ONE

INTRODUCTION

> Laws of distribution can only be arrived at by comparative study of the different groups of animals, for this study we require a common system of regions and a common nomenclature.
>
> **Alfred Russel Wallace (1894:612)**

CLASSIFICATION IN SCIENCE

Biogeography is a comparative science. Classification is the foundation of comparative science. Whenever we compare two objects, we rely on a classification to decide whether they should be placed in the same group or in different groups. A scientific classification has two qualities (Szostak, 2005:2): it should first identify an exhaustive set of types, such as the Periodic Table of chemical elements, and second be based on some

Box 1.1 Universal Systems and General Laws

- A *Universal System* is an inclusive plan, arrangement, or classification that is characterized by repeatability and predictability. The Periodic Table of the Elements is a Universal System.
- A *General Law* is an immutable expression of the relationship among a series of observations. The notion that gradual changes in the Earth over long periods of time explain the origin and history of biodiversity and geodiversity is a General Law.

theoretical ordering principle, such as atomic number. In physics, the classification of colors was pioneered in the symmetrical six-color circle or wheel of German poet, writer, and naturalist Johann Wolfgang von Goethe, first published in *Zur Farbenlehre* (1808–1810; Goethe, 2006). Goethe's color wheel is still used today in science and industry, often in a modified form, such as the circular chart of Munsell (1905; see Platts, 2006). The elegantly simple color wheel represents a scientific classification. It incorporates the range of colors in the visible spectrum and places them in order of wavelength: red, orange, yellow, green, blue, purple. In geology, classifications are essential for the identification of rocks and of their minerals. *A System of Mineralogy, Fourth Edition,* by 19th-century naturalist James Dwight Dana (1854) introduced a chemical classification, grouping minerals into now familiar categories such as sulfides, silicates, and oxides (Hawthorne, 1985; see Ferraiolo, 1982).

The value of such natural classifications is that they accommodate *all possible* histories; hence, they are *universal* and have great predictive (or retrodictive) value. Without natural classifications, we cannot make meaningful comparisons of biological, chemical, or physical forms. Individual histories are not universal and cannot be used to classify or compare forms. The swimming performance of a particular species of tuna, for example, cannot tell us whether other fish species swim as fast or as slowly. Such individual histories play almost no role in predicting what other histories may be discovered. Knowing what other species are classified in the tuna family allows predictions about form and function of those species.

To understand a vast and complex system of interactions, we generalize our observations and experiences to recognize either *Universal Systems* or *General Laws*. A General Law is resistant to other possible explanations and can reject a Universal System. Scientific classifications should be Universal Systems, not General Laws. Classifications that are Universal Systems provide a stable foundation for all scientific fields.

Box 1.2 Léon Croizat (1894–1982)

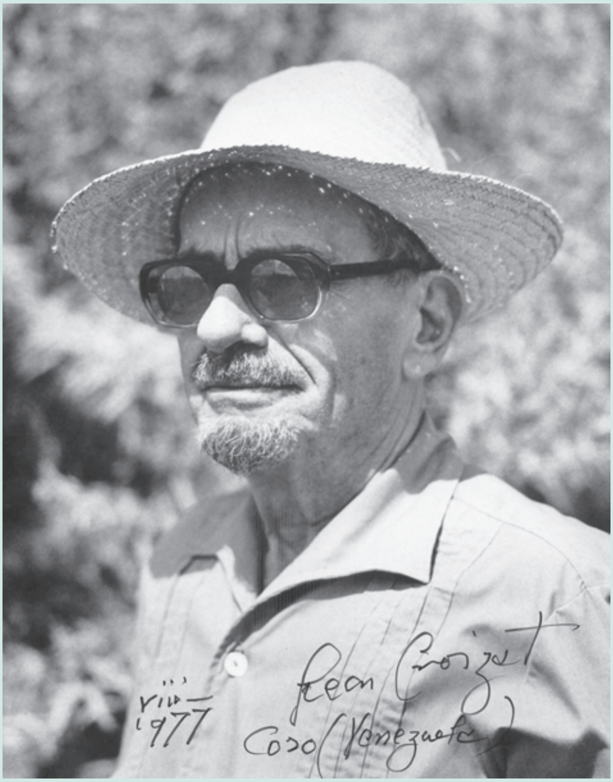

Figure 1.1. Léon Croizat in Coro, Venezuela, August 1977. [Photograph courtesy of Ricardo Callejas and Beatriz Rivera.]

Léon Croizat is the father of modern biogeography. He formalized the concept of a dynamic Earth evolving along with the organisms that inhabit it, now sometimes called panbiogeography. Croizat, an Italian emigrant to the United States, was employed as a technical assistant at the Arnold Arboretum, Harvard University, from 1937 to 1946. In 1947, he moved to Venezuela, where he held several academic positions and worked on various field expeditions as a botanist, including his first exploration of the upper Orinoco. His experience and skill as a field botanist and scholar led him to write several groundbreaking works: *Manual of Phytogeography* (1952), *Panbiogeography* (1958), *Principia Botanica* (1961), and *Space, Time, Form: The Biological Synthesis* (1964) (see Craw, 1984). *(continued)*

Croizat's panbiogeography was an advance in comparative biogeography as it focused on organisms and geographical areas as distinct, yet interactive, entities. *Panbiogeography* was unique as most other biogeographical fields were developed against a backdrop of a static or slowly changing Earth. Croizat's idea that organisms naturally disperse and become geographically isolated within existing geographic ranges gave birth to the concept of vicariance (see Chapter 5). Croizat is a controversial figure in biogeography; the importance of his contributions continues to be debated (e.g., Seberg, 1986; Craw et al., 1999; Grehan, 2006). His extensive writings are most appreciated by those who take the time to read them: Croizat's ". . . flood of words has raised the sea of biogeography to a new level. . . . [His] victory is the defeat of hypotheses of chance dispersal: he has given us whereon to stand" (Corner, 1963:244–245).

EARTH AND LIFE EVOLVED TOGETHER

The catchphrase of Léon Croizat (1964:605), ". . . earth and life evolve together," refers to the dynamic interaction of biology and geology—a cornerstone of panbiogeography and one of the principles that we and many other biogeographers have adopted.[1] The concept of an Earth that changes along with the organisms that inhabit it has been controversial and is far from universally accepted as part of the foundation of biogeography. British geologist Charles Lyell outlined a General Law on the history of the Earth in his three-volume masterpiece, *Principles of Geology* (1830–1833). Lyell's General Law of gradual change over long periods of time was used to explain how the Earth was formed and to explain the origin and history of *biodiversity* and *geodiversity*. We call it a General Law because it was resistant to and rejected other possible explanations. Noted for his profound influence on geology, Lyell was one of the first to propose an explicit dispersalist biogeography which maintained that evolution of the Earth and distribution of life on it are disjunct mechanisms (see Camerini, 1993:705; Bueno-Hernández and Llorente-Bousquets, 2006). As we shall explain, the influence of such strict dispersalist views impeded progress in the science of biogeography.

The proposal of continental drift by German scientist Alfred Lothar Wegener (1915, 1929) diminished Lyell's notion of gradualism. Continental drift is a theory of Earth history based on the outline and positional relationships of continents as evidenced by the relationships of their biological and geological diversity. A supercontinent, Pangea, was formed and then subsequently broke apart, and over millions of years its sections or continents drifted to the positions they occupy today.[2] Late-19th- and early-20th-century biologists were intrigued by the growing evidence for past continental connections and interpreted the biogeographic patterns with respect to Earth history: Irish naturalist Robert Scharff's (1911) monumental *Distribution and Origin of Life in America* is a modern-in-tone refutation of the permanence of ocean basins and an argument for past land connections. Wegener's theory of continental drift was rejected by early-20th-century geologists, and hence by most other scientists as well, because he proposed no plausible explanatory mechanisms of continental formation or movement. The discovery of spreading mid-oceanic ridges in the mid-20th century vindicated Wegener and led to the proposal of a mechanism of an evolving Earth: plate tectonics and seafloor spreading (Hess, 1962). A new geological synthesis, incorporating a dynamic Earth, was adopted rapidly by geologists and other scientists (e.g., Dietz and Holden, 1970; Hallam, 1973). The development of a theory of plate tectonics dramatically altered our understanding of the Earth and changed perspectives on the patterns and mechanisms of extinction and evolution of life (see also Heads, 2005a). A dynamic Earth—not the passive, slowly eroding Earth, punctuated by catastrophes, as perceived by Lyell and other 19th-century naturalists—is taken for granted today.

Ironically, biogeography was led by 19th-century naturalists who gave in to the concept of a static Earth after considering a mobilist perspective (see also Chapter 2). British naturalist and biogeographer Alfred Russel Wallace, co-proposer with Charles Darwin of a theory of organic evolution (i.e., natural selection), argued first that geographical relationships of plants and animals, as detailed on maps, ". . . provided the crucial link between biological processes (the production of new species from existing ones) and geological processes . . ." (Camerini, 1993:723). Wallace even advocated major continental movements, but then changed his mind, as explained by Camerini (1993:726), who notes that Wallace argued,

> Just as geological and physical features provide clues to biological evolution, the evolutionary relationships and geographical distribution of animals provide essential clues to former land connections. On this point, however, we find in 1863 a shift from the reliance on major continental movements to a belief in the permanence of the major continental land

> masses. . . . The pro-permanence view provided solid ground for [Wallace's] subsequent treatises on geographical distribution and earned him the full support of Lyell and Darwin.

Had Wallace maintained a mobilist view of the world and its biota, we could now be in the second century of discovery of biogeographic patterns that incorporate Earth history. Instead, following in the Wallace-Darwin-Lyell biogeographic tradition, overwhelming biogeographical patterns that link continents, such as coherence of life around the Pacific basin, have been explained away as being irrelevant or as being driven by mechanisms such as long-distance dispersal of individual clades (e.g., Darlington, 1957; Carlquist, 1965; Briggs, 1974; and more recently de Queiroz, 2005; see Chapter 7). Geology and biology have been kept apart.[3]

Explanatory Mechanisms

Development of the phylogenetic systematic or cladistic methods (Hennig, 1950, 1965, 1966; Nelson and Platnick, 1981) to discover and rigorously diagnose monophyletic groups of organisms—and hence to build natural biological classifications—has been the greatest advance in evolutionary biology since the modern synthesis combined genetics with biological evolution (Mayr, 1942), and in systematic morphology since the reestablishment of Owen's special homology by Naef (1919). Biological classification changed in the mid-20th century in response to the rise of cladistic methodology rather than in response to the modern synthesis (e.g., Mayr, 1974; Ragan, 1998) or to the acceptance of the notion of a dynamic Earth. Biological classification, once largely gradistic, was replaced by a phylogenetic or cladistic classification system. In a cladistic classification, only monophyletic groups are named; in a gradistic classification, paraphyletic as well as monophyletic groups are named. A paraphyletic group, such as the Algae, Invertebrata, or Reptilia, is an artificial and non-evolutionary category that cannot be used to explain phylogenetic history.

Today biogeographic theories acknowledge the decisive role of phylogeny. Multiple phylogenies are mandatory to identify patterns. Without a biogeographical classification that incorporates natural biotic area groups based on a phylogenetic classification, we must explain each incidence of conformation to a pattern *as if it were not part of the pattern*. In effect, we give up the opportunity to compare. One pattern

Box 1.3 Cladistic versus Gradistic Classification

- Cladistic Classification: A biological classification in which only monophyletic groups are named. A monophyletic group, or *clade,* contains all, and only, the descendants of a common ancestor.
- Gradistic Classification: A biological classification in which names may be applied to both monophyletic and paraphyletic groups, emphasizing the differences among taxa. A paraphyletic group, or *grade,* contains descendants of a common ancestor yet excludes those descendants that have diverged from their close relatives.

If taxon A evolves into taxon B, all members of taxon A are paraphyletic because some members of taxon A are more closely related to members of taxon B than they are to any other taxon. If we assume that ancestors are found at the nodes of phylogenetic trees, then groups at the terminal branches are *grades,* not *clades*.

expressed by many different organisms is meaningful and has predictive power, even without a ready explanatory mechanism. The problem with particular explanatory distributional mechanisms—such as individual episodes of long-distance dispersal—is not that they fail to explain distributions and biodiversity, but that these explanations cannot be refuted empirically. Such explanatory hypotheses lack empirical rigor and are untestable. Only with a natural classification of taxa and biotic areas are we able to compare distributions and discover historical biogeographical patterns. This is what this book is about.

Life and Earth and Earth and Life

Clades form phylogenetic patterns because they share a common history and, therefore, their homologous characters (such as feathers in birds, seven cervical vertebrae in mammals, spinnerets in spiders, and so on). Abiotic patterns in geology involve structure and composition of minerals and rocks; their explanations perhaps allude to similar conditions under which they were formed (such as sedimentation or volcanism) or to geomorphological structures (asymmetrical and symmetrical rippling). These inorganic classifications reflect the types of environments that existed, but the structures are not necessarily related by common history. Ripples like those we see in coastal inlets or in tidal rivers are similar to the ripples we see in sedimentary rocks. Discovery of such rocks in association with other, similar structures that indicate a coastal or tidal environment leads to identification of patterns suggesting, in turn, that a current mountainous or arid terrane may have once been a coastline. Thus, ripples in various places or at different times are caused by similar mechanisms, but may not be caused by precisely the same event.

Inorganic classifications, furthermore, can never provide evidence as to what taxa lived in past environments. If we identify a coastal environment based on geological or geographical evidence, it still cannot tell us what families of fishes or gastropods, for example, may have lived there. No matter how much we know of a past environment, even its chemical or climatic composition, those data alone will not confirm what taxa lived there. The fossil record has shown in many instances that similar environments can support many different types of biota through time.

BIOGEOGRAPHY

The word *biogeography* was coined by the German geographer Friedrich Ratzel (1891:9):

> . . . Vereinigung der Pflanzen- und Tiergeographie mit der Anthropogeographie zu einer allgemeinen Biogeographie, einer Lehre von der Verbreitung des Lebens auf der Erde.

> . . . the unification of plant and animal geography with anthropogeography [human geography] in order to form a General Biogeography, the study of the distribution of life on Earth.

Ratzel's General Biogeography possibly combines all known methods, theories, and techniques of biogeography, including human geography, anthropology, and social change (see Müller, 1995). Here, we limit biogeography to the study of the relationship between the organic part of the world, the biosphere, and the inorganic, the physical Earth. The timeframe of biogeography spans nearly 4 billion years, from when life first appeared on Earth as simple cells, to the present day. In practice, biogeography does not extend much beyond some 570 million years ago (mya), when organisms became more complex and evolved hard parts that could be fossilized (see Tarling and Tarling, 1975).

Biogeography is a naturally integrative field of study that encompasses a broad range of methods, data, habitats, and organisms, as well as practitioners and goals.[4] Biogeography helps us understand our planet and its geography, geology, and organisms, where they have interacted through time, evolving together to form the places we know today. Most important, biogeography is a comparative science that interprets the complexity of relationships and distributions of life on Earth with respect to its geological history.

The common goal of all biogeographers is to understand the relationship between life and its distribution. After that, agreement is infrequent (see, e.g., Crisci, 2006; Crisci et al., 2003, 2006). Cladistic methods have been applied to biogeography in a variety of methods, many with contradictory aims (viz. Nelson and Platnick, 1981; Morrone and Carpenter, 1994; Humphries and Parenti, 1999; Brooks and McLennan, 2002; see Chapters 5 and 6). The method of Comparative Biogeography and its incorporation of Systematic and Evolutionary Biogeography is introduced below and detailed more fully in Chapters 3, 4, and 7. Other biogeographic methods and distributional mechanisms are reviewed with respect to the comparative biogeographic method in Chapters 5 and 6.

COMPARATIVE BIOGEOGRAPHY

Biogeography can be a powerful tool to explore data on the diversity, phylogeny, and distribution of organisms, to reveal the biological and geographical history of Earth. We aim to unite the many aspects of biogeography under one banner: *Comparative Biogeography*. Comparative biogeography uses the naturally hierarchical phylogenetic relationships of clades to discover the biotic area relationships among local and global biogeographic regions. One biotic area, A, may be said to be related to another, B, more closely than either is to a third, C, if the taxa of the biotic areas reflect a three-area relationship: C(AB). Such proposals of area relationship are three-area relationships or *area homologs:* hypotheses of area relationships that may be expressed in a general classification of areas.

To introduce comparative biogeography, we differentiate between the two types of biogeographic investigation that it encompasses: systematic biogeography and evolutionary biogeography.

Systematic Biogeography is the study of biotic area relationships and their classification and distribution. For example, the distribution and relationships of numerous taxa may be expressed in a hierarchy as Eastern South America (Africa, India), meaning that organisms in Africa have their closest relatives in India and that together they are in turn related to organisms in eastern South America. Examples include such diverse taxa as vascular plants, fishes, birds, and dinosaurs.

Evolutionary Biogeography is the proposal of evolutionary mechanisms responsible for organismal distributions. Possible mechanisms responsible for the distribution of organisms related as in the area homolog Eastern South America (Africa, India) include widespread taxa disrupted by continental break-up or individual episodes of long-distance movement, to name just two.

Systematic versus evolutionary is one historical division of biogeographers as well as of biologists and their methods. The division is analogous to investigation of "classification versus explanation" or "patterns versus mechanisms." This division dates from the earliest formulations of evolutionary theory (Camerini, 1993; see Chapter 2). The modern synthesis emphasized process or mechanism over pattern, and, according to Ghiselin (2006), at the level of species or below, with scant concern for geological processes (Chapter 2). Evolutionary biology under the modern synthesis did not focus largely on a dynamic Earth, emphasizing instead mechanisms such as dispersal, and species interactions, such as competition, mutualism, and predation. The dynamic Earth is more than just drifting and colliding continents; it is all the geological processes linked explicitly to events such as climate change, sea level changes, erosion and weathering, frequent volcanism, earthquakes, tidal waves, changes in atmospheric chemistry, changes in soil chemistry, and so on. Ultimately, it involves the close relationship between organisms and the environment, seen in major animal constructions such as coral reefs, and acting at all levels.

CLASSIFICATION OF AREAS: SYSTEMATICS AND BIOGEOGRAPHY

Classification of biotic areas is the goal of our comparative biogeography just as classification of taxa is the goal of systematics (Chapter 2). Biotic areas are what we compare and classify in biogeography. Biotic areas are defined by both the aggregate taxa and the areas in which they live.

Once comparative biogeography is more fully implemented, we will be able to replace the traditional classifications of biogeographic regions and realms with natural, homologous areas (sensu Wallace, 1894; Chapter 2). Arbitrary areas (e.g., an abiotic geographic entity, such as "Australia," "Borneo," or "the Philippines") have little meaning in comparative biogeography unless they are occupied by a monophyletic biota. For a variety of reasons, it is not surprising that some geographically delineated regions may also be recognized in area homologs.

TOWARD A COMPARATIVE BIOGEOGRAPHY

Comparative biogeography provides biologists with a rigorous empirical theory and with methods of analysis for interpreting Earth history. Comparative biogeography diagnoses and classifies biogeographic areas by incorporating data from a broad array of taxa, their phylogenetic hypotheses, and geological and geographic variables. It grapples with the potentially enormous amounts of data of comprehensive biogeographical analyses by providing a classification of organic areas which forms a biogeographical framework. It implements a classification or universal system *before* exploring explanatory mechanisms or hypotheses.

Comparative biogeography empirically examines the common historical processes that may be postulated to explain biotic distributions and diversity. It does not emphasize molecules over morphology, nor does it emphasize vicariance over dispersal (Chapter 5). This search for common patterns does not emphasize the simple over the complex (viz. Brooks, 2005). Simple mechanisms can produce highly complex, repetitive, nested patterns (Wolfram, 2002). Nature endlessly repeats (Croizat, 1958). This repetition, the observation of the same distribution over and over, in many different and unrelated taxa, led to the identification of natural biogeographic features which Croizat illustrated as lines on maps or tracks (Figure 1.2; also Chapter 2). Tracks drawn as networks or reticulations do not identify area homologs. The repeated features of global biogeography, trans-Pacific, trans-Atlantic, boreal, austral, Indian Ocean, and so on down to the lowest levels, when defined as area homologs and classified hierarchically, will form the framework of a comparative biogeography.

Biogeographers have swung between two extremes, from rejecting geological history as too old to have affected biological distribution, to interpreting distributions explicitly with respect to current theories of geology. We adopt the view of early cladistic biogeographers such as American ichthyologist and biogeographer Donn Eric Rosen (1978; Chapter 7), who states that biological and geological patterns provide "reciprocal illumination" or shed light on each other, but do not test, and therefore cannot reject, one another.

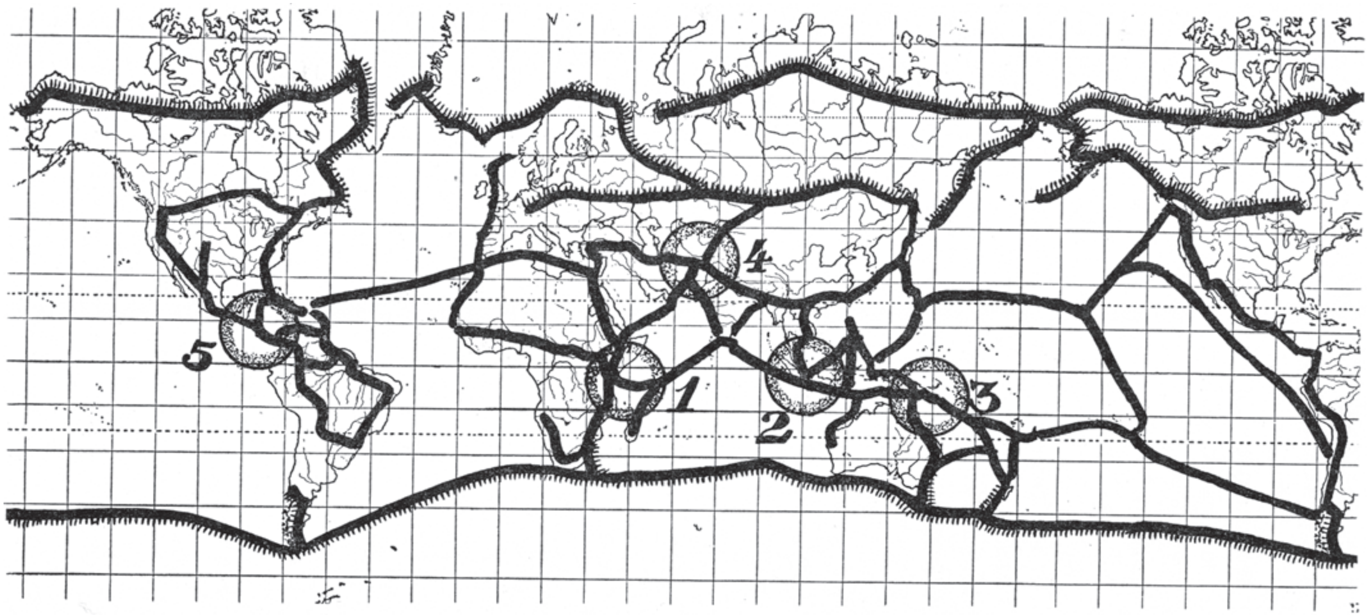

Figure 1.2. Croizat's (1958, IIb: 1018, figure 259) summary of the major features of global biogeography of both plants and animals. The lines are generalized tracks or repeated distributions of organisms. Numbered areas are panbiogeographic nodes, or major intersection points, of the generalized tracks. Hatched lines represent boreal (in the north) and austral (in the south) distribution patterns. [Image courtesy of John R. Grehan.]

Biogeographic patterns are not all necessarily explained by current, generally accepted, well-known geological hypotheses or familiar details of plate tectonic theory. Many biogeographers have long called for the recognition of a formerly closed Pacific basin to explain the distribution of its life (Chapter 8). This theory is still controversial, and many geologists reject the notion of a closed Pacific basin as folly. But more data, both biological and geological, may change this, just as Wegener's notion eventually changed the accepted early-20th-century paradigm of Earth history. Seen until now as part of a widening rift in biology, the interdisciplinary approaches of systematics and evolutionary biology are united with Earth history under the multidisciplinary comparative biogeographical approach.

ORGANIZATION OF THIS BOOK

The core of this book is organized into three parts:

Part I: History and Homology In Chapters 2, 3, and 4, we detail the foundations of comparative biogeography and explain how they relate to the interconnected fields of systematic and evolutionary biogeography. Endemism, the restriction of organisms to particular places, is introduced as one of the core concepts in biogeography. Our thesis is that discovery of a classification of endemic biotic areas that specifies a pattern of area relationships logically precedes inferences about the mechanisms or processes that may have caused biotic distribution.

Part II: Methods We review current methods of biogeography, especially with regard to how they relate to the goal of biotic area classification, in Chapters 5 (Processes) and 6 (Methods and Applications). Our aim is not to exhaustively critique all biogeographic methods, an activity which would be well beyond the scope of this book, but rather to contrast some of the methods, and especially their assumptions, with those of comparative biogeography. In Chapter 7, we outline our method of systematic biogeography, which is discovering a global biotic area classification.

Part III: Implementation We address the relationship between Earth history (geology) and biological distribution in comparative biogeography in Chapter 8. We then tackle the complex biogeography of the Pacific in Chapter 9 to implement our method, demonstrating the power of biogeography to discover and interpret natural patterns.

We close with Chapter 10, our vision for a global biogeography. We argue that biogeography is Big Science and deserves the attention and resources given to other large-scale, global scientific efforts.

NOTES

1. Panbiogeography, formulated by botanist and biogeographer Léon Croizat (see Box 1.2), documents and interprets distribution patterns with respect to each other without relying on or specifying particular phylogenetic hypotheses. We share many basic principles with panbiogeographers, but we differ in the use of phylogenetic patterns in biogeography.

2. The first proposal of an ancient supercontinent, Pangea, is often credited to the 18th-century French naturalist Georges-Louis Leclerc, Comte de Buffon (1766). In contrast, Papavero et al. (2003) argue that Buffon borrowed the idea from German scholar and collector Johann Wilhelm Karl Adolph von Honvlez-Ardenn, Baron von Hüpsch (1764), who published it two years earlier.

3. Darwin, as well as Wallace, fell under the influence of Lyell. Craw (1984:49) argues that "Darwin, in his first 'Transmutation of Species' notebook (1837–1838) used biogeographic evidence to erect novel geological hypotheses. These included a continental drift theory in which all the continents were grouped together into the middle of the Pacific Ocean. . . . Subsequently in his 'On the Origin of Species' (1859) he rejected that view and argued vehemently in favour of the permanence of continents and oceans. . . . In his mature work particular geological theories were used as the basis upon which biogeographic narratives were constructed."

4. We see the field of biogeography as logically integrative because it combines biology, ecology, geology, geography, paleontology, and so on. All biogeography is "integrative biogeography," and this view has a well-established historical foundation. The phrase "integrative biogeography" has been used to endorse a particular set of methods (sensu Donoghue and Moore, 2003) or to inflate artificial divisions, such as that between phylogeny and ecology (Wiens and Donoghue, 2004; see Chapter 5).

FURTHER READING

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