Fundamentals of Conservation Biology

For Aram Calhoun, who inspires us with her delight in the natural world and dedication to conservation.

Fundamentals of Conservation Biology

Third Edition

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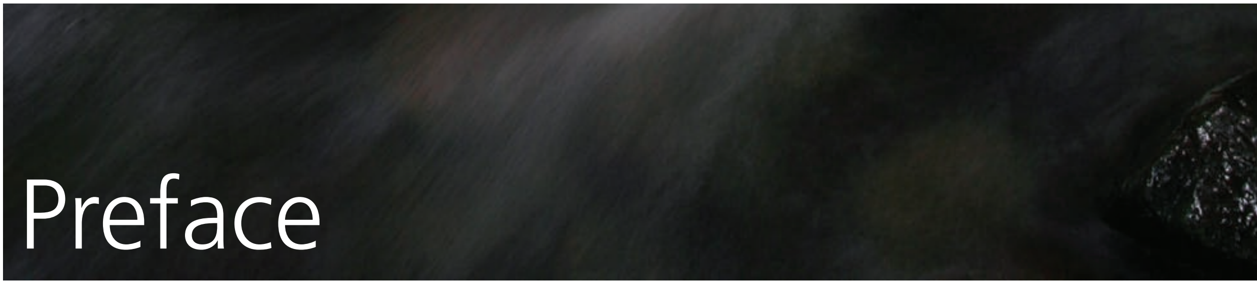

Preface

11:15 P.M. 20 June 1990 I'm not used to being this hot so late at night. I don't know the sounds coming through the window . . . crickets? . . frogs? . . . a wheezing air-conditioning system? I don't know what to do.

I'm in a dorm at the University of Florida; the fourth meeting of the Society for Conservation Biology has just ended; I'm sifting through various conversations of the last 4 days. I wonder if I should postpone my plans to write a sequel to my book on managing forests for biodiversity – a sequel that would focus specifically on tropical forests. At the meeting I've discovered that professors are using my book for a much broader range of conservation courses than I ever anticipated and that tells me that there is a niche to be filled.

Apparently various multiauthored books on conservation biology topics are not filling the need for a basic text. Perhaps I should add a brick to the foundation of the discipline before pursuing a more specific project. Now if I can rough out an outline before I get too sleepy.

27 August 1993 Over three years later and I have just finished the first draft. Actually the writing went reasonably quickly (I did not begin in earnest until May of 1992) because I chose a sort of stream-of-consciousness approach in which I wrote only what I knew or thought I knew. Now I look forward to spending the next several months combing the literature, correcting, refining, and updating this draft. It might seem that this approach would make it easier to convey my original thinking about conservation biology as opposed to reporting on everyone else's thinking. Perhaps so, but I claim no truly original thoughts. I tend to think each person is no more than a unique melting pot for a vast community of ideas.

Unfortunately, I have already nearly reached my target for final length and thus keeping the book to a reasonable size and cost will be a challenge. Perhaps the best index of this is the fact that in *Wildlife, Forests, and Forestry*, I described managing forest ecosystems for biodiversity in 370 pages; in this draft the subject is covered in four pages. It has been particularly difficult trying to balance spanning the breadth of conservation biology with plumbing its depths. I have tended to err on the side of breadth on the assumption that most readers will use the book as part of a conservation biology class, and the instructor can easily focus on depth, for example, by describing applications of the principles outlined here.

24 August 1994 Sifting through the literature of conservation biology has been great fun, although it has entailed some difficult choices. If many of my readers will be North American, should I keep things familiar and easy by illustrating general principles with redwoods, bald eagles, and well-known foreign species like tigers? Or should I try to open some vistas by describing fynbos, huias, and thylacines? Many years of working abroad predispose me toward the latter approach, but I have curbed this temptation to some degree, partly to save the space it would take to describe the fynbos, and partly because I have tried to select literature that will be reasonably accessible.

As I enter the final stages of production I often think about my readers and how they will use this book. My primary audience is students who have some background in biology and ecology but who have not taken a previous conservation biology course. I also hope to reach some general-interest readers and have tried to keep the prose fairly lively so that they can manage at least half an hour of bedtime reading before dozing off.

This is an opportune place to explain two features of the book. First you will note that there are no scientific names in the text; they are all in a separate list of scientific names, which also constitutes an index to all the species mentioned in the text. Furthermore, the `literature cited' section constitutes an index to authors, because after each citation the pages where it is cited are listed.

27 December 1994 Two more days before the book goes out to copy-editing, and it is time to start listing all the scores of people who have helped, in an acknowledgment section. I particularly want to thank Andrea Sulzer, the friend and artist who illustrated the book; the Department of Wildlife Ecology of the University of Maine, where a relationship that began in 1970 has recently led to a professorial chair endowed by the Libra Foundation; and Aram Calhoun who has shared all but a month of our marriage with this book. Finally a special thanks to everyone who buys this book for all its royalties are allocated to a fund to support conservation students from developing countries.

When I began writing this book my goal was to fill a gaping hole, but now my colleagues have produced two other credible conservation biology textbooks (Primack 1993, Meffe and Carroll 1994), and more are in the pipeline. Still, I have absolutely no regrets about having embarked on this project for I have thoroughly enjoyed it, and if a small portion of my enthusiasm reaches my readers, it will be well worth the effort.

Second edition: January 26, 2001 Before undertaking this second edition I was rather dreading the prospect of replowing old ground, tearing apart my first edition and putting it back together again. In hindsight, the last nine months of sorting through the conservation biology literature have been rather enjoyable, especially after I realized that it was okay to be selective in my reading. With 651 new references there is a lot of fresh material to chew on here; most of it is very recent (my last trip to the library was this morning) although I have also added some older papers from the "classical period" of conservation biology (the 1980s). Some scepticism about the "authority" of information found on the world wide web has severely limited my use of these sources, but on the other hand I have provided many URLs to give readers a gateway to the organizations that make conservation biology happen. A new glossary and many new illustrations are also prominent features of this edition.

Third edition: 15 May 2006 I am returning home from a four-month sabbatical in Australia, where weekends were spiced with pursuing wombats, whale sharks, and lyre birds, just in time to work on the production phase of this book. Two years ago when I decided to invite a coauthor to join me it took about ten seconds to identify James Gibbs and, the next day, it took even less time for him to accept. I have worked with James for 25 years, since he was a new student at the University of Maine and I was a new professor, and it has always been a pleasure. James' expertise with genetics and population biology, complementary experiences with field conservation projects around the world, and his willingness to dive into the social sciences was just what was needed to strengthen this edition.

Another salient feature of this edition is a strong shift from Andrea Sulzer's pen-and-ink drawings to color photographs. Finding photos for this edition has been an enjoyable challenge and we are grateful to the many photographer/artists whose works appear here. They are named in the legends but special recognition must go to Marc Adamus whose photos grace the cover, three section frontispieces, and two other figures. We have also expanded our visual breadth to include many other artists–ranging from the anonymous cave painters of Lascaux to Monet and Rubens and particularly, Debbie Maizels and the staff of Emantras.

Of course the substance of revising any textbook lies in new literature and the field of conservation biology remains vigorous in this regard. The 762 new references added are just a small sample of the high-quality research that characterizes the discipline. We have also added three new case studies, holding back somewhat because we think case studies should largely be generated and presented by faculty and students based on their own experiences and interests. Overall the book is about 6% longer than previous editions as measured by the number of words, but 50 pages shorter because of more compact formatting.

As with earlier editions, the royalties are going into a fund to support conservation students from developing countries, most recently the fieldwork of a student from Argentina studying cavity-nesting birds in the Andes for her dissertation. In time the royalties will be sufficient for an endowed, perennial source of support for similar aspiring conservationists.

M. L. Hunter, Jr.

For instructors, if you did not receive an artwork CD-ROM with your comp copy, please contact this email address: artworkcd@bos.blackwellpublishing.com

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On the production side many folks have worked hard to create this book. These include, in roughly chronological order: Jane Humphreys, Simon Rallison, Bob Calhoun, Julie Dodge, Chris Halsted, Shirley Moulton, Lincoln Hunt, Shawn Girsberger, Elizabeth Frank, Nancy Whilton, Sarah Graves, and Janey Fisher.

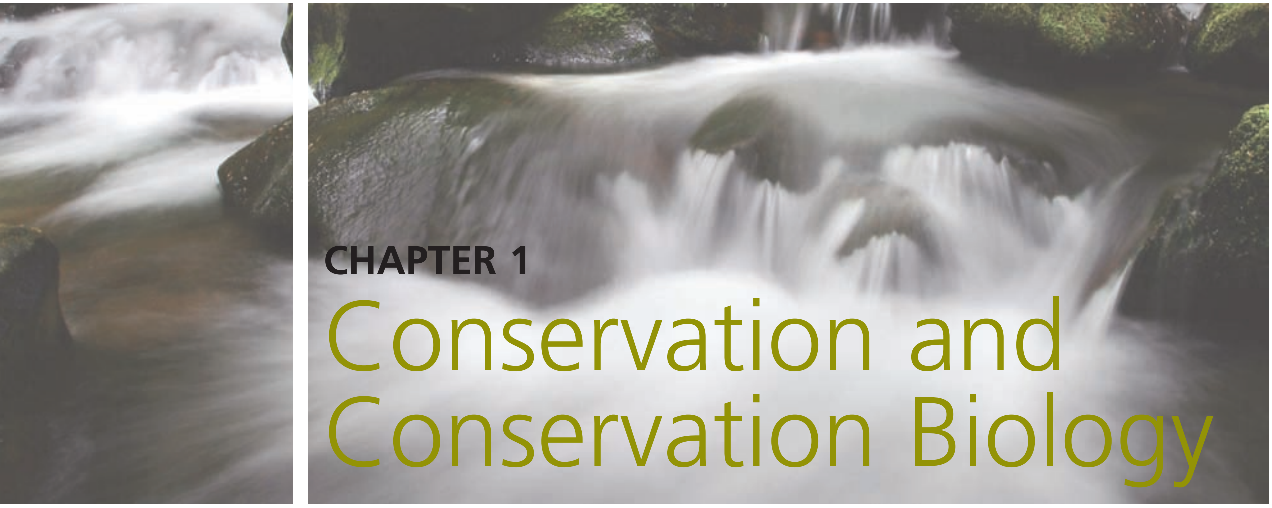
Last but not certainly not least, are our partners in life and conservation, Aram Calhoun and Thane Joyal, who have helped with this book in many direct and indirect ways.

PART I

Biodiversity and Its Importance

Think about our world and its wild things: a marsh splashed and flecked with the colors of flowers and dragonflies, the rhythmic roar and swoosh of waves punctuated by the strident calls of gulls, a dark forest pungent with the odors of unseen life teeming below a carpet of leaves and mosses. Imagine a future world utterly dominated by concrete and regimented rows of crops – a monotonous, ugly, and unhealthy home for us and the species we have chosen for domestication. This book is about hope in the face of forces that would degrade our world. It is about the rich tapestry of life that shares our world now and about how we can maintain it.

Photo opposite: Spring Falls © Marc Adamas



CHAPTER 1

Conservation and Conservation Biology

What Is Conservation?

Since the beginning of humanity people have been concerned about their environment and especially its ability to provide them with food, water, and other resources. As our numbers have grown and our technology has developed, we have become increasingly concerned about the impact we are having on our environment. Newspapers herald the current issues:

- "Conservationists call for tighter fishing regulations."
- "Ecologists describe consequences of warmer climates."
- "Environmentalists criticized by chemical industry."
- "Preservationists want more wilderness."

They also reveal an ambiguous terminology. Are we talking about conservation or preservation? Are the issues ecological or environmental? Students deciding which university to attend and which major to select are faced with a similarly bewildering array of choices – soil and water conservation, environmental studies, natural resource management, conservation biology, wildlife ecology, human ecology, and more – that intertwine with one another and often cut across traditional departmental and disciplinary lines. In this chapter we will try to resolve these ambiguities by examining how they are rooted in human history and ethics. To start on common ground we will briefly examine some of the differences and similarities among conservationists, preservationists, environmentalists, and ecologists. In the second part of the chapter we will see where conservation biology fits into this picture.

A *conservationist* is someone who advocates or practices the sensible and careful use of natural resources. Foresters who prudently manage forests, hunters and fishers who harvest wild animal populations sustainably, and farmers who practice the wise use of soil and water are all conservationists. Citizens who are concerned about the use of natural resources are also conservationists, and they often assert that the activities of foresters, fishers, farmers, and other natural resource users are not prudent, sustainable, or wise. In theory arguments over who is, or is not, a conservationist should turn on the issue of what is sensible and careful. In practice, the foresters, farmers, ranchers, etc. have largely ceded the title "conservationist" to their critics. They have become reluctant to call themselves conservationists and instead use the word to describe the people they consider adversaries.

A *preservationist* advocates allowing some places and some creatures to exist without significant human interference. Most people accept the idea that conservation encompasses setting certain areas aside as parks and maintaining certain species without harvesting them. The divisive issues are how many areas and which species. Many resource users believe that enough areas have already been closed to economic use, and they use “preservationist” as a negative term for people they consider to be extremists. Because of this pejorative use relatively few people call themselves preservationists. People who find themselves labeled preservationists by others usually prefer to think of preservation as just one plank in their platform as conservationists.

An *environmentalist* is someone who is concerned about the impact of people on environmental quality. Air and water pollution are often the proximate concerns; human overpopulation and wasteful use of resources are the ultimate issues. There is enormous overlap between environmentalists and conservationists. Many environmentalists would say that environmentalism encompasses conservation, while many conservationists would say the reverse. The difference is a matter of emphasis. By focusing on air and water pollution and their root causes, environmentalists often emphasize urban and suburban situations where human-induced problems and human well-being are paramount. Because conservationists focus on natural resource use, they tend to emphasize rural areas and wildlands, as well as their associated ecosystems and organisms, including people.

Traditionally, an *ecologist* is a scientist who studies the relationships between organisms and their environments. However, in the 1970s the term developed a second meaning when the public failed to distinguish between environmentalists and the scientists (ecologists) who provided the scientific basis for the environmental movement. The confusion was understandable because most ecological scientists are also, politically speaking, environmentalists. Now “ecologist” is often used in the popular press as a synonym for “environmentalist.” To make a hairsplitting distinction we can let the second definition of ecologist be a person who is concerned about the relationships between organisms (including people) and their environments.

A Brief History of Conservation

The roots of conservation are lost in prehistory (Fig. 1.1). No doubt there was a time when human reason, growing ever more sophisticated through the millennia, began to extend the idea of deferred gratification (“save this fruit to eat tomorrow rather than now”) over much longer periods. “Leave these tubers so there will be more next year when we pass this place.” “Take this calf home so that we can raise it and eat it next winter when it is bigger and we have little food.” Certainly, such practices were simple, almost analogous to the food hoarding exhibited by many animals, but they represent conservation nevertheless. The roots of preservation are probably quite ancient too. With the development of spirituality and castes of priests and priestesses, some species were given special status as gods or totems that protected them from exploitation. Sometimes, large areas such as sacred mountains were decreed off-limits or visited only on religious occasions (Fig. 1.2).

Figure 1.1 The roots of conservation can probably be found among the earliest *Homo sapiens*, such as the people who painted this mural in the Lascaux cave in France. (Photo from Art Resource, New York.)

Leaping forward, history records many examples of conservation throughout the ages and across cultures. For example, the biblical story of Noah's ark remains a popular metaphor for conservation. The Bible also contains the first-known game conservation law:

> If you come on a bird's nest, in any tree or on the ground, with fledglings or eggs, with the mother sitting on the fledglings or on the eggs, you shall not take the mother with the young. Let the mother go, taking only the young for yourself, in order that it may go well with you and you may live long. (Deuteronomy 22:6–7)

(In other words, don't kill mother birds.)

A far broader law was promulgated by Asoka, emperor of India 274–232 BCE (Before Common [or Christian] Era):

Figure 1.2 Mount Fuji has been a sacred mountain for the Buddhists and Shintoists of Japan for many centuries. (Painting by Katsusika Hokusai from the British Museum, London; photo from HIP/Art Resource, New York.)

Twenty-six years after my coronation I declared that the following animals were not to be killed: parrots, mynahs, the aruna, ruddy geese, wild geese, the nandimukha, cranes, bats, queen ants, terrapins, boneless fish [shrimp] ... tortoises, and porcupines, squirrels, twelve-antler deer, ... household animals and vermin, rhinoceroses, white pigeons, domestic pigeons, and quadrupeds which are not useful or edible. ... Forests must not be burned.

Many laws focused on regulating rather than prohibiting the exploitation of species. For example, Middle Eastern pharaohs issued waterfowl hunting licenses, and night hunting was banned in the city-states of ancient Greece (Alison 1981). Early regulations emphasized trees and birds, mammals, and fish caught for food, but all species and whole ecosystems benefited from the popularity of declaring preserves. Starting at least 3000 years ago with Ikhnaton, king of Egypt, and continuing with the royalty of Assyria, China, India, and Europe, as well as with the Greeks, Romans, Mongols, Aztecs, and Incas, history has recorded many decrees setting aside land to protect its flora and fauna (Alison 1981).

Conservation was an issue during the period when European states were colonizing the rest of the world, because colonization often led to disruption of traditional systems of natural resource use and rapid overexploitation, despite the protestations of some sensitive, farsighted people who argued for moderation. This was particularly true on some small, tropical islands such as Mauritius and Tobago, where the consequences of overexploitation became apparent very quickly (Grove 1992, 1995). Freedom from feudal game laws was often a significant stimulus to colonization. Imagine how attractive the promise of abundant, free game would seem to people who feared for their lives whenever their appetite for meat led them to poach one of the king's deer. The promoters of colonization knew this, and their claims became so exaggerated that one writer felt compelled to set the record straight:

> I will not tell you that you may smell the corn fields before you see the land; neither must men think that corn doth grow naturally (or on trees), nor will the deer come when they are called, or stand still and look on a man until he shoot him, not knowing a man from a beast; nor the fish leap into the kettle, nor on the dry land, neither are they so plentiful, that you may dip them up in baskets, nor take cod in nets to make a voyage, which is no truer than that the fowls will present themselves to you with spits through them. (Leven 1628, quoted from Cronon 1983)

Of course, bountiful game did not fare well under the onslaught of hungry colonists and native people armed with modern weaponry, and soon the colonists found that they had to regulate themselves. As early as 1639 it was illegal to kill deer between May 1 and November 1 in parts of Rhode Island (Trefethen 1964), and the Cape Colony in southern Africa had game laws by 1822 (MacKenzie 1988). This basic pattern – human populations growing, expanding into new areas, developing new technology, and then responding to overexploitation with an array of ever more restrictive conservation regulations – has been repeated across the globe and continues to this day.

With increasing human impacts, the abuse of resources other than trees and large animals also began to be recognized, albeit slowly for species that lack obvious economic value, such as most invertebrates, small plants, amphibians, and reptiles. Aldo Leopold (1949) called for saving every species with his well known admonition "To keep every cog and wheel is the first precaution of intelligent tinkering," but it was not until the 1960s and 1970s that the idea of "endangered species" became a major issue for conservationists. During this period many nations passed laws (e.g. the United States Endangered Species Act) to form an umbrella under which all animal and plant species threatened with extinction can, in theory, benefit from conservation activities. In practice, however, smaller plants and animals still are not given equal treatment, and other biological entities, such as microorganisms, genes, and ecosystems, are usually not explicitly under the umbrella at all.

This brings us to the point of departure for conservation biology and this book, but first let us briefly return to preservation, environmentalism, and ecology to see where they fall in this history of conservation.

Preservation

Although the early roots of preservation may lie in the proscriptions of religious leaders and royalty, many people would identify the establishment in 1872 of Yellowstone National Park, the world's first national park, as the beginning of governmental policy codifying the value of preservation. Here were 9018 square kilometers of evidence that society recognized the importance of removing some natural resources from the path of economic development. The national park movement has developed throughout the world and has been modified in many ways – some preserves are off-limits even to tourists, while some parks, especially in Europe, maintain traditional cultural practices such as historic livestock grazing regimes – but the underlying value system remains largely intact. This same preservationist value system has also ended the exploitation of many species. Some of these are species on the brink of extinction; some are simply species for which preservation seems preferable to utilization. Many countries, for example, have banned the harvesting of all songbirds even though some species could be harvested in a sustainable manner.

Environmentalism

The first environmentalists were probably citizens of our earliest cities, more than 3000 years ago, who complained of water pollution and demanded the construction of sewer systems. The industrial revolution accelerated urbanization and brought its own problems, such as coal burning and factory discharges into water bodies. Environmental issues became much more high profile after the publication of Rachel Carson's 1962 treatise on pesticides, *Silent Spring*, and a global environmental movement finally coalesced at the first United Nations Conference on the Human Environment, in Stockholm in 1972. This event marked the beginning of an era of considerable environmental activity at the global, national, and local levels, with many organizations created, laws passed, and treaties ratified.

Ecology

As is true of most sciences, elements of ecology can be traced to Hippocrates, Aristotle, and other Greek philosophers, but it was not until 1869 that the word "ecology" was coined. Scientific societies of ecology and ecology journals followed in the early 1900s, and ecology soon proved useful in developing a scientific basis for forestry and other areas of natural resource management. However, ecology did not move into the public eye until the advent of environmentalism. As the environmental movement spawned new government agencies, advocacy groups, and consulting firms, universities educated large numbers of ecologists to fill these organizations. Schools at all levels began informing students about the relationships between organisms and their environment. Consequently, there are now many professional ecologists at work solving environmental problems and many more people who call themselves ecologists out of concern for these issues.

An Overview of Conservation Ethics

It is easy to describe the history of conservation in terms of political benchmarks such as the passage of laws, but these are only a manifestation of a more fundamental process: the evolution of human value systems or ethics. We will encounter conservation ethics in many chapters and will focus on the topic in Chapter 15, "Social Factors," but a brief preview here will complement our history of conservation and will provide a foundation for later chapters.

A milestone paper, "Whither conservation ethics?" by J. Baird Callicott (1990), placed conservation ethics into a historical context using the writings of three people – John Muir, Gifford Pinchot, and Aldo Leopold – to describe three ethics: the Romantic-Transcendental Preservation Ethic, the Resource Conservation Ethic, and the Evolutionary-Ecological Land Ethic, respectively (Fig. 1.3).

Figure 1.3 Put yourself in the shoes of Aldo Leopold, John Muir, and Gifford Pinchot (depicted from left to right) to view the landscape opposite. How does this influence your perspective? (Photos from Aldo Leopold Foundation, USDA Forest Service, Yosemite National Park Archives, and M. Hunter.)

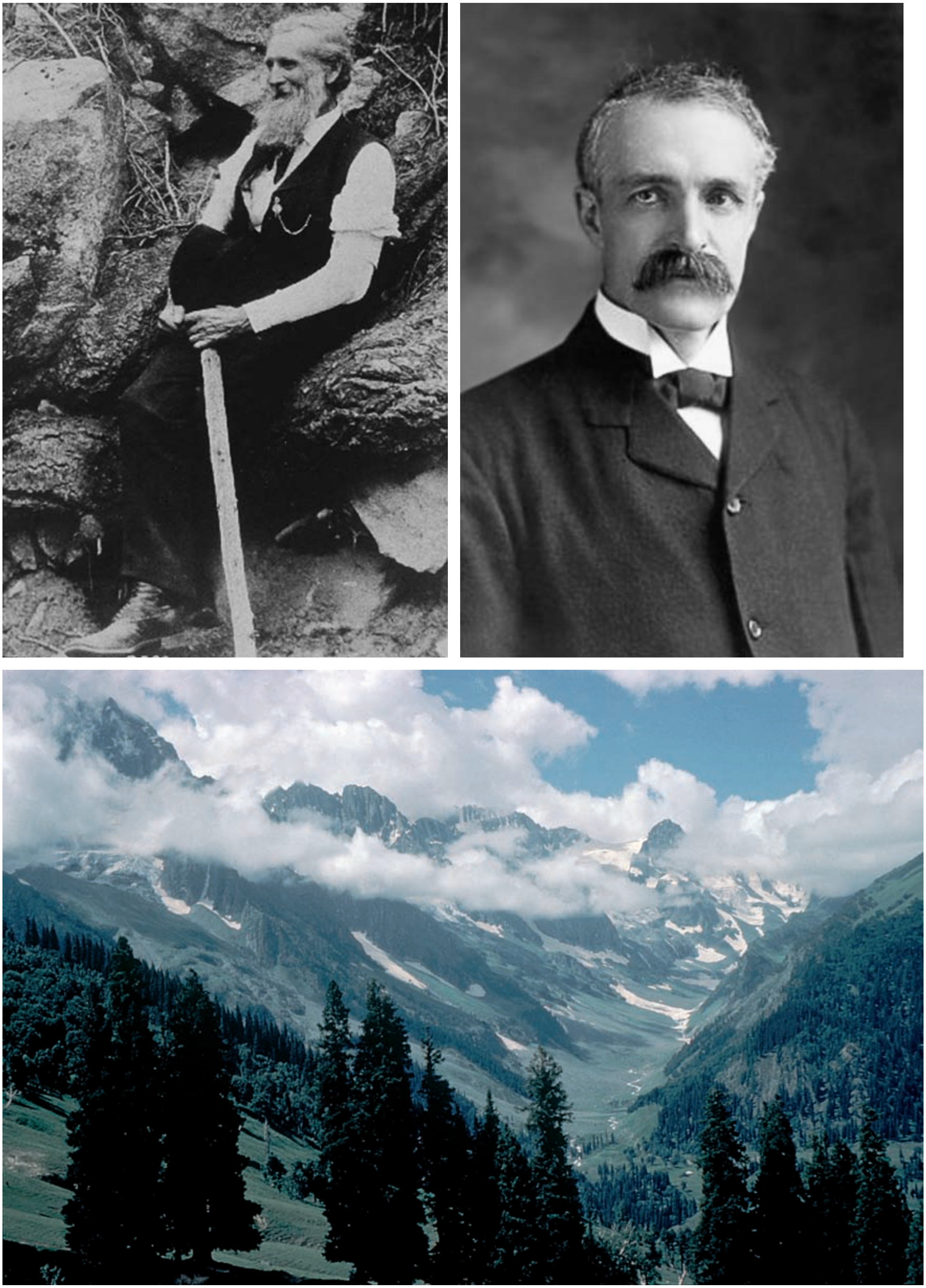


Figure 1.3 Contd.

The Romantic-Transcendental Preservation Ethic became the basis for political action in the hands of John Muir (1838–1914), the writer and naturalist who founded the Sierra Club and who was best known in some circles for climbing trees during storms to experience nature at its fullest. Muir believed that communion with nature brings people closer to God (thereby providing a "transcendent" experience) and that visiting ancient forests and alpine meadows for this purpose is morally superior to using them to cut timber or graze livestock. In other words, nature is a temple that is sullied by the economic activities of people. Obviously, such an ethic puts a high premium on establishing parks and similar areas where nature is preserved reasonably intact.

At about the same time that Muir was calling for the preservation of extensive lands, Gifford Pinchot (1865–1946) was formulating a very different value system, the Resource Conservation Ethic. Pinchot was a forester and politician, the founder of the US Forest Service. To Pinchot, nature consisted solely of natural resources and should be used to provide the greatest good for the greatest number of people for the longest time. This was not a call to plunder the land, but a call to use it in a way that distributes benefits fairly and efficiently among many people, rather than among a handful of lumber barons and cattle kings. It also advocated wise, judicious use of natural resources so that future generations would not be shortchanged. By recognizing aesthetics as a resource, the Resource Conservation Ethic even found room for a modest amount of preservation to accommodate Transcendental philosophers and Romantic poets. Given these precepts and a history of overexploitation of the nation's natural resources, Pinchot believed that natural resources should be owned or regulated by the government.

Although there was a profound gap between Muir's and Pinchot's ethics, they both espoused an anthropocentric (people-centered) view of nature. They both wrote of nature's utility – its *instrumental value* in the terminology of philosophers. One promoted nature as a source of spiritual enlightenment, the other as a source of commodities, but neither claimed that nature had *intrinsic value*, value independent of its usefulness. However, in his journals, which were published posthumously, Muir seemed to entertain the idea that nature may have intrinsic value as a work of God:

> Why should man value himself as more than a small part of the one great unit of creation? And what creature of all that the Lord has taken the pains to make is not essential to the completeness of that unit – the cosmos? The universe would be incomplete without man; but it would also be incomplete without the smallest transmicroscopic creature that dwells beyond our conceitful eyes and knowledge. (Muir 1916)

With the arrival of the science of ecology and the writings of Aldo Leopold (1886–1948) – founder of wildlife conservation as a professional discipline, a man who began his career eradicating predators, but ended it as a strong advocate of wilderness – one finds a utilitarian perspective of species being questioned:

> Ecology is a new fusion point for all the sciences. … The emergence of ecology has placed the economic biologist in a peculiar dilemma: with one hand he points out the accumulated findings of his search for utility or lack of utility in this or that species; with the other he lifts the veil from a biota so complex, so conditioned by interwoven cooperations and competitions, that no man can say where utility begins or ends. (Leopold 1939)

Leopold was saying that because nature is a complex system rather than a random set of species with positive, negative, and neutral values, each species is important as a component of the whole. In other words, species have instrumental value because of their utility in an ecosystem. This was the key idea that spawned the Evolutionary-Ecological Land Ethic. It was a fundamentally different idea that took Leopold's ethical vision beyond the choice of either preserving nature as inviolate or efficiently developing it. Muir wrote of the equality of species in religious terms; Leopold expressed equality in ecological terms. Pinchot (1947) stressed the dichotomy between people and nature ("there are just two things on this material earth – people and natural resources"); Leopold thought of people as citizen-members of the biotic system. Leopold's ideas gave people the right to use and manage nature *and* the responsibility of doing so in a manner that recognized the intrinsic value of other species and whole ecosystems. Indeed, he contended that the very tools that had been so frequently used to destroy the environment (namely the axe and the plow) could also be creatively applied to heal it, especially if informed by science.

All three of these ethics are still thriving. The Resource Conservation Ethic guides the actions of natural resource-based industries and their associated government agencies, although some would argue that the profit motive is too often the stronger guide. Many private conservation/environmental organizations are wedded to the Romantic-Transcendental Preservation Ethic, reflecting a membership that uses nature primarily for spiritual rejuvenation during brief forays out of the cities and suburbs. The Evolutionary-Ecological Land Ethic characterizes some conservation groups and government agencies (e.g. many park and wildlife agencies) that try to balance the needs of people and wildlife (Clark 1998). The idea that people have the rights and responsibility to manage nature carefully may be strongest in Europe, where the hand of humanity is conspicuous on virtually every landscape, and in developing countries, where the urgency of providing for the needs of poor, rural people is widely recognized.

In the conclusion to his essay, Callicott (1990) challenged conservationists with a provocative idea. If people are valid members of the biotic community as Leopold asserts, why do we turn to landscapes without people (at least without agricultural-industrial age people) to set benchmarks for what is natural? If beavers and reef-building corals can shape landscapes in positive ways, why can't people? Can people improve natural ecosystems? These are not simple issues, and we will return to them frequently in this book because this dynamic, often difficult, interface between people and nature is the crux of conservation and conservation biology.

What Is Conservation Biology?

Conservation biology is the applied science of maintaining the earth's biological diversity. A simpler, more obvious definition – biology as applied to conservation issues – would be rather misleading because conservation biology is both less and more than this. It is narrower than this definition because there are many biological aspects of conservation, such as biological research on how to grow timber, improve water quality, or graze livestock, that are only tangentially related to conservation biology. On the other hand, it reaches far beyond biology into disciplines such as philosophy, economics, and sociology that are concerned with the social environment in which we practice conservation, as well as into disciplines such as law and education that shape the ways we implement conservation (Jacobson 1990; Soulé 1985). Because conservation biology is a mission-driven discipline, conservation biologists often find themselves in the arena of political advocacy, a tendency that has earned conservation biology some criticism for straying too far from the accepted value-neutral domain expected of most scientific disciplines.

Forty years ago maintaining biological diversity meant saving endangered species from extinction and was considered a small component of conservation, completely overshadowed by forestry, soil and water conservation, fish and game management, and related disciplines. Now with so many species at risk and the idea of biological diversity extending to genes, ecosystems, and other biological entities, conservation biology has moved into the spotlight as the crisis discipline focused on saving life on earth, perhaps the major issue of our time.

Susan Jacobson (1990) devised a schematic model to illustrate the structure of conservation biology from an educational perspective (Fig. 1.4). As you can see, conservation biology sits between basic biologic sciences and natural resource sciences because it originated largely with basic biologists who have created a new, applied natural resource science. It is different from traditional natural resource sciences because it places relatively greater emphasis on all forms of life and their intrinsic value, compared with other natural resource sciences, which usually focus on a few economically valuable species (Soulé 1985). Like natural resource sciences, conservation biology is influenced by the physical sciences because it addresses issues with strong ecological and environmental linkages. Similarly, it is influenced by social sciences, law, education, and other disciplines because it operates in the world of human socio-economic-political institutions and seeks to change those institutions to allow people to coexist with the rest of the world's species.

This model also shows how students wishing to become conservation biologists need to focus on courses in the basic biologic sciences and the applied sciences of natural resource management while acquiring some understanding of the subjects that shape the arena within which conservation operates. These include physical sciences such as geology and climatology, social sciences such as economics and politics, and subjects such as law, education, and communication that provide a vehicle for changing the structure of society.

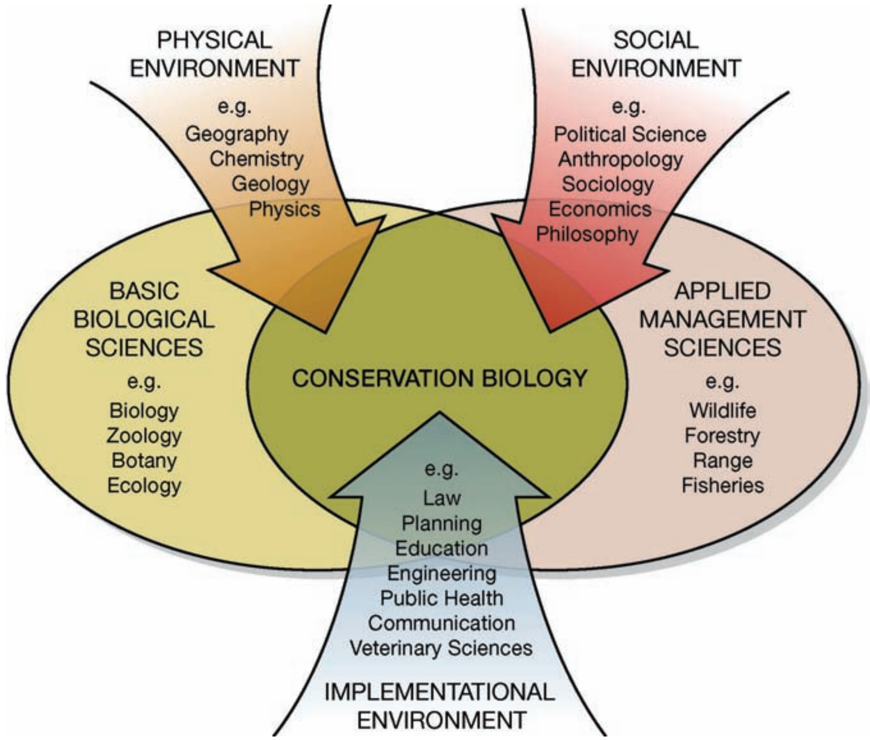


Figure 1.4 A schematic view of the relationship between conservation biology and other disciplines. (Redrawn after Jacobson 1990.)

A Brief History of a Young Discipline

The deepest roots of conservation biology are widespread but its emergence as a discipline is usually attributed to the First International Conference on Conservation Biology held in San Diego, California, in 1978, and to the book that followed, *Conservation Biology*, edited by Michael Soulé and Bruce Wilcox (1980). Eight years after this small beginning the Society for Conservation Biology was formed, and it launched a new journal, *Conservation Biology*, in 1987 (Fig. 1.5). The society and its journal flourished, and universities, foundations, private conservation groups, and government agencies nurtured this growth with an array of conservation biology programs (Jacobson 1990; Meine et al. 2006).

The founders of conservation biology had many more links to institutions of basic biological sciences (e.g. genetics, zoology, botany) than to natural resource management institutions and they wove some novel and diverse intellectual threads into the conservation tapestry. Ideas from evolutionary biology, population dynamics, landscape ecology, and biogeography provided a new understanding of the diversity of life, how it is distributed around the globe, and what most threatens it.

Figure 1.5 The Society for Conservation Biology began publishing *Conservation Biology* in May 1987 and held its first conference that June.

CASE STUDY

Return of the Tortoises to Española[1]

The year is 1960. On the island of Española, a low dry expanse of eroding lava far to the southeast in the Galápagos Archipelago, a giant tortoise rests under a bush and gazes out to sea. The edges of her shell flare out dramatically – a distinctive characteristic of her lineage – but lichens cover the shell, a sign that she has not bred in decades. Moreover, her head lies weakly on her outstretched forelimbs, her body withering within her shell. Beyond the small bush sheltering her from the blazing sun hooves thud against rock and dust swirls as a herd of goats mills about. Kids bleat hungrily after their mothers. The island is devastated, and even the goats are starving. The magnificent stands of arboreal cactus that once crowned the island are gone, torn down and stripped of their pads. Gone also is the carpet of fragile herbs and grasses that once covered the island. Even the finches and mockingbirds that flitted about noisily in search of seeds and insects have mostly disappeared. Little remains but patches of prickly mesquite and expanses of exposed, powdery earth, from which a lava block occasionally protrudes, polished brightly by the shells and claws of thousands of generations of giant tortoises. But they too are now all gone. Seemingly only the old female tortoise remains.

By the 1950s the tortoises of Española Island had been given up as extinct. The island was low and accessible and the first stop for many whaling ships visiting the Galápagos in the 1800s. These sailing ships disgorged hungry sailors, who wobbled on their unstable “sea legs” deep into the trackless island, smoking clay pipes and clutching precious water supplies in fragile, hand-blown glass bottles. After much searching these sailors – mostly poor men conscripted from coastal villages along the northeastern coast of the United States – used make-shift stretchers to haul back down the island what may have been thousands of the giant tortoises collectively. These they rowed back in long boats to the ships and stored below decks for up to a year, without food or water, and, back under sail, the sailors slaughtered the tortoises one-by-one to provide occasional fresh meat for the often scurvy-ridden crew. After several decades of such depredations even the whaling ships stopped visiting Española once word got around that the tortoises were all gone. The introduction of goats to the island (presumably to supply another source of meat for future visits) made matters even worse. By the 1950s observations from boats passing the island of the enormous goat population and wasted landscape confirmed that the famous Española tortoises must be gone forever.

One person, however, held out hope. Miguel Castro had been recently appointed as the first tortoise warden ever in the Galápagos Islands. He had a tough task ahead of him: starting the first program to protect these magnificent reptiles, which had been subject to plunder for two centuries and remained mere sources of bush meat in the eyes of most local people. Castro sailed to Española and made a brief reconnaissance trip in August 1963 in hope that some tortoises might still exist. After much wandering around he found to his great surprise a single tortoise eating a torn-down cactus in the company of 15 goats. If there was one, perhaps there might be more. His curiosity piqued, Castro made a second trip in November 1963. Again he saw mostly goats, thousands of them, busily stripping bark from cactus tree roots, causing the cacti to fall over. Remarkably, he also found the same tortoise he had found in August. He then found another tortoise, in a different part of the island. The signs were positive that perhaps a small nucleus of tortoises might survive.

Further trips to Española located a few more individuals. In desperation, the director of the Charles Darwin Research Station, Roger Perry, ordered the removal of all animals that could be found to captivity at a safe location at the research station on another island. Some 14 were eventually located. Once they were together in captivity mating quickly ensued among the tortoises, perhaps the first breeding to occur in a half-century! But producing young tortoises was not easy. No one had bred giant tortoises successfully in large numbers before. Even the best zoos of Europe and the United States had tried in vain.

Through trial and error, another individual, Fausto Llerana, along with many helpers and advisors, gradually developed tortoise husbandry at the Research Station. Nesting initially failed because improper soil was provided. Some females laid their eggs on the soil surface, where the eggs were promptly attacked by birds. Others used the sandy soil provided, but it did not adhere well and this prevented females from digging proper nests. They often slipped on the edges of their nests while attempting to gently arrange their eggs with their rear legs at the end of the laying process, damaging the eggs in the process. Better soil was provided and hatching rates improved.

Figuring out the best diets for the animals was also a challenge, as well as how to keep these large herbivores happy and well fed on a tiny budget. A variety of local foods was offered, and slowly a tortoise diet was developed that balanced palatability, nutrition, availability, and cost. Despite these initial problems the tortoises began to reproduce well, and the effort showed that it was quite possible to establish a functional breeding colony in the Galápagos. Moreover, natural climatic conditions, local plants for foods, and native soils for nesting eliminated most of the reproductive, veterinary, dietary, and housing costs experienced by "high tech" zoos overseas.

One lingering problem was that the small nucleus of adults remaining had a very skewed sex ratio. Either by chance or because males tend to be more aggressive, larger, and conspicuous to tortoise hunters, the remaining population was heavily skewed: 12 females and just two males. So the international search for more Española tortoises began. Old records were unclear but suggested that a group of tortoises had been removed from Española and shipped to San Diego around 1934–6. Perhaps some survived 35 years later in distant California. Further investigation revealed that there was indeed a male still alive from that shipment – a third known living male for Española. So-called "Diego" was large and still extremely vigorous. He was boxed and after several false starts trying to find an aircraft suitable to transport him, he was finally flown to Ecuador and then sailed back to Galápagos in August 1977. Diego was apparently thrilled to finally arrive back home after a 40-year absence: the captive population became surprisingly productive shortly after his arrival. By 1976, 88 young had been produced, increasing the population from 14 to 102 in just five years. Diego is to this day a prolific breeder.

The captive Española tortoises also had a major, unanticipated, and ancillary benefit: educational and public relations value. Local people, especially school children, and tourists visited the rearing center with its breeding enclosures and incubators. The tortoise conservation program was a huge hit for all. Visitors could see the little hatchlings clustered around their water baths. In one exhibit they could even walk among and view without barriers some older tortoises from other islands. The breeding program came to serve as a prime example of what needed to be done to preserve what remained and to reclaim some of what had been lost in Galápagos. It remains a major attraction to visitors.

Once numbers in captivity had built up and the Española tortoises were out of danger of outright extinction, the Galápagos National Park Service turned its attentions to remedying the problems on the tortoises' home turf back on Española. During the 1970s, about 3000 goats were eliminated from Española through an intense campaign by guards of the Galápagos National Park Service. Groups of guards with rifles, stout boots, and jugs of water would go to the field for weeks and even months and hunt down the goats. The terrain was difficult and the comforts were few. They lived largely off what they hunted. Huge numbers of goats were culled early in the process but the very last goats took many months to eliminate. The last goats were of course the wiliest ones of all; the hunters knew each by its coat color. The guards eventually succeeded, through sheer dedication and skill, and now just skulls of goats litter the island, weathering to bright white in the blazing sun. The nutrients the goats took from the ecosystem are being slowly incorporated back into it as the plant and animal communities reorganize themselves and begin to recuperate after being turned upside down by goats for at least a century.

After the goats were removed the repatriations of the first hatchling tortoises began in 1975. Areas of the island with the last remaining patches of cactus were chosen as special release sites because the cactus provides critical food, moisture, and shade for young tortoises. Boxes of five-year-old hatchlings were transported first by sea and then up the rocky slopes of the islands in backpacks and released one-by-one. By August 2002, the captive population had generated 1200 offspring that were repatriated to Española. The vegetation has recuperated rapidly, with the exception of the slow-growing cacti, which remain scattered and rare and evidently much reduced in number. But even the cacti are showing signs of recovery now that the tortoises are back to disperse their seeds. Of the repatriated tortoises, perhaps half die of natural causes but half survive and grow well. Most significantly, after nearly 30 years of reintroductions, some of the first repatriates have grown to adulthood. These repatriated tortoises are now reproducing among themselves on Española (Fig. 1.6). Nests can be found, as can, occasionally, a soft-shelled, tiny tortoise newly emerged from its nest.

The Española tortoises, once abandoned and quietly relegated to extinction, have returned to their native ground. They are now essentially taking care of themselves. Humans can step back out of the picture, after being a destructive force and then a healing one in it for two centuries. We can now let the tortoises and the ecosystem of which they are part resume interacting as they have done for thousands of years previously.

Coda

Here on Española Island, conservation has succeeded. It was accomplished by a cadre of dedicated individuals, mostly Ecuadorian park managers and scientists with some foreign support, working with scarce funds. It is an example of the awesome power of humans to control the fate of wild life. It is also an example of how we can be both agents of destruction and benevolent stewards. This book seeks to explore these issues with you in much greater detail and to provide guidance on achieving positive outcomes for the many creatures around the world that, like the Española tortoises, are still struggling to survive.

Figure 1.6 This Española tortoise was among the very first repatriated to the island as a small hatchling some 25–30 years ago, once goats had been removed and the island's habitat restored. It is likely one of the tortoises now responsible for the new hatchlings appearing again on the island, representing the first reproduction in this population in many decades. (Photo from J. Gibbs.)

1 Primary sources for this section are Marquez et al. (1991), Milinkovitch et al. (2004), and personal observations.

By forming a new professional society dedicated to the maintenance of biological diversity, conservation biologists overlapped some of the domain of some older professional societies. This was especially true of The Wildlife Society, which, on the first page of the first issue of *The Journal of Wildlife Management*, described wildlife management as "part of the greater movement for conservation of our entire native flora and fauna" (Bennitt et al. 1937). Despite some broad goals the dominant concern of wildlife management in its early years was managing populations of mammals and birds for sport hunting. Today wildlife managers place an ever-growing emphasis on endangered and nongame species, including reptiles, amphibians, and sometimes even invertebrates and plants, but much, arguably most, of their attention is still focused on game species. Perhaps, if more wildlife managers had reached out to embrace all forms of life that are wild, not just the vertebrates, and to work with a constituency of all people who care about nature, not just hunters and anglers, then conservation biology might not have arisen as a separate discipline. This is especially apparent if one defines "wildlife" as "all forms of life that are wild," a definition that overlaps substantially with biodiversity. (To make it clear that this book uses a broad definition, the original, two-word spelling, "wild life," will be used.)

Summary

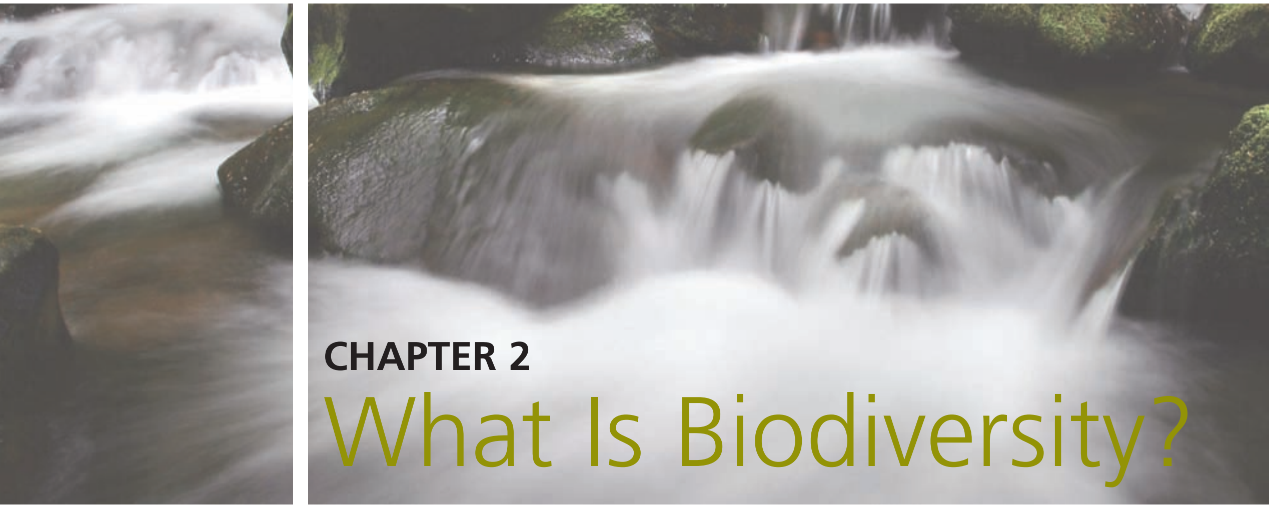
People who care about nature and the natural resources we obtain from nature, such as clean air and clean water, come with many labels: conservationists and preservationists, environmentalists and ecologists. Although these people share many goals, their priorities can differ. For example, conservationists advocate the careful use of natural resources, whereas environmentalists often emphasize maintaining an uncontaminated environment. The history of conservation has a recurring theme: people being forced to limit their use of natural resources more and more as human populations grow and technological sophistication increases. Conservation history is marked by laws regulating our use of natural resources, but more fundamental is the evolution of our ethical attitudes toward nature and its intrinsic and instrumental values. Callicott (1990) has described three such ethical positions: (1) the Romantic-Transcendental Preservation Ethic (briefly, nature is best used for spiritual purposes); (2) the Resource Conservation Ethic (nature is natural resources to be carefully developed for human purposes); and (3) the Evolutionary-Ecological Land Ethic (people are part of nature and have both the right to change it and a responsibility for respecting the intrinsic value of other species and ecosystems in general). Conservation biology is the applied science of maintaining the earth's biological diversity. It is a cross-disciplinary subject lying between basic biologic sciences and natural resource sciences. It differs from basic biologic sciences because it reaches out to economics, law, education, politics, philosophy, and other subjects that shape the human world within which conservation must operate. It differs from traditional natural resource sciences because it places relatively greater emphasis on all forms of life and their intrinsic value, compared with other natural resource sciences, which typically focus on a few species with high instrumental (usually economic) value.

FURTHER READING

A comprehensive world history of conservation would be a weighty tome but one succinct treatment is available (Hughes 2001a). Many books cover certain times, phenomena, and places; for example, the sixteenth to eighteenth centuries (Richards 2003), the twentieth century (McNeill 2000), European colonization (Grove 1995), collapse of civilizations (Diamond 2005), Costa Rica (Evans 1999), south and southeast Asia (Grove et al. 1998), the United Kingdom (Moore 1987), and the United States (Nash 1990). Related books include histories of ecology (Worster 1994) and environmental ethics (Nash 1988). Also see Hughes (2001b) and the journal Environmental History for an entreé into the literature. Articles by Soulé (1985), Callicott (1990), and Jacobson (1990) form a foundation for the latter parts of the chapter and merit further reading. For relevant websites, check out the Society for Conservation Biology's website at www.conservationbiology.org and some of the major international conservation groups at www.iucn.org, www.wwf.org, www.nature.org, www.conservation.org, and www.worldwildlife.org.

TOPICS FOR DISCUSSION

1. Do you think of yourself primarily as a conservationist, environmentalist, ecologist, or preservationist, or none of these? Why?
2. Which of the three ethics described by Callicott do you think will be predominant 50 years from now? Why? Would you feel comfortable promoting one of these ethics among your friends and family?
3. Name some organizations that exemplify each of the three ethics today. Have any of these organizations changed their philosophy?
4. Can you identify some specific examples of how each of the disciplines in Fig. 1.4 has contributed to conservation biology?



CHAPTER 2

What Is Biodiversity?

A tropical forest ringing with a cacophony of unseen frogs, insects, and birds; a coral reef seething with schools of myriad iridescent fishes; a vast tawny carpet of grass punctuated by herds of wildebeest and other antelope – these images are well known, and for many people they all revolve around a central issue and a single word, "biodiversity" (Fig. 2.1). Some have argued that "biodiversity" is too vague and trendy to be a useful word, but it does succinctly imply a fundamental idea: life on earth is extraordinarily diverse and complex. This idea is not as well captured in other words such as "nature" or "wild life." Furthermore, "biodiversity" has entered the public vocabulary at a time when global concerns about the survival of life are at their zenith, and thus to many people the term carries a conviction to stem the loss of the planet's life-forms.

Definitions of biodiversity usually go one step beyond the obvious – the diversity of life – and define biodiversity as the variety of life in all its forms and at all levels of organization. "In all its forms" reminds us that biodiversity includes plants, invertebrate animals, fungi, bacteria, and other microorganisms, as well as the vertebrates that garner most of the attention. "All levels of organization" indicates that biodiversity refers to the diversity of genes and ecosystems, as well as species diversity. The idea that biodiversity has levels of organization introduces a depth of complexity that we will explore in the next three chapters, "Species Diversity," "Ecosystem Diversity," and "Genetic Diversity," after a brief overview here.

Species, Genes, and Ecosystems

It is easiest to comprehend the idea of maintaining biodiversity in terms of species that are threatened with extinction. We know about blue whales, giant pandas, and whooping cranes, and we would experience a sense of loss if they were to disappear, even though most of us have never encountered them except in films and magazine articles. For most mosses, lichens, fungi, insects, and other small species that are unknown to the general public, it is much harder to elicit concern. Nevertheless, many people are prepared to extend some of the feelings they have for whales, pandas, and cranes to species they do not know, as an expression of their belief that all species have some intrinsic value.

Like tiny obscure species, genes are rather hard to understand and appreciate. These self-replicating pieces of DNA that shape the form and function of each individual organism are obviously important, but so are water, oxygen, and thousands of other molecules. It is not the genes themselves that conservation biologists value; it is the

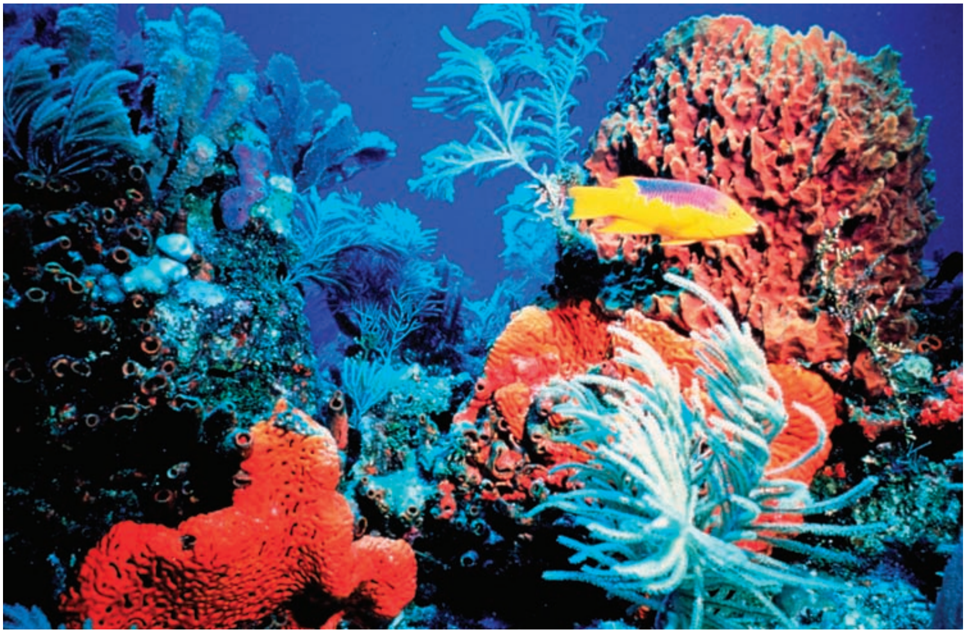


Figure 2.1 There are few places where biodiversity is as conspicuous as a coral reef. (Photo from the Florida Keys National Marine Sanctuary Staff.)

diversity that they impart to organisms that is so essential. If two individual strawberry plants have a different set of genes, one of them might be better adapted to fluctuations in water availability and thus would be more likely to survive a period of climate change. One of them might be less susceptible to damage from ozone and other types of air pollution. The fruit of one might be more resistant to rotting and therefore its progeny might prove useful to strawberry breeders and farmers. Perhaps the fruits simply taste different and thereby provide aesthetic diversity. The diversity of life begins with genetic differences among individuals and the processes of evolution that lead to differences among populations, species, and ultimately the higher taxonomic levels: genera, families, orders, and so on.

Unlike genes, ecosystems are large and conspicuous, and thus anyone with the most rudimentary understanding of ecology appreciates the value of lakes, forests, wetlands, and so on. Nevertheless, ecosystems can be hard to define in practice. Where do you draw the boundary between a lake and the marsh that surrounds it when many organisms are moving back and forth between the two? This sort of problem can complicate the role of ecosystems in biodiversity conservation. Conservation biologists often advocate protecting examples of all the different types of ecosystems in a region, but how finely should differences be recognized? Is an oak–pine forest ecosystem that is 60% oak and 40% pine appreciably different from one that is 40% oak and 60% pine? If you look hard enough, every ecosystem will be unique. The rationale for protecting ecosystem diversity also differs. Some conservationists advocate protecting ecosystems as independent biological entities that are not just a loose assemblage of species, whereas others think of protecting ecosystems simply as an efficient way to protect the species that compose the ecosystem.

Structure and Function

The definition of biodiversity provided above emphasizes structure – forms of life and levels of organization – but sometimes ecological and evolutionary functions or processes are also included in a definition of biodiversity. For example, the Wildlife Society (1993) defines biodiversity as "the richness, abundance, and variability of plant and animal species and communities and the *ecological processes that link them with one another and with soil, air, and water*" (emphasis added).

The diversity of ecological functions is enormous. First, each of the earth's millions of species interacts with other species, often many other species, through ecological processes such as competition, predation, parasitism, mutualism, and others. Second, every species interacts with its physical environment through processes that exchange energy and elements between the living and nonliving worlds, such as photosynthesis, biogeochemical cycling, and respiration. All of these functional interactions must total in the billions. The diversity of evolutionary functions is even more complex. It includes all these ecological processes because they are key elements of natural selection, in addition to processes such as genetic mutation that shape each species' genetic diversity.

Functional biodiversity is clearly important. For example, a management plan designed to keep a species from becoming extinct will almost certainly fail in the long run unless the processes of evolution, especially natural selection, continue, allowing the species to adapt to a changing environment. Sometimes, focusing on a functional characteristic – for example, the hydrological regime of a wetland (Turner et al. 1999) – is the most efficient way to maintain the biodiversity of an ecosystem. Nevertheless, conservation biologists usually focus on maintaining structural biodiversity rather than functional biodiversity for two reasons. First, maintaining structural biodiversity is usually more straightforward. In particular, it is easier to inventory species than their interactions with one another. Second, if structural diversity is successfully maintained, functional biodiversity will probably be maintained as well. If we can maintain a species of orchid and its primary insect pollinator together in the same ecosystem, then we will probably have a pollination interaction between the two. Similarly, if we can maintain the orchid's genetic diversity, we will probably have orchid evolution. The qualifier "probably" has been added here because one can imagine circumstances in which structural diversity is maintained without maintaining functional biodiversity in full. For example, natural selection may not have the opportunity to operate on the genetic diversity represented in the seeds that plant breeders store in a freezer to maintain the structural diversity of a crop plant species. On the other hand, it is much easier to think of circumstances where some major ecological processes are maintained, but structural diversity is severely degraded; for example, a plantation of exotic trees that maintain normal rates of photosynthesis and biogeochemical cycling.

In short, both the structural and functional aspects of biodiversity are important; however, if genetic, species, and ecosystem diversity are successfully maintained, then ecological and evolutionary processes will probably be maintained as well.

Measuring Biodiversity

It is easy to provide a simple definition of biodiversity, such as "the variety of life in all its forms and at all levels of organization," but this is only a starting point. To monitor biodiversity and develop scientific management plans, we should have a quantitative definition that allows us to measure biodiversity at different times and places.

Ecosystem A	Ecosystem B	Ecosystem C
Black oak	Black oak	Black oak
White pine	White pine	White pine
Red maple	Red maple	Red maple
Yellow birch		

Table 2.1 Hypothetical lists of species for three ecosystems.

The first step in measuring biodiversity is to determine which elements of biodiversity are present in the area of interest. Ideally, we would have a complete inventory, including genes, species, and ecosystems. In practice, logistical constraints commonly limit us to a partial list of species, often listing only vertebrates and perhaps vascular plants. (Sometimes a list of ecosystems is compiled, although the basis for distinguishing among the different types is often unclear; we will focus on the species level of biodiversity here for simplicity.) Lists can be tallied to provide a crude index of biodiversity. In Table 2.1, for example, ecosystem A is easily recognized as more diverse than B or C because it has four species instead of three. This characteristic is called *species richness* or just richness, and it is a simple, commonly used measure of diversity.

Ecologists also recognize a second component of diversity called *evenness*, which is based on the relative abundance of different species. In Table 2.2 ecosystem C is more diverse than B because in C the three species have similar levels of abundance, or high evenness. The concept of evenness is not as intuitively obvious as the idea of richness. It may help to think of a jury that has five women and five men versus one that has eight women and two men; the five plus five jury is more diverse because it is more even.

The ecological importance of species richness seems quite evident, especially if you consider the loss of richness through extinction. Similarly, most conservation

Ecosystem	A	B	C
Black oak	40	120	80
White pine	30	60	60
Red maple	20	20	60
Yellow birch	10		
Richness	4	3	3
Evenness	0.92	0.88	0.99
H	0.56	0.39	0.47

H = $-\Sigma p_i \log p_i$, where p_i is a measure of the importance of the *i*th species.
Evenness = H/H_{max}, where H_{max} is the maximum possible value of *H*.

Table 2.2 Abundance of species (number/hectare) in three ecosystems and measures of richness, evenness, and the Shannon diversity index (*H*), one of many ways to combine richness and evenness quantitatively (Magurran 2004).

biologists would be concerned about any process that reduced evenness, because this would mean uncommon species are becoming less common, while common species are becoming more common. To return to our jury metaphor, this would be analogous to losing a man from the jury that only had two men. Richness and evenness are often combined into a single index of diversity using mathematical formulae (Table 2.2) but, as we will see in the next section, such indices are of limited utility.

The Mismeasure of Biodiversity

Often, being precise and quantitative will reveal solutions to a difficult problem, but using quantitative indices of diversity can be misleading when maintaining biodiversity is the goal. Consider the following three lists of species, each one representing (in very abbreviated form) a sample of the species found in three different types of ecosystems.

Forest	**Marsh**	**Grassland**
Black oak	Reed-grass	White prairie-clover
Shagbark hickory	Painted turtle	Horned lark
Gray squirrel	Red-winged blackbird	Black-footed ferret
White-tailed deer	Muskrat	
Raccoon		

If someone were asked which of these tracts is most important from the perspective of maintaining biodiversity, one measure of biodiversity – species richness – would suggest that the forest be chosen. However, if you knew that the black-footed ferret is one of the rarest mammals in the world and that all the other species listed are very common, you might well select the grassland tract. Why?

The simple answer is that all species may count the same when tallying species richness, but conservationists almost always consider additional information such as the likelihood of a species becoming extinct, its role in an ecosystem, and more. Consequently, all species are not equal from a conservation perspective. We will return to this issue in other chapters, but we need to build a foundation here by considering how conservation decisions are shaped by patterns of diversity and risk of extinction at different spatial scales.

Biodiversity and Spatial Scales

Extinction usually refers to the disappearance of a species from the earth, but the term is also routinely used, with modifiers, to describe the disappearance of a species from a smaller area. For example, when a species disappears from a small area, this is called a *local extinction*, even though the area may later be recolonized by immigrants, e.g. when beavers return to a valley from which they had disappeared. On a somewhat larger scale one can refer to *regional extinction*. Extinctions that are not global in scope are sometimes called *extirpations*. Although conservation biologists are most concerned about global extinctions, smaller-scale extinctions are also of some concern because they may foreshadow extinctions on a larger scale and because they may represent a loss of genetic diversity. Another key term is *endemic*, which

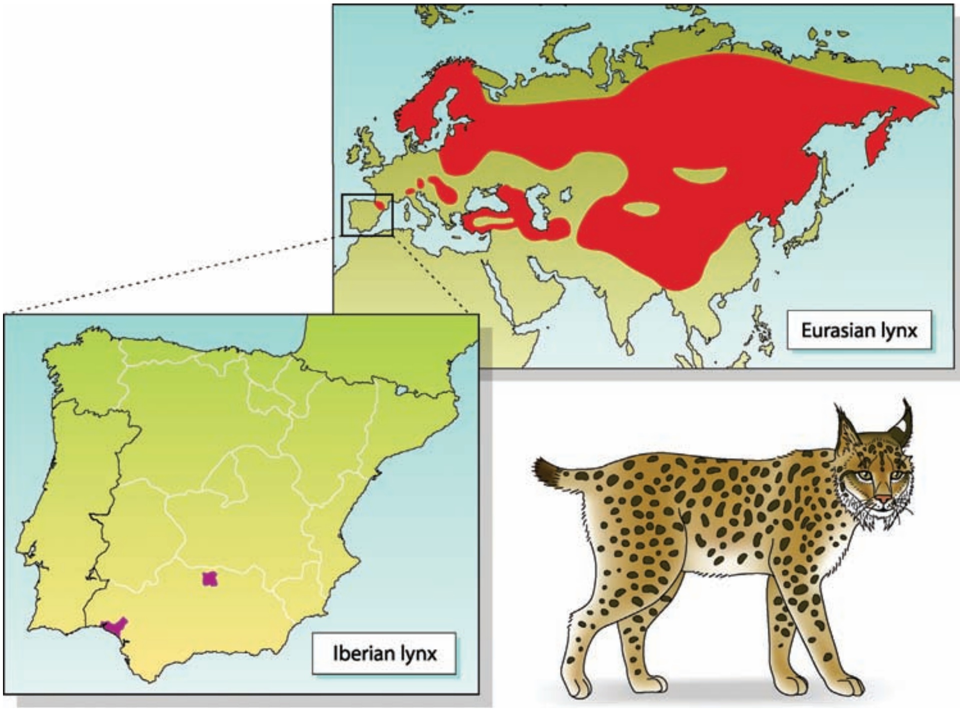


Figure 2.2 Conservationists do not consider all species to be equally important. For example, the Iberian lynx, a species confined to southern Spain, is a higher priority for Spanish conservationists than the Eurasian lynx, which has a huge range that just reaches northern Spain.

refers to species found only in a defined geographic area; thus, koalas are endemic to Australia. If a species is found only in a small area (e.g. many inhabitants of the Galápagos and other isolated islands), it is called a *local endemic*.

The risks of extinction at different spatial scales are a key consideration when deciding which endangered species are a high priority. The larger the scale at which an extinction is likely to occur, the more important it is to try to prevent it. For example, Spanish conservationists place a higher priority on protecting the Iberian lynx, a species endemic to southern Spain and Portugal that faces global extinction, than on the Eurasian lynx, a species threatened with regional extinction from the Pyrenees Mountains along the Spanish–French border, but still relatively secure in much of eastern Europe and Asia (Fig. 2.2).

The ecologist Robert Whittaker (1960) devised a simple system for classifying the scales at which diversity occurs; he described three scales of diversity as alpha, beta, gamma (A, B, C in Greek). *Alpha diversity* is the diversity that exists within an ecosystem. In Fig. 2.3 two hypothetical lizard species, spotted lizards and long-tailed lizards, illustrate alpha diversity by coexisting in the same forest, living at different heights within the forest. A third species, banded lizards, illustrates *beta diversity* (among ecosystems diversity) by occurring in a nearby field. Finally, if you imagine spotted, long-tailed, and banded lizards living on one island, and a fourth species, speckled lizards, living a thousand kilometers away on another island, this would represent *gamma diversity*, or geographic-scale diversity.

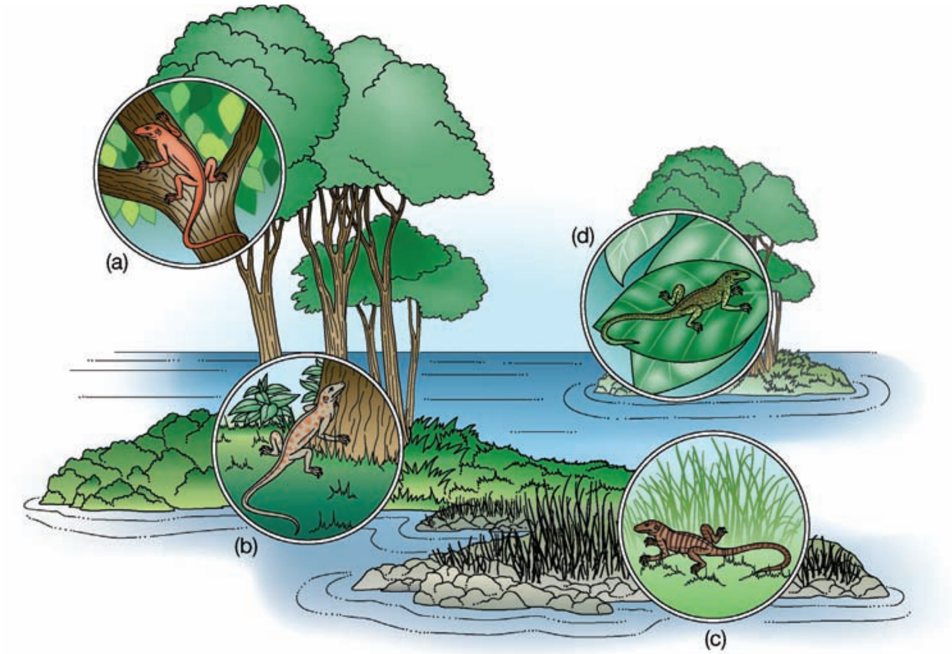


Figure 2.3 The distribution of four hypothetical lizard species showing alpha diversity (within an ecosystem, A plus B), beta diversity (among ecosystems, A/B plus C), and gamma diversity (geographic scale, A/B/C plus D). See text.

We can use this hypothetical example to show how a narrow-scale perspective on maintaining biodiversity can lead would-be supporters of biodiversity astray. Some people might look at Fig. 2.3 and think, "There are more lizard species in forests, so let's plant trees in the field." By doing so they might increase the alpha diversity of the field from one lizard to two (from banded lizards to spotted and long-tailed lizards), but they might also decrease the beta diversity of the island from three species to two because banded lizards would no longer have any suitable habitat. Similarly, they might think, "Let's bring some of the speckled lizards from the other island to our forest and have four species here." However, the speckled lizards might outcompete and replace one of the local lizards or introduce a disease. The whole archipelago could end up with only three, two, or one lizard species instead of four and thus decreased gamma diversity.

The idea of spatial scale is so fundamental to maintaining biodiversity that a mnemonic phrase is worth remembering: "Scale is the tail that *w-a-g-s* biodiversity" (*w*, within ecosystem diversity; *a*, among ecosystem diversity; *g-s*, geographic-scale diversity).

Diversity components usually vary dramatically from one scale to another, but not always. Take the extreme case of the flowering plants of Antarctica. They include just two species – a grass, *Deschampsia antarctica*, and a cushion-forming plant, *Colobanthus quintensis* – that usually co-occur at the same sites. This is a very rare case where alpha and gamma diversity are the same.

Perspicacious readers may think that some intuitively obvious ideas are being belabored here, but these ideas are frequently overlooked in the real world of natural resource management. For example, natural resource managers who manage large tracts of contiguous forest often claim that they can increase the biodiversity of their forest by cutting moderate-sized patches in their forest (Hunter 1990). This claim is usually true; cutting some patches in a mature forest typically increases species richness by providing new habitats for many early successional species, while most of the species associated with a mature forest ecosystem will persist in the remaining uncut forest. On the other hand, what about the few forest species that may not survive after cutting? For example, some plant species may disappear because deer populations often increase dramatically after cutting (Miller et al. 1992; Kirby 2001). Global populations of some species found in the interior of mature forests are probably declining as large tracts of unbroken forest become scarcer. If they become extinct, then global diversity will have been reduced, while the beta diversity of some forested landscapes was being increased. In sum, whenever we manipulate diversity at a local scale, we should consider the consequences at a larger scale and not rely on simple measurements of local biodiversity to judge the outcome. The following case study illustrates this issue well.

Biodiversity Verbs

People change, manipulate, and manage the world and, consequently, affect biodiversity. Most of our activities have a negative impact on biodiversity; conservation biologists promote positive actions and use a variety of verbs to describe these activities. The verb *maintain* is dominant in this book because a major goal of conservation biology is to keep all the elements of biodiversity on earth, despite human-induced changes that tend to diminish biodiversity. In this section we will evaluate some alternative verbs that are often encountered in the conservation biology literature. This may seem like a pedantic exercise, but some verbs carry implications that are not always consistent with the goal of maintaining biodiversity. For example, to *maximize* biodiversity implies manipulations such as increasing the alpha diversity of an ecosystem, even importing exotic species, without considering the big picture. What is the natural level of biodiversity in that type of ecosystem? What will be the consequences for biodiversity at a larger scale? Manipulating the lizard populations in Fig. 2.3 is a good example of this. To *increase* or to *enhance* biodiversity may imply the same shortsightedness, unless we are referring to an ecosystem in which biodiversity has been diminished by previous human activity and the goal is to return it to its previous state. If this is the case, it is probably best to refer to *restoring* biodiversity. *Protecting* biodiversity is similar to maintaining biodiversity but with a heavier emphasis on the negative impact of most human activities. To *preserve* biodiversity carries a connotation comparable with "to protect," but it may also imply that the only way to maintain biodiversity is to isolate it from human influence as much as possible; this is not always feasible or desirable. To *benefit* or *optimize* biodiversity is rather vague, and these terms are sometimes used by people who have unusual ideas about what is beneficial or optimal. Finally, to *conserve* biodiversity implies using it carefully in a manner that will not diminish it in the long term. This is a reasonable goal, but it tends to overlook the idea that many elements of biodiversity have little or no instrumental value for people.

The Related Concepts of "Integrity" and "Sustainability"

"Biodiversity" is only one of several concepts that have been competing for the attention of natural resource managers in recent years; it has been joined by "sustainability," "ecosystem integrity," "biotic integrity," and others. In this section we will attempt to clarify the linkages and differences between these terms and biodiversity with a distillation of two syntheses, Callicott et al. (1999) and, primarily, Hunter (1999) (Fig. 2.5).

CASE STUDY

Clear Lake

In the northeastern corner of California lies Clear Lake, a large body of water (17,760 ha) that is shallow, warm, and productive; thus it supports a great abundance of fish. Originally, Clear Lake was home to 12 native kinds of fish, at least three of which were endemic to the lake: the Clear Lake splittail, Clear Lake hitch, and Clear Lake tule perch (Moyle 1976a, personal communication) (Fig. 2.4). Two of the native species, Pacific lamprey and rainbow trout, migrated between tributaries of the lake and the sea and practically disappeared from the lake when a dam was built on the lake's outlet. Other species were decimated largely because of human attempts to increase the fish diversity of the lake by importing exotic species, primarily sport fish sought by anglers. By 1894 carp and two species of catfishes had been introduced to Clear Lake, and they flourished there. During the twentieth century 13 additional species were introduced, primarily members of the Centrarchidae family (sunfishes and basses) native to the eastern United States. One species introduced in 1967, the inland silversides, soon became the most abundant species in the lake. In the face of this competition, the native species have declined dramatically, and only four native species remain common in the lake. Worse still, two of the native species that have disappeared from the lake (the Clear Lake splittail and the thicktail chub) are globally extinct. The net scorecard: misguided attempts to enrich the fish fauna of Clear Lake have increased the number of fish species there from 12 to 25 by adding 16 exotic species, but these introductions have decimated the lake's native fish fauna, eliminating two elements of biodiversity from the entire planet and reducing gamma diversity. This was not a very good trade.

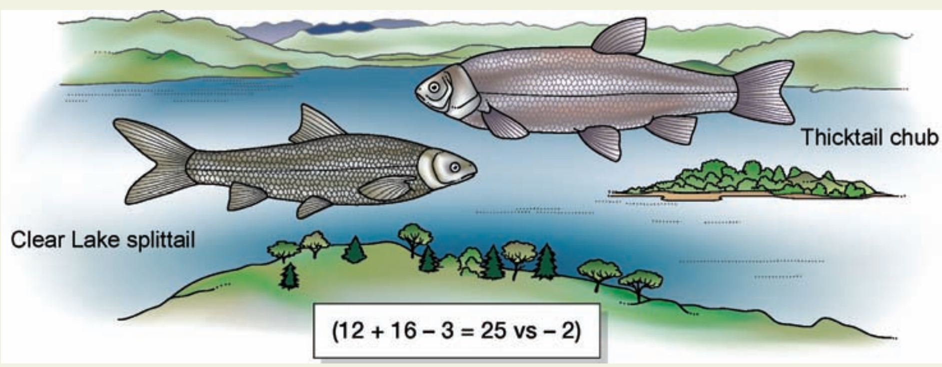


Figure 2.4 Clear Lake in northern California used to be inhabited by 12 native species of fish until fisheries managers began introducing new fish species, 16 in all. These introductions decimated the native fish populations, but still produced a net increase in alpha diversity of 13 species. This increase came at the expense of global diversity because two of the original species, the Clear Lake splittail and the thicktail chub, are now globally extinct.

Biotic Integrity

Biotic or biological integrity refers to the completeness or wholeness of a biological system, including the presence of all the elements at appropriate densities and the occurrence of all the processes at appropriate rates (Angermeier and Karr 1994), and thus it is quite similar to the concept of biodiversity. The difference is mainly a matter of

Figure 2.5 What is the state of this Pacific kelp forest? From a biodiversity perspective we would focus primarily on having a complete set of the native species (especially any that might be in danger of disappearing from the system), as well as genetic and ecological attributes. A biotic integrity perspective would be similar, but would put more emphasis on having an appropriate density of each species and the appropriate rate of ecological processes. In terms of ecosystem integrity, the emphasis would be on the ecological processes driving this system. A focus on sustainability would center on the prospects for maintaining this system in the future. (Photo from David Zippin.)

emphasis. Biotic integrity emphasizes the overall balance and completeness of biological systems, while biodiversity emphasizes that all the biotic elements are present. Furthermore, biotic integrity gives almost equal weight to functions and structure, whereas biodiversity usually emphasizes structure. Consequently, a person who was judging the biotic integrity of an ecosystem would be likely to focus on the ecosystem's key species and processes and might overlook the disappearance of a rare species. The well-being of rare things – species, ecosystems, and sometimes genes – is always in the spotlight from a biodiversity perspective. A biotic integrity perspective does avoid some of the misunderstandings about biodiversity described earlier in this chapter. This is accomplished primarily by focusing on the condition of an ecosystem with respect to a reference condition, usually what the ecosystem would be like if it were in a natural state (Hunter 1996; Angermeier 2000). For example, no one could ever claim that they had increased biotic integrity by increasing the number of fish species in Clear Lake.

Ecosystem Integrity

Ecosystem health and ecosystem integrity (or ecological health and integrity) are effectively synonymous. "Ecosystem integrity" is generally a preferable term because the inevitable analogy between ecosystem health and human health can be misleading (to take just one example, an ecosystem that is profoundly affected by a native pathogen is not necessarily unhealthy) (Suter 1993; De Leo and Levins 1997; Rapport 1998). In some ways, ecosystem integrity is broader than both biotic integrity and biodiversity because it encompasses the physical environment; for example, soil erosion and sedimentation are key aspects of ecosystem integrity. Because ecosystem ecologists often focus on overall processes, ecosystem integrity is usually evaluated in terms of ecosystem functions, rather than the suite of species that constitute the biological portion of an ecosystem (Callicott et al. 1999). From an ecosystem integrity perspective the productivity or water quality of Clear Lake might be considered as important as the species composition of the fish fauna.

Sustainability

"Sustainability" is simply the ability to maintain something over time without diminishing it. In a natural resource management context, sustaining the resources that are most directly used by people – timber, fisheries, water, recreational opportunities, and so on – usually comes first (Lélé and Norgaard 1996). The key idea here is "intergenerational equity" or, in plainer language, not messing things up for our children and grandchildren. Obviously conservation biologists support sustaining biodiversity, but they are not all comfortable with the term, partly because it implies that the status quo is a desirable state and partly because the term is primarily associated with the instrumental value of natural resources demanded by people (Newton and Freyfogle 2005a, b). For example, sustaining the sport fisheries of Clear Lake has not required sustaining the native fishes.

Values

People's values are clearly reflected in their choices of what should be sustained. It is also true, but less obvious, that the ways we judge biotic integrity and ecosystem integrity are also shaped by values (Lélé and Norgaard 1996; De Leo and Levins 1997; Lackey 2001). Proponents of the biotic integrity concept are quite explicit that their ideas about "all appropriate elements and occurrence of all processes at appropriate rates" are based on using natural systems as benchmarks, that is, those with little or no human influence (Angermeier and Karr 1994; Hunter 1996). For example, they would decide whether a particular species of lizard belongs on a given island by whether it would be there without human intervention. Many biologists would share this standard, but there is nothing sacred about using a natural system as the basis for comparison. For example, Robert Lackey (1995) has argued that "An undiscovered tundra lake and an artificial lake at Disneyland can be equally healthy." For him the key question is whether the lake is in a desired state, i.e. is it satisfying human expectations? The bottom line is that to use any of these concepts, including biodiversity, requires some kind of benchmark, and the selection of benchmarks inevitably reflects human values.

Summary

Biodiversity is the variety of life in all its forms (plants, animals, fungi, bacteria, and other microorganisms) and at all levels of organization (genes, species, and ecosystems). Biodiversity includes these structural components, as well as functional components: that is, the ecological and evolutionary processes through which genes, species, and ecosystems interact with one another and with their environment. Conservation biologists focus on maintaining structural biodiversity because if genetic, species, and ecosystem diversity are successfully maintained, then the diversity of ecological and evolutionary processes will probably be maintained as well.

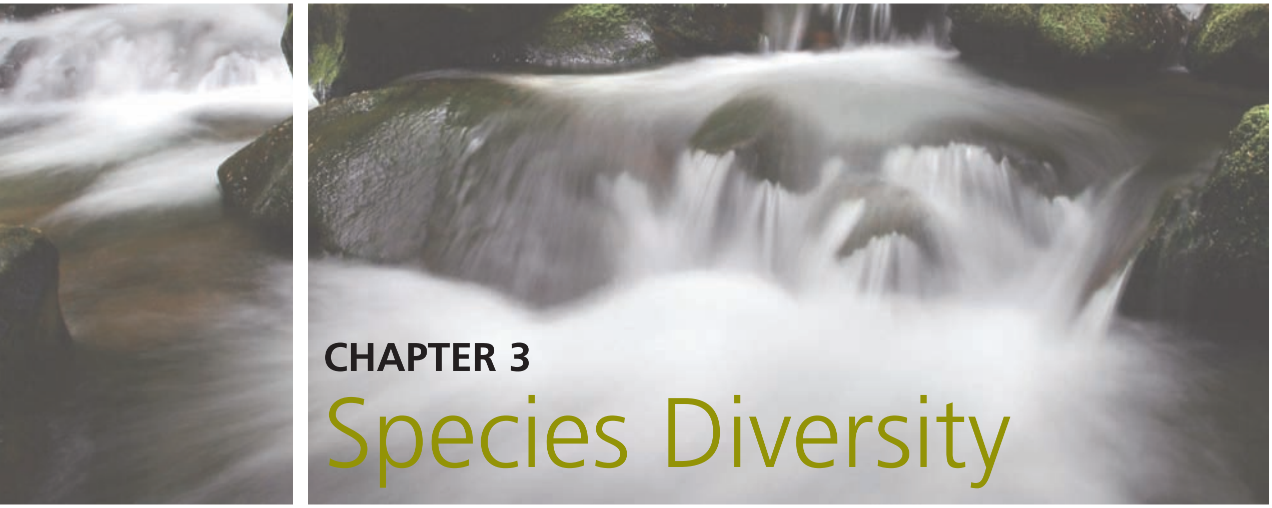
Some elements of biodiversity can be measured with quantitative indices of diversity based on richness, the number of elements of biodiversity (usually number of species), and evenness (their relative abundance). However, these indices can be misleading because a higher biodiversity index is not always desirable if the goal is maintaining biodiversity. It is more important to assess the risk of extinction of different species and emphasize those that are most endangered. The risk of extinction needs to be evaluated at different scales, and emphasis needs to be placed on those species most at risk at the global scale because they are irreplaceable. The biodiversity and scale issue can also be addressed by thinking of diversity on three scales (alpha, within an ecosystem; beta, among ecosystems; and gamma, geographic scale) and by always assessing the large-scale consequences whenever one manipulates biodiversity at a small scale. Thinking about biodiversity at large scales will often reveal that it is inappropriate to advocate maximizing biodiversity. Instead, the goals should be to maintain natural levels of biodiversity or to restore biodiversity in ecosystems degraded by human activity. The goal of maintaining biodiversity is closely related to some other goals, such as maintaining ecosystem or biotic integrity and ensuring sustainability of natural resource management.

FURTHER READING

Wilson (1992) and Heywood and Watson (1995) provide good introductions to the concept of biodiversity, and Angermeier (2000), Povilitis (1994), and Hunter (1996) discuss some of the difficulties in moving from a conceptual definition to action. DeLong (1996) reviews definitions of biodiversity. The two major biodiversity journals are *Conservation Biology* and *Biological Conservation*, but there are many other journals also worth perusing for conservation biology topics: *Biodiversity and Conservation*, *Bioscience*, *Ecological Applications*, *Ecology and Society*, *Oryx*, and *Pacific Conservation Biology*, to name just six among dozens.

TOPICS FOR DISCUSSION

1. Given a choice between conserving an ecosystem that was functioning properly (as measured by productivity, nutrient cycling, and similar parameters) and one that had a complete set of native species, which would you choose? Why?
2. Is it desirable to increase alpha- and beta-scale diversity if it can be done without apparently decreasing gamma-scale diversity?
3. If you were managing a forested stream valley, would you consider putting a small dam on the stream to add a pond ecosystem to the valley? What if the pond would be inhabited by a globally endangered species of turtle?
4. Think of some places in which you have observed ecosystems change over time. How did these changes affect biodiversity? Can you identify examples of both positive and negative changes?



CHAPTER 3
Species Diversity

Imagine flocks of parrots flashing green and gold over the piedmont forests of Virginia, a raft of penguin-like birds paddling up a Norwegian fjord, or a marsupial wolf coursing kangaroos through the eucalypt woodlands of Australia. These sights will never be seen again because the Carolina parakeet, great auk, and thylacine are gone forever. And they are not alone. Over a thousand species are known to have been driven into extinction by people just since 1600 (Hanski et al. 1995), and we can only guess at the total number of species that have disappeared because of human activities. Nothing highlights the need for maintaining biodiversity like the fate of these species and the many more that still survive but are sliding toward extinction. Keeping the wave of species extinctions from becoming a flood is the core of conservation biology.

In this chapter we first address two fundamental questions: (1) What is a species? (2) How many species are there? Then we explore the importance of species diversity in terms of both intrinsic and instrumental values.

What Is a Species?

When we try to classify the natural world, it seems relatively easy to recognize different species – peregrines and redwoods are readily distinguished from other birds and trees, but even experts will argue about where to draw the line between different kinds of ecosystems and genes. Nevertheless, the question "What is a species?" is more complex than most people realize. One widely used definition is based on reproductive isolation: "Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups" (Mayr 1942). For example, mammalogists classify brown bears in Eurasia and North America as the same species, even though they have been separated by the Bering Strait for about 10,000 years, because they would interbreed given the opportunity. On the other hand, American black bears and brown bears are considered separate species because they do not interbreed despite having overlapping ranges. Occasionally, interbreeding does occur between two apparently distinct species, and the offspring are considered hybrids. Here some difficult questions arise (Grant et al. 2005). How much hybridization can occur before you decide that the two parent species are really just one species? And what if the hybrid offspring form self-perpetuating populations? These issues have come to the fore as biologists work to determine if North America is inhabited by up to four species of the genus *Canis* (gray wolves, coyotes, red wolves, and eastern timber wolves) or as few as two species, with other forms being of hybrid origin (e.g. some biologists believe that coyote–gray wolf hybridization produced the red wolf) (Wayne and Gittleman 1995; Wilson et al. 2000, 2003; Nowak 2002).

Questions about hybrids are more familiar to botanists than to zoologists. Look through any comprehensive list of plant species, and you will find many listings such as *Typha angustifolia* × *latifolia*, indicating that hybrids of the narrow-leaved cattail (*angustifolia*) and the broad-leaved cattail (*latifolia*) occur routinely. However, this is only the tip of the iceberg; it has been estimated that 70% of angiosperms (flowering plants) owe their origins to hybridization (Whitham et al. 1991; Arnold 1992). Plant species are also harder to define in terms of reproductive isolation than animal species because they are more likely to exhibit asexual reproduction, self-fertilization, polyploidy (multiple sets of chromosomes), and other variants of what we usually consider "normal" reproduction. Similarly, most microorganisms reproduce asexually, thus confounding the idea of reproductive isolation. Their extremely rapid reproduction and thus evolution adds another complexity: is the bacterium that embarks on a transoceanic voyage with a ship's crew the same species when it returns to shore a week later? Note, too, that species definitions fail to represent well some of life's odder forms, such as prions, which are infectious self-reproducing proteins (some of which cause serious disease risks to humans, e.g. bovine spongiform encephalopathy, also known as mad cow disease), and viruses, which reproduce by invading other cells and commandeering the cellular machinery that viruses lack for reproducing themselves.

Evolutionary biologists and taxonomists are wrestling with these issues and have proposed many other species definitions: evolutionary, phylogenetic, ecological, cladistic, morphological, and more (see Claridge et al. 1997 and Coyne and Orr 2004 for reviews). Different definitions serve different purposes, and no one of them is "best" or "correct." The differences among definitions would be an academic issue except that species identified by different definitions do not always correspond to one another. For example, there may be from 1 to 30 species of *Drimys*, a kind of tree, in New Guinea, depending on the definition you use (Stevens 1989), and this would be an important issue for a conservation biologist trying to protect *Drimys* diversity.

Conservation biologists need to be aware of the debate over species definitions because it can have profound implications (Agapow et al. 2004; Mace 2004), but they cannot allow themselves to be paralyzed by it. It is better to use a fallback definition such as a species is "what a competent taxonomist says it is" (Stevens 1990), rather than do nothing for lack of definitive information. Fortunately, uncertainty over species definitions actually bolsters the overall goal of maintaining biodiversity because it highlights the critical importance of maintaining diversity below the species level, namely genetic diversity. This means that conservation biologists can sometimes sidestep the definition of species and use a term such as "evolutionarily significant units," or more succinctly "taxa," to refer to both species and subspecific groups such as subspecies, races, varieties, or even populations (see Fig. 3.1 and Fraser and Bernatchez 2001). As we will see in Chapter 5, "Genetic Diversity," all of these merit some attention from conservationists.