

FORUM ON BIOGEOGRAPHY: INTRODUCTION

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The process of unifying biogeography has had its many champions. Originally, in pre-evolutionary Europe, biogeography was unified by the common aim of uncovering the centre of origin, a concept derived from biblical texts. Organisms either were created in the places they were found or they moved there from elsewhere (Buffon, 1766; Sclater, 1858). Whether or not the organisms evolved was not an issue in biogeography. Organisms had a centre of origin (either by creation or evolution) from which they moved, thus forming the strange distribution patterns both in living and fossil species. The advent of Darwinian evolutionary theory, a process (natural selection) proposed to explain biogeographical distribution, was seen to be a unifying theme. Organisms had one centre of origin. Ernst Haeckel, who was deeply influenced by Darwin's work, proposed a centre of origin for mankind. At first he believed it was the lost island of *Lemuria*, sunk off the coast of Pakistan. In a later revision he moved it to present day Afghanistan (see Haeckel, 1876). Earth at this time was thought to be static, continents were set rigid and only oceans and climate were seen to be dynamic. The unifying theme of biogeography relied on the actions of ocean currents and climate to explain odd distributions of living and fossil taxa. Matthew (1915), Darlington (1957), Simpson (1965) and MacArthur & Wilson (1967) were champions of static Earth biogeography, a theme united by dispersals and centres of origin. But unity did not last long.

The discovery of diverging plate margins after the Second World War was the final clinching argument for continental drift and a dynamic Earth (see Hess, 1962). The works of Taylor (1910), Wegner (1915), du Toit (1937) and Carey (1976) finally came to the forefront. The role of continental drift explained disjunct fossil distributions, but more importantly it highlighted the speed at which plates could move and topology could change. Léon Croizat was the first to champion the idea that Life and Earth evolved together as a unifying theme for biogeography (Croizat, 1958, 1964). Donn Rosen (1978), Gareth Nelson, Norman Platnick (see Nelson & Platnick, 1981), Robin Craw, Michael Heads and John Grehan (see Craw & al., 1999) developed Croizat's ideas further. The search for centres of origin was a task that no longer unified biogeography. Earth was dynamic, older areas were impossible to find, and many living species had a

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poor fossil record. The cladistic revolution in systematics also highlighted the need for monophyletic groups in order to discover historical patterns of taxa (Williams & Ebach, 2004). Biogeography under the Croizatian unification was historical and focused on discovering patterns and then explaining them. Discovery

for some, however, is not separate from explanation or mechanical processes (see Hull, 1988).

Proponents of phylogenetic systematics are convinced that transformational optimizations in phylogenetic trees offer the best way to approach biogeography. All phylogenetic lineages have separate centres of origin which by way of discovery, offer a better explanation for distributions and diversity. Recently, Brooks (in press) and Donoghue & Moore (2003) have argued that Life and Earth, in fact, do not evolve together, thus leaving the pursuit of centres of origin and direction of dispersal once again open for debate. Naturally each author realises the impact of a dynamic Earth, but not as the main aim of biogeography.

A similar reaction had occurred in molecular systematics. The advent of molecular data in systematics and its eventual focus on biogeography is the next and latest unification in biogeography. All unifications before were based on morphological data and aimed at species level and above. Molecular data in biogeography, championed by phenetists such as Sokal (1979), were concerned with comparing genetic with geographical distance. Unification came in the form of the most accurate measurement for genetic distance and genetic relationships. Phylogeography is now the leading molecular biogeographical theory.

The island biogeographers stemming from MacArthur & Wilson (1967) relied on unification via statistical measurement of diversity and proposing accurate models with which to predict future and past distributions. The dynamic Earth had little effect on island biogeography, as it is still mostly concerned with ecology, or simply biological interactions. Walter (2004) states that unification can be achieved by integrating "all available

historic and present biogeographic information for the development of predictive distribution models” (Walter, 2004).

Unification in biogeography exists in three different states:

1. Unification as life and Earth evolving together.
2. Unification as the most appropriate method.
3. Unification as a relevant model.

Biogeography as one independent field is unified in three different ways by the proponents of integrated fields. An ecologist is more likely to be an island biogeographer, a molecular systematist a phylogeographer and a morphologist a historical biogeographer. These associations are not exclusive but rather highlight the areas from which the calls for unification originate.

Unification is not an easy task for biogeography. The different answers given by Avise, Parenti and Humphries, and Walter in this forum, highlight the various affinities of biogeographers. The question of unification, however, still remains open. Do we return to Darlington and Matthew and find centres of origin and explain pathways of dispersal unified by a method (sensu Lieberman, 2003)? Can we continue to unify an integrated field of ecology, genetics, geology and history by uncovering patterns caused by a dynamic Earth? Are we bound to find one universal statistical model that unifies biotic distribution (see Hubbell, 2001)?

Biogeography is an historical science, but at the same time is shaped by history. The path we as biogeographers or as students in biogeography choose now will influence decisions and the way we do biogeography in the future. Unification will also be challenged and bear its champions. In order for us to know how biogeography is to be unified and where it will progress lies in our ability to understand its past.

The purpose of this Forum is to analyze biogeography for the researcher and student of biology, geography, and palaeontology currently faced with a daunting number of theories and methods. It explores the wide range of differing approaches to biogeography told in the words of some of today’s leading biogeographers. Biologists representing historical biogeography, island biogeography and phylogeography, have been asked to respond to four basic questions:

1. How would you define biogeography and its goals?
2. Why are there so many biogeographical theories and methods?
3. In recent years there has been a call for the integration or unification of biogeography. Do you think this is necessary?
4. Has the use of molecular data changed the goals and therefore future development of biogeography?

The responses to these questions reveal that biogeography continues to be a diverse science with many

active and dynamic areas.

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BIOGRAPHICAL SKETCH

Malte Ebach's research includes the history, philosophy, theory and methodology of systematics and biogeography, trilobite systematics and the development of computer software for three-item analysis. Recently he has been investigating the impact of Goethean science in comparative biology.

What is the field of biogeography, and where is it going?

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INTRODUCTION

Biogeography can be both an eclectic and a unifying discipline—eclectic by virtue of the diversity of technical and conceptual approaches from which it borrows; and unifying by virtue of drawing together inputs from diverse fields (ranging from molecular biology to ecology to historical geology) in its attempts to understand the spatial and temporal dynamics of organismal distributions. Here I offer several personal thoughts on the history and possible future of biogeography, with special reference to the role of molecular phylogeographic analyses in forging helpful connections between microevolutionary and macroevolutionary perspectives on biogeographic phenomena.

HOW WOULD YOU DEFINE BIOGEOGRAPHY AND ITS GOALS?

Biogeography can be briefly defined as the science that attempts to describe and interpret the geographic distributions of organisms. Its ultimate goal is to achieve comprehensive understandings of biological and physical processes (at both ecological and evolutionary timeframes) that have shaped the spatial arrangements of the Earth's species and biotas (Cox & Moore, 1993). In spite of (or perhaps because of) its central position at the intersectional crossroads of various biodiversity and geophysical sciences, biogeography has seldom been sanctioned as a formal academic discipline: "In general, there are no institutes of biogeography; there are no departments of it...no professors of it, no curators of it" (Nelson, 1978). Nevertheless, biogeographic analyses (explicit or implicit) are an important component of what many scientists—ranging from anthropologists to botanists, zoologists, ecologists, naturalists, population geneticists, systematists, phylogeneticists, and others—actually do.

WHY ARE THERE SO MANY BIOGEOGRAPHICAL APPROACHES?

Heterogeneity among the scientific backgrounds of biogeography's diverse practitioners probably accounts

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in large degree for the wide variety of the field's theories and methods. For example, many ecologists often tend to view current abundances and distributions of species as being mostly reflective of contemporary habitat conditions (including biotic interactions), whereas many systematists and phylogeneticists tend to be more inclined to consider geological

forces also, as well as other evolutionary processes that may have been at work in the near and distant past. A tension between ecological and historical perspectives in biogeographic investigations was recognized by the Swiss botanist Agustin de Candolle (1820) nearly two centuries ago, and to some extent these two traditional biogeographic orientations continue to march side-by-side, sometimes competitively, even today.

Within historical biogeography, another tension has been between proponents of vicariance as opposed to dispersal. When biogeographers of earlier times interpreted plant and animal distributions against the backdrop of a supposedly static physical Earth, they were often forced to hypothesize dispersal events from evolutionary centers of origin to account for the disjoint ranges of many biotas (e.g., Wallace, 1876; Matthew, 1915; Darlington, 1957). But in the 1960s, with the rejuvenation of interest in Wegener's (1915) pioneering notions regarding continental drift, and more generally with the idea that numerous geophysical features of the planet are themselves highly dynamic, the vicariance school of thought arose (Rosen, 1978). Many biological range disjunctions then were reinterpreted to reflect evolutionary or ecological forces that may have sundered the formerly continuous distributions of particular taxa. A rapid growth of interest in historical vicariance was closely associated with the rise of cladistic biogeography (Nelson & Platnick, 1981; Humphries & Parenti, 1986; Wiley, 1988), which itself was inspired by Hennig's (1966) principles of phylogenetic systematics. In cladistic biogeography, scientists search for correspondences between the geophysical histories of areas and the phylogenetic histories of clades (monophyletic groups)

inhabiting those areas, with particular kinds of outcomes interpreted to reflect either vicariant or dispersal events of the past.

Crisci & al. (2003) reviewed and compared nine different technical and philosophical approaches to historical biogeography. One of these—intraspecific phylogeography—is the study of how biological and physical processes have exerted influence on the spatial distributions of genetic lineages within species and among closely related taxa. The field began as an empirically motivated outgrowth of molecular studies on mitochondrial (mt) DNA, a cytoplasmically-housed set of molecules that is maternally inherited and evolves rapidly in nucleotide sequence in most animal taxa. Within a given species, population-genetic surveys of mtDNA typically revealed a medley of matrilineal or “female family names” that can be interpreted as being highly analogous to patrilineal surnames in many human societies. Furthermore, mtDNA’s non-recombining mode of asexual transmission meant that phylogenetic (i.e., genealogical) relationships among mitochondrial genotypes (“haplotypes”) and matrilineal clades could be recovered from the molecular data. In principle and sometimes in practice, comparable analyses can also be applied to DNA sequences from the nuclear genome, although the technical complications are usually much greater. Phylogeographic analyses then seek to interpret branching structures in such “gene-trees” in a spatial context that includes consideration of both historical and contemporary processes. In general, phylogeography has revolutionized biogeographic analyses at microevolutionary scales of reference, much as did cladistic biogeography at deeper temporal scales and at higher taxonomic echelons.

Intraspecific phylogeography merits distinction from traditional cladistic biogeography in several respects. First, it extends phylogenetic principles and reasoning to the intraspecific level. Traditional wisdom was that cladistic methods do not strictly apply within the “tokogenetic” realm (Hennig, 1966) of intraspecific evolution, because the potential for interbreeding within any extended reproductive community of sexual reproducers would seem to invite genetic reticulations (anastomotic relationships among individuals) that in turn would violate the basic assumptions of phylogenetic reconstruction methods. However, as clearly demonstrated by asexually transmitted mtDNA, non-reticulate genealogical histories are recorded within the non-recombined nucleotide sequences of particular tightly linked runs of DNA. In other words, stretches of nucleotide sequence within which there has been little or no inter-allelic genetic recombination (over the evolutionary timeframe under scrutiny in a given investigation) can contain genealogical data that lend themselves perfectly well to phyloge-

netic analysis. The intraspecific “gene trees” that emerge from such empirical molecular appraisals are non-reticulate and hierarchically branched, just as are the supra-specific phylogenies traditionally generated for species lineages and higher taxa.

On the other hand, a second important realization is that multitudinous quasi-independent gene trees are contained within (and in effect truly comprise) any extended population pedigree (Maddison, 1995). An mtDNA gene tree can be interpreted as a genealogical record of matrilineal heredity through a pedigree, i.e., as the extended history of female to female to female transmission (F→F→F...). For nuclear genes, however, many such hereditary pathways collectively exist. Most nucleotide sequences on the mammalian Y-chromosome, for example, have traversed a male to male to male (M→M→M...) transmission route, whereas DNA sequences at autosomal loci will have transited the generations through a multitude of different hereditary pathways involving both sexes (Avise & Wollenberg, 1997). Such considerations led to several rather novel insights relevant to biogeographic reconstructions, such as the fundamental distinction between a gene tree and a population tree or species tree, and the inevitable variance among gene-tree structures within one-and-the-same organismal pedigree. Indeed, phylogeographic perspectives have raised and also partially answered several questions about the fundamental nature and even the meaning of phylogeny itself at the microevolutionary level.

From this growing appreciation of distinctions between gene trees and population trees, a third realization arose of relevance to biogeography—namely, that by hard criteria, multiple lines of “concordant” biogeographic evidence are normally required before deep genealogical splits in a gene genealogy can necessarily be interpreted to indicate deep historical splits at the population or species level (Avise & Ball, 1990). Concordance can have several aspects, including: phylogeographic agreements across the genealogies of unlinked genes; similar positions of intraspecific genealogical breaks across multiple co-distributed species; and agreement of historical partitions in reconstructed gene trees with traditional taxonomic partitions based on morphological comparisons of particular species, or with biogeographic evidence on the boundaries between historical biotic provinces. Searches for concordant phylogeographic evidence soon led researchers into broader comparative analyses that involve, for example, examination of the genealogical content of multiple unlinked genes within a species (Hare, 2001), and of phylogeographic patterns across multiple species within a regional biota. The latter has been termed the “regional” (Avise, 1996), “landscape” (Templeton & Georgiadis, 1996), or comparative (Bermingham & Moritz, 1998) approach to phy-

logeography, and it is likely to become a focus of much more phylogeographic research in the future.

A fourth general realization was that genealogical outcomes within and among conspecific populations are inextricably linked to the demographic histories of those populations. In other words, the shape and depth of any gene tree reflects to a large degree historical population demographic parameters such as means and variances in offspring production among parents, and magnitudes and patterns of gene flow among demes. Indeed, these inherent connections between genealogy and historical population demography motivated the rise of modern coalescent theory (Hudson, 1990), which provides a formal mathematical and statistical framework for interpreting various gene-tree structures. What has emerged is a burgeoning new field known as “statistical phylogeography” (Knowles & Maddison, 2002; Knowles, 2004) in which explicit biogeographic hypotheses are generated and formally tested with reference to the theoretical expectations of coalescent theory and population-demographic models. Interestingly, demographic considerations almost never arose (although they probably should have) in discussions of phylogenetic relationships of related species and higher taxa, but they clearly are of cardinal importance for interpreting phylogeographic patterns at the intraspecific level.

These and other broad conceptual insights (Avisé, 2004) were an important aspect of the emergence of phylogeography as a recognizable academic discipline, but the empirical datasets themselves were undoubtedly of greater motivational importance. In molecular-genetic surveys of mtDNA conducted across the geographic ranges of literally hundreds of animal species (and later of chloroplast DNA in many plant species; Schaal & al., 2003; Soltis & al., 1992; Petit & Verdramin, 2004), the architectures of organelle gene trees revealed a wide variety of distinctive phylogeographic patterns. Nearly all examined species proved to be genealogically structured across geography, often at various spatial and temporal scales that seem to make considerable sense in terms of each species’ known or suspected ecology and natural history, demography, and biogeographic past (Avisé & al., 1987). Of special note were the well-earmarked phylogeographic subdivisions often observed within particular species. Sometimes referred to as “evolutionarily significant units” or “intraspecific phylogroups”, these genetically distinctive and spatially coherent regional assemblages of conspecific populations often appear quite relatable to past biogeographic agents (such as the presence and spatial arrangements of Pleistocene refugia). Collectively, such empirical findings, accumulated for large numbers of species, amply evidence the importance of historical (as well as modern) biogeographic factors in having shaped the genealogical

relationships of geographic populations within species. The finding of salient but formerly cryptic historical partitions within various species has also proved to be of considerable relevance to conservation biology (Avisé & Hamrick, 1996; Frankham & al., 2002).

IS AN INTEGRATION OR UNIFICATION OF BIOGEOGRAPHY DESIRABLE OR NECESSARY?

Phylogeographic perspectives have highlighted one key sense in which an integration and unification of biogeography is indeed desirable. Throughout the 20th century (and before), there were at least two distinct academic traditions in evolutionary genetics, one in the macroevolutionary arena of phylogenetics above the level of biological species, and the other in the microevolutionary arena of population genetics within a species. Typically, a professional systematist would be well versed in the language and concepts of phylogenetics and would likely be a taxonomic expert on a particular organismal group, but might have had relatively little training in such classical and oft-mathematical population-genetic topics as gene flow, natural selection versus genetic drift, genetic recombination as a function of mating systems, and so on. Conversely, a traditional population geneticist might well be familiar with these latter topics but would not necessarily have had much exposure to phylogenetic principles and concepts. By extending “phylogenetic” reasoning to the realm of population genetics (as described above), phylogeographic perspectives helped to build conceptual and empirical bridges between the formerly disengaged fields of phylogenetic biology and population genetics (Avisé, 1989). This was important, because at least with respect to genealogy, macroevolution is ineluctably an extension of microevolution (all extant organisms had parents who in turn had parents, and so on in an unbroken chain of ancestry leading back in time). Similar arguments can be made for phylogeography’s role in building links between biogeographic assessments at micro- and macroevolutionary timescales.

I would argue that phylogeography is also helping to ease tensions between ecological and historical perspectives in biogeography. As mentioned above, phylogeographic analyses at the intraspecific level have revealed how both past and modern processes can have major impacts on the observed spatial arrangements of gene genealogies. Contemporary patterns of dispersal and gene flow certainly can imprint a species with characteristic phylogeographic signatures, but so too can more ancient factors such as population isolations and subsequent patterns of dispersal from glacial refugia (e.g.,

Hewitt, 1996; Weiss & Ferrand, 2004). The realized molecular phylogeographic structure of almost any species or taxonomic assemblage is likely to reflect some blend (often empirically estimable by empirical genetic findings interpreted under coalescent theory) between current and former biogeographic processes.

HAVE MOLECULAR DATA CHANGED THE GOALS AND FUTURE DEVELOPMENT OF BIOGEOGRAPHY?

Apart from extending genealogical approaches to the intraspecific level, and thus permitting phylogeographic assessments within as well as among species and broader biotas, molecular data have probably not appreciably altered biogeography's general mission of understanding organismal distributions. They have, however, considerably heightened the prospects that biogeography's grand goals will someday be realized. Thanks in no small part to the development and application of various classes of "molecular markers", the future for biogeographic research appears bright.

One way that molecular data have expanded biogeographic horizons is by facilitating temporal appraisals of past vicariant or dispersal events, even when the fossil record or geological evidence is poor. Particular gene sequences (such as those in mtDNA) typically evolve at fairly standard rates across related lineages (e.g., Li, 1997), and this has motivated the notion that "molecular clocks," when properly calibrated for particular taxonomic assemblages, can offer unprecedented power in biogeographic analyses. Of many examples that could be cited, I'll mention just two. Near the microevolutionary end of the phylogenetic continuum, scientists used magnitudes of mtDNA sequence divergence to estimate evolutionary dates for the origination of speciation events (Klicka & Zink, 1997), and also mean temporal durations of the geographic speciation process (Avisé & Walker, 1998), for numerous extant sister species of birds. At a much deeper evolutionary timeframe, Hedges (1996) used a variety of molecular data and molecular clocks to deduce that over-water dispersal events scattered across the past 60 million years (rather than more ancient vicariant separations) had been responsible for the introduction of various terrestrial vertebrate lineages onto Caribbean Islands from continental sources.

In the final analysis, the biodiversity patterns that biogeographers seek to characterize are genetic diversity patterns. Before the molecular revolution in ecological and evolutionary genetics, systematists and biogeographers had to content themselves with analyzing organismal phenotypes (behaviors and external morphologies,

for example) whose specific genetic underpinnings typically remained unknown. Thus, the observable phenotypes of organisms were merely surrogates (often rather inadequate) for genotypic distributions that ultimately provide true genealogical records of life. Today, it is hard to imagine a comprehensive discipline of biogeography that is not intimately tied to the secure kinds of genealogical and phylogenetic information that molecular markers often provide.

Emphatically however, this is not to say that molecular genetic data should be considered in isolation in biogeographic appraisals. To the contrary, molecular biogeographic reconstructions are almost invariably of greatest interest and utility when interpreted in conjunction with traditional sources of biogeographic inference, such as historical geology, fossil evidence, and organismal phylogenies as derived from morphological or other evidence. The hackneyed "molecules versus morphology" debate that characterized earlier decades of the molecular revolution in systematics (see, e.g., Patterson, 1987), beginning in the 1960s, should now be relegated to the status of a rather unfortunate footnote in the sociopolitics of science. The truth is that molecular and morphological approaches are mutually informative, and indeed benefit tremendously from one another's services. Any molecular phylogenetic or biogeographic appraisal can be intellectually quite sterile unless employed as a historical backdrop against which to interpret the temporal or spatial distributions of organismal phenotypes. Conversely, attempts to understand the spatial and temporal histories of organismal phenotypes are almost always greatly enhanced by molecule-informed appreciations of the phylogenetic relationships of the creatures displaying those phenotypes.

CONCLUSION

The empirical and conceptual richness of biogeography stems from the field's central and integrative position at the intersection of several biodiversity disciplines and the physical Earth sciences. Biogeography's diverse philosophies and methods likewise arise from heterogeneous inputs to the field from many different sources, ranging from molecular genetics to the geophysical sciences, and from ecology to systematics and phylogenetic biology. Although differing perspectives have sometimes generated tensions (as well as stimulated much research) within the field, it is time now to fully embrace and interconnect the diversity of biogeographic approaches, much as the discipline itself has always embraced efforts to understand the multiple sources of causation that underlie the rich spatial and temporal diversity of life.

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FURTHER READING

- For an extended treatment of the history, purview, and findings from the field of phylogeography, see **Avisé, J. C.** 2000. *Phylogeography: The History and Formation of Species*. Harvard Univ. Press, Cambridge, Massachusetts.
- For a broad-ranging introduction to the use of molecular markers in ecology and evolution, see **Avisé, J. C.** 2004. *Molecular Markers, Natural History, and Evolution*, ed. 2.

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For a comprehensive advanced discussion of molecular phylogenetic methods in evolutionary biology, see **Felsenstein, J.** 2004. *Inferring Phylogenies*. Sinauer Associates, Sunderland, Massachusetts.

For a simpler treatment of molecular phylogenetic methods, see **Hall, B. G.** 2004. *Phylogenetic Trees Made Easy*, ed. 2. Sinauer Associates, Sunderland, Massachusetts.

For an overview of the broader field of biogeography, see **Brown, J. H. & Lomolino, M. V.** 1998. *Biogeography*, ed. 2. Sinauer Associates, Sunderland, Massachusetts.

BIOGRAPHICAL SKETCH

The author is a Distinguished Professor in the Department of Genetics, University of Georgia, Athens. Research in the Avisé laboratory involves the use of molecular markers to study ecological and evolutionary processes, including biogeographic phenomena. In particular, Avisé has been interested in the development of molecular methods and conceptual approaches in the relatively young but growing field of intraspecific phylogeography, which deals with the spatial distributions of genealogical lineages in microevolutionary time.

Historical biogeography, the natural science

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INTRODUCTION

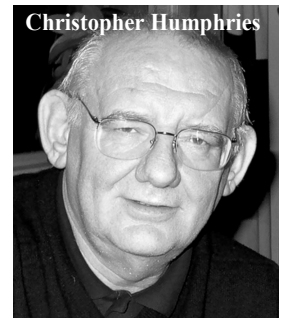
Twenty years ago we wrote a monograph on historical biogeography that was published in 1986 in the Oxford University Press Monograph Series on Biogeography (Humphries & Parenti, 1986). We summarized and interpreted the field of cladistic biogeography as it stood at the time for the undergraduate, graduate student and professional biologist, and as it had developed in concert with the cladistic revolution in phylogenetic methods (i.e., Hennig, 1966; Nelson & Platnick, 1981; Wiley, 1981). During the following decade, biogeography enjoyed a renaissance, particularly in methodology, and we wrote a second edition of our book in large part to summarize advances made during the 1990s (Humphries & Parenti, 1999).

A challenge facing biologists today is to understand the enormous amount and variety of information that is being generated and archived in databases, particularly those in systematics collections documenting global species diversity over time for discovering a pattern. Biogeographic patterns provide an organizing framework within which we may interpret biological data, as well as provide the basic information for understanding relationships among areas. Well-corroborated biogeographic patterns have a high predictive value. They may inform other phylogenetic studies, by predicting where a primitive sister group may live; reinforce conservation studies, by identifying species, endemic areas and complementary hot spots; or simplify our understanding of, hence our explanations for, patterns of diversity, by proposing a common cause of our observations in the sense of Life and Earth evolving together rather than a series of unrelated events, such as dispersal scenarios.

Biogeography is more relevant now than it has perhaps ever been, and it is time for yet another renaissance. Many terms have been coined that pull together diverse bits of biological information: biodiversity, bioinformatics, biocomplexity, and so on. None of these can replace the power of “historical biogeography” that asks a simple question: What lives where, and why? And, the subject is bold enough to suggest some answers to that ques-



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tion. So, in the spirit of vicariance biogeography or area cladistics, we provide answers below to the questions posed to all of the authors in this forum.

HOW WOULD YOU DEFINE BIOGEOGRAPHY AND ITS GOALS?

Having identified, named, systematized, and classified organisms, biogeographers ask a simple question: what lives where, and why? (Platnick & Nelson, 1978; Nelson & Platnick, 1981). Answering the first part of this question—what lives where—is an important first step in describing the global distribution of plants and animals, and it remains perhaps the most critical phase of the biogeographic enterprise. None can doubt the value of distribution maps (e.g., for freshwater fish families in Berra, 2001; for plants in the Pacific in van Balgooy, 1963–1993, or ultimately, indeed, all organisms on Earth) for gaining an understanding of, and appreciation for, fundamental global distribution patterns.

Answering the second part of the question—why—is more difficult and requires analysis, although the possible answers are straightforward: a taxon lives in an area because it evolved there or it evolved elsewhere and dispersed into that area (Platnick & Nelson, 1978). Two processes, vicariance and dispersal, are recognized as forming basic global biogeographic patterns. Dispersalist explanations for distributions of plants and animals largely reflect the present-day habitats of those organisms; i.e., if an animal can tolerate salt-water during part

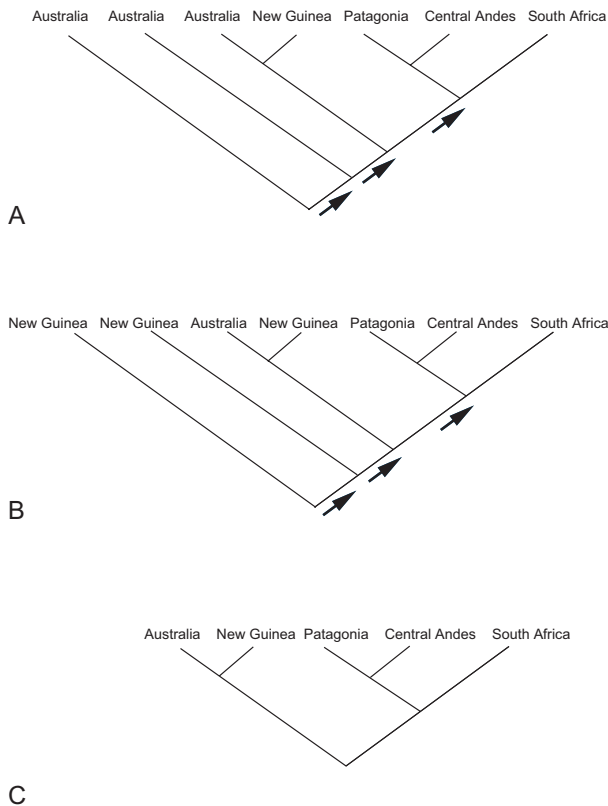


Fig. 1. A, hypothetical area cladogram of the southern hemisphere with repeated taxa in Australia. Arrows indicate path of inferred dispersal from Australia under a center of origin hypothesis. B, hypothetical area cladogram of the southern hemisphere with repeated taxa in New Guinea. Arrows indicate path of inferred dispersal from New Guinea under a center of origin hypothesis. C, general pattern for southern hemisphere areas as indicated by area cladograms 1A and 1B. Repetition of pattern and extinction may result in pattern 1A or 1B.

of its life history pattern, dispersal through the seas is often invoked as a biogeographic process. Further, dispersalist explanations are often proposed for a single taxon without asking whether or not it conforms to a general pattern. This is one facet of phylogenetic biogeography that is most concerned with species history and inferred migration routes from centres of origin, especially of populations within a single species. It represents a return to *generation* rather than *discovery* in science (see Ebach & Humphries, 2002). It echoes the migration-dispersalist scenarios of Matthew (1915) and others, and finds its origins in the works of Linné (1781). In contrast, discovery puts primary emphasis on identifying a common pattern of area relationships among a group of taxa, not on habitat or physiological similarities or differences, to interpret distributional history and ulti-

mately infer the process by which the pattern was formed. Sharing a pattern implies sharing a history. Both vicariance and dispersal can be used to interpret a distributional history. Area cladograms provide the raw data for biogeographic analysis. How those raw data are used—to generate or to discover—distributional histories, has sparked the ongoing methodological debates in biogeography.


WHY ARE THERE SO MANY BIOGEOGRAPHICAL THEORIES AND METHODS?

Biogeography follows systematics (Humphries & Parenti, 1986, 1999). Just as systematists may be concerned with a wide range of tasks such as species descriptions, enumeration of taxa, writing of floras or faunas, comparative morphology, cytogenetics, molecular systematics, or phylogenetics, biogeographers may focus on local, small-scale distribution patterns of populations or species, on more broadly-distributed genera or families, or global distribution patterns through time.

The relationship between methods developed for systematics and biogeography has not always been obvious, in large part because the goals of biogeographic analyses have not always been understood or stated clearly (see Brooks, 1981; Page, 1990). Early cladistic biogeographers aimed for a single area cladogram in the same way that phylogeneticists aimed for a single cladogram of taxa. The analogy between phylogenetics and biogeographic analysis is not complete, however. Taxa have one history¹; areas do not, especially over long geologic periods (Page, 1990; Ebach & Humphries, 2002). A single phylogenetic tree reflects our understanding that a group of organisms has but one evolutionary history. A single area cladogram may lead to the erroneous conclusion that a group of areas has had one relationship throughout geological time (e.g., Grande, 1985; Cracraft, 1988). Methods such as PAE (Parsimony Analysis of Endemicity) or Brooks Parsimony Analysis adopt protocols directly from phylogenetic systematics, and violate some of the basic assumptions of cladistic biogeography (see Crisci, 2001; Crisci & al., 2003).

One of the most common misapplications of a cladistic method to a biogeographic problem is optimization of areas on the internal nodes of an area cladogram analogous to optimization of characters on the internal nodes of a taxon cladogram (Bremer, 1992; Enghoff, 1993). It is inappropriate to optimize areas onto an area cladogram to interpret, for example, the ancestral area or centre of origin of a taxon. Optimization does not ask

¹ Although some would argue that different plastids and endosymbionts have different histories within organisms.

whether vicariance or dispersal is the best supported explanation for the distribution pattern, but dismisses vicariance at the outset in favour of a “centre of origin” hypothesis. A hypothetical example is given in Fig. 1. Optimization of areas of Fig. 1A implies dispersal from a centre of origin in Australia. Optimization of areas of Fig. 1B implies dispersal from a centre of origin in New Guinea. The general pattern to be inferred from both Figs. 1A and 1B is shown in Fig. 1C. It is not contradicted by either Fig. 1A or 1B and includes all of the information on area relationships contained in both figures. Repetition in area cladograms is the rule ed now at the beginning. Botanist and biogeographer Léon Croizat (1958, 1964) emphasised that nature endlessly repeats. Extinction could make the individual area cladograms that form a general pattern look different, but this should not make us overlook their shared, non-contradictory information. Extracting the common patterns has been made easier over the last decade or so through developments in cladistic biogeography that have removed spurious effects by removing paralogous geographical nodes from the cladograms and applying subtree analysis to resolve the common area relationships (Nelson & Ladiges, 1996; Ebach & Humphries, 2002).

IN RECENT YEARS, THERE HAS BEEN A CALL FOR THE INTEGRATION OR UNIFICATION OF BIOGEOGRAPHY. DO YOU THINK THAT THIS IS NECESSARY?

Biogeography is naturally an integrative field. It requires a thorough knowledge of geography as well as biology, and a basic understanding of geology. As Croizat (1964) declared: The world and its biota evolved together. Biology is not separate from geology, nor are the distributional histories of taxa in a biota separate from each other. Greater collaboration between biogeographers and geologists and/or geographers, as well as between botanists and zoologists, is welcome.

Area cladograms and geological reconstructions provide data that allow us to interpret the history of the world and its biota. No theory should take precedence over the other, however. Although it is important to make comparisons between taxic/area cladograms and geographical/geological reconstructions, it is critical not to interpret one in terms of the other as is done in event-based methods (e.g., Hovenkamp, 1997; Ronquist, 1997). Integration, or unification, should not come by accepting popular or consensus explanations for distribution patterns and dismissing alternative explanations. Marine fishes are rarely interpreted within a vicariance framework because they are assumed to disperse through

the seas (Briggs, 1974). This assumption has kept vicariance analyses to a minimum despite evidence that distribution of marine taxa can be explained by concordance with geological features (Springer, 1982). The assumption should be rejected. Present-day ecology does not dictate the process of formation of distribution patterns (Parenti, 1991, for marine and freshwater fishes), rather, long-term historical events associated with changes in the topography of the Earth have been fundamental.

HAS THE USE OF MOLECULAR DATA CHANGED THE GOALS AND THEREFORE FUTURE DEVELOPMENT OF BIOGEOGRAPHY?

Molecular data may provide novel hypotheses of cladistic relationships of taxa that challenge conventional wisdom (e.g., Miya & al., 2003, for spiny-finned fishes; APG group for angiosperms, see Peter Stevens' website at www.mobot.org/MOBOT/Research/APweb/welcome.html). Early applications of molecular data to biogeography tended to look for common patterns and to reject the Simpsonian (Simpson, 1965) view of the world that relied on dispersal from a centre of origin, usually hypothesised as the oldest fossil locality (see Nelson & Ladiges, 2001). More recently, however, fossils have been replaced by molecules to hypothesise patterns of ancestry, dispersal routes, and centres of origin (Nelson, 2004). There are exceptions. Molecular data have been used to interpret phylogenetic patterns of cichlid fishes, for example, that in turn have been interpreted as congruent with Gondwanan fragmentation patterns (Sparks, 2004).

Phylogeography (Avice, 2000) was formulated as a method that combined phylogenies with geographic distribution patterns to infer evolutionary processes. One hypothesis that may be tested for any such species tree is: is genetic distance correlated with geographic distance? Lucid phylogeographic studies at the population level (e.g., Taylor & Hellberg, 2003, on the cleaner goby, *Elacatinus evelynae*) have supported the notion that even though some taxa have the ability to disperse great distances, they do not. At higher taxonomic levels and across broader geographic distances, however, asking this question is similar to invoking dispersal without consideration of vicariance, as in the above example of optimizing nodes on an area cladogram. All phylogenetic biogeography is not cladistic biogeography, in the sense of Humphries & Parenti (1999). The ease of collection and analysis of molecular data, however, has proven attractive to biologists who wish to generate rapidly a phylogenetic hypothesis and interpret a distribution pattern. Many interpretations are untestable, irrefutable sce-

narios of dispersal—part of the world of generation rather than of discovery in science (e.g., de Bruyn & al., 2004).

CONCLUSION

Biogeography is a lively field of scientific investigation as this Forum demonstrates. We have no agreed-upon methodology of historical biogeography, and there are at least nine different classes of technique all vying for attention, as Crisci & al. (2003) so aptly observed. Perhaps hoping for consensus is unrealistic and even undesirable. At the least, however, we require methods that search for biogeographic patterns, not individual explanations, and only those that follow the principle that the world and its biota evolved together.

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BIOGRAPHICAL SKETCHES

Lynne R. Parenti joined the National Museum of Natural History, Smithsonian Institution, in 1990, as a Curator of Fishes and Research Scientist. Her research specialities include the systematics and biogeography of tropical bony fishes, development of new character systems in the study of bony fish phylogeny, and the theory and practice of historical biogeography. She is co-editor of *Interrelationships of Fishes* (1996, Academic Press), and *Ecology of the Marine Fishes of Cuba* (2002, Smithsonian Institution Press), and co-author of *Cladistic Biogeography* (1986, 1999, Oxford Univ. Press).

Christopher J. Humphries has been with the Natural History Museum, London, since 1972. His research has concentrated on several problems in historical biogeography, both theoretical and empirical, angiosperm systematics, biodiversity measurement, and methods of priority selection in conservation. He is now on the editorial board of *Taxon* and *Journal of Biogeography*.

Understanding places and organisms in a changing world

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INTRODUCTION

The recent literature revival of the preeminent naturalist Alfred Russel Wallace reminds us not only of his genius and energy as explorer and scientist but also of his unusual concern about the vulnerability of nature in a human-dominated world. His plea for conservation of habitats and species (Wallace, 1905, 1910; quoted by Berry, 2002, pp. 146–153) in temperate and tropical regions was well ahead of his contemporaries in the 19th century. In many ways we are not much further along than at Wallace's time. Conservation has become more urgent than ever before, with some areas of the tropics having still not been explored, and many invertebrate taxa hardly known at all. But we also have a vastly increased knowledge of the living world.

There has never been a better time for being a biogeographer than today. Computers, GIS, and DNA tests combined with worldwide ecological monitoring, and a steadily increasing database of biotic taxa and their distributions, make biogeography a science for the future and an indispensable discipline for ecosystem analysis, regional biodiversity management, and long-term species conservation planning.

HOW WOULD YOU DEFINE BIOGEOGRAPHY AND ITS GOALS?

My definition of biogeography has changed markedly over the past forty years, a reflection of a rapidly moving discipline and my own wanderings among the life and earth sciences. Initially, the goal appeared to be gaining an understanding of biotic distribution patterns with the help of historical (palaeontological) data. Later, it included spatial processes causing or contributing to distribution patterns. Recently, I added functional space as an important concept for understanding the dynamics of biotic space. My current definition reads as follows: *biogeography studies the interface between places, biota, and people along spatial and temporal scales*. This definition is general and broad, possibly encompassing all of biogeography. It sets a pointed accent, however, by putting “places” ahead of biota and people. There are two reasons for this unorthodox emphasis: (1) biogeography



is not only or not any more simply a subdiscipline of evolutionary biology and systematics, and (2) new techniques and the megainfluence of global change provide a great opportunity (and scientific responsibility) for an earnest focus on the places where biota thrive or fail.

Biogeography is an exceedingly broad field, which is typical for much of geography and systematic biology. The former does not lend itself to reductionist thinking characteristic of the hard sciences today. This is so because no two spots or landscapes on the earth are identical. This basic truth of geography has been of profound influence for the evolution of the biosphere and for taxon speciation.

For most of the last 200 years biogeography has played a major role in the study of evolution since distribution pattern and processes of dispersal and vicariance substantially assist and enable our understanding of present and past biodiversity. The recent textbook by Brown & Lomolino (1998) states that “biogeography is a branch of biology” and formulates as its *fundamental question*: “How are organisms distributed over the surface of the earth and over the history of the earth?” This approach seems limited as it omits the most interesting question “Why?” and neglects to inform the reader about biogeographic work in anthropology, agriculture, palaeontology, and, of course, in various subdisciplines of geography (see Gade, 1999). Biogeography resembles a central node in an amoeba-like corpus of data, terminologies, hypotheses, and concepts that intersects with several disciplines at the periphery of the life sciences.

The goals of biogeography today can be found by grouping significant biogeographic work into a number of focus areas. They are:

A. Taxon Evolution and Persistence. — A vast number of biogeographers work at or below the species level to unravel the evolutionary history and spatial differentiation at the population level. Work on higher taxa

often includes a comparative perspective of lower taxa (historical biogeography). Example: the genus *Pinus* (Richardson, 1998). Modern phylogeographic work falls neatly into this focus. Molecular data reveal often surprising historical geographical phenomena that are undetectable by morphological assessments (Klicka & Zink, 1997; Petit, 2004). For birds, some recent examples are the California thrasher *Toxostoma redivivum* (Sgariglia & Burns, 2003), the bay wren *Thryothorus nigricapillus* (Gonzalez & al., 2003), and the two Palaearctic wagtails *Motacilla flava* and *M. citreola* (Pavlova & al., 2003).

B. Area Structure and Function. — The range of a taxon on earth is a uniquely valuable dataset: it is the manifestation of the interface between the taxon, its environment, and human presence and agency. GIS techniques and organized region-wide censuses and atlas work have vastly improved our understanding of range structure and boundaries. See Sauer (1988), Hengeveld (1990), Maurer (1999), Ponder & Colgan (2002), Gaston (2003), Humphries & Bourgerou (2003), and Walter (2004).

C. Regional Diversity. — The focus on biodiversity of ecosystems, habitats, hot spots, islands or parks is a modern version of chorological or areographic analysis. Who occurs where? How unique, rich or poor is a particular region at different spatial and taxonomic scales? This focus has seen intense efforts and the development of huge databases over the past 20 years or so. Examples: the global and regional biodiversity catalogues and richness summaries, often collected and published by major conservation NGOs (Berthold, 1993; Kunkel, 1993; Dumont, 1998; Stattersfield & al., 1998; Abell & al., 2000; Stein & al., 2000; Gillespie & Walter, 2001; Mayr & Diamond, 2001; Woods & Sergile, 2001; Walter & Breckle, 2002; Wikramanayake & al., 2002).

D. Landscape Ecology. — This is an ecological and geographic approach to the interrelationships between certain biotas and their dynamic habitats and landscape parameters. How do certain features of the terrain and human-built environment affect biotic distribution and dispersal? This focus area makes use of GIS techniques and plays an increasingly important role in the design of conservation-benign landscape systems in regional planning (Brown, 1995; Bissonette, 1997; Kraus & al., 2003).

E. Island Biogeography. — This involves the continuation of proving or applying the island biogeographic theory of MacArthur & Wilson (1967) to islands and to mainland isolated habitat areas or bounded reserve and parklands. The importance of islands as an engine of biogeographic work and stimulation cannot be emphasized enough. Beginning with Darwin & Wallace (Wallace, 1869, 1880; Berry, 2002) this focus continues to produce meaningful and creative work and new ques-

tions (Diamond, 1975; Lack, 1976; Gilbert, 1980; Williamson, 1981; Solem, 1990; Whittaker, 1995; Thornton, 1996; Walter, 1998; Whittaker, 1998; Mayr & Diamond, 2001; Thornton & al. 2001; Haila, 2002). There may never be a better and more popular book about island biogeography than *The Song of the Dodo* (Quammen, 1996). Many students have developed a serious interest in biogeography because of this book.

F. Human Impact. — This includes significance of exotic species in terrestrial and marine ecosystems, invasion biology, domestication, origin and spread of cultivated taxa, extirpation and extinction histories and pathways, and comparing prehistoric and ongoing extinction scenarios. These are all exciting and expanding research areas fueled by regional and worldwide patterns of habitat destruction and landscape homogenization. Characteristic literature: Olson (1990); Steadman (1997); Cowie (2001); Leveque & Mounolou (2003); Ruiz & Carlton (2003); Lydeard & al. (2004).

G. Global Change. — This differs from F in that physical factors and systems may play a large role in addition to anthropogenic pollution factors. It also includes potential shifting of distribution of taxa, habitats, and entire biomes plus analyses of previous climate change and modeling of future climate scenarios and the shifting of vegetation and species boundaries. Literature: MacDonald (1993); Mace & al. (1998); Shugart (1998); Schneider & Root (2001).

H. Conservation and Management. — This focus involves application of biogeographical principles to parks, reserves, and other human-controlled landscapes/ecosystems. Literature: Diamond (1975); Wilson & Willis (1975); Laurance & Bierregaard (1997); Stattersfield & al. (1998); Whittaker (1998); Amler & al. (1999); Abell & al. (2000); Wikramanayake & al. (2002).

I. Theory and Integration. — This is the eternal quest for an underlying and universal principle explaining all or most of the biogeographic phenomena; in its sub-format, it is striving for concepts and frameworks that illuminate relevant processes or functions and provide new insights. Important milestones are Preston (1960), MacArthur (1972), Rosenzweig (1995), Brown (1995), Rhodes & al. (1996), Hubbell (2001), and Whittaker & al. (2001).

WHY ARE THERE SO MANY BIOGEOGRAPHIC THEORIES AND METHODS?

Actually, there are few theories that are exclusive to biogeography. In order to substantiate this statement, I went through my (incomplete) files and some 2200 entries in the invaluable dictionary on evolution and bio-

geography by Sedlag & Weinert (1987). Fewer than 20 still relevant theories or hypotheses qualified (age and area, dispersal center/refugium, climate rules, species-area curve, extinction theories, equilibrium and non-equilibrium theory of island biogeography (ETIB), disturbance, vegetation succession, plant sociology, landscape ecology (percolation theory), regional classification, synanthropy, cytogeography, dispersal, vicariance, panbiogeography, ice age dynamics). Most methods and concepts of interest to biogeographic inquiry are shared with or derived from neighbouring disciplines (examples: niche, cladogram, speciation, vagility, habitat, species-area curve).

Reading a biogeographic journal is always a *tour de force* even for seasoned experts because nobody today can be familiar with the special biology and geography of all plant and animal taxa requiring the application of hundreds of taxon-specific methods of collection, observation, and cataloguing. The excitement and challenge of biogeography lies in this extraordinary diversity of research on often unfamiliar taxa from distant and near corners of the earth. The quantification of current research means, however, that a fair understanding of a relatively few major statistical techniques is required for the full “enjoyment” of published work.

To become proficient in biogeography, it is advisable to become thoroughly familiar with the biology and geography of one taxon group (raptors, land snails, orchids, lichens), to construct a database, and to use the latter for testing and comparing relevant biogeographic concepts and hypotheses.

IN RECENT YEARS THERE HAS BEEN A CALL FOR THE INTEGRATION OR UNIFICATION OF BIOGEOGRAPHY. DO YOU THINK THIS IS NECESSARY?

Advancement in science is usually accomplished by a relatively small sector or subdiscipline. A breakthrough can be accomplished with a new method or tool as well as with a new integrating or unifying concept. True integration in biogeography will not be possible for two simple reasons: (1) the various phyla of the earth have adaptations and life forms that defy any integration beyond utter simplicities (such as needing energy), and (2) there are still too many focus areas of interest to biogeographers (see above) that span the history of the field as well as many life science specialties.

Many of the integrative concepts of the past thirty years come from ecology and are based on data from vertebrate communities. Competition theory has been in vogue but fares poorly with invertebrates such as mol-

lusks (Solem, 1990). As a result, I am not convinced that ecosystems in general are packed “as a zero sum game” (Hubbell, 2001). Most importantly, ecologists have routinely neglected the terrain on which or in which life persists. This is the landscape in all its manifestations that co-evolves with taxa. Even Hubbell (2001) admits that he has based his unification theory on a constant physical environment. This is simply unrealistic and demands different approaches for the study of biodiversity in time and place.

Recently, I proposed the *eigenplace* concept defined as the functional spatial complex of existence (Walter, 2004). The purpose of this concept is a place-based perspective on natural diversity rather than the traditional species- and community-based approach. It will be possible to develop an eigenplace theory, but its purpose would not be to unify the discipline. Rather, it might assist with tackling and solving the enormous biodiversity-related management and preservation problems accompanying global warming and global and regional change in general.

Finally, if we wish to integrate the biogeographic enterprise we might want to attempt to pool and focus our research efforts more deliberately towards the near future. This suggestion parallels a recent effort by American ecologists to focus on “an ecology for the future” (Palmer & al., 2004). Phylogeographic studies, palaeofloras, and prehistoric extinction waves may all teach us something about the changing life on earth tomorrow. For lack of a better term, I have coined *progressive biogeography* as the focused effort to use our combined knowledge of the past and present biodiversity to “progress” to future predictability of the place-biota-people interface. This may not be a necessary step, but certainly a desirable one for the discipline. A progressive biogeographer therefore attempts to integrate all available historic and present biogeographic information for the development of predictive distribution models. A series of papers in the special issue of the *Journal of Biogeography* (Nos. 10/11, 2002) on the history and future of the New England landscape may serve as examples for a progressive biogeography (Foster, 2002a, b; Foster & al., 2002; Motzkin & al., 2002).

HAS THE USE OF MOLECULAR DATA CHANGED THE GOALS AND THEREFORE FUTURE DEVELOPMENT OF BIOGEOGRAPHY?

As Gaston (2003) correctly points out, we understand far more about the structure of species ranges today than is commonly known. The addition of molecular analysis permitting an exact determination of the timing

of even tiny mutations, dispersal, and vicariant events, makes biogeography more relevant, even necessary for an in-depth analysis of the entire history of a taxon in space and time. In an age of globalization where a catastrophic mixing of long isolated biotas takes place on islands and mainlands around the world, comparative phylogeography will be of great assistance in sorting out the amount of introgression, hybridization, and origin of invasive taxa (Petit, 2004).

Phylogeographic techniques will become indispensable tools for biogeographers, and I advocate the establishment of phylogeographic laboratories even in geography departments. But the goals of biogeography are likely to remain the same because the questions have not gone away because of a new technique: phylogeography will just give us additional and better answers! And that will generate new questions.

CONCLUSION

In all probability, the future will see more and more multidisciplinary research teams that will include one or more biogeographers because of their sophisticated tools (phylogeographic and GIS) and their expertise of the essential biogeographic interface. In my work experience, the ideal young biogeographer has come from a museum-systematics background, is field-oriented, and has a good grasp of quantitative techniques and Internet databases. This background helps to discuss biogeographic principles and theories as well as research design. The more geography the student has the better prepared she/he will be for a progressive analysis of the state of biodiversity in a changing world.

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FURTHER READING

A. Journals. — The three journals *Journal of Biogeography*, *Diversity and Distributions*, and *Global Ecology and Biogeography* contain a perfect mix of articles representing all of biogeography.

B. Books. — Sooner or later one has to access the original papers of our founders. Here is an easy source: **Lomolino, M. V., Sax, D. F. & Brown, J. H.** 2004. *Foundations of Biogeography: Classic Papers with Commentaries*. Univ. Chicago Press, Chicago. An easy and enjoyable access to the distant and recent history of biogeography (and much of modern biology) can be found in D. Quammen's book *The Song of the Dodo* (1996); it is up-to-date until about 1994 but does not discuss more recent revisions and improvements of island biogeographic theory.

BIOGRAPHICAL SKETCH

At fourteen, Hartmut S. Walter became a collaborator of the Museum A. Koenig (Bonn) with interest in birds, dragonflies and lizards. He studied zoology, botany, and chemistry at Bonn (Germany) and Cagliari (Italy), did his doctorate on the ecology of Eleonora's falcon *Falco eleonora* (field work in Crete and Morocco), then worked in environmental conservation for UNESCO (East Africa). He has been a professor at the University of California, Los Angeles (UCLA) since 1972, teaching and researching biogeography, field ecology, and conservation science in the Department of Geography. His particular interest concerns island biotic systems, conservation science, and applied biogeographic theory.