

COPYRIGHT NOTICE:

Seth R. Reice: The Silver Lining

is published by Princeton University Press and copyrighted, © 2001, by Princeton University Press. All rights reserved. No part of this book may be reproduced in any form by any electronic or mechanical means (including photocopying, recording, or information storage and retrieval) without permission in writing from the publisher, except for reading and browsing via the World Wide Web. Users are not permitted to mount this file on any network servers.

For COURSE PACK and other PERMISSIONS, refer to entry on previous page. For more information, send e-mail to permissions@pupress.princeton.edu

*Chapter 1 The More Things Change,
the More They Stay the Same*

Nature is an endless combination
and repetition of a very few laws. She
hums the old well-known air through
innumerable variations.

—Ralph Waldo Emerson, “History,” in
Essays (First Series, 1841)

*Yellowstone National Park, August 20, 1988:
“Black Saturday”*

It was very hot and dry. Winds had been blowing from the west for weeks. These hot winds sucked the moisture from the leaves, from the trees, from the Earth itself. An ancient 100-foot-tall Lodgepole Pine bent with the force of the wind. Its sap grew sticky and began blistering. The once green needles were drying, falling, and forming a deep brown carpet on the ground. Overhead, a dark cloud, a thunderhead, blotted out the sun. Instantaneously, the air cooled by a few degrees and everything was still: even the birds were silent. Suddenly, there was a

brilliant flash of light, then a roar of thunder. A lightning bolt raked the old Lodgepole Pine and its sap burst into flame. The flame was fanned by the wind and the tree blazed. The carpet caught fire. The flames were whipped by the wind. The fire spread to the old pine's neighbors. Dry trees exploded as the wall of heat reached them, sending burning debris in every direction, consuming the tons of fuel that had built up over decades. The fire rushed along valleys and up to the ridgetops, creating its own wind. Firestorm!

The fires of 1988 raged for days. They devoured 989,000 acres of America's first and most revered national park, Yellowstone. Millions of trees were destroyed. In a nightmarish scene right out of *Bambi*, the mammals fled before the flames. The fire was so intense and spread so rapidly that the young and very old, the sick and the slow could not run fast enough to save themselves. Insects, the most abundant animal life in the forest, had no chance to escape, and millions upon millions were incinerated. Yet, the more mobile animals, the birds and mammals, did survive. The number killed was amazingly low. Night after night, the TV news was filled with pictures of flames leaping hundreds of feet into the air. Images of charred forest were seared into the American consciousness. The message was that this was a terrible "National Tragedy," a loss of America's national treasure. The public, led by the TV news media, looked for someone to blame. "Who was the villain who stole our national park from us?" The implication was

that someone or something evil was among us. As Pogo said: “We have seen the enemy and they are us.”

This fire was a natural disaster, but was it really a tragedy? From our human perspective it may seem to be a catastrophe, but let’s look at the fire from the perspective of the forest ecosystem. Is fire solely evil, or is fire actually part of the natural life cycle of the forest? Can it be seen as a positive force? Was the Yellowstone ecosystem more in harmony with its environment before or after the fire?

Disturbances help generate the mosaic makeup of the habitat. A fire burns out a patch of forest and opens it up to sunlight. Now, small plants, which had been suppressed by the shade of the trees, can thrive, and then a meadow can develop. Every organism is uniquely adapted to a particular type of habitat and a diverse array of habitats can support many more species than a uniform habitat. A variety of habitat patches, in turn, supports a diversity of species and communities. This biodiversity is the foundation of the natural ecosystem services upon which all life depends. Contrary to common thinking, disturbances are not bad, but rather they are valuable—indeed, they are essential for healthy ecosystems. Even the Yellowstone fires brought some important benefits. They created beautiful and diverse meadows of wildflowers and revitalized the forests. The nature of nature is change.

All disturbances are not alike. Some, like wholesale human alterations of natural systems (e.g., dams that

“permanently” flood whole river valleys), can be devastating to their ecosystems. In this book, I will address the issues of scale and intensity of disturbances and their effects. Then, armed with these insights, I will examine changes in ecosystem management, and in our own lives, that are necessary if we are to live in harmony with nature’s changing rhythms.

How Do Ecosystems Really Work?

The idea that a forest fire is a disaster for the forest is grounded in a long ecological tradition. For a century, we have assumed that constancy is the natural order of things. This basic idea is called an *equilibrium model*. This model presents an entire structure of thinking about nature, a paradigm. In this view, communities and ecosystems are supposed to remain constant. Is this a realistic view? Do communities really stay the same or are they constantly, naturally changing?

A community is the collection of all the organisms that live together in a place. It is composed of all of the animals, plants, fungi, bacteria, and viruses in a known area. We can thus refer to the “forest community” of Yellowstone National Park. As we descend through the Grand Canyon of the Yellowstone to the Yellowstone River, we will find that the community of the canyon walls is different from the community of the high plateau, and the community of the river is even more different. The plateau has Lodgepole Pines, caribou, deer,

wolves, voles, and grasses. In the Yellowstone River, the terrestrial plateau community is replaced by something completely distinct. The river community is composed of aquatic algae and reeds, mayflies, dragonflies, and fish. Most people, and all ecologists, recognize that communities change in response to changes in climate and environment.

In contrast, our attitudes about how communities respond to variations over time have been very different. We generally expect things to be constant, to continue in the same way, making a tacit assumption that nature is unchanging, constant, forever. We may want it to be true, but that's not the way nature works. Change is the only constant.

My wife and I recently discovered a waterfall in western North Carolina called Catawba Falls. We loved the sight and sound of the water's 150-foot plunge, with its multiple chutes and torrents. The trees alongside the falls were tall and erect. Spruces and firs made a green cloak for the silver, dancing cascade. A large dead log spanned the stream at the base of the falls, at the perfect height to make a bench for us to sit on and soak up the beauty of the scene. We went back to the same spot a year later. We found that many trees had been blown down in a storm and lay strewn like pickup sticks crisscrossing the formerly unblemished cascade. I was disappointed: my waterfall had changed and our "bench" was gone. I felt a sense of loss. Yet, as I stood watching the falls, the altered beauty of the scene slowly transformed my disappointment into a sense of wonder and

admiration. This new and revised edition of Catawba Falls was just as beautiful, just as awe inspiring as the previous edition. And the former edition was not the first edition, either. These falls have been transforming for millennia.

This changing waterfall is the life-sustaining environment for the host of aquatic insects and mosses that live in that part of the river. As you look at any river or stream, you can see tremendous variety in the flow of the water. In the midst (and the mist) of Catawba Falls are hundreds of different flow rates. In some places the water is rushing, churning, and frothing into whitewater (the white color is caused by the air bubbles trapped within the water), yet only a meter away the water is perfectly still. The rushing water was diverted by a boulder. Sheltered by the giant rock, a pool of quiet water was formed. These different places, or microhabitats, are filled with different groups of organisms, each adapted through natural selection to live only there. In the fast-flowing chutes are aquatic mosses with net-spinning caddisflies clinging to them. The water carries food to their nets for them to eat. In slightly faster water, blackfly larvae sit, clinging to scoured boulders, with their filtering fans projected up into the flow to catch their dinner. In the quiescent pools, burrowing mayflies feed on the animals deposited in the sediments. At the surface, water striders perch delicately balanced on the surface film, hunting for smaller terrestrial insects trapped on the water's surface. Each of these animals is well suited ("adapted") to its own microhabitat, its own special

place in the river. Where the confluence of all their requisite environmental factors occurs, that's where you'll find them. That is what ecologists call their *physical niche*. I use "niche" as in ordinary common usage; it is an organism's place or role in nature.

However, microhabitats and environments change. If a tree falls in the forest, and lands in the river, it will change all of the flow patterns near it. What was once a fast reach can be stilled. As the water seeks a downstream path around the log, a new chute will form. The microhabitats have all changed, and the community must change, too. What was once an excellent blackfly habitat is no longer suitable for the flies. The animals have to move to survive. Some won't make it. Some were crushed when the tree fell on them. Some will get stranded and die. Some will get up and go. Change is endless and has consequences for all living things. It is as obvious as day follows night and the change of the seasons. What is rare is constancy.

Yet, people are drawn to an image of nature—a model—which assumes a constant environment. We can justify this obviously false assumption because we are overwhelmed by nature's complexity. An ecologist, working even in a rather simple community, must consider dozens of species, all interacting with one another. Some compete with each other for food, while some are food for each other. Just mapping out the feeding relationships, the food web (who eats whom), among the species in a community is a daunting task. Because in all communities, as in Catawba Falls, environmental

change (e.g., from a simple treefall to a major disturbance) can rearrange all of the relationships, it is not surprising that ecologists have sought a way of simplifying the complexity.

Ecologists have often assumed that the environment is constant. The equilibrium model starts like old school math proofs: “All things being equal.” We know now—as we suspected back in high school—that all things are never really quite equal. Ecologists have built growth, change, and evolution into the equilibrium model of the community. The process of community change is called *succession*. Succession is viewed as an orderly, sequential process, and its endpoint, the culmination, is called the *climax community*. Each stage, however transitory, can be treated as an intact community. The climax community is the ultimate, the Platonic ideal community for that environment, “the way things are supposed to be.” This traditional, orderly view of nature requires that you have a constant environment to allow the community to reach the climax stage, that is, to equilibrate. This ideal climax community can become a reality only if the environment is actually constant. If the environment is in perpetual flux, then the climax community becomes impossible.

The traditional (equilibrium) perspective also dictates how one views the forces that structure natural communities. If you believe that the proper state of nature is to be in balance, then natural disturbances can be dismissed as aberrant. In contrast, from the newer,

nonequilibrium point of view, disturbances are very important agents for promoting biological diversity.

To understand this dilemma, we need a few clear definitions. *Community structure* is the term that describes how the community of organisms of a given area (a stream reach or a forest tract) is organized. The key idea in community structure is biodiversity. The most basic question about the structure of any community is: "How many different species are there in the community?" To answer that question, we sample the community and count up the different species, a measure called the *species richness*. If you list all the names of all the species in the community, species richness is the tally at the bottom of the list.

In practice, this species list is abbreviated. In many communities we don't know everyone's name. There are thousands of species of microarthropods (e.g., mites and springtails) in the soil, too many to identify. The number of species of bacteria in soil or in water are myriad and extremely difficult to identify. So, in most analyses of the community, only the well-known and accessible groups are identified and tallied. For example in the Yellowstone mountain forests there are only eight common species of trees, about sixty-five species of birds, and about twenty-five species of common mammals. However, we have hardly any idea how many species of bacteria there are. Sometimes, people refer to local groups of similar species as if they were whole communities, for example, the tree community or the bird

community of a forest, when the whole living forest (trees and shrubs, birds and bugs) is the community.

Biodiversity is more than species richness. It includes, among other things, the differences among individuals in populations, the differences among populations, and the relative abundance (or distribution) of individuals among species in a community (the evenness). For now, let's stick to species richness as our primary measure of biodiversity. Communities with higher species richness are more diverse than communities with fewer species. The high biodiversity of the macrobenthic invertebrates (macro = big; benthic = bottom dwelling; invertebrates = animals without backbones, mostly insects) of streams stands in striking contrast to the relative paucity of macrobenthic species in ponds. Ponds have fifteen to thirty species, while streams have nearly ten times as many. Why should neighboring systems with similar, even evolutionarily related groups of organisms (with overlapping families and genera), have such different community structures? What can explain these dramatic differences in biodiversity among similar communities? Understanding the underlying causes of differences in biodiversity is the central question of community ecology. As the great ecologist G. Evelyn Hutchinson asked in 1959, "Why are there so many kinds of animals?" The same question can be asked about plants as well. We are still striving to answer this most fundamental question. Let me give you a preview of where I am heading: to show that disturbance is emerging as a key force in creating and maintaining biodiversity.

What Determines Community Structure?

Historically, ecologists have been divided about what factors are most responsible for determining the structure of the community. The debate began early in the 1900s, when the basic issue was (and still is) whether the most important factors are biological or environmental. Are communities structured by the interactions among the organisms (e.g., competition, predation, etc.), or does the physical and chemical environment set the array of organisms? At its simplest level, the community is composed of the organisms that are able to live there. We don't find cacti in the rain forest, or tropical mahogany trees in the Rocky Mountains. One view is that the environment sets the community composition, meaning its membership and the relative abundance of its members. The presence or absence of a given organism in a given place is based on the ability of the organism to get there, to survive there, and to reproduce there. The physical and chemical environment sets the range of conditions for colonization, survival, growth, and reproduction of all possible residents of the community.

However, for any environment, the membership in the community is not fixed. There are far more potential species that can live there than are actually found there. Consider your choices when you plant your garden. When you go to the garden shop or the farmers' market, you can choose from a wide selection of annual plants. You can plant your garden with petunias (many varieties) or marigolds (all sizes and shapes and colors).

You make your selection for your garden from among dozens of species and hundreds of varieties. You are the selective agent, determining the species composition of your garden, the structure of the community of annual plants. Charles Darwin, in the *Origin of Species*, taught us that there were more individuals and varieties of a species than could survive and reproduce. Similarly, there are more species than can fit into any environment. He offered the idea of natural selection (or survival of the fittest) as a general explanation of the species that we see. Community structure follows the same pattern: it results from sorting out the various potential occupants of an area. How does this work in nature?

Charles S. Elton, one of the first great ecologists of the twentieth century, emphasized the role of interspecific interactions in determining the “limited membership” of the community. Interspecific interactions refer to the whole range of contacts, such as competition and predation, among different species. Elton did a clever thing. He examined the published surveys of fifty-one animal communities from all over the globe and from twenty-one different habitat types. He tallied the number of genera (groups of closely related species) and the number of species in each of the fifty-one communities. (This analysis makes the typical assumption that members of the same genus are more ecologically similar than species from different genera, which is usually a safe bet.) Then Elton computed the average number of species per genus in each community. He found that in his fifty-one surveys there were, on average, only 1.38

species per genus in each of these communities, or just a fraction more than one per genus. Then he compared this number to comprehensive taxonomic lists of species per genus in several well-studied groups across a wide variety of habitat types and communities (notably insects from all habitats in the United Kingdom). He found that, on average, across a range of communities, there were 4.23 species per genus.

Elton concluded that any given habitat has far fewer species per genus than are available in the larger world. Membership in the community was limited to about one species per genus, so only a small fraction of the total number of species that could potentially colonize an area actually coexists there. Why should this be? Elton's argument was that the interactions among the species, especially competition, determine community structure. He argued that these competitive interactions should be more intense among the species of the same genus, since they are morphologically and ecologically more similar than representatives of different genera. Elton's results can be generalized to conclude that biotic interactions determine community structure and biodiversity. Competing species contest each bit of turf. Predators ("red of tooth and claw") stalk their prey and eat them. Elton viewed the environment merely as the backdrop against which the real drama of the interactions among species is played out.

In this scenario, the environment is viewed as static and passive. If it varies at all, then the impact of the variation is considered trivial compared to the conse-

quences of the interactions among species. The presumption of the preeminence of biotic interactions is not so strange, since ecologists are, after all, people. We are all drawn to the dramatic moment. Scenes of animals struggling together, fighting, or preying on each other is the main attraction of nature programming on television. Competition and predation attract ecologists, too. Mutualism, the study of how organisms help and benefit one another, gets very little press. Studies of mutualism account for less than one percent of the number of studies on either competition or predation.

The long-held assumption of environmental constancy is also understandable, since communities superficially appear to be constant and stable. The trees that were there yesterday are generally still there today. Yesterday's weather is a fine predictor of today's weather. Elton helped set the stage for ecologists to minimize the influence of the environment on community structure.

This equilibrium model of community structure is based on the interactions among species, and each species' relative strengths and abilities. Since the outcome is predictable, determined by the players, their characteristics, and their relative abundances, it is called a *deterministic model*. Much of traditional ecological theory is structured this way. Mathematical models predict the numbers of individuals of the competing species or the predators and their prey, given the species, their characteristics, and their relative abundances. Once you start building ecological models, which predict the future community structure, the models get very complex very

quickly. In order to limit the complexity of these models, the first simplifying assumption that is made is to assume that the environment is not changing. We solve the equations for that moment when the abundances of all the individuals of each species are neither growing nor declining. That is, we solve them at equilibrium. This body of theory has structured ecologists' worldview for nearly a century. It can be called the *equilibrium paradigm*. It is the core concept organizing how nature is viewed by many people, often called the "balance of nature." The equilibrium paradigm has subtly guided how we manage our environment. It is the underpinning of the Smokey Bear syndrome of suppressing forest fires and is the conceptual framework behind the construction of dams for flood control. In short, it serves as a guiding principle of how the world is "supposed to be." It is loaded with value judgments, for example, that climax communities are good and disturbed communities are less desirable or somehow spoiled. However, as Bob Dylan sang, "The times they are a changing."

A new paradigm about how nature works has been emerging. Over the last two decades, an alternative worldview to the equilibrium model has gained strength in ecology. This is the concept of nonequilibrium dynamics of communities and is at the core of disturbance theory. In this view, communities are commonly disturbed, whether by fire, storm, drought, flood, or earthquake. Disturbance theory takes into account the changes that "disasters," both great and small, bring about in the natural world. Disturbances create new

habitats and new opportunities for species to thrive, enhancing biodiversity. In this new paradigm, the normal state of the community can be thought of as recovering from the last disturbance, with the only constant being change. The goal of this book is to explore the meaning and consequences of this paradigm shift. If the environment is not constant, and if nature is not in balance, then where do we stand? How do we approach a world that is not now, nor ever will be, in equilibrium? The crux of this debate is whether interactions between species or forces of the environment (disturbances in particular) control community structure.

***Nonequilibrium Determinants of Community Structure:
The New Paradigm***

The realization that real environments are constantly changing has renewed the fundamental debate in ecology over whether natural systems are dominated by the interactions among species or, alternatively, by environmental fluctuations and perturbations. In the 1950s, the big ecological debate was over how single-species populations were regulated, that is, why population sizes tend to stay within seemingly proscribed bounds. Now the focus is on what determines the structure of entire communities.

In the late 1960s and 1970s, the equilibrium model of community dynamics was crystallized by a group of ecologists led by Robert MacArthur. MacArthur and

E. O. Wilson's *The Theory of Island Biogeography* (coincidentally also published by Princeton University Press) is the epitome of an equilibrium model of community structure. They argued that the species richness on an island is controlled by the trade-off between immigration and extinction; the only role for the environment is to provide a set of resources. The only place the environment was included was as the size of the island. The environment was considered only a static "fruit bowl" of resources. Neither variation in space or time nor variation in the abundance or availability of resources was considered. The model argued for the absolute primacy of species interactions. In the theory, the solution to the number of species on an island is obtained when immigration and extinction balance exactly—when they are at equilibrium. It is noteworthy that this model of island biogeography still is widely used to predict the optimum size of nature reserves (such as national parks) to preserve biodiversity.

As is clear by now, equilibrium models presume a constant environment. Such models exclude disturbances, and any other environmental fluctuations. In this view, it is a simple step to conclude that biotic interactions are the key determinants of community structure. Under equilibrium conditions, the community is the direct result of the competitive and predator-prey relationships among and between species. The environment is viewed as predictable, regular, and constant.

In all of these equilibrium ideas, the environment is the backdrop, not the actor. It is as if the waterfall at

Catawba Falls were just so much scenery and the real actors were the animals and plants and bacteria and fungi, living on and among the rocks. What's missing here is the understanding that the species only exist there because the waterfall suits them and the flow meets their needs, creating the conditions for successful survival and reproduction. If a drought dried up the Catawba River, nearly all the animals would die, and species richness would nosedive. In the period between disturbances, significant competition or predation may well be occurring, so that a quasi-equilibrium begins to become established. Yet when the next storm-driven flood hits, all bets are off. Surviving the flood becomes everyone's first and only priority.

Reconsider the Yellowstone fires. Walt Disney had it right in *Bambi*. The environment was ablaze. It was the fire that made the animals run. In the film, we saw predators and prey all mixed together, fleeing before the flames. Foxes and rabbits ran away from the heat, together. When the great fire sweeps through the forest, no one stops to eat; all notions of competition and predation are gone. Survival is the order of the day. Disturbances change all the rules. After the fires cooled, the entire community of Yellowstone was restructured. The environment was anything but passive. It played a pivotal role, as it always does. This applies not only in Yellowstone, but everywhere.

As the Catawba Falls and Yellowstone examples illustrate, the concept of a natural ecosystem at equilibrium

is only an ideal, a vision of a world where species interact with one another, unconstrained by pressures from their environment. It is also a way by which ecologists, as biologists, have elevated the importance of biological interactions as determinants of community structure. Note that disturbance theory does not ignore competition and predation as important factors in community structure; it just puts them in perspective with the other vital forces of nature.

Are disturbances common and important enough to finally dethrone the equilibrium paradigm? They certainly are. Disturbances are common in all ecosystems. Table 1.1 gives a listing of disturbance frequency and predictability in natural ecosystems pointing out the major disturbance types that impact the world's ecosystems. It is not exhaustive, and you may be able to think of others. Some of these disturbances will be discussed in detail in chapter 2.

A false friend has fostered our attitudes toward disturbances. Smokey Bear was a National Forest Service creation born of equilibrium thinking about community dynamics and ecosystem management. Smokey taught generations of people that forest fires were bad, and that "Only *you* can prevent forest fires!" However, Smokey got us into trouble. In Yellowstone, management policy was to suppress all forest fires. Without fire suppression, there would have been many smaller fires over time, reducing the fuel load (the dead trees and branches) and lowering the density of trees. Since

TABLE 1.1
Disturbance Frequency and Predictability in Natural Ecosystems

<i>Ecosystem Type</i>	<i>Disturbance</i>	<i>Frequency*</i>	<i>Predictability</i>
TERRESTRIAL			
Deciduous forest	Fire	1/40–200 years	None
	Windstorm	1/10–25 years	None
	Insect defoliation	Rare	None
Coniferous forest	Fire	1/20–40 years	Moderate
	Windstorm	1/10–25 years	None
	Insect defoliation	Rare	None
Rain forests			
Tropical	Windthrow	Frequent	None
	Fire	Frequent	None
Temperate	Fire	1/200–500 years	None
	Storms	1/50–100 years	None
Chaparral	Fire	1/15–25 years	High
Grasslands	Fire	1/5–10 years	Moderate
Desert	Frost	1/50–200 years	None
Pocosins	Fire	1/10–25 years	None
FRESHWATER			
Streams and rivers	Floods		
	Spring snowmelt	Annual	High
	Storms	0–15/year	None
	Drying up	0–2/year	Moderate to high
	Freezing/Anchor	0–2/year	High
Ice			
Lakes	Storms	0–4/year	None
	Freezing (Winter Kill)	0–1/year	High
Ponds	Freezing	0–1/year	High
	Drying up	0–2/year	Low to high

TABLE 1.1 (cont.)

<i>Ecosystem Type</i>	<i>Disturbance</i>	<i>Frequency*</i>	<i>Predictability</i>
MARINE			
Intertidal zone	Hurricanes	1/20 years	Low
Beaches	Tornadoes	1/20 years	Low
	Log damage	Annual	Low
Pelagic zone	Storms, hurricanes	Aperiodic	Low
Deep-sea benthos	Storms, hurricanes	Aperiodic	Low
	Submarine volcanoes	Aperiodic	Low
	Whale carcasses	Aperiodic	Low

* Number of disturbances/unit time

smaller fires had been suppressed for decades, the fuel load in Yellowstone in 1988 was immense, and as a result the 1988 fires were devastating. The timing of the fires was unpredictable, although the conditions that allowed the fire to start had been building for generations. The destruction wrought by the 1988 fires would have been far more limited if previous natural fire disturbances had run their course.

What was the real threat to Yellowstone, then? Strange as it may seem, it was not the fires. The fires opened up the forest and allowed many trees to germinate for the first time in decades. The fires cleared out the deep litter, exposing soils to sunlight and allowing many wild-



Figure 1.1 The Yellowstone fires of 1988 created a patchy mosaic of regrown and unburned areas. (Photo by S. R. Reice, 1998)

flowers to bloom and reproduce. The fires re-created the patchy mosaic landscape of burned and unburned stands, of meadows among the forests (see fig. 1.1). The real threat to Yellowstone was the fire suppression policies of the National Park Service, which created the conditions for this conflagration in the first place. This may seem counterintuitive, but this book will argue that the absence of disturbance, not the disturbance itself, is the real danger. Communities and ecosystems require disturbances for their very survival. In this book we will take a closer look at the positive role of disturbances in nature and show that they are vital to maintaining the integrity and health of natural ecosystems, upon which all

life depends. This is the silver lining in the storm cloud we must learn to seek out and value.

Further Reading

- Botkin, D. B. 1995. *Our Natural History: The Lessons of Lewis and Clark*. New York: Grosset/Putnam.
- Darwin, C. 1988 [1859]. *On the Origin of Species*. New York: New York University Press.
- Elton, C. S. 2000 [1927]. *The Ecology of Invasions by Animals and Plants*. Chicago: University of Chicago Press.
- MacArthur, R. and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.
- Quammen, D. 1997. *The Song of the Dodo: Island Biogeography in an Age of Extinctions*. New York: Touchstone Books.