SECOND EDITION

BIOGEOGRAPHY

INTRODUCTION TO SPACE, TIME, AND LIFE

GLEN M. MACDONALD

WILEY Blackwell

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Second Edition

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PREFACE TO THE 2ND EDITION

The general goals of this 2nd Edition remain similar to the 1st edition. These are to provide an introduction to biogeography that reflects the fascination and importance of the field, but is understandable and engaging to university students from a wide variety of educational backgrounds and interests. The overall organization of the book has also remained similar to the 1st edition. In Part I we review some relevant concepts from the life and physical sciences. We then embark on an exploration of the current geographic distribution of life on the planet and its relationship to the environment. In Part II we explore the trajectory of the planet and life over geologic time. We consider the responses of species to changing environments through processes of dispersal, evolution and extinction. We include our own species in this consideration and examine the evolution of humans and our impact on the climate and the biosphere. In Part III we examine some of the important practices that biogeographers employ to collect data on plant and animal distributions, and some theories that have arisen in biogeography to provide general explanations for the patterns that are revealed. An important focus of Part III is studying the geographic patterns seen in global biodiversity. The final chapter of Part III tackles how biogeographic practices and theory can be applied to assist in addressing the pressing conservation challenges the world faces today. Biogeography is a field of study that is by its very nature global in scope. Accordingly, the research and examples presented here are drawn from throughout the world. Although the general goals and organization of the book remain the same, the world, and the discipline of biography, in important ways that must also be reflected in the new edition.

The 1st edition of *Biogeography: Space, Time and Life* was published two decades ago. Over that time the science of biogeography has advanced significantly. Techniques and data-sets related to field surveying, geographic positioning systems, remote sensing, geographical information sciences, molecular genetics analysis, species distribution modelling and so on have seen remarkable growth. Citizen scientists are using mobile phone apps to greatly increase our knowledge of the geographical distributions of species and the environments they inhabit. Studies of the geologic history of the Earth, past environments, and the evolution and extinction of species have added incredible amounts of new information and refined our perspectives of life over time. The growth of biogeography and the new information on the spatial and temporal patterns of life on Earth has allowed biogeographers to refine previous theory, develop new theory, and in some cases discard previous ideas. It is hoped that this new edition, with many new examples, figures, tables and sources, captures and conveys this exciting growth. As a discipline, biogeography has also become more diverse in the past twenty years. Scholars from throughout the world are contributing important new information and insights. The ideas and examples presented in this text represent the work of thousands of scientists and scholars. These are cited at the end of each chapter. Hundreds are new to this edition. I encourage the readers to dive into these primary sources and learn and be inspired by the works I have drawn upon and been inspired by.

Over the past twenty years the impact of humans on the environment and the species we share the planet with has intensified. Significant forest and woodland clearances have occurred in many countries across the globe. It has been estimated that over 77,000 species of animals and plants are threatened by extinction, and it is widely acknowledged that this may be just the tip of the iceberg. Emissions of greenhouse gasses by human activities have increased and the global surface temperature has risen by about 0.2°C per-decade. The acceleration of human impacts on the Earth's environment have prompted some scientists to declare that we have entered a new geologic Epoch – the Anthropocene. The challenges posed to the sustainability of our planet are considerable. The current state of many of these challenges is provided in this new edition. Biogeography is playing an important role in tackling the sustainability challenges of the Anthropocene. The need for the insights and conservation solutions provided by biogeography is pressing. It is hoped that this book will help inspire you to take up these challenges, as a concerned citizen or a scientist yourself. You can make a very real and positive difference to the fate of life on our planet.

In closing, I wish to thank all of those who have made this second edition possible. The editorial and production staff at John Wiley & Sons who believed in the project, and provided support and patience during its long gestation are owed a debt of gratitude. Many colleagues at UCLA and elsewhere have kept me intellectually stimulated and generously shared their knowledge with me. I continue to learn so much from my undergraduate and graduate students. I thank them for sharing their questions, knowledge and energy with me. In particular, I thank my graduate students Joan Chimezie, Elly Fard, Jessie George, Jiwoo Han, Scott Lydon, Lisa Martinez and Ben Nauman for keeping me inspired during the heaviest research and writing for this edition. Finally, I owe a huge debt of gratitude to another biogeographer who also hails from the University of Toronto, my wife Joanne. Her understanding of the work, her support and her patience have been invaluable.

ABOUT THE COMPANION WEBSITE

This book is accompanied by a companion website:

www.wiley.com/go/macdonald/biogeography2e

The website includes:

- PowerPoints of the figures
- Gallery of images and videos

CHAPTER 1

AN INTRODUCTION

There cannot be many people who have never marveled at an unusual flower or animal, or contemplated the deeper history of the human race and how they, themselves, originated. Even those with the most casual interest in the environment know that today the earth abounds with an incredible diversity of interesting plants and animals, but many are facing grave threats due to habitat destruction, overhunting, and climate change. You may have wondered: How did this wonderful diversity of life, including our own species, arise; how did we get to this present state of environmental crisis; and what can we do about it? These are big questions, and in picking up this book you might be wondering what the science of biogeography can tell us about all of this.

If this is your first exposure to the science of biogeography, you probably have three basic questions: What exactly is biogeography? Why should I bother studying it? How will this book help me understand biogeography? Let's start with a simple answer to the first question. **Biogeography** is the study of the past and present geographic distributions of plants and animals and other organisms.[1] Of course, there is much more to it than that. We will explore this question further and expand on this definition presently, but first let us consider why you might want to study biogeography as an aid in understanding both the diversity of life and how we might conserve that diversity.

More than most sciences, biogeography helps us to understand and appreciate the living environment that we experience every single day. Biogeography helps us answer questions such as how the great diversity of life that we experience today arose, where the modern human species came from, and what we can do to preserve the natural environment in the face of increasing human population growth and environmental change. How does answering such questions directly affect you? When we think of nature we tend to think about distant national parks and wildlands. These are important, but let's think about closer to home. You cannot set foot outside your door without seeing plants that are growing around you. Many of the plants you see are native to the area in which you live, but many others are exotic species that have been recently introduced by humans. You cannot escape hearing the calls of wild birds, some of which are native and some of which have been introduced. Even if you do not know the scientific names of the plants and animals near your home, you are familiar with the way they look and sound. At some point you must have wondered how this diversity of life around you arose and specifically where all of these different plants and animals that live near you originated. These plants and animals fill your neighborhood with beauty and interest. They can also provide more tangible benefits such as the trees that provide shade or shelter from winds, or the small fish that keep populations of mosquitos in check. These tangible benefits that arise from the diverse plants and animals around you are called **ecosystem services**. Biogeography helps you understand the plant and animal life that you encounter everyday where you live and that provide important ecosystem services to you on a daily basis.

If you have ventured far from your home, perhaps visiting another state, province, or country, you have undoubtedly noticed differences in the vegetation and animal life you encountered. For example, during the winter millions of people travel from the northeastern United States and Canada to enjoy the sunshine and palm-lined beaches of southern Florida. The green vegetation of Florida contrasts greatly with the cold and leafless winter forests of the Northeast. Many animals

[1] Throughout the text, key terms and concepts will appear in bold lettering. Short definitions for these terms and concepts can be found at the end of the book.

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found in Florida, such as alligators, are not found in the northeastern United States or in Canada. Why are alligators and most other plants and animals found in southern Florida not found in the Northeast? The obvious answer might be that these plants and animals require the warm and humid environment of Florida to survive. However, many plant and animal species from Florida are also absent from the other warm tropical and subtropical areas of the earth. Travel to South America, West Africa, Southeast Asia, or northeastern Australia and you will see palm trees and many interesting animals, including relatives of alligators such as crocodiles, but not a single native alligator (Fig. 1.1). Surprisingly, however, you will find native alligators in southern China. Why are certain plant and animal species limited to relatively small areas of the earth? Why are other types of organisms widely distributed? Why can't you grow many of the plants found in Florida in a garden in New York?

An important role of biogeography is to record such geographic differences in vegetation and wildlife and seek to explain them. Biogeography can tell us why North American alligators *(Alligator mississipiensis)* are found only in warm, moist areas such as Florida and adjacent states. Biogeography can also help us to understand why alligators are also found in China *(Alligator sinensis),* and not in tropical regions of Africa and Australia. In studying biogeography, you will come to understand that a combination of geographical, environmental, and historical factors led to the great diversity and current geographic distribution of plant and animal life. In studying biogeography, you can develop a much greater awareness, understanding, and appreciation of the wonderful diversity of plant and animal life found on a global basis as well as the diversity of life that you encounter every single day.

The study of biogeography also helps us to appreciate the development and history of our own species. We do not stand as far apart from the natural world as we might think. Our development, both biologically and culturally, is influenced by geography, the earth's physical environment, and interactions with other organisms. The evolution and spread of humans around the world make up one of the great stories of biogeography. At present, humans play an increasingly greater role in changing the world's environments and have a significant impact on the lives of plants and animals with which they share the earth. We have helped some species spread throughout the world while driving others from much of their former habitat. Some plants and animals owe their existence to human activity. Sadly, many more species owe their extinction to us. Since our existence depends on our relationships with the other species of the earth, our future will ultimately be determined by how we treat them. Biogeography helps us understand where living organisms, including humans, have come from and where we and earth's other inhabitants are potentially headed.

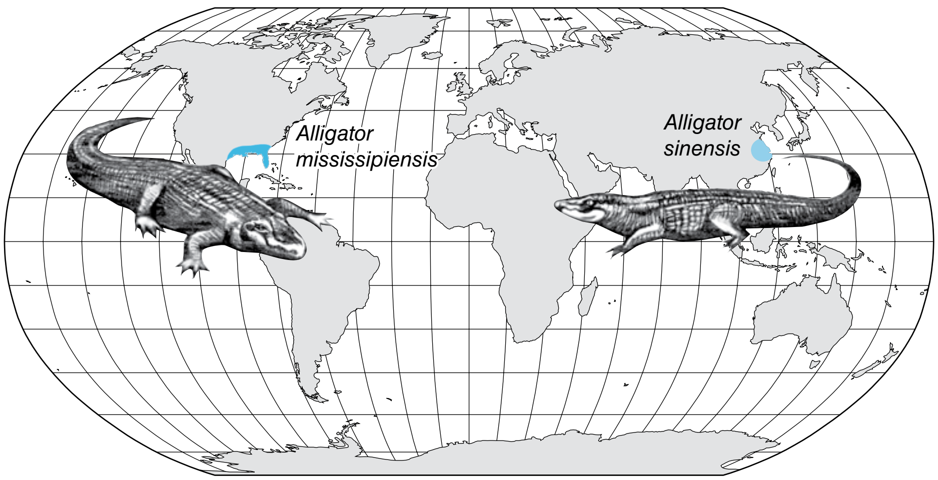

FIGURE 1.1 The world distribution of alligator species *(Alligator mississipiensis* and *Alligator sinensis).* Understanding why alligators are found only in North America and China is a classic biogeographical question. Alligators are found in warm subtropical regions because they cannot tolerate prolonged exposure to cold and freezing temperatures. In the geologic past, Europe, Asia, and North America were joined together in one large continent that experienced relatively warm climates. Therefore, the geographic range of the ancestors of modern alligators was much larger than it is today. Over time, as continents shifted, climate changed, and alligators faced competition from crocodiles and caimans, the geographic range of alligators became fragmented and small.

The ability of humans to alter the environment and affect the survival of plants and animals bestows a great deal of responsibility upon us. We are responsible for making sure our actions cause as little damage as possible to the natural environment. In this effort we will always face tradeoffs between the needs of people for food, resources, living space, and recreational areas, and the preservation and conservation of nature. In some cases, we can alter our activities to lessen the damage we cause. In other instances, we might try to restore damaged areas to a semblance of their natural state. In these enterprises, biogeography can provide important guidance. By examining the long-term histories of plant and animal communities, biogeographers provide information on how humans have altered the environment. In studying the natural distributions of plants and animals, biogeographers can help preserve nature. Biogeography provides important guidance on how we are affecting the environment and what actions we can take to conserve resources and preserve natural environments.

The contrasting state of health of the North American alligator and its relative, the Chinese alligator, underscores the conservation challenges facing biogeographers. According to the Wildlife Conservation Society, there are only 120 Chinese alligators remaining in the wild. This makes it the most endangered crocodilian (crocodiles and their relatives) in the world. Why are the North American alligator populations relatively healthy today and their Chinese relatives so endangered? What might be done to alleviate the risk to the Chinese alligator? Biogeography has much to contribute to such questions.

Let us now turn to further defining biogeography. In studying the present and past distributions of life, biogeographers have two basic tasks: description and explanation. Describing where a plant or animal species occurs today is the easiest part, and yet this task remains incomplete for vast numbers of plants, animals, and other organisms. So far, less than 3 million living species of plants, animals, and other organisms have been identified. It is thought that there may be a total of over 8 million eukaryotic species (organisms such as mammals, birds, insects, and plants that have cells contained in membranes) of which many remain to be discovered and scientifically described. When prokaryotic organisms such as bacteria are included, the total may jump to 2 billion or more. If our knowledge of present-day species remains incomplete, it is even more difficult to reconstruct the past distributions of organisms because we must rely on fossil records that are often fragmentary and difficult to interpret. Explaining exactly how present and past distributions are controlled by the complex geographic, environmental, and historical factors that affect all organisms presents the greatest challenge. In order to understand how the physical and biological environment controls the distribution of plants and animals today, biogeographers must be familiar with concepts and techniques in physiology, anatomy, genetics, ecology, geomorphology, pedology (the study of soils), climatology, limnology (the study of lakes), and oceanography. In order to study how plants and animals were distributed in the past, biogeographers must know some basic geology, paleontology, and evolutionary biology. In studying our own biogeographic history and the relationship between humans and the other species of the earth, biogeographers also intersect in their interests with disciplines such as anthropology and archaeology. Since biogeography requires knowledge from a wide variety of other disciplines, it is called a synthetic science. The interests of the biogeographer blend and overlap with the interests of the ecologist, the evolutionary biologist, and the paleontologist to such an extent as to make the identification of firm boundaries between biogeography and these disciplines difficult. Indeed, it might be argued that from a life sciences perspective, all of these disciplines are subfields of biogeography. Given the synthetic nature of the field, it is not surprising that biogeographers can be found working in many different university departments, including geography, environmental science, sustainability, biology, geology, paleontology, and anthropology. Biogeographers can also be found working in park services, forestry services, environmental services, conservation groups, and private consulting firms.

Clearly, biogeography encompasses a huge area of the natural sciences. One way in which biogeographers tackle the complexity of their subject is to break it down into different subdisciplines. **Phytogeography** studies the present and past distributions of plants. **Zoogeography** examines the present and past distributions of animals. The biogeographic study of the modern relationships between organisms and the environment is called **ecological biogeography.** Some biogeographers concentrate on studying past distributions and the evolution of life. This line of inquiry is called **phylogeography** or **historical biogeography.** The field of **analytical biogeography** is concerned with developing general rules that explain how geography affects the evolution and distribution of plants and animals and how past distributions and evolutionary history are reflected in modern distributions. The application of the lessons learned from ecological, historical, and analytical biogeography, including the protection or restoration of the natural environment, is called **conservation biogeography.** In recent years much attention has been placed on the expanded concept of **ecological sustainability,** which is the capacity of the biosphere to meet the present and future needs of humans and other species. Biogeography has an important role to play in achieving this important goal for our planet.

So, what are the aims of this textbook, and how can it help you understand this fascinating and diverse field? The book is written to provide you with a solid introduction to the field of biogeography. It does not assume extensive background knowledge of biology, geography, or geology. There are, however, fundamental terms and concepts from these three fields that all biogeographers must know, and so they are outlined in this book. In Chapter 2 you will be introduced to some important basics of biology and physical geography including climatology, oceanography, and limnology. Later, in Chapter 7, we will explore some important concepts from geology regarding the history of the earth. Chapter 9 will provide some further primer material on genetics. Throughout the text, you will also be introduced to widely applied concepts from ecology and evolutionary biology. These concepts will be explained in detail, and their importance to biogeography will be highlighted.

In recognition of the ecological, historical, and analytical facets of biogeography, the book is divided into four major sections. The first section, called Space and Life, is concerned with ecological biogeography. In these chapters we will examine how present physical and biological conditions affect organisms and their distributions. Chapter 3 describes how physical conditions affect organisms and control their geographic distributions. In Chapter 4 we will look at the interactions that occur between different organisms and discuss how these biological factors can control geographic distributions. In Chapter 5 we will examine how disturbances such as fires or floods impact ecosystems and influence the geographic distribution of organisms. In Chapter 6 we will in particular explore the classification of life into global biomes that reflect the strong control of climate on vegetation.

The second section of the book concerns historical biogeography and is entitled Time and Life. In Chapter 7 we will discover how the physical geography of the earth has changed over the past 500 million years. We will also explore how the earth's climate has undergone natural periodic changes. We will pay special attention to the shifts between glacial and nonglacial conditions that have occurred over the past 2 million years. We will conclude the chapter with a consideration of how human activity, particularly that related to increases in greenhouse gases, is now changing the climate of the planet. Chapter 8 will delve into how organisms change their distributions in response to changing geographic and environmental conditions. In Chapter 9 we will explore how the processes and patterns of evolution and extinction relate to changing environmental conditions and how geography affects these processes. Chapter 10 discusses how past and present processes play out in determining the major biogeographic regions of the earth. Chapters 11 and 12 examine the fascinating story of human evolution and some of the impacts of our species on the biosphere.

In the third section, entitled Theory and Practice, we put the concepts we have learned together to understand global distributions of plants and animals and how biogeography can be applied to their conservation and the sustainability of the earth. In Chapter 13 we will examine different general geographic patterns observed in the spatial distributions of species. Chapter 14 explores how overall biodiversity is distributed across the planet and the roles the environment, geography, and past history have on biodiversity.

Some people have argued that humans have so altered the planet that we have entered a new geological epoch referred to as the **Anthropocene.** Chapter 15 provides an exploration of conservation and ecological sustainability concepts and potential solutions to some of today's challenges provided by biogeography. The final chapter will provide an outline of some of the current scientific tools and approaches that biogeographers use in conservation work.

One of the greatest attractions of biogeography comes from the wonderful variety of life and the fantastic adaptations that allow organisms to live in environments ranging from the coldest depths of the ocean to the hot sands of the Sahara Desert. Biogeography is a science concerned with life, and it should be lively! In this book you will be introduced to many examples of fantastic and wonderful plants and animals. These organisms, and the many interesting environments and communities in which they live, will be used to illustrate the concepts and theories of biogeography. We will also examine many real-world examples of how biogeography has impacted people and how human activity has affected other organisms. These examples should make your studies more enjoyable and allow you to translate your knowledge of biogeography to the real world. In the end, when you travel across the world, walk down your own street, or look at yourself in the mirror, you will realize that you and every single plant, animal, and person you encounter is a result of, and contributor to, the biogeographical story of life.

KEY WORDS AND TERMS

Analytical biogeography
Anthropocene
Biogeography
Conservation biogeography
Ecological biogeography
Ecological sustainability
Ecosystem services
Historical biogeography
Phylogeography
Phytogeography
Zoogeography

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PART I

SPACE AND LIFE

CHAPTER 2

SOME BASICS

Biogeography is a very wide ranging science, and accordingly biogeographers are a highly diverse group of scientists in terms of interests and perspectives. This multidisciplinary scope is one of the most satisfying aspects of biogeography—and one of the most challenging. Anthropology, biology, climatology, geography, and geology all contribute concepts, specialized vocabularies, and ways of classifying information that are important to biogeography. In order to understand and appreciate the science of biogeography, we must therefore have some knowledge of its foundations in these other sciences. Before we get down to the business of biogeography, we will review some key concepts from some of these associated disciplines. In this chapter, we will concentrate on aspects of biology and physical geography that are fundamental to biogeography. Later in this book we will discuss some concepts from geology and physical anthropology that are also important to biogeography. Much of the material that we cover here will be familiar to anyone who has taken introductory courses in biology and physical geography. However, even for those with such a background, a little review won't hurt.

BIOLOGY AND THE HIERARCHIES OF LIFE

Biology can be defined as the science of life and all of its phenomena. Life on earth includes millions of different types of organisms, ranging from viruses to whales. The study of any of these organisms could include examination of myriad phenomena, from biochemical reactions within plant cells to the social behavior of pods of whales. It is clear that biologists face a daunting challenge! The science of biology tackles this immense task by breaking it down into smaller components that can be studied individually. One way to categorize and organize the constituent units of a large entity is to develop a hierarchy. A **hierarchy** is a system of organization in which components are ordered by rank. Most corporations are good examples of hierarchies. A large group of office staff is under the direction of one office manager, who, along with several other managers, is under the direction of the vice president of operations. The vice president, along with two or three other vice presidents, reports to the president of the firm. The president occupies the upper-most level of the corporate hierarchy, and the office staff provides its base. Every biogeographer should be familiar with three important biological hierarchies: the taxonomic hierarchy, the ecological hierarchy, and the trophic hierarchy. We will examine each of these.

Taxonomic Hierarchy

Taxonomy is the subdiscipline of biology concerned with the classification and naming of organisms. Taxonomy is also known as **systematics** when the main goal is to determine the evolutionary relationship between groups of organisms. In this case, taxonomists are also called systematisists. The evolutionary histories of organisms that are reconstructed by systematisists are referred to as phylogenies. Taxonomists use observable traits, referred to as characters or character states, to group similar individual organisms together and to separate groups of different organisms. The groups that taxonomists develop are called **taxa** (the singular form is **taxon**). The characteristics that taxonomists use to classify organisms usually start with physical differences, such as color variations in flowers or

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in the plumage of different birds. Taxonomists may also consider differences that are apparent through chemical analysis of the tissue or fluids of the organism. Such studies are referred to as chemotaxonomy. Finally, cytotaxonomists examine the chromosome structure of organisms to detect genetic similarities and differences in order to classify organisms.

The classification and naming of organisms by individual taxonomists would not be very useful if everyone had their own system and terminology. Fortunately, there is a single system of taxonomic classification that is generally accepted by all biologists and biogeographers. The development of our present taxonomic system is at the foundation of biology and biogeography. It is a history that can be traced back to ancient Greece. The roots of the modern taxonomic system began with Aristotle (384–322 BCE[1]). Aristotle, a student of Plato, is best known as a philosopher but was also active in biology, physics, astronomy, and psychology. He developed an early scientific system for classifying animals into groups that shared similar features. Aristotle believed that the specific form and behavior of individual plants and animals were inherited and immutable. He considered that all individuals belonged to groups, or **species** (from the Greek word *eidos*), of taxonomically similar individuals. Aristotle believed that the form and behavior of these species did not change from generation to generation. He taught that dogs form one species and cats another. Aristotle also argued that plant and animal species formed a hierarchy ranging from simple organisms, such as worms, to the most complex organism, which he considered to be humans. In the Middle Ages, European scientists, influenced by Aristotelian logic, grouped organisms that appeared to be generally, but not exactly, similar to each other into taxonomic units called **genera** (the singular form is **genus**). A genus would include, for example, the Scots pine trees of Scandinavia and the Mediterranean pines of southern Europe. Both the Scots pines and the Mediterranean pines belong to the genus called *Pinus*.

Before we proceed, let's examine the words *genus* and *species* and consider the continuing role of Latin in biology and biogeography. Genus is the Latinized form of the Greek word *genos*. In the Middle Ages the language of scholarship in Europe was Latin, and the names of the genera came from that language or are latinized versions of words from other languages. For example, in Latin the genus for pines is called *Pinus*. In comparison, the genus for cats is *Felis*. Although Latin is no longer widely spoken or understood, the formal names of organisms are still written in that language. The benefit of this convention is that no matter which language the scientist is working in, the names of the organisms are always presented in Latin using the Latin alphabet. Even papers and books written in Russian Cyrillic or in Chinese characters will always present the scientific names of organisms in the Latin alphabet. Biologists and biogeographers always know which organisms are being discussed, even if they can read nothing else in the document. The use of the proper scientific names for organisms is also important for avoiding confusion among scientists who speak the same language. Take pines, for example. In North America we have many different trees that are closely related and belong to the genus *Pinus*. In the South Pacific we might encounter a tree that is commonly called the Norfolk Island pine. This plant, however, is unrelated to our North American pines and belongs instead to the genus *Araucaria* (Fig. 2.1). In many instances the same plant or animal will have several different common names, but every organism has only one accepted scientific name. In addition, the Latin names of organisms often contain descriptions that can be understood by people with only a limited knowledge of Latin.

So what is the difference between a species and a genus? It is recognized that genera of plants and animals contain organisms that are related but are consistently distinguishable on the basis of their morphology. In addition, many of these taxa, though members of the same genus, cannot interbreed. These different members of a genus are species. For example, people in eastern North America will be familiar with the eastern white pine, and those in the western part of the continent might know the lodgepole pine. Both species belong to the genus *Pinus* and share certain broad similarities, such as long thin needles, cones, and upright growth (Fig. 2.2). There are, however, clear differences

[1] BCE stands for Before Common Era and is equivalent to the previously used notation BC. CE (Common Era) is equivalent to the previously used notation AD. Both notation systems are based on the Gregorian calendar which was introduced by Pope Gregory XIII in 1582 and used throughout the world today. The year 322 BCE is exactly equivalent to 322 BC, and 2019 CE is equivalent to 2019 AD. In this book, years that are within the Common Era will be cited without adding the CE notation; for example, 2019 = 2019 CE.

FIGURE 2.1 White pine trees of the genus and species *Pinus strobus* growing in the Pocono Mountains of Pennsylvania (*a*) and so-called Norfolk Island pines of the genus and species *Araucaria heterophylla* from Norfolk Island in the South Pacific (*b*). Although both species are called pines, they are unrelated, and only white pine is actually a member of the pine genus.

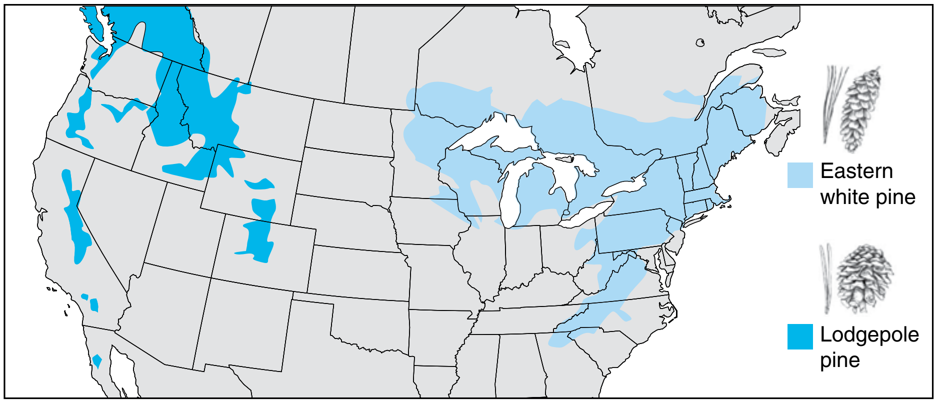

FIGURE 2.2 The needles, cones, and shapes of a mature eastern white pine *(Pinus strobus)* and a western lodgepole pine *(Pinus contorta)*. Notice that both pine species share a general resemblance but possess clear differences in terms of their needles, cones, and mature form.

between the trees. White pines can grow to well over 30 meters in height, whereas most lodgepole pines achieve heights of only 20 meters. The white pine carries its needles in bundles of five. In contrast, the lodgepole pine has bundles of two needles. The white pine has large cones that open immediately upon ripening and release their seeds. Lodgepole pines have small cones, many of which remain closed and retain their seeds until a fire causes the cone scales to open. In addition, eastern white pine and lodgepole pine cannot interbreed. The two trees are recognized as different species within the genus *Pinus*. Following the concepts of Aristotle, the English scholar John Ray (1627–1705) attempted to systematically define a species. He concluded that if seeds came from the same plant, the seedlings must be related and similar in character. He recognized that variations might occur between seedlings from the same parent, but he considered these to be "accidents." Ray's conception of species can be paraphrased as "Like begets like."

Since the time of Ray, species have formed the basic unit of the modern taxonomic system, but there remains much debate among scientists as to just how a species should be defined. Three main definitions are in use today. The phylogenetic species concept identifies a species as a group of sexually reproducing organisms that share at least one diagnostic character that is present in all members of the species but absent in other organisms. Unique behavioral traits are accepted as defining characters. This concept does not adequately take into account natural variations within species, such as differences in human hair color. If this concept were widely applied by biologists, far more species would be identified than is now the case. In addition, the phylogenetic species concept does not consider reproductive interactions between members of the species or their evolutionary history. The biological species concept defines a species as a group of organisms that can interbreed freely under natural conditions. This definition was articulated by the great evolutionary biologist Ernst Mayr in 1942, although its roots extend into the early part of the twentieth century. It remains the most widely used definition of a species in biology. Finally, paleontologists who study the fossil record often use the evolutionary species concept. Evolutionary species are organisms that have a direct ancestor-descendant relationship that is traceable in the fossil record. Usually, such a relationship is inferred from morphological similarities such as the size or shape of the fossils. This is because morphological features are generally all that is available from the fossil record. New species are differentiated when there are clear divisions of one evolutionary line into two or more new lineages. The evolutionary species concept allows for morphological changes in the species over time as evolution occurs.

In practice, biogeographers combine these concepts and view species as organisms that are morphologically similar and can interbreed freely under natural conditions. It is assumed that such organisms must share a common ancestor. Although this sounds pretty straightforward, we still encounter problems in defining species due to natural variability in the morphology and reproductive behavior. In addition, species are generally thought of in terms of sexually reproducing organisms. Organisms that reproduce asexually raise difficulties when the common phylogenetic and biological species definitions are used.

Until the eighteenth century, scientists named species simply by adding some descriptive words to the name of the genus. The eighteenth century was a period of great geographical and biological exploration and discovery when many new genera and species were found and described. To differentiate these newly discovered species, their names often became polynomials containing a dozen or more Latin words. Clearly, this system was unwieldy. The simplified system of naming organisms that we use today was invented in the mid-eighteenth century by the great Swedish scientist Carolus Linnaeus (1707–1778). He attempted to catalog all of the known species of the world. Linnaeus was trained as a medical doctor but inherited a keen interest in plants and natural history from his father. Many of the species he identified and described are still accepted by taxonomists today. Linnaeus introduced the binomial system whereby every organism could be identified by a unique combination of a generic (genus) and specific (species) name. For example, white pine is known as *Pinus strobus,* while lodgepole pine is known as *Pinus contorta*. These related species share the same genus, *Pinus,* but are differentiated by their species names, *strobus* and *contorta*. Species with the same generic names are assumed to be related. With the binomial system, different species can also share the same specific name. This occurs frequently because the specific names often describe some feature of the organism. As an example, the scientific name for white oak is *Quercus alba,* whereas the scientific name for a seabird known as the snowy sheathbill is *Chionis alba*. In this case, the word *alba* refers to the light coloring of the organisms and in no way implies a genetic relationship.

Because different, unrelated species can share the same specific name, a species is never referred to by its specific name alone—the genus must be indicated. If it is clear which genus is being discussed, you can use the first initial of the generic name instead of spelling the complete name (i.e., *Quercus alba* can be referred to as *Q. alba*). By convention, the generic and specific names are always italicized, and the generic name starts with a capital letter. The specific name starts with a lower-case letter. In this book you will find the scientific names of important genera and species in parentheses following the first usage of the common name. Sometimes the scientific name of a species is followed by the full name, abbreviated name, or initials of the taxonomist who first described it. A scientific name followed by the letter L, such as *Quercus alba* L., means that the species was first described by Linnaeus himself.

So what does the modern taxonomic hierarchy consist of? As we have seen, species form the lowest level of the hierarchy, although some species may be further subdivided into distinctive subspecies and races. Collections of species that are similar to one another, and presumably genetically related, are grouped together in the next level, the genera. Genera that are morphologically similar and likely possess evolutionary linkages are grouped together as **families.** Oaks, for example, belong to the family of trees called Fagaceae. This family also includes the genus beech *(Fagus)* and several other genera of trees. How higher taxonomic groups are classified remains a subject of revision and debate. According to a widely used system, families that are related are grouped together in taxonomic **orders.** The order for oaks is Fagales. In turn, orders are grouped into **classes.** All flowering plants are grouped into one of two classes. The oaks are members of the class **Magnoliopsida** (sometimes called **dicotyledons**). Among other traits, plants in this class have seeds that produce two initial leaves, or cotyledons, when they germinate. Many of the familiar trees of the deciduous forest, such as maples *(Acer),* birch *(Betula),* elm *(Ulmus),* willows *(Salix),* and garden flowers such as roses *(Rosa)* and daisies *(Aster)* are Magnoliopsida. The other class for flowering plants is **Liliopsida** (also called **monocotyledons**). Some examples of Liliopsida include orchids *(Orchidaceae)* and grasses *(Poaceae)*. When the seeds of these plants germinate, they produce one cotyledon.

Classes of plants are grouped together into **divisions** (in the case of animals, the term **phyla** is used for this level of the hierarchy—the singular being **phylum**). The division for the Magnoliopsida and Liliopsida is **Magnoliophyta.** The Magnoliophyta are also referred to as the flowering plants or the **angiosperms. Conifers** (cone-bearing plants) such as the pines *(Pinus),* the spruces *(Picea),* and the firs *(Abies)* are neither Magnoliopsida nor Liliopsida. They do not belong to the Magnoliophyta but are instead members of the division **Pinophyta** and are also known as **gymnosperms.** Finally, at the highest level, plants are all grouped into the kingdom **Plantae.** Both the Magoliophyta and the Pinophyta have vascular systems to transport water and nutrients and are grouped together in a subkingdom called the **Tracheobionta.** Life is often grouped into **kingdoms** and sometimes a lesser number of higher-level **domains.** Debate continues on how to classify organisms at many levels, including these highest levels. According to one commonly used system, the kingdoms include Monera, Protista, Fungi, Plantae, and Animalia. The Monera are simple prokaryotic organisms such as bacteria. The Protista are single-celled eukaryotic organisms such as amoeba. You can probably guess who the members of the Fungi, Plantae, and Animalia kingdoms are. Thus, we can trace the affinity of every organism, including humans (Table 2.1), up through the taxonomic hierarchy to a kingdom. However, the exact number of kingdoms continues to be debated and numbers up to eight have been proposed in recent years. For example, the Monera are often subdivided into Bacteria and Archaebacteria kingdoms.

Notwithstanding continuing debate on specific aspects of it, the taxonomic hierarchy provides a convenient and generally accepted way to classify life. It should be remembered, however, that this

TABLE 2.1 A Systematics (Taxonomic Hierarchy) of Eastern White Pine *(Pinus strobus)* and Humans *(Homo sapiens sapiens)*

	White Pines		Humans
Species	*Pinus strobus*	**Species**	*Homo sapiens*
Genus	*Pinus*	**Genus**	*Homo*
Family	Pinaceae	**Family**	Homonidae
Order	Pinales	**Order**	Primates
Class	Pinopsida	**Class**	Mammalia
Division	Pinophyta	**Phylum**	Chordata
Kingdom	Plantae	**Kingdom**	Animalia

system is not static. Terminology associated with its subdivisions has evolved over time. New species are continuously being discovered and added. At times, new genera and families are added. The status of some of the kingdoms remains hotly debated. In addition, taxonomists may change the genus or family of older recognized species when new information comes to light. It sometimes happens that several taxonomists identify the same species and give it different names. These names are referred to as synonyms, and the earliest published name generally takes precedence.

Ecological Hierarchy

The taxonomic hierarchy provides for a division and ranking of life based on the morphology and the genetic relationship of organisms. It is the foundation for many aspects of biological research. There is, however, a need to consider a different hierarchy used to organize and interpret observations for the ecologist or biogeographer who goes out into the field to study and categorize how organisms are affected by the environment or how they interact with other species. It would be an intractable task to study the relationships between every organism on earth and the environment, or the interrelationships among all the organisms that populate the planet. Therefore, ecologists and biogeographers often concentrate on specific spatial and taxonomic scales of study. These different levels of ecological study can be organized into a hierarchy that reflects the increasing geographic and taxonomic scale being examined.

The lowest scale of study that is of interest to the biogeographer is the **individual** organism. For example, scientists might put a radio tracking collar on one Arctic fox *(Alopex lagopus)* and monitor its movements. At the next level, they might consider studying a **population** of Arctic foxes. A population is defined as all individuals of a given species in a prescribed area. Usually, members of the same population are assumed to be in close enough proximity to be able to interact and interbreed frequently. Of course, in many cases, members of the same species are found in different locations and do not interact on a regular basis. Interbreeding and other interactions between these separated populations of the same species may only occur infrequently. Such populations are referred to as **metapopulations.** The term was coined by the biologist and philosopher Richard Levins in 1969 to describe this concept of studying populations of separated populations of the same species. Metapopulations are found both in terrestrial and marine settings. Two broad types of metapopulations can be recognized. Loose metapopulations consist of subpopulations of the same species that live in different locations and interact with other subpopulations very infrequently. The distance between subpopulations is farther than most individuals travel during their life spans. Tight metapopulations consist of subpopulations that are close enough for individuals to travel between them and thus interact more frequently. The Arctic fox populations living on different islands in the Canadian Arctic separated by large expanses of water are an example of a loose metapopulation. Birds that live and nest in different woodlots that are separated only by agricultural fields are an example of a tight metapopulation.

We might also consider examining the interaction of our fox population with all the other species of organisms in its environment. In this case, we are studying an ecological **community.** A community can be broadly defined as all populations of organisms that live and interact within a prescribed area. Ecological research that focuses on one species is sometimes referred to as **autecology,** while research that focuses on the interactions between species in communities is referred to as **synecology.** Some ecologists and biogeographers limit their studies of communities to subsets of the total community. For example, phytogeographers might restrict their study to flowering plant species only. Some biogeographers would refer to this as the flowering plant community. However, other ecologists and biogeographers feel that the term community should only be used to refer to all species of organisms in an ecosystem. Subsets of a community, such as the flowering plant species, are often referred to as **assemblages.** One important subset of the complete community is the **guild.** Guilds are groups of animal species within a community that have similar forms, habitat, and resource requirements. The insectivorous bird species form one guild in a community, while the seed-eating bird species form another.

If we were to consider the relationship between the species of our community and the physical factors of the environment, particularly when we examine flows of energy and matter through this biophysical system, we would be conducting research at the scale of the **ecosystem.** It could be argued that the spatial boundaries of any ecosystem extend over the whole earth. Even the smallest area is linked to the world at large by physical processes such as global rainfall patterns and biological processes such as bird migrations or the input of tiny airborne microorganisms such as fungal spores. In practice, the boundaries of ecosystems are often defined by the researcher and can vary from very small areas such as the trunk of a decaying tree to large areas such as the tundra of Baffin Island in Arctic Canada. Very large areas of the earth's surface that have a similar climate and vegetation are referred to as **biomes.** The biomes are an important area of research in biogeography, and we will discuss them in detail later. Finally, all of life on the planet is collectively referred to as the **biosphere**—the highest and broadest level of ecological research. The other realms of the earth are physical ones of the **atmosphere, hydrosphere,** and **lithosphere.** The atmosphere includes all the components of the air; the hydrosphere includes all the water in the oceans, lakes, streams, and ground; and the lithosphere is the solid earth of rock and sediment. Although the research of biogeographers may focus on smaller levels such as ecosystems, the end goal of biogeography is to combine the results from all of these more specific studies and draw general conclusions about how the biosphere functions today, how it developed, and where it might be headed in the future. Remember, our future and that of the biosphere are really one and the same.

Trophic Hierarchy

A third way of ordering the biosphere is to examine the flow of energy through ecosystems. The various levels through which energy flows from its initial capture by the biosphere until its dissipation as waste heat are called **trophic levels.** The biosphere functions through the acquisition of energy by organisms and the flow of energy from one organism to another. With very few exceptions, all life is dependent on the sun to provide the energy that is consumed. Notable exceptions are the amazing ecosystems that have developed around undersea volcanic vents (Technical Box 2.1).

Most of the solar energy that reaches the earth is visible light, which is a form of short-wave radiation. The electromagnetic waves that make up visible light range in wavelength from approximately 0.4 microns to 0.6 microns. Of this incoming energy, approximately 32% is reflected back into space by the earth's atmosphere. Roughly 18% is absorbed by the earth's atmosphere. The surface of the earth absorbs about 50% of the incoming radiation, and about 20% of this is used in evaporation. Visible light energy from the sun is absorbed by the atmosphere and the earth's surface and then

TECHNICAL BOX 2.1

Deep-sea crabs and other marine life near a "black smoker" hydrothermal vent in the deep ocean. Illumination for the picture is provided by artificial lighting from a deep-sea submersible vehicle. *Source:* W.R. Normark, Dudley Foster / Wikimedia Commons.

Chemosynthesis and the Ecosystems of Oceanic Hydrothermal Vents

In 1977 scientists discovered that hydrothermal vents located 2500 meters below the ocean surface near the Galapagos Islands supported unexpectedly dense concentrations of organisms. Over 100 similar vents have been discovered throughout the world's oceans. The biomass of these vents is astounding and can range as high as 20 to 30 square kilometers. The vent organisms include giant red worms *(Riftia pachyptila),* large clams *(Calyptogena magnifica),* and mussels *(Bathymodiolus thermophilus)*. In addition, various species of crabs, shrimps, and sea anemones are found at some vents. In all, some 700 new species, previously unknown to science, have been discovered near undersea hydrothermal vents. How can such fauna be supported so far from the upper ocean waters where photosynthesis occurs? These vents emit mineral-laden waters at temperatures ranging up to 450° C. When mixed with the cold ocean waters, this produces temperatures in the vent area of 8° C to 23° C. Hydrogen sulfide (H_2S) is particularly abundant in these plumes. Studies have revealed that these vents support a food chain based entirely on geothermal energy. At the base of the food chain are bacteria that oxidize the sulfur from the vents to form carbohydrates. In contrast to photosynthesis, this process is called **chemosynthesis** and proceeds as follows:

$$CO_2 + H_2S + O_2 + H_2O \rightarrow CH_2O + H_2SO_4$$

The CO_2 and O_2 in the process come from the sea water. The bacteria are then eaten by primary consumers such as limpets, mussels, and clams. Chemosynthetic bacteria utilizing hydrogen and aluminum have also been found in environments such as the hydrothermal vents, cold marine vents, and sunless caves.

radiated as long-wave (3-micron to 25-micron wavelength) thermal energy. This long-wave radiation is what we sense as heat. It is clear that almost 100% of the incoming solar radiation is reflected back into space or used in heating and evaporation. What then powers the biosphere? The entire biosphere, including the human race, is supported by a tiny fraction of the incoming solar radiation. The amount of solar energy captured for direct use by the biosphere is only 0.1% to 0.3% of the total input!

The solar energy used to power the biosphere is captured through the process of **photosynthesis.** For most plants, the radiation used for photosynthesis falls in the red through blue visible light (approximately 0.4-micron to 0.6-micron wavelength) portion of the electromagnetic spectrum. This light is referred to as photosynthetically active radiation, or PhAR. Most of the solar energy that the earth receives is PhAR, so it is no coincidence that plants evolved to use this portion of the electromagnetic spectrum in photosynthesis. It is also not surprising that our eyes are adapted to detecting radiation in these wavelengths. We can see visible light spectrum energy but not ultraviolet or infrared energy.

During photosynthesis, atmospheric carbon and water vapor are transformed into sugar, water, and oxygen. The energy for photosynthesis comes from PhAR. The process takes place in chloroplasts, which are small, green bodies within plant cells. The chloroplasts hold chlorophyll, which is the primary light capturing the pigment of plants. The overall process can be summarized as follows:

$$\underset{\text{Carbon Dioxide}}{6CO_2} + \underset{\text{Water}}{12H_2O} \xrightarrow{\text{Light}} \underset{\text{Sugar}}{C_6H_{12}O_6} + \underset{\text{Water}}{6H_2O} + \underset{\text{Oxygen}}{6O_2}$$

The CO_2 enters the leaves of plants through openings created by specialized sets of cells called **stomata.** The stomata also allow the release of oxygen and water vapor from the interior of the leaf.

There are three different biochemical pathways that green plants use in photosynthesis. Most plants capture energy using the **C_3 pathway** described by Melvin Calvin of the University of California at Berkeley. In C_3 plants, the CO_2 from the atmosphere is converted into a 3-carbon molecule called 3-phosophoglyceric acid. In the 1960s it was discovered that sugar cane converts CO_2 into two 4-carbon molecules: malic and aspartic acid. This process became known as the **C_4 pathway.** Finally, some plants, such as the prickly pear cactus *(Opuntia),* use a modified form of photosynthesis called **crassulacean acid metabolism (CAM).** In CAM plants, CO_2 is absorbed at night and stored as malic acid. During the light of day, photosynthesis is conducted by the C_3 pathway. The term *C_2 photosynthesis* is also encountered when discussing photosynthesis and relates to the process of photorespiration whereby high light intensity and temperatures lead to a process with decreased photosynthetic efficiency. This will be discussed further in Chapter 3. In general, C_4 plants have the highest rates of photosynthesis, while CAM plants display the lowest rates. Interestingly, however, all plants are relatively inefficient in terms of energy fixation through photosynthesis. Only about 1% to 3% of the light hitting a leaf is transformed into chemical energy in the form of simple carbohydrates such as the sugars glucose and fructose.

Photosynthetic plants are the foundation of the trophic hierarchy almost everywhere except places like hydrothermal vents or sunless caves (Fig. 2.3). Plants are referred to as primary producers because they fix the energy of the sun into chemical energy used to power the biosphere. This term is slightly misleading, for plants cannot actually produce energy but merely transform it from one state to another. Plants are also referred to as **autotrophs** or phototrophs because of their ability to fix energy through photosynthesis rather than derive it from the consumption of other organisms. Organisms that eat plants to obtain energy are called primary consumers. Species that eat the primary

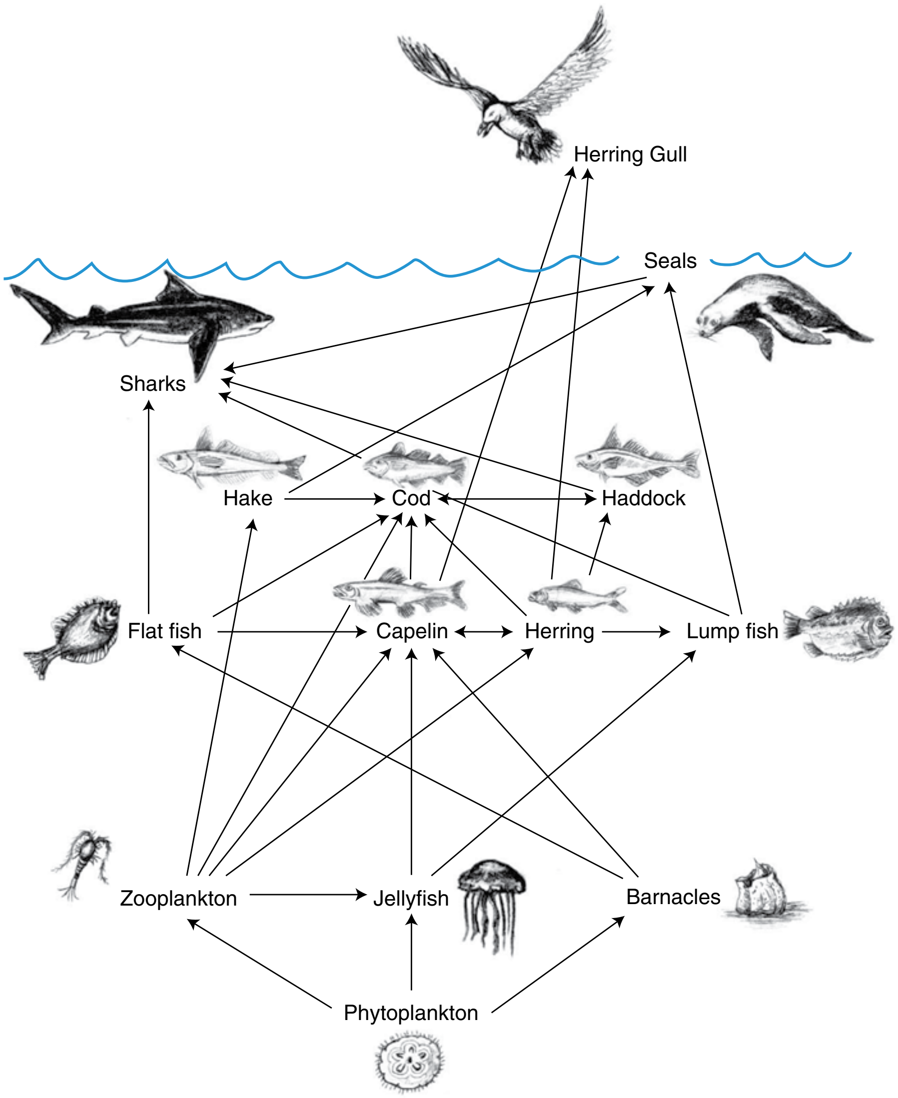

FIGURE 2.3 The complexity of energy flow within an ecosystem illustrated by a simplified and small part of the food web for the northwestern Atlantic Ocean (after Lavinge, 1992). Despite its complexity, a trophic hierarchy with planktonic plants at the base and sharks, mammals, and birds at the top is still apparent.

consumers are referred to as secondary consumers, while species that eat secondary consumers are referred to as tertiary consumers. Plant-eating species are also called herbivores, and meat-eating species are called carnivores. Animals that eat both meat and vegetable matter, such as most humans, are omnivores. When plants and animals die, decomposers consume them. Decomposition is the ultimate fate of all trophic levels. Herbivores, carnivores, omnivores, and decomposers are collectively known as **heterotrophs** because they rely on other organisms to provide energy.

The trophic levels extending from primary producers to the highest level of consumers are sometimes called food chains. However, the idea that energy flows in a linear fashion up the trophic hierarchy is simplistic and misleading. Generally, there is a skipping of levels and a back-and-forth exchange between different levels of consumers and decomposers. As a result, the actual flow of energy in an ecosystem is more like a **food web** than a linear chain (Fig. 2.3). The English ecologist Charles Sutherland Elton (1927) was one of the earliest scientists to identify the importance of ordering ecosystems according to energy flows. He also recognized that the flow of energy was more complex than a simple linear chain. The work of American ecologist Raymond Lindeman in 1942 was the first attempt to formally conceptualize and quantify the flow of energy within food webs. The study of food webs is the basis of modern systems ecology. It has been suggested that understanding food web structure is fundamental to understanding basic ecosystem structure, function, and response to disturbance and change.

Relatively complex trophic hierarchies have been identified from both terrestrial and marine ecosystems. However, tracking and quantifying the flow of energy in such systems are not easy. The three approaches commonly used to investigate and define food webs are direct observation of feeding habits, inspection of the stomach contents of dissected organisms, and use of radioactive tracers such as phosphorus-32 (^{32}P), which are introduced through injection into the vegetation and can be easily traced in tissue samples from animals.

The average length of time during which energy captured through photosynthesis is held by living plants in food webs varies from a few days in the open ocean to 3 years in grasslands and 22 to 25 years in some forests. Energy captured by photosynthesis can also be held in plant litter for significant periods of time before being used by decomposers. In the tropics, the energy held in plant litter may be released within 3 months, while it can be held for over 100 years in the litter of temperate and northern forests. However, studies using radioactive tracers show that, despite the potential long residence time of energy in plants and litter, much of the energy captured by photosynthesis moves very quickly through the food web. In both terrestrial and freshwater ecosystems, some of the energy captured by photosynthesis is passed up to the highest trophic levels within a matter of weeks.

Elton noted that trophic hierarchies appeared to be limited to only four or five levels. More recent examinations of the number of trophic levels in many food webs ranging from invertebrate communities living in dung to birds in forest stands to fish, birds, and mammals of the Antarctic pack-ice have found that most ecosystems support only three to six trophic levels. Why is this? It has been argued that since the transfer of energy between different trophic levels is relatively inefficient, the energy available to higher trophic levels will rapidly decrease. All organisms use energy to function through the process of **respiration,** which is the oxidative reaction that breaks the high-energy bounds of carbohydrates to release energy for the organism's metabolism. Thus, respiration is the reverse of the process of photosynthesis, with metabolic energy being produced, as shown here:

$$\text{Energy} + \underset{\substack{\text{Carbon}\\\text{Dioxide}}}{6CO_2} + \underset{\text{Water}}{12H_2O} \xleftarrow{\text{Metabolic Energy}} \underset{\text{Sugar}}{C_6H_{12}O_6} + \underset{\text{Water}}{6H_2O} + \underset{\text{Oxygen}}{6O_2}$$

On average, only about 10% of the energy of any trophic level is passed on to the next trophic level. This generalization is known as the 10% rule. As a result of the 10% rule, each trophic level is expected to have about 90% less energy available to support it than the preceding trophic level. There is a high degree of variation in the actual energy efficiencies of different organisms in food webs. Birds and mammals are the least efficient because they use energy to maintain constant body heat. They assimilate