

Evolutionary Biogeography

— *An* —

INTEGRATIVE APPROACH

with CASE STUDIES



JUAN J. MORRONE

EVOLUTIONARY BIOGEOGRAPHY

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An Integrative Approach with Case Studies

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COLUMBIA UNIVERSITY PRESS



NEW YORK

Columbia University Press
Publishers Since 1893
New York Chichester, West Sussex

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Library of Congress Cataloging-in-Publication Data

Morrone, Juan J.

Evolutionary biogeography : an integrative approach with case studies / Juan J.

Morrone.

p. cm.

Includes bibliographical references.

ISBN 978-0-231-14378-3 (cloth : alk. paper)—ISBN 978-0-231-51283-1 (ebook)

1. Biogeography. 2. Biogeography--Case studies. I. Title.

QH84.M665 2009
578.09—dc22

2008038927



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Printed in the United States of America

c 10 9 8 7 6 5 4 3 2 1

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In memory of my mother, Lidia Lupi (1937–2008), who inspired me to love nature and truth.

There are three things that last forever: faith, hope, and love; and the greatest of the three is love.

—1 Corinthians 13:13

When the miracle occurs, as it sometimes does; when, on one side and the other of the hidden crack, there are suddenly to be found cheek-by-jowl two green plants of hidden species, each of which has chosen the most favourable soil; and when at the same time two ammonites with unevenly intricate involutions can be glimpsed in the rocks, thus testifying in their own way to a gap of several tens of thousands of years suddenly space and time become one: the living diversity of the moment juxtaposes and perpetuates the ages. Thought and emotion move into a new dimension where every drop of sweat, every muscular movement, every gasp of breath becomes symbolic of a past history, the development of which is reproduced in my body, at the same time as my thought embraces its significance. I feel myself to be steeped in a more dense intelligibility, within which centuries and distances answer each other and speak with one and the same voice.

Claude Lévi-Strauss (1955), *Tristes tropiques*

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Preface

The aim of this book is to provide a theoretical and practical guide to evolutionary biogeography for advanced undergraduate and beginning graduate students, academics, and anyone concerned with the study of biogeographic patterns and their evolution. It provides an introduction to evolutionary biogeography, its basic concepts, history, approaches, methods, developments, and case studies. I have assumed that the readers have a basic knowledge of phylogenetic systematics, so cladistic methods are not detailed. Some existing books deal with a specific biogeographic approach or with several methods but fail to provide a coherent framework from which one can choose the most appropriate, leaving the reader uncertain about how to address a particular problem. I discuss the available methods and suggest the appropriate step of a biogeographic analysis in which to use any particular one. The case studies (most from my own research) are intended to help the reader make a rational choice from among the approaches and methods available. I have also included problems, questions for discussion, and a glossary that can be used in the classroom.

In recent decades, biogeography has undergone much debate. Dispersalists, panbiogeographers, cladistic biogeographers, ecological biogeographers, macroecologists, and phylogeographers, among others, have disputed the relative merits of their approaches but have not worked toward their integration. However, a few authors have noted this lack of interaction recently and have stated that the integration of approaches and methods in biogeography is a salient issue. I hope this book can contribute to a future integrative biogeography.

I am indebted especially to my students for their insights and inspiration. Many thanks to my friends and colleagues Roxana Acosta, Alfredo Bueno Hernández, Angélica Corona, Dalton de Sousa Amorim, Malte Ebach, Tania Escalante, David Espinosa Organista, Oscar Flores Villela, John Grehan, Gonzalo Halffter, Michael Heads, Analía Lanteri, Livia León Paniagua, Jorge Llorente Bousquets, Ana Luz Márquez, Susana Magallón, Juan Márquez Luna, Rafael Miranda Esquivel, Adolfo Navarro Sigüenza, Gareth Nelson, Silvio Nihei, Federico Ocampo, Jesús Olivero, Rod Page, Gerardo Pérez-Ponce de León, Paula Posadas, Raimundo Real, Sergio Roig-Juñent, Adriana Ruggiero, Luis A. Sánchez-González, Claudia Szumik, Hernán Vázquez, and Mario Zunino for helpful and stimulating discussions. I am also indebted to Malte Ebach, Tania Escalante, John Grehan, David Hafner, Michael Heads, Analía Lanteri, Rafael Miranda, Silvio Nihei, Federico Ocampo, Jesús Olivero, Lynne Parenti, Paula Posadas, and Adriana Ruggiero for valuable comments on parts of the manuscript. Patrick Fitzgerald (Columbia University Press) and three anonymous reviewers provided very useful suggestions. In recent years my research has been supported by the Universidad Nacional Autónoma

de México, the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, and the Consejo Nacional de Ciencia y Tecnología, México; the National Geographic Society, United States; and the Fundación Carolina, Spain. Parts of this book were written in Paris and Málaga; thanks to my colleagues from the Université Pierre et Marie Curie and the Universidad de Málaga for hosting me during my sabbatical leave. For the last twelve years, Adrián Fortino has provided love, support, and encouragement.

Mexico City, February 20, 2008

EVOLUTIONARY BIOGEOGRAPHY

CHAPTER 1

Introducing Evolutionary Biogeography

Biotas are complex mosaics originated by dispersal and vicariance, having reticulate histories, which should be studied through different methods. Evolutionary biogeography integrates distributional, phylogenetic, molecular, and paleontological data in order to discover biogeographic patterns and assess the historical changes that have shaped them, following a stepwise approach. In this chapter I briefly introduce the steps of this approach.

What Is Evolutionary Biogeography?

One hundred fifty years ago, Charles Darwin published *On the Origin of Species*. The geographic distribution of plant and animal taxa was among the evidence he provided to support evolution. Although the fact that continents have their own distinctive biotas has been known for some time, from Darwin we learned that these biotas evolve, that their composition changes over time. In the nineteenth and twentieth centuries, biogeographers extensively debated the mechanisms leading to biotic evolution. In recent years some authors have concluded that dispersal and vicariance are both relevant processes. When climatic and geographic factors are favorable, organisms actively expand their geographic distribution according to their dispersal capabilities, thus acquiring their ancestral distribution (dispersal). When the organisms have occupied all available space, their distribution may stabilize, allowing the isolation of populations in different sectors of the area and the differentiation of new species through the appearance of geographic barriers (vicariance).

To analyze the resulting complex patterns, we should identify particular questions, choose the most appropriate methods to answer them, and finally integrate them in a coherent framework. Most of the authors who are involved in the theoretical development of biogeography or who apply their methods usually conceive them as representing alternative schools; however, they can be used to answer different questions. Evolutionary biogeography integrates distributional, phylogenetic, molecular, and paleontological data in order to discover biogeographic patterns and assess the historical changes that have shaped them. It follows a stepwise approach (fig. 1.1). Each of its steps is discussed in a different chapter of this book.

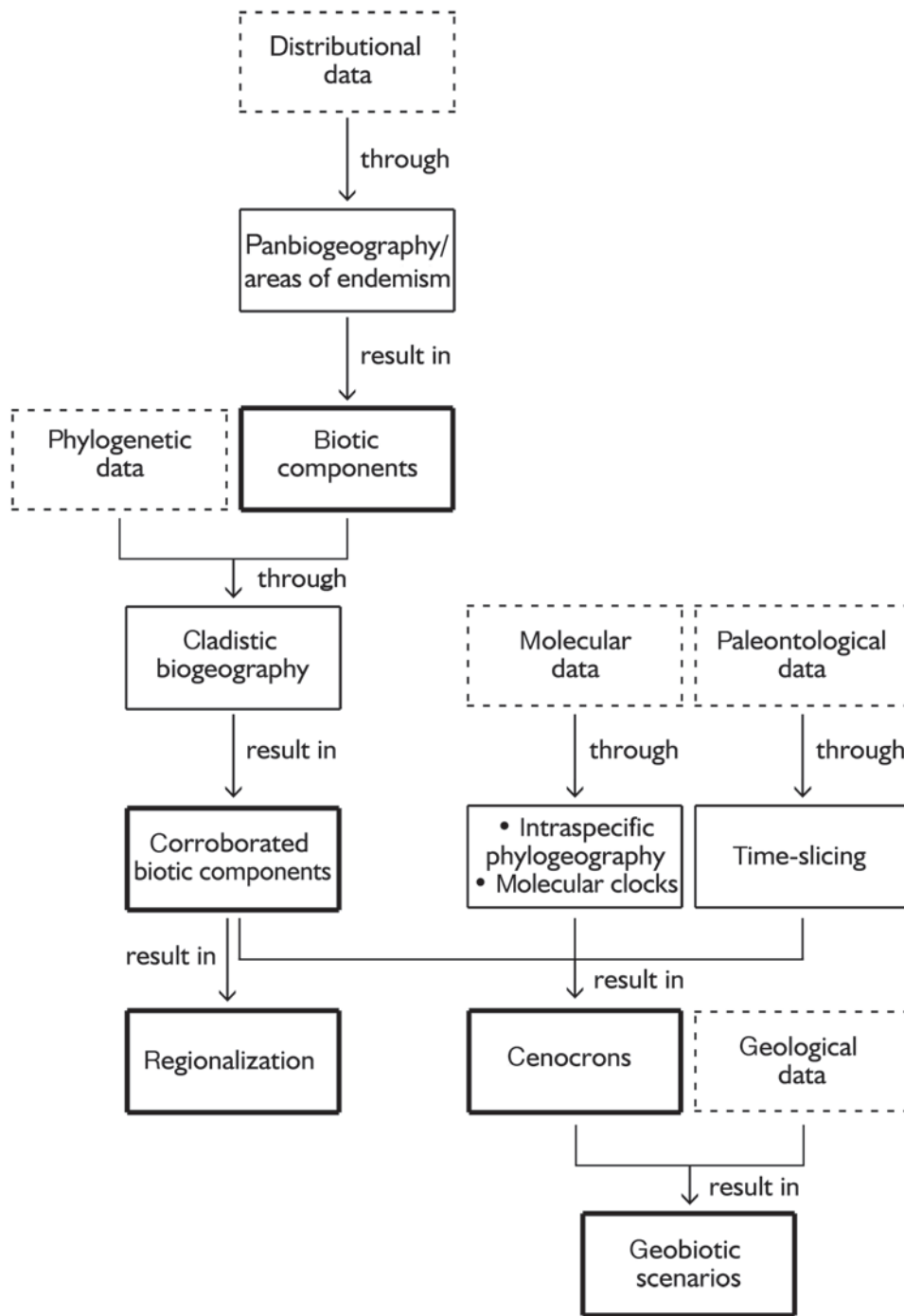


Figure 1.1 Flow chart with the five steps of an evolutionary biogeographic analysis.

Step 1: Identification of Biotic Components

Biotic components are sets of spatiotemporally integrated taxa that coexist in given areas. Their identification is the first stage of an evolutionary biogeographic analysis. There are two basic ways to represent biotic components: generalized tracks and areas of endemism. The former are studied by panbiogeography, whereas the latter are the units of cladistic biogeography.

Panbiogeography emphasizes the spatial or geographic dimension of biodiversity to allow a better understanding of evolutionary patterns and processes (Craw et al. 1999). A panbiogeographic analysis comprises three basic steps: (1) constructing individual tracks for two or more different taxa, (2) obtaining generalized tracks based on the comparison of the individual tracks, and (3) identifying nodes in the areas where two or more generalized tracks intersect. Individual tracks are the basic units of panbiogeography, representing the primary spatial coordinates of species or supraspecific taxa, which operationally correspond to line graphs connecting the different localities or distributional areas of a taxon according to their geographic proximity. Generalized tracks result from the significant superposition of different individual tracks and indicate the preexistence of ancestral biotic components that became fragmented by geologic or tectonic events. Nodes are complex areas where two or more generalized tracks superimpose and are usually interpreted as tectonic and biotic convergence zones.

Areas of endemism are areas of nonrandom distributional congruence between different taxa (Morrone 1994b). Müller (1973) suggested a protocol that has been applied to identify areas of endemism and that consists of plotting the ranges of species on a map and finding the areas of congruence between several species. This approach assumes that the species' ranges are small compared with the region itself, that the limits of the ranges are known with certainty, and that the validity of the species is not in dispute.

Step 2: Testing Relationships Between Biotic Components

Cladistic biogeography assumes a correspondence between the phylogenetic relationships of the taxa and the relationships between the areas they inhabit (Platnick and Nelson 1978). Cladistic biogeography uses information on the cladistic relationships between the taxa and their geographic distribution to postulate hypotheses on relationships between areas. If several taxa show the same pattern, such congruence is evidence of common history. A cladistic biogeographic analysis comprises three basic steps: (1) constructing taxon–area cladograms from the taxonomic cladograms of two or more different taxa by replacing their terminal taxa with the areas they inhabit, (2) obtaining resolved area cladograms from the taxon–area cladograms (when demanded by the method applied), and (3) obtaining a general area cladogram, based on the information contained in the resolved area cladograms.

Taxon–area cladograms are obtained by replacing the name of each terminal taxon in the cladograms of the taxa analyzed with the area where it is distributed. Their construction is simple when each taxon is endemic to a single area and each area has only one taxon, but it is more complex when taxonomic cladograms include widespread taxa, redundant distributions, and missing areas. In these cases, some methods require that taxon–area cladograms be turned into resolved area cladograms (Morrone and Crisci 1995; Nelson and Platnick 1981). General area cladograms based on the information from the different resolved area cladograms represent hypotheses on the biogeographic history of the taxa analyzed and the areas where they are distributed.

Step 3: Regionalization

Because the geographic distributions of taxa have limits, and these limits are repeated for different taxa, they allow the recognition of biotic components. Once they have been identified, they may be ordered hierarchically and used to provide a biogeographic classification. This stage of the analysis takes place before cenocrons are elucidated and a geobiotic scenario is proposed.

Biogeographic regionalization implies the recognition of successively nested areas for which classically the following five categories have been used: realm, region, dominion, province, and district. Sometimes it is more difficult to determine the exact boundaries of two realms or regions, and authors have described transition zones. These zones represent events of biotic hybridization, promoted by historical and ecological changes that allowed the mixture of different biotic components.

Step 4: Identification of Cenocrons

Cenocrons are sets of taxa that share the same biogeographic history, constituting identifiable subsets within a biotic component by their common biotic origin and evolutionary history from a diachronic perspective. After biotic components are established, time slicing, intraspecific phylogeography, and molecular clocks can help establish when the cenocrons assembled in the identified components, incorporating a time perspective in the study of biotic evolution.

Events of biogeographic convergence produce reticulated area histories that decrease the chances of establishing area relationships through congruence. The solution to problems posed by instances of biogeographic convergence is time slicing (Upchurch and Hunn 2002). Whereas assessments of faunal similarity usually are undertaken with faunas of successive geological ages, cladistic biogeography has used only data on organism relationships and spatial distributions on a single time plane (usually the present). Time slicing may reconcile the use of time and a synchronic approach. Ideally, it is possible to use a synchronic approach for each time slice identified.

Intraspecific phylogeography studies the principles and processes governing the geographic distribution of genealogical lineages, especially those within and between closely related species, based on molecular data (Avice et al. 1987). Once the population genetic structure has been assessed based on mitochondrial DNA (mtDNA), it is possible to obtain a network or cladogram of haplotypes, which allows us to analyze historical patterns and the processes that shaped them (e.g., dispersal, vicariance, range expansion, and colonization), sometimes under a statistical framework. This knowledge can suggest when recent cenocrons incorporated into a biotic component.

Cladograms based on molecular data may be used as raw data in cladistic biogeography and intraspecific phylogeography. In addition, the assumption that the rate of molecular evolution is approximately constant over time for proteins in all lineages allows the inference of a clock-like accumulation of molecular changes (Zuckerland and Pauling 1962), where the “ticks” of the clock, which correspond to mutations, do not occur at regular intervals but rather at random points in time (Gillespie 1991). This time is measured in arbitrary units and then calibrated in millions of years by reference to the fossil record or geological data (Magallón 2004; Sanderson 1998), giving minimum estimates of the age of a clade, which in turn may help elucidate the relative minimum ages of the cenocron to which it belongs.

Step 5: Construction of a Geobiotic Scenario

Once we have identified the biotic components and cenocrons, we may be able to construct a geobiotic scenario. By accounting biological and nonbiological data, we can integrate a plausible scenario to help explain the episodes of vicariance or biotic divergence and dispersal or biotic convergence that have shaped the evolution of the biotic components analyzed.

Biogeographers have classified geographic features in terms of their impact on dispersal and vicariance. The most important are barriers (geographic features that hinder dispersal) and corridors (geographic features that facilitate dispersal). In dealing with long-term changes in the biotic distributional patterns, continental drift may be a relevant factor (Briggs 1987; Cox and Moore 1998). Not only do the splitting and collision of landmasses directly affect distributional patterns, but also new mountains, oceans, and land barriers change the climatic patterns on the landmasses.

How to Read This Book

There are different ways to read this book. You may select an individual chapter to address your particular interests (e.g., chapter 2 if you are interested in conceptual issues, chapter 3 if you are interested in the history of biogeography, chapter 4 if you are interested in panbiogeography, chapter 5 if you are interested in cladistic

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