JP. 1974. Multiple stable points in natural communities. *Am Nat* **108**: 859–73.
- Usher MB. 1981. Modelling ecological succession, with particular reference to Markovian models. *Vegetatio* **46**: 11–18.
- Walters C and Kitchell JF. 2001. Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. *Can J Fish Aquat Sci* **58**: 1–12.
- With KA, Pavuk DM, Worchuck JL, *et al.* 2002. Threshold effects of landscape structure on biological control in agroecosystems. *Ecol Appl* **12**: 52–65.
- Woolhouse MEJ, Haydon DT, Pearson A, and Kitching RP. 1996. Failure of vaccination to prevent outbreaks of foot and mouth disease. *Epidemiol Infect* **116**: 363–71.