

Chapter One

INTRODUCTION

THIS BOOK brings together my two strongest interests in research: understanding nutrient cycling and limitation in terrestrial ecosystems, and understanding the ecosystems of the Hawaiian Islands. I have been fascinated by nutrient cycling and limitation since I chose to pursue a research career in ecology in 1970. I followed that fascination through analyses of temperate forest ecosystems and human influences on them, learning the dynamics of particular forests in New Hampshire, Indiana, North Carolina, and California as I moved through graduate school and a succession of university positions in those states. I worked in continental tropical forests in Costa Rica, Brazil, and Mexico, and led cross-site comparative analyses and syntheses of nutrient cycling in forest ecosystems. Shortly after moving to Stanford University in 1984, I began research in the Hawaiian Islands—where I had always intended to work, someday—and since then my research has been increasingly, now almost exclusively, focused there.

Why Hawai‘i, and why nutrient cycling and limitation? The personal reasons for Hawai‘i are easy to explain. I was born and brought up in Hawai‘i, and most of my family remains there. It is the place I am most at home, with both land and culture. However, that sense of place is not a sufficient reason for devoting most of my research to Hawai‘i, even though “a feeling for the land” does contribute substantially to that research. Still less is it sufficient reason for any agency or foundation to support my research. Part of the reason I have worked so actively in Hawai‘i, and the main reason I have been able to do so, is that the Hawaiian Islands represent an extraordinary model system for the analysis of many ecosystem properties and processes. Chapters 2 and 3 develop this part of the answer to “why Hawai‘i?”; they explain the concept of model systems and its application in other fields, and they show how features of islands in general—and the Hawaiian Islands in particular—make them useful model systems for answering a broad range of ecological questions.

Why I am interested in nutrient cycling and limitation is more difficult to explain—why do any of us choose the broad research areas we do? Having made my choice, though, it is easy to explain why understanding nutrient cycling and limitation is both interesting and important. The more compelling reasons include:

1. The availability and/or supply of essential nutrients demonstrably shapes the productivity, composition, diversity, dynamics, and interactions of plant, animal, and microbial populations in many terrestrial, aquatic, and marine ecosystems. N and/or P in particular are often in short supply, relative to the needs of many organisms (Schindler 1977, Vitousek and Howarth 1991, White 1993).
2. Nutrient limitation is economically important—as illustrated most directly by the fact that humanity spends tens of billions of dollars annually on fertilizer.
3. There is a fascinating question at the heart of N limitation. Biological N fixers that can draw upon the vast pool of atmospheric N₂ are ubiquitous. It seems that such fixers should have a competitive advantage in N-limited ecosystems, and as a byproduct of their activity they should boost N inputs substantially. Just that happens in most temperate freshwater ecosystems; cyanobacterial N fixation brings N supply more or less into equilibrium with the next most limiting resource (Schindler 1977). How can N limitation persist in many terrestrial ecosystems despite the presence of biological N fixers (Vitousek and Howarth 1991, Vitousek and Field 1999)?
4. The global cycles of N and P have been altered substantially by human activity. Anthropogenic N fixation for fertilizer, during fossil fuel combustion, and in legume crops is greater than natural biological N fixation on land (Smil 1990, Galloway et al. 1995, Vitousek et al. 1997a, Galloway and Cowling 2002), and the mining and mobilization of P for use in fertilizer and industrial processes exceeds the weathering of P from rocks (Carpenter et al. 1998, Smil 2000, Bennett et al. 2001). Many organisms and ecosystems now receive “unnaturally” large quantities of these elements—and function differently as a consequence. At the same time, the responsiveness of many terrestrial plants and ecosystems to the ongoing anthropogenic increase in CO₂ is constrained in part by N and/or P limitation (Schimel et al. 1997, Lloyd et al. 2001, Oren et al. 2001)—and understanding these limitations is crucial to predicting the future composition and dynamics of terrestrial ecosystems.

My goal in this book is to contribute to the understanding of nutrient cycling and limitation, using the Hawaiian Islands as a model system. Accordingly, this book is not intended as a synthesis volume for ecosystem research in Hawai'i, but rather as an analysis that makes use of unique characteristics of the Hawaiian Islands to understand the mechanisms driving nutrient availability, cycling, and limitation in terrestrial ecosystems more generally. I do not attempt to present a consensus view of

ecosystem ecology, or even the consensus of my colleagues and students who have worked on Hawaiian ecosystems; this is a personal view of how I think nutrient cycling in terrestrial ecosystems works, and why. Some of the fundamental questions that I believe can be answered more straightforwardly in Hawai'i than anywhere else include:

How do biological and geochemical processes that operate on very different timescales interact to cause, sustain, or offset nutrient limitation? “Nutrient cycling” encompasses a wide range of processes that occur on very different timescales, from the turnover of available nutrients in soil solution (minutes to days, for an essential element in short supply) to the development of acidic, deeply leached tropical soils (millions of years). I will focus on four timescales here: (1) nutrient supply into biologically available pools versus organisms’ demand for those nutrients, over minutes to days; (2) the cycling time of nutrients from soils to plants and back—generally years in forests—and the development of plant-soil-microbial feedbacks that can slow or speed nutrient cycling; (3) the accumulation of nutrient pools within plant biomass and soil organic matter, which can continue for decades to centuries or more, and how these pools function as sources and sinks for biologically available nutrients; and (4) the balance between inputs of elements to ecosystems and losses of elements from them, as these change over millennia to millions of years during long-term soil and ecosystem development. Despite their very different timescales, these processes interact strongly to control nutrient availability, cycling, and limitation in terrestrial ecosystems—and I believe we can understand most of these timescales and their interactions better in the Hawaiian Islands than elsewhere.

How are element inputs to and losses from terrestrial ecosystems regulated, and what are the implications for nutrient cycling and limitation? A decade ago, the prevailing conceptual model for the control of element inputs to and outputs from terrestrial ecosystems held that most inputs are controlled by processes occurring outside of ecosystems, while outputs are controlled in part by biological processes that cause nutrients in short supply to be retained within terrestrial ecosystems. Hedin et al. (1995) then suggested that nutrient limitation could be caused or sustained by losses of nutrients in forms that are not accessible to organisms, and so cannot be retained by them. How important are what I will call “demand-independent” element losses? Conversely, are there important pathways of element inputs that are “demand-dependent” (in addition to biological N fixation)? What are the implications of these pathways of element inputs and losses for the functioning of terrestrial ecosystems?

How do the cycles of different elements interact? Many analyses of nutrient cycling and limitation evaluate one element at a time, focusing for

example on the dynamics of the N cycle; others consider multiple elements, but do so sequentially. However, organisms require a suite of elements simultaneously, at ratios that differ among organisms, and the processes that drive element inputs and output also affect multiple elements simultaneously. A recent analysis by Sterner and Elser (2002) expanded upon earlier work (Redfield 1958, Reiners 1986) to demonstrate that understanding the ratios of elements in organisms and ecosystems—their biological stoichiometries—can contribute substantially to understanding nutrient cycling and limitation. Can we integrate the biological stoichiometries of plants, animals, and decomposers with the geochemical stoichiometries of element inputs, outputs, and transformations, and develop a more fundamental analysis of biogeochemistry?

How do genotypes, species, and communities of organisms affect nutrient cycling and limitation in ecosystems? Many recent studies have evaluated the influences of particular species, functional groups, and/or levels of diversity on ecosystem productivity and nutrient retention (Tilman et al. 2001, Hooper et al. in press); other studies have demonstrated that although components of global change (e.g., warming, elevated CO₂) alter nutrient cycling directly, they have greater effects indirectly through their alteration of species composition (Hobbie 1995). One of the features that makes the Hawaiian Islands a useful model system is their low species diversity. I use this low diversity to evaluate the importance of population-level variation within species, and I use the consequences of biological invasions by species from outside Hawai'i to ask how nutrient cycling and limitation might differ in a more biologically diverse region.

These questions represent threads that run throughout this book, and I return to them in the last chapter for a more extended discussion. I do not answer all of these questions, or indeed any of them completely—rather I think research in Hawai'i has contributed to answering some of them, and to developing perspectives and informed speculations on the rest.

A brief road map for the book is as follows: chapter 2 begins by defining model systems, and describing how they are used in other fields. I briefly summarize the natural history of the Hawaiian Islands, and illustrate how Hawai'i has been used as a model system in analyses of evolution/speciation, conservation biology, and culture as well as ecosystem studies. In chapter 3, I focus on the extraordinary environmental gradients within Hawai'i, describing how the combination of remarkable constancy in some of the environmental factors that control terrestrial ecosystems (sensu Jenny 1980), coupled with wide and well-defined gradients in other factors, makes the Islands useful for understanding nutrient cycling in particular. I conclude chapter 3 by describing a 4.1 million year substrate age gradient across Hawai'i that provides the focus for most of the remainder

of the book. Chapter 4 describes patterns in productivity, nutrient availability, and nutrient cycling across that gradient, demonstrating that a biologically regulated positive feedback strongly reinforces the underlying geochemical controls of nutrient cycling as soils and ecosystems develop. In chapter 5, I summarize experimental studies of nutrient limitation across this substrate age gradient—evaluating which nutrients limit productivity in young, intermediate-age, and old sites, and with what consequences for nutrient cycling in ecosystems. Chapter 6 summarizes the inputs of elements to all of the sites along the age gradient, in the process demonstrating that long-distance transport of continental dust to Hawai'i contributes substantially to maintaining productivity and soil fertility there in the long term. In chapter 7, I evaluate the outputs of nutrients from sites along the gradient, and compare calculations of inputs versus outputs. These input-output budgets provide an independent check on estimates of inputs and outputs, and in the process demonstrate that there remains a lot about Hawaiian ecosystems that I do not understand. Finally, in chapter 8, I return to the questions raised above, and combine analyses based upon a simple simulation model with field results from Hawai'i and elsewhere to summarize what I think we know—and don't know—about nutrient cycling and limitation in terrestrial ecosystems.