

Hares and Tortoises: Interactions of Fast and Slow Variables in Ecosystems

Stephen R. Carpenter*¹ and Monica G. Turner²

¹*Center for Limnology, University of Wisconsin, Madison, Wisconsin 53706, USA; and* ²*Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706, USA*

Components with diverse turnover times establish the tempo of ecosystem dynamics. The gradient of turnover times within an ecosystem is more than a useful device for understanding; it has practical value as well (O'Neill and others 1986). When initiating a study of a particular ecosystem process, ecologists know that the context is set by other processes with longer turnover times, while the mechanisms derive from another set of processes with shorter turnover times. With the help of the template formed by context, process, and mechanism, the investigator formulates hypotheses, chooses approaches and methods, and prioritizes the research objectives. Skilled modelers know that the essential dynamics of a given ecosystem phenomenon can be captured by including the key processes with longer and shorter turnover times (slower or faster turnover rates). Slow processes are treated as parameters, whereas fast processes may be solved at equilibrium.

The range of turnover times in ecosystem components spans at least 12 orders of magnitude. At one extreme, the turnover times of limiting nutrients in pelagic ecosystems are less than a second; at the other, the weathering of rock formations can take millions of years. Organismic turnover times range from about a day for microbes to centuries for old-growth trees. Disparities in turnover times make ecological legacies possible. Extensively weathered landscapes may have phosphorus-limited vegetation, whereas glacially reworked land-

scapes support nitrogen-limited vegetation. Dead trees in forests support insects and birds or serve as nurse logs for extended periods of time. Large, infrequent disturbances may structure an ecosystem for centuries, and the effects of human land use can persist in ecosystems long after the activity has ceased (Turner and Dale 1998). Ecosystem dynamics are history-dependent because of the coupling of events across a range of cycling times.

"Big effects from small causes" (Ricker 1963) are among the more spectacular consequences of coupled slow-fast cycles in ecosystems. These phenomena appear as rapid, large changes in ecosystem structure that are difficult to reverse. Reversal, when it is possible, may involve a different pathway than the original shift. In African savanna, for example, woodlands are stabilized by low fire frequency, whereas grasslands are stabilized by high elephant densities (Dublin and others 1990). The reduction of elephant densities by hunting can cause grassland to shift to woodland. However, elephant browsing alone is insufficient to convert woodland to grassland. For this transition, frequent fires are necessary. The nesting of turnover times in ecosystem responses is clearly evident in trophic cascades (Carpenter and Kitchell 1993). Large cohorts of relatively long-lived fishes structure the food web for the lifetime of the cohort, and transitions among cohorts can have sharp impacts on more rapidly cycling components of the ecosystem. The community structure of zooplankton and phytoplankton, ecosystem production and respiration, and limitation of primary producers by phosphorus vs nitrogen depend on the trophic ecology of the dominant fishes.

The vast range of turnover times in ecosystems

leads to the paradox of predictability. On the one hand, it is possible to build predictive ecosystem models for a given time horizon. To make the modeling problem tractable, detail is suppressed by running fast variables to equilibrium. Slower variables are treated as parameters. On the other hand, the only constant feature of ecosystems is change (Botkin 1990). Constraints and context (and hence parameters) can change qualitatively, essentially changing the rules of the game. There is no balance of nature; endless change and the ongoing creation of novelty are the rule. Thus, no single ecosystem model can make useful predictions for all time horizons. Predictive models are specific to particular time scales. It is particularly difficult to predict the fate of ecosystems over evolutionary time. Slow variables create the arena in which evolution occurs; in Hutchinson's (1965) evocative phrase, they are the ecological theater for the evolutionary play. But some slow variables are themselves subject to evolutionary change. Thus, the feedbacks between ecology and evolution are an important frontier for building a predictive science of ecosystems. A more immediate concern is the current decline in biodiversity and its effects on ecosystem processes. In addition to any direct impacts of biodiversity decline, the loss of biotic variability diminishes potential evolutionary change, with implications for future ecosystem patterns and processes.

The multiplicity of turnover times in ecosystems creates a fundamental problem that hampers the integration of ecological and social sciences. Ecological models are usually built to help us understand the present by examining the past. Rival models are compared on the basis of their capacity to explain the sequence of events that led to current conditions. Models that are successful in explaining the extant data may then be used to forecast future scenarios. Social science, on the other hand, builds models to help explain the behavior of large numbers of individuals, each engaged in forward-looking behavior. Each of these individuals uses experience and communication to learn, and acts upon individualistic expectations about the future of a world they are all co-creating. However, social context can also change qualitatively—as witnessed, for example, by the emergence of environmentalism or the collapse of the Russian economy. The multiple time scales and slow variables of ecology have profound implications for forward-looking human behavior toward the environment.

It is easy to see how failures of foresight, explainable in part by insufficient knowledge of slow variables, can lead to environmental collapse. The history of Easter Island is a salient example (Redman 1999).

The Easter Islanders felled large old-growth trees to build sea-going canoes used for harvesting porpoises, a staple food. The logs were also used to transport and erect the statues for which Easter Island is famous. Deforestation caused soils to erode and degrade, preventing forest regrowth and diminishing the fleet of canoes needed to harvest porpoises. People turned to seabirds and coastal animals for food, decimating these populations. With no wood to build houses, the declining human population, moved into caves. Over a period of several hundred years, the Easter Island civilization underwent a massive, inexorable ecological and social decline. How could this intelligent, creative group of people be caught in such a collapse? If they had understood weathering, soil dynamics, and forest regeneration, could they have chosen a more sustainable path?

While it is tempting to draw analogies between Easter Island and the world's environmental predicament, we must recognize that current issues in ecosystem management differ in many ways. Nevertheless, a lack of understanding of slow ecological variables, and the concomitant poor integration of such variables into policy choice, is one characteristic that we apparently share with the Easter Islanders. The practice of discounting, for example, limits the time horizons of economic decisions to around 30 years (Heal 1997). Although a 30-year span may seem farsighted in human terms, it is severely myopic with respect to slow ecological variables. A better understanding of slow ecological variables and their links to faster variables critical for human welfare should help to correct this myopia.

For this issue of *Ecosystems*, we have invited a number of distinguished ecologists from diverse subdisciplines to write about linkages of slow and fast variables. Levin discusses the ubiquity of multiscale dynamics in ecosystems with respect to biodiversity change and the mismatches between human and ecological time scales. Rinaldi and Scheffer offer a graphical approach for understanding the mathematical basis of changes caused by the interaction of slow and fast variables. Hotchkiss, Vitousek, Chadwick, and Price describe the interactions of climate change and soil development over time scales of a few thousand to a few million years. Camill and Clark examine the dynamics of landscapes that may be dominated by peatlands or woodlands, depending on feedbacks of vegetation and disturbance that are difficult to predict. Kitchell and others describe the nested turnover rates present in the Lake Superior food web and explore the ways in which they have changed due to the introduction of exotic salmonids and more intensive fishing. Reed-Andersen, Carpenter, and Lath-

rop present a model of phosphorus flow in a watershed–lake system and show how lake dynamics are controlled by relatively slow soil processes.

We hope that these papers establish a theme that will be developed more fully in the pages of this journal over the next few years. Interactions across time scales are responsible for some of the most fascinating ecological phenomena, as well as principles that help to unify ecosystem ecology. In addition, slow–fast interactions play a fundamental role in prediction. Promoting a better understanding of interactions across slow and fast time scales is one of the most important contributions that ecologists can make to wise environmental policy.

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