

## CHAPTER ONE

# The Balance of Nature: What Is It and Why Care?

## 1.1 BALANCING A NOISY SYSTEM

Each spring as the sun begins to strengthen again, I walk the trail that surrounds our house. Unfailingly, I am met by the steady green carpet of plants, the chorus of songbirds, the scurrying of squirrels, and the occasional hawk presiding over the forest floor. On any spring night I may find myself awakened by the unmistakable cry of coyotes to find that the night is alive with the peeping and buzzing of frogs and insects. At a very rough observational level, the main groups of players that make up this localized food web (i.e., plants, herbivores, predators) appear to be consistently present from year to year. If these observations are correct, we can say that this system is stable in the sense that the species assemblage persists intact over ecological time scales. We as casual observers have grown to expect this consistency. Much of this book is concerned with this aspect of stability, often called persistence in the ecological literature. I would argue that this persistence-based notion of stability has fascinated humans throughout history precisely because they have casually observed this pattern for such a long time and depended upon it for their survival.

Despite the pleasing notion that the world's ecosystems harbor a great steadiness or a perfect balance, the more detailed observer is uncomfortable with this statement. Most biologists today would in fact be quick to argue that if we can expect anything in ecological systems, we can expect change (Levin, 2003). As an example, if we look closer at the lush green carpet of plants, we may find there are far more goldenrods this year than last year. Upon further inspection we may also find that last year's summer storms, more frequent than normal, knocked down many large silver maples, leaving behind forest gaps and impressive new understory growth. Thus, the level below the apparent consistency harbors considerable variation within the plant species themselves. This same phenomenon is true for animals. Some years may see enormous

insect outbreaks, followed several years later by the increased presence of insectivorous species that during breeding capitalized on the pulse of abundant prey. Simply put, ecosystems are dynamic entities, waxing and waning at a variety of temporal and spatial scales. As we focus in on them, this beautiful, endless, dynamic mosaic appears to be everywhere, and yet, amazingly, the net result at a more macroscopic level (e.g., that of the casual walking observer) is a complex system that harbors some degree of stasis (i.e., a similar assemblage).

There is something calming to the human mind about this consistency in species assemblage, and there is also something unsettling when things do change dramatically in an ecosystem. In her 1962 book, *Silent Spring*, Rachel Carson (1962) documented the loss of birds to DDT. “Silent spring” referred to the fact that our human expectation of nature (i.e., the sound of birds in spring) had been abruptly altered. Although many challenged her scientific assertions, the book and its ideas endured, trumpeting in the modern environmental movement. Carson’s ideas were tangible in that both scientists and lay people were able to observe the loss of a major group of species as a result of a human activity. In a sense, the consistency of our forests, our parks, and our backyards had been threatened.

This loose, persistence-based definition of stability is at the heart of most of the more mathematically rigorous definitions that ecologists have historically employed. Variability, or the coefficient of variation, CV (variation/mean), is a common measure of stability in both experiments and recent theory. The logical argument behind this metric of stability is that the more variable a species’ population dynamics are, the more likely that species is to attain dangerously low densities. High variability, all else equal, therefore implies a greater risk of local extinction.

Similarly, resilience, so common to many theoretical equilibrium studies, was argued to be an appropriate measure of stability because a resilient population rapidly returned to near equilibrium densities after a perturbation (Pimm et al., 1991). Thus, if a species is perturbed to low densities, a rapid return time to equilibrium means that this same species quickly rises away from near-zero densities and, in doing so, avoids the threat of local extinction. A slowly returning species, on the other hand, is more likely to be subjected to the vagaries of nature’s noisy world for a much greater time and so has a significantly higher risk of extinction. So even mathematically based definitions, which assume equilibrium, are in a real sense attempting to speak to the consistency of a species assemblage in a variable world. Clearly though, theory needs to further explore this casual assumption, and many researchers have started to look more rigorously at the fascinating interaction between environmental

variability and population stability [e.g., see Ives and Carpenter (2007); Ives et al. (2008)].

There is a long history of ecologists seeking to understand what factors contribute to the stability of ecological communities. Early ecologists pointed to the role diversity plays in stability. This idea remains to some degree today, but most researchers now seek a more explicit understanding of the mechanisms behind stability. It seems likely that if diversity does truly correlate with stability, this is not because of diversity per se but rather because of some fundamental structures embedded in diversity itself (May, 1974b). This biological structure can be at the population scale (e.g., age structure), the community scale (e.g., food web structure), or the ecosystem scale (e.g., size of detrital compartment). The task remains to uncover these fundamental natural structures—a difficult task for sure because the balancing act of nature couples interactions over an enormous range of spatial scales. At local scales (e.g., 1-m<sup>2</sup> plots), nature's balance seems amiss, with organisms varying in number in both space and time. At large enough scales, local variance may in fact cancel itself out to become a flatlined equilibrium process. Local variability can beget regional stability.

Along these lines and within a single trophic level context, Tilman and others (Tilman et al., 1998; Doak et al., 1998) have recognized that species level variation, under various sets of conditions, can ultimately lead to relatively constant competitive communities. Variation at the plant population level, for example, can sum to give a relatively constant plant community as long as not all species increase or decrease together. These researchers, in a sense, changed the stability question by embracing population level variation in density and focusing on the implications of population variability for whole-plant community stability. Once aware of this complex mosaic of spatial and temporal variance, it becomes interesting to consider how this variation itself may play a role in the stability and sustainability of ecosystems. As such, variation in space and/or time may be considered a form of natural structure that organisms have adapted to thrive within. This book will argue frequently that this may indeed be the case. I will also further argue that most human impacts tend to restructure the landscape with broad, homogenizing strokes. Species loss aside, such actions may remove the intricate, detailed spatial and temporal structure that underlies most pristine ecosystems.

This precise aspect of an ecosystem—the multilayered complex of interacting organisms that transcends small to large spatial and temporal scales—is also the toughest part to study. One can ignore interactions by focusing on an isolated box (e.g., population ecology), yet these scale-dependent connections cannot be easily ignored for large ecological problems like ecosystem stability

and function. When ecologists, for example, purposefully separate this scale dependency in controlled microcosm experiments, such as simplified and spatially restricted laboratory universes, these mini-ecosystems often fail rapidly after a few violent oscillations in population dynamics. In aquatic microcosms these spatially simplified worlds almost always end up dominated by bacteria. This experimental result may speak to the notion that ecological systems are enormously dependent on the interconnections that span huge ranges in spatial scale. If so, human actions that leave behind fragmented and less spatially connected ecosystems ought to put ecosystems at grave risk of collapse.

In summary, there appears to be a balance of nature, but it is highly unlikely that we are talking about a system in equilibrium. Rather, the persistence of highly diverse complex ecological systems is an emergent property of an intensely interactive and variable underlying dynamical system. I would argue that ecologists never saw the balance of nature as a perfect equilibrium process and that to attack the concept interpreted as such is to take down a straw man. Within this more generalized definition of balance, it remains an important task to ask what it is about nature that allows it to maintain itself and how these complex natural entities adapt in the face of such a variable world. These scientific tasks are closely aligned with the applied societal need to understand how human modifications will impact the diversity, sustainability, and functioning of ecological systems.

This book is an attempt to conceptually synthesize our current understanding of one of the big questions in ecology and evolution—What governs the stability of ecological systems? Although we have briefly discussed stability above, it is obviously critical to more rigorously define what we mean by stability. In the remaining sections of this chapter, I first define stability, discuss the role whole systems play in governing stable ecosystem function, and punctuate the stability problem with case studies of examples of instability in ecological systems. This final aspect of the chapter is included to convince the reader that there are already numerous examples of ecological instability and ecosystem collapse.

## 1.2 ECOSYSTEM STABILITY AND SUSTAINABILITY

It is commonly asserted that different definitions of stability often lead to different answers about what governs nature's stability (Ives and Carpenter, 2007). As an example, although Ives and Carpenter (2007) found differences between a number of stability definitions in terms of whether diversity begets stability, they also found that all definitions that involved dynamics

consistently gave the same qualitative answer. I will show throughout this book that dynamical definitions of stability are often consistent, and when they are not, it is informative to consider why, as suggested by Ives and Carpenter (2007). For instance, attributes that are stable in one sense (e.g., a population return forms a large perturbation rapidly) may be destabilizing in some other important sense (e.g., the same rapidly returning population overshoots the equilibrium and oscillates). I will show that this dynamic trade-off (i.e., fast return–big overshoot) is common in both population and consumer-resource models and that this result is useful in developing a synthetic theory for stability in more complex food web models.

I now define some common measures of stability. These definitions require some understanding of common terms, such as “equilibrium”, used in theory. For those having difficulty with terminology, it may be worth reading the mathematical review of chapter 2 before reading the stability definitions below.

### 1.2.1 PERSISTENCE-BASED METRICS OF STABILITY

Much of the theory I will discuss in this book relies on the following broad group of stability metrics (Pimm, 1982, 1984; McCann et al., 2000). I am referring to this set of metrics as persistence-based because they are an attempt, through various means, to quantify how likely the system as a whole is able to persist intact. Persistence-based definitions of stability effectively assume that the underlying dynamical system (i.e., an  $n$ -member mathematical model) is not changed by a perturbation (i.e., perturbation does not remove a species).

#### 1.2.1.1 *Engineering Resilience*

A measure that assumes system stability increases with decreasing return time to an attracting state (e.g., equilibrium) after a perturbation. The faster the return time, the more stable the system. In this book the term “resilience” will refer to engineering resilience.

#### 1.2.1.2 *Equilibrium Resilience*

The state being returned to after a perturbation is an equilibrium attractor. Mathematically, it is measured by the inverse of the maximum eigenvalue (i.e.,  $1/\lambda_{\max}$ ).

### 1.2.1.3 *Nonequilibrium Resilience*

The state being returned to after a perturbation is a nonequilibrium attractor (e.g., a limit cycle, a chaotic attractor).

### 1.2.1.4 *Variance Stability*

The variance in population densities over time, usually measured as the coefficient of variation, CV (variance/mean). High variance implies a greater chance of extinction, especially with external perturbations which are common in experimental tests of stability.

### 1.2.1.5 *Bounded or Minima Stability*

A system is more stable than another system if its global minimum density is bounded further away from zero densities than that of the other system. Here, “bounded further away from zero” simply implies that the minimum population density is further away from zero and so less likely to go extinct in a variable environment or after a perturbation.

### 1.2.1.6 *Sustainability*

A system is said to be sustainable if its' component members are able to persist in the face of a specified perturbation [either a continuous perturbation (i.e., a press perturbation) or a discrete perturbation (i.e., a pulse perturbation)].

## 1.2.2 CHANGE-BASED METRICS OF STABILITY

Persistence-based notions of stability, in some sense, all concern themselves with the likelihood that the  $n$ -member system persists over ecological time scales. There are also metrics of stability that assume a system can change. With this assumption, stability metrics become more concerned with quantifying how a perturbation changes the system and the extent of the change. This has become very popular with the realization that ecosystems may flip from one attractor to another after a perturbation [called an *alternative state* (Scheffer et al., 2001)]. Some common stability metrics of this sort are the following (Holling, 1996).

### 1.2.2.1 *Alternative State Stability I*

A system is deemed less stable the more alternative states it has. All else equal, the more alternative states, the greater the likelihood a given perturbation will flip the system to an entirely different state.

This focus on multiple attractors has led Holling to define a related alternative state–based measure of stability (Holling, 1996).

### 1.2.2.2 *Alternative State Stability II (Holling’s Resilience)*

A measure of the amount of change or disruption (i.e., the size of the perturbation) that is required to transform a system from being maintained by one set of mutually reinforcing processes and structures (a given attractor) to a different set of processes and structures (another attractor with potentially different species).

### 1.2.2.3 *Resistance Stability*

Resistance is a metric that quantifies the change of a system after a perturbation. The smaller the change of the system after the perturbation, the more resistant the system. This metric is commonly used when we consider a perturbation that changes the structure of the system, such as the complete removal or addition of a species. A relatively common use of this occurs in the network literature where resistance is related to the number of other species extinctions (secondary extinctions) after the removal or addition of another species [e.g., (Dunne et al. 2004)].

Note: There is no real reason to expect persistence-based metrics to give the same answer as the change-based metrics above. In fact, one may expect the opposite. Let us imagine, for example, a resilient plant monoculture. After a small perturbation in its own density, the resilient monoculture returns rapidly because of its high growth rate. However, this same monoculture can also be enormously sensitive to an invading herbivore (e.g., its high growth rate correlates with its being highly edible) and so have a low resistance. As noted by Ives and Carpenter (2007), it behooves us to begin to consider these multiple axes of stability and how nature struggles with different aspects of stability.

## 1.3 OF FOOD WEBS, STABILITY, AND FUNCTION

When considered at all scales, from a local patch to the entire biosphere, a food web governs the flux of energy and nutrients throughout our natural

world. This flux and its fate ultimately drive a number of critical functions. Ecosystems recycle nutrients, decompose wastes, and produce primary and secondary biomass. All these major functions of an ecosystem ultimately service humans and frequently do so with such a consistency that people doubt ecosystems will ever stop serving them. Some of the services offered to humans are plant food, animal food, water purification, hospitable climate, detoxification, crop pollination, seed dispersal, wood, carbon storage, energy (e.g., water power, wood), and landscape stabilization. It is estimated that the services provided by natural ecosystems are worth more than 33 trillion U.S. dollars each year (Costanza et al., 1997). The actual number is debatable, but there is little doubt that ecosystems service humans in a way that we tend to overlook.

Stability, in the sense defined above, can be thought of as both a function and a property of an ecosystem. An imbalance of function can be costly to a society. If a fishery that depends on secondary production (e.g., the cod fishery of the North Atlantic) is lean for many years, this causes obvious problems for an economy. Similarly, outbreaks in pests and diseases incur great societal costs to agricultural crops and bodies of water (e.g., lost forestry or fisheries production). Both are examples of either a drastic reduction in a key species (e.g., cod) and/or a drastic increase in an unwanted organism (e.g., mountain pine beetle). They represent, at the least, a temporary loss in the consistency of the assemblage at both a local (e.g., 1-m<sup>2</sup>) and a regional (e.g., ocean, forest stand) scale such that the system is tipped excessively one way or another. We now consider some examples of such documented instability and collapse that appear to be driven, at least to some extent, by human activity.

#### 1.4 ECOLOGICAL INSTABILITY AND COLLAPSE

Rachel Carson's book *Silent Spring* was driven by a large-scale human action, the widespread application of DDT (Carson, 1962). One of the odd things about human impact is that it can occur at such enormous spatial and temporal scales. As DDT made bird eggs less viable, this global human impact directly knocked out a group of highly visible species. There was no refuge in space or time from the DDT, so the influence had direct consequences for birds and many other vulnerable species. Many other influences of DDT, though, were likely less direct and less obvious. I am not aware of anyone considering how the reduction in birds and other vulnerable organisms changed the rest of the ecosystem. One can imagine a huge array of potential indirect cascades throughout terrestrial and aquatic food webs. Perhaps nothing so dramatic

occurred. It is possible that other organisms competing with birds rose slightly in density with the simultaneous reduction in birds. If so, nature may have had a way of balancing itself in the face of such a massive human perturbation, a way we just did not empirically detect. Unfortunately, we do not know what happened. We simply tend to hope that such human-induced perturbations find a way of working themselves out in a manner that does not influence our way of living.

Perhaps ecosystems are so robust that they almost always work themselves out without strongly influencing us, or perhaps we humans are just blissfully unaware that we are eroding critical components of an ecological system—the very attributes that allow the system to right itself in the face of our massive earth experiments. Even one counterexample forces us to recognize that instability and collapse are a real possibility. There are, in fact, numerous suggestions that we are tipping the scales of nature's balance. Below, I cover just a few of the emerging examples to highlight the fact that at least some human actions seem to be intricately linked to a loss in stability that results in the collapse of whole ecosystems.

#### 1.4.1 NUTRIENTS ON THE LANDSCAPE

One commonly observed driver of ecosystem collapse is the large-scale anthropogenic movement of nutrients on the landscape. In a series of influential papers, empirical ecologists [reviewed in Polis and Holt (1992)] made the point clear that ecological systems are never isolated. Frequently, for example, nutrients are shunted around the landscape from one ecosystem to another, and in many cases this shunting of nutrients can play a large role in the dynamics of an ecosystem (Polis and Holt, 1992). Large-scale human impact and examples of instability and imbalance often fall within this subsidy framework. A classic example of such ecological instability and collapse driven by a human subsidy was brought to the attention of the ecological world by Bob Jefferies and his colleagues (Jefferies et al., 1994, 2004). Their long-term research on the Hudson Bay snow geese populations allowed them to closely monitor explosive population growth in snow geese. This explosive growth in herbivores has led to destructive overgrazing, an enormous loss of diversity, and a completely altered ecosystem (figure 1.1).

The cause of this unbridled growth in snow geese appears to be driven by a human subsidy that arises thousands of miles south of the impacted Hudson Bay lowlands. Population densities of snow geese are strongly correlated with the intensive increase in the application of nitrogen to cereal crops in the southern states (Jefferies et al., 2004). Nutrient-rich fields of cereal crops allow the snow geese to thrive before they leave in flocks for northern nesting grounds.



FIGURE 1.1. The destructive power of herbivores as shown by Jefferies et al. (2004). The top left photo is a relatively pristine ecosystem. All the others show the destructive power of herbivory. The bottom left photo contrasts a rich plant community (exclosure) against the barren landscape after herbivory. This is an example of what Don Strong has referred to as “runaway consumption” (Strong, 1992). Photo courtesy of Bob Jefferies.

The luxurious southern bounty of cereal crops manifests as healthy snow geese offspring that will ultimately return south to thrive on the rich crops before moving north to breed and consume the marsh. The result of this boom in geese has been devastating for the Hudson Bay lowlands. Lush fields of sedges have been replaced by salty nutrient-poor mud flats (figure 1.1). Geese are destructive feeders, removing even the roots of plants in an activity called *grubbing*. With the loss of plants and their roots, the soil is eventually destabilized, and so water running over the landscape carries off rich topsoil and nutrients in the process. The loss of plants in turn also exposes the soil to the sun. Under such conditions the salinity of the soil, is substantially increased and the ecosystem becomes inhospitable to most plant life.

In sum, runaway herbivory has led to ecosystem level feedbacks that have reduced this once-rich system to a barren landscape. Sadly, it appears that reversing the ill effects of this human subsidy will not be trivial. This research not only highlights how a human-driven subsidy has led to massive habitat

destruction but is also a salient example of the enormous scale that ecological systems operate over. The world is indeed intimately connected.

Nutrient runoff also influences recipient aquatic ecosystems. Lake Erie and the Gulf of Mexico are two of many examples where terrestrial nutrient runoff fuels algal growth that cannot be rapidly assimilated by the pelagic component of the aquatic ecosystem (Dodds, 2006; Wilhelm et al., 2006). These unconsumed algae end up in the sediment, where they foster an explosive growth of bacteria. The bacterial boom in turn causes an oxygen deficit in the depths of aquatic ecosystems that can extend over enormous spatial scales in large bodies of water. In the face of such harsh conditions, many bottom-dwelling (benthic) organisms die and consequently reduce the flux of biomass up to higher-order predators. Thus, the direct reduction in benthic biomass and production likely cascades through these aquatic food webs, although the full extent of this cascade is unknown. These areas have become appropriately referred to as *dead zones* and are not trivial in size. For example, the Mississippi River drains enough nutrients into the Gulf of Mexico, to produce a dead zone of over 100 km<sup>2</sup>. Dead zones are examples of runaway microbial activity, a seemingly common phenomenon in collapsed ecosystems (both natural and laboratory-created ecosystems, as mentioned earlier).

Intact seagrass beds are wonderfully diverse and productive coastal ecosystems, but natural variation in human densities around different beds has repeatedly created gradients in species diversity (figure 1.2a). Alex Tewfik, a student and colleague of mine, found that as human density increased, these ecosystems lost top predators, detritus, specialist consumers, and edible seagrass (Tewfik et al., 2007a; Tewfik et al., 2007b). At high enough human densities, the systems are reduced to a homogenized habitat dominated by a single relatively inedible seagrass and an explosion of sea urchins (figure 1.2a–d). The reason for this changing structure is not fully known, but early findings suggest that generalist urchins consume increased algal production driven by the increased loading of nutrients in the water around heavily populated coastal areas. The human-induced nutrient subsidy, with the simultaneous loss of top-level predators through culling, promotes an elevated density of urchins, which drives runaway herbivory and extreme habitat homogenization.

An idea lurking behind the above stories is that certain organisms are poised to take advantage of human subsidies. When they do, they gain an excessive advantage and explode in biomass. This imbalance drives a cascade of consequences, which usually means a great loss of diversity and homogenization of the habitat. Further, in all the above cases, there are undoubtedly enormous human costs that accompany these collapses.

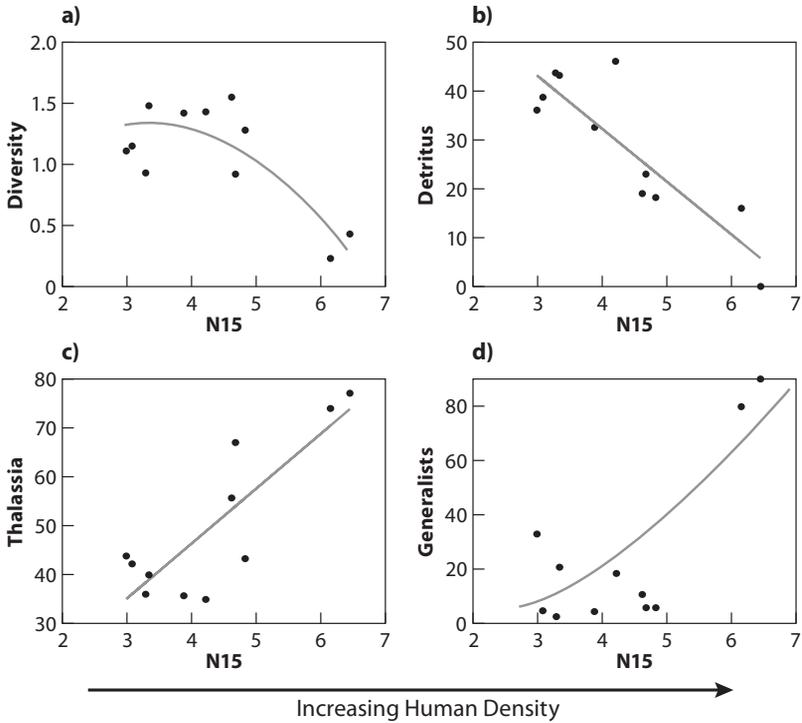


FIGURE 1.2. Some changing attributes of seagrass food webs across a gradient in the nitrogen isotope N-15 which correlates with human density (Tewfik et al., 2007a). (a) Data show a sudden jump to low diversity at high N-15 levels. (b) Detritus declines steadily with increases in N-15. (c) The relatively inedible seagrass *Thalassia* increases steadily with N-15. Not shown, the more edible *Syringodium* declines. (d) Generalist consumers show a sudden leap to extremely high densities at high N-15, mostly urchins at the endpoint. Figure modified from Tewfik et al. (2007a).

#### 1.4.2 HARVESTING, FRAGMENTATION, AND RUNAWAY HERBIVORY

While the previous section outlined the bottom-up influences of nutrients on whole food webs, there is also abundant evidence that humans impact the top of the food web. Harvesting, for example, tends to be focused on the higher-order predators in both terrestrial and aquatic landscapes (Pauly et al., 1998; Jackson, 2001; Terborgh et al., 2001). Further, because these higher trophic level organisms are frequently large and mobile relative to lower trophic level organisms, they are also often the most negatively influenced by habitat fragmentation.

In an excellent review of human impact on coastal ecosystems, Jeremy Jackson and colleagues documented in detail the historical removal of large consumers by humans in coastal marine ecosystems and the subsequent delayed collapse of these food webs (Jackson, 2001). They argued using historical data that ecological extinction caused by overfishing precedes that caused by all other human disturbances in coastal ecosystems. Further, there is often a significant lag in time before ecosystems collapse, simply because unfished species take over the role of lost species until they too are negatively influenced by exploitation or disease. It appears as though changes induced by humans in coastal ecosystems have tended to drive a preponderance of microbial production and dominance (Jackson, 2001), much like the fate of most microcosm studies and the aquatic dead zones discussed above. Jackson (2001) referred to this as “microbilization” of the coastal ocean (Wilhelm et al., 2006). Perhaps, as suggested earlier, this microbial dominance is the signature of a complete collapse of a once-diverse ecosystem.

A recent well-explored example of the effects of such species removal has been uncovered in Yellowstone National Park. In Yellowstone, wolves, one of the major historical apex predators in the ecosystem, were completely eliminated by hunting by the 1930s. Fairly recently, wolves have been reintroduced into the park. The history of the park with and without wolves has been followed closely by a number of ecologists [e.g., Ripple et al. (2001)]. Once they were gone, the loss of wolves cascaded through the ecosystem, influencing both density and diversity in the park. Where the system consisted of a broad range of herbivores, elk grew in density to dominate herbivores in the absence of wolves. Further, the elk, no longer fearing predation, began to move into riparian areas they normally would not have visited in the presence of wolves (Ripple et al., 2001). The increased densities of elk and their accompanying consumption impact on riparian vegetation in turn has greatly altered the riparian zone. The Yellowstone story is reminiscent of Aldo Leopold’s essay, “Thinking Like a Mountain”, which predicted the runaway consumption impacts of herbivores and great losses in diversity resulting from the removal of wolves. Yellowstone has recently reintroduced wolves, and this reintroduction has proven relatively successful. Elk, now fearing predation near the more open riparian zone, have adjusted by moving higher in the landscape, leaving riparian vegetation to flourish (Ripple et al., 2001).

In another example, Terborgh and colleagues (Terborgh et al., 2001) took advantage of a hydroelectric dam that flooded a large terrestrial area in the tropics. The dam flooded the landscape such that the highland areas became islands surrounded by a sea of water. Top predators were eliminated from most islands (especially the small islands) but not the mainland, allowing comparison of the

influence predators had on overall ecosystem structure. Again, herbivore abundance increased enormously in the absence of predators; predator-free islands had herbivore densities several orders of magnitude (10–100 times) higher than those in nearby mainland areas with top predators (Terborgh et al., 2001). This heightened herbivore density, not surprisingly, had dramatic implications for the density of understory seedlings and saplings. Again, top predators appeared to be playing a major role in promoting the persistence of a given assemblage of species. The collapse of diverse pristine assemblages seems to be relatively common when top predators are removed. Later in this book, I will return to some of these cases to suggest that this impact may be dependent on ecosystem size (McCann et al., 2005).

#### 1.4.3 WATER IMBALANCE AND ECOSYSTEM COLLAPSE

Humans also frequently affect the balance of water on the landscape with dramatic food web consequences. The Aral Sea in Central Asia, at one time one of the largest inland seas on the planet, has seen a change of horrific proportions (Smith, 1994; Assessment, 2005). In an attempt to increase cotton production in the region, longstanding waterways were rerouted to croplands. This change in water use reduced the Aral Sea to a fraction of its original size. This dramatic change led to an enormous loss of native plants in the area surrounding the sea. With the loss of plants, the soil dried out and soil erosion increased, so that rain moving over the landscape took with it critical nutrients. Again, as in the snow geese example, the dry, sun-baked soil then increased in salinity. There are even large-scale climatic feedbacks that contribute to such “desertification” (Assessment, 2005). Windswept, barren areas increase the heat and dryness of the area and so reduce precipitation. This type of positive feedback is common to what ecologists now refer to as “alternative states” (Scheffer et al., 2001; Folke et al., 2004). Essentially, systems are changed enough that they cross a tipping point where the new system has positive feedbacks (e.g., loss of soil nutrients, inhospitable saline soil, and a dryer climate) that suddenly preserve it in its altered state. In the Aral Sea example, there are even arguments that in this region disease has become rampant and entire fisheries have been lost (increased water salinity likely contributes to this)! The region has been dealt enormous economic and social blows.

Restoration of a system that does not want to change easily obviously becomes an expensive endeavor. Examples of desertification (sometimes from increased herbivory) abound (Srivastava and Jefferies, 1996), and other examples of ecosystems switching into very different, often economically unfortunate states are emerging (Scheffer et al., 2001; Folke et al., 2004; Assessment, 2005).

#### 1.4.4 HUMAN ECOSYSTEMS AND THE PARADOX OF ENRICHMENT

We have to this point discussed the impact of humans on natural ecosystems. There is also the case of human-made ecosystems that are frequently relatively spatially unstructured compared to their more natural counterparts (e.g., monocultures of plant crops, aggregations of fish for food, and monocultures of trees for lumber). In a sense, these homogenized ecosystems represent an extreme departure from pristine ecosystems where spatial and temporal variations seem to be the rule (Levin, 1999). As such, human-made ecosystems can be seen as an experiment in what happens when systems become strongly homogenized. While maximizing the area of a wanted biological product, humans have a long and costly history of defending these ecosystems against nature clawing back.

Agricultural and silvicultural ecosystems, for example, are frequently subjected to enormous outbreaks of pest species (Cappuccino et al., 1998; Logan et al., 2003). These pest species are fueled dynamically by the excess of resources concentrated in space (i.e., a nutrient-subsidized crop). Their populations explode locally and then spreads across the homogenized landscape like a wildfire. Fish farms have had similar issues, with the recent documentation of increased parasitic loads, disease, and contamination (deBruyn et al., 2006). In some cases, penned fish with their heightened disease burden have been shown to transmit contagion to nearby wild fish. There is a theoretical idea in ecology called the paradox of enrichment. I will discuss it in detail in this book, and it will become a foundation for the ideas laid out here. This idea is presented in many ways, but in its most qualitative presentation it suggests that predator-prey interactions in a well-mixed productive setting ought to readily drive boom-and-bust dynamics (i.e., an unstable situation by persistence-based metrics). In a sense then, boom dynamics are arguably a manifestation of the first half of this theory (i.e., that predators, pests, or diseases explode in number under such conditions). However, the second half of the theory—that resource populations are ultimately suppressed—is not always fully realized because humans go to great cost to alleviate the suppressive pressure of such pests.

### 1.5 A THEORY FOR FOOD WEBS

Here I have briefly laid out examples where humans have appeared to ignite collapses in ecological systems. I have also occasionally emphasized that this imbalance probably comes at a significant cost. Real ecosystems are indeed collapsing on the landscape. It therefore remains an important task to understand these complex natural entities in relation to their modified counterparts (i.e., urban ecosystems).

TABLE 1.1. Some Literature Examples of Major Ecosystem Impacts on an Ecosystem Following Some Perturbation(s)

<i>Ecosystem</i>	<i>Perturbation</i>	<i>Impacts</i>	<i>Citation</i>
Tropical islands	Hydroelectric dam (loss of top predators)	Runaway herbivory	Terborgh et al. (2001)
Yellowstone National Park	Loss of top predators (wolves)	Runaway herbivory	Ripple et al. (2001)
Marine ecosystems	Fishing (loss of top predators)	Unknown	Myers and Worm (2003)
Coral reefs and Estuaries	Fishing and eutrophication	Microbes dominate	Jackson et al. (2001)
Kelp forests	Loss of top predators	Runaway herbivory	Tegner and Dayton (2000)
Seagrass beds	Loss of predators and eutrophication	Runaway consumption	Tewfik et al. (2007a)

The examples presented above argue that human changes often reduce diversity, homogenize, and fragment the landscape. This creates wholesale rerouting of energy and nutrient fluxes throughout food webs such that a once-minor species can become a dominate biomass on the landscape. These changes alter feedbacks at local to global scales, feedbacks that are not easily predicted. At the very least, we are experiencing a period of great loss of natural beauty, and at the most, we are destroying the underlying life support we take for granted one ecosystem at a time.

Having laid out arguments that understanding the stability of ecosystems is a fundamental societal need, the rest of this book endeavors to understand how complex ecological systems work. I believe that our increased ability to understand these complex entities will ultimately form the conceptual infrastructure we need to deal with this rapidly changing world that is currently undergoing major habitat fragmentation, climatic change, and significant biodiversity loss.

This book proceeds by first presenting an introduction to dynamical systems theory. Here, my intention is to simply allow readers entry into this seemingly formidable area of math. As a result, I do not go into technical detail (although I will give references for the curious reader) but rather give the reader an intuitive walk through this fascinating area of math. The basic ideas behind the math are often quite simple, and I believe they are accessible to all readers. The ideas discussed here are then used throughout the remainder of the book in order to develop a theory about food webs.

In the second section of the book I examine the results from single-species models to small subsystem models (i.e., two-, three-, and four-species models, now commonly referred to as *modules*). In this part of the book I emphasize the role of interaction strength in the dynamics and develop some energetically driven principles that will form a backbone for more complex food web theory. The final section will expand upon this simple theory by extending the principles from modular theory to fit within a whole ecosystem context and all its accompanying complexities. Wherever possible I relate empirical and experimental results to the theory. Laid out in this way the book synthesizes results from single population models (including age structure) to whole ecosystem models that include nutrient recycling. I argue that there is a surprisingly coherent theory about food webs and ecosystems that sets the framework for understanding how perturbations (such as human impact) ought to influence the sustainability of ecosystems.