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Vicariance Biogeography

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Introduction

Vicariance biogeography seeks geo-physical explanations for disjunct distributions of organisms. Optimally, vicariance hypotheses are tested on the basis of the comparison of unrelated lineages of organisms that share geographic arenas. The fundamental approach is to marry geology and biology in the study of current and historical patterns of biodiversity. As a science, vicariance biogeography grew out of a synthesis of Alfred Wegener's continental drift as realized by the plate-tectonic mechanism, Léon Croizat's track analyses, and Willi Hennig's phylogenetic systematics into a discipline with more readily testable hypotheses than those from classical dispersal biogeography. Vicariance biogeography, at the time of its emergence in the mid-1960s, offered a common explanation for many of the most puzzling disjunct-distribution patterns across the globe. From the 1960s to the early 21st century, vicariance biogeography dominated the field, marginalizing inquiries into geographic distributions on the basis of dispersal explanations, in part because center-of-origin ideas had fallen into disrepute. However, with the realization that vicariance hypotheses fail to explain an array of biogeographic patterns, including both isolated biotas on oceanic islands and many groups spread over previously connected landmasses, dispersal's role in disjunct distributions of living things has been resurrected. The current consensus is that both processes play key roles in shaping the distribution of organisms through time.

General Overviews

An excellent primer for the scholar seeking insight into vicariance biogeography is the voluminous collection of foundational papers assembled in Lomolino, et al. 2004. This collection includes key early papers, with commentaries, on the role of vicariance by early authors as outlined in the Introduction, including Joseph D. Hooker, Alfred Wegener, George G. Simpson, Lars Brundin, Anthony Hallam, Philip J. Darlington, and many others. Wiens and Donoghue 2004 discusses the chasm between ecological and historical biogeography and the great potential in their integration. Cowell and Parker 2004 and Young, et al. 2004 review biogeography from the perspective of geologists. However, most early-21st-century overviews of historical biogeography are incorporated in general publications on biogeography, such as within biogeographical monographs and textbooks (see Textbooks). For example, Lomolino, et al. 2016 (cited under Textbooks) offers a detailed account of tectonic-plate theory and vicariance in chapters 8 and 12, including the history of the theories.

- **Cowell, C. Mark, and Albert J. Parker. 2004. Biogeography in the *Annals*. *Annals of the Association of American Geographers* 94.2: 256–268.**

  Discusses fundamental areas of biogeographic research covered in this journal devoted to geography. A good summary of biogeography through the eyes of geographers, with a review of the evolution of the discipline.

- **Lomolino, Mark V., and Richard Field. 2014. Re-articulation and re-integration of publications: Monographs in biogeography. *Frontiers of Biogeography* 6.2: 57–59.**

  A succinct summary of foundational monographs on biogeography published outside mainstream publication venues for biogeography research.

- **Lomolino, Mark V., Dov F. Sax, and James H. Brown, eds. 2004. *Foundations of biogeography*. Chicago: Univ. of Chicago Press.**

A thorough introduction to, and reproduction of, influential papers on biogeography, from preevolutionary and precontinental-drift thinking to the beginning of the molecular revolution. An essential overview of early literature.

- **Wiens, John J., and Michael J. Donoghue. 2004. Historical biogeography, ecology and species richness. *Trends in Ecology & Evolution* 19.12: 639–644.**

  An influential commentary on the existing chasm, and potential synergic interplay, between ecological and historical biogeography. Highlights research agendas and modeling approaches in historical and ecological biogeography that have since been better integrated into the discipline.

- **Young, Kenneth R., Mark A. Blumler, Lori D. Daniels, Thomas T. Veblen, and Susy S. Ziegler. 2004. Biogeography. In *Geography in America at the dawn of the 21st century*. Edited by Gary L. Gaile and Cort J. Willmott, 17–31. Oxford: Oxford Univ. Press.**

  A chapter within a book exploring the state of the art in geography in America. Provides an overview of and prospects for biogeography from geographic perspective and practice, including key references in the field.

Journals

No single journal is dedicated to vicariance per se, but several focus on biogeography. The *Journal of Biogeography* and *Global Ecology and Biogeography* are two of the most prominent journals in the field; the former is especially important for students of vicariance biogeography, emphasizing both empirical and theoretical studies on the subject. Within geography, biogeographic research with broad appeal sometimes appears in the *Annals of the Association of American Geographers*. Two widely respected journals publishing paleoecology research are *Quaternary Research* and *Quaternary Science Reviews*. Research on vicariance biogeography is also published in a variety of journals with a broader focus on systematics, most notably *Systematic Biology* and *Molecular Phylogenetics and Evolution*, and in multidisciplinary journals such as *PLoS ONE*.

- ***Annals of the Association of American Geographers*.**

  The most prestigious journal of the Association of American Geographers; publishes biogeographic studies based on research by geographers.

- ***Global Ecology and Biogeography*.**

  Emphasizes biogeographical research in a macroecological context, but with a broad geographic, taxonomic, and temporal scope; encompasses various aspects of historical biogeography.

- ***Journal of Biogeography*.**

  A leading journal of biogeographic research, and a prestigious outlet both for empirical and theoretical papers on vicariance biogeography, with broad taxonomic, spatial, and temporal scope.

- ***Molecular Phylogenetics and Evolution*.**

  A prominent and high-throughput outlet for molecular phylogenetic and biogeographical research. One of the journals publishing the highest absolute number of biogeographical articles.

- ***PLoS ONE*.**

  An extremely productive open-access interdisciplinary journal well known for judging papers on science only, not potential impact of articles. Among the high volume of articles are numerous biogeographical studies.

- ***Quaternary Research: An Interdisciplinary Journal*.**

  Includes original research on paleogeography, paleoecology, and paleoclimatology, along with research from other disciplines, including geoarchaeology and geomorphology.

- ***Quaternary Science Reviews*.**

  Reviews developments in science related to the Quaternary, encompassing all areas of Quaternary research, including paleogeography.

- ***Systematic Biology*.**

  A flagship journal of systematics: publishes theoretical, methodological, and empirical research on systematics, with many papers focusing on historical biogeography.

Textbooks

Textbooks addressing biogeography as a discipline offer in-depth overviews of the role of vicariance. The most comprehensive, useful to students and professors alike, is Lomolino, et al. 2016, which is richly illustrated and includes numerous empirical examples well integrated into portraying the major subdisciplines. It devotes a chapter (chapter 8) to plate tectonic theory, its history, and its eventual integration with phylogenetics to lay the foundations for modern vicariance biogeography (see also chapter 12). Cox, et al. 2016 offers a somewhat shorter overview of biogeography, with chapter 5 focusing on plate tectonics. Ebach 2015 provides a unique perspective, studying the early history of biogeography through the lenses of less well-known biogeographers. Crisci, et al. 2009 emphasizes methods in historical biogeography, offering considerable detail on selected methods. Parenti and Ebach 2009 includes a thorough historical summary of theory and practice in the discipline, a review of a large variety of methods, and their implementation. Morrone 2008 surveys various approaches to and theories of evolutionary biogeography, emphasizing how different questions require different methods and tools. MacDonald 2003, written from a geographic perspective, is a concise introductory biogeography textbook, but is now somewhat outdated.

- **Cox, C. Barry, Peter D. Moore, and Richard Ladle. 2016. *Biogeography: An ecological and evolutionary approach*. Hoboken, NJ: John Wiley.**

  A voluminous textbook written by biologists and ecologists for students with a variety of backgrounds. Approaches biogeography from a myriad of perspectives, including evolution, taxonomy, ecology, geology, paleontology, and climatology. One of the few textbooks in the field with a marine biogeography component.

- **Crisci, Jorge, Liliana Katinas, Paula Posadas, and Jorge Víctor Crisci. 2009. *Historical biogeography: An introduction*. Cambridge, MA: Harvard Univ. Press.**

  Emphasizes methods and topics of interest in historical biogeography. Cladistics, phylogenetics, panbiogeography, and other topics are covered, with a broad focus on historical distributions of plants and animals.

- **Ebach, Malte Christian. 2015. *Origins of biogeography*. New York: Springer.**

  An account of the history of early biogeography, focusing on the pioneering work of early but less discussed practitioners such as Eberhard A. W. von Zimmermann, Friedrich Stromeyer, Augustin Pyramus de Candolle, and Alexander von Humboldt.

- **Lomolino, Mark V., Brett R. Riddle, and Robert J. Whittaker. 2016. *Biogeography: Biological diversity across space and time*. 5th ed. Sunderland, MA: Sinauer.**

  The most comprehensive biogeographical textbook. Offers detailed accounts of plate tectonic theory, its history, its driving forces, and its impact on biological distributional patterns, supported with very numerous and excellent illustrations. Provides a broad selection of examples of vicariant biogeographical patterns and discusses numerous key papers spanning over three hundred years of the history of biogeography.

- **MacDonald, Glen. 2003. *Biogeography: Space, time, and life*. Hoboken, NJ: John Wiley.**

  Introductory text that explores the field of biogeography explicitly from a geographic perspective. Unique chapter on the biogeography of human evolution. Appropriate for introductory biogeography classes with students from a wide array of backgrounds and little prior exposure to biology or ecology.

- **Morrone, Juan. 2008. *Evolutionary biogeography: An integrative approach with case studies*. New York: Columbia Univ. Press.**

  Offers a comprehensive treatment of historical biogeography and an excellent overview of the state of the art in the first decade of the 21st century, including classical methods—some now further developed, others slowly disappearing.

- **Parenti, Lynne R., and Malte C. Ebach. 2009. *Comparative biogeography: Discovering and classifying biogeographical patterns of a dynamic earth*. Berkeley: Univ. of California Press.**

  Brings multiple comparative tools and perspectives to a more unified discipline of biogeography; thoroughly reviews the history and the theory of biogeography and the development and use of methods and offers prospects for the future of the discipline.

Brief History of Vicariance Biogeography

In the 19th and early 20th centuries, the common view was that the earth's landmasses and ocean basins were static. In this context, disjunct distributions were explained by long-distance dispersal, rafting, or migration across land bridges. Early evolutionary biologists viewed dispersal as central to explaining disjunct distributions, but they still saw the importance of geological change, even before defensible continental-drift ideas had surfaced. Both Charles Darwin and Alfred Russel Wallace viewed geological changes as a major driver in biogeography. They agreed on the importance of ocean-level changes and land rise and decline. Wallace also put his faith in land bridges, while Darwin rejected most land-bridge hypotheses in favor of dispersal. However, both considered long-distance dispersal as the most important explanation for disjunct distributions, and Darwin made numerous observations and experiments to demonstrate the feasibility of overwater dispersal. Joseph D. Hooker is often referred to as the father of vicariance biogeography due in part to his disdain for dispersal hypotheses. He developed and applied two key principles of the discipline: the idea that the splitting of ancestral ranges was a key biogeographical force and the approach of comparing disjunction patterns across evolutionary lineages. However, much later and after the emergence of plate tectonics, the term *vicariance* was first used in the context of historical biogeography in Croizat, et al. 1974, an important paper, aiming to provide a new approach by uniting plate tectonic theory, Léon Croizat's pangeographical *track analyses*, and Willi Hennig's phylogenetic systematics (Hennig 1966). Lars Brundin, in a series of papers starting with Brundin 1966, first developed phylogeny as a fundamental component of historical biogeography. Phylogenetic vicariance biogeography was then further developed in Nelson 1974, Nelson 1978, Platnick and Nelson 1978, Rosen 1978, Nelson and Platnick 1981, Wiley 1988a, Wiley 1988b, and Bremer 1992. With the advent of molecular phylogenetics/omics and more-powerful statistical software, the field of vicariance biogeography continues to rapidly develop (see Current Practice in Vicariance Biogeography).

- **Bremer, Kåre. 1992. Ancestral areas: A cladistic reinterpretation of the center of origin concept. *Systematic Biology* 41.4: 436–445.**

  Reestablishes the goal of inferring ancestral areas for lineages as valid, since the ancestral area for a lineage was probably smaller than the current area occupied by its descendants for many groups. Introduces a cladistic analysis for single lineages to assess the probability of a geographic area being ancestral for the in-group. Vicariance in this context is seen as the subset of inferred histories in which the ancestral area is identical to the current area.

- **Brundin, Lars. 1966. *Transantarctic relationships and their significance, as evidenced by Chironomid midges: With a monograph of the subfamilies Podonominae and Aphroteniinae and the Austral Heptagyiae*. Stockholm: Almqvist & Wiksell.**

  A landmark synthesis of emerging theories of systematics and plate tectonics in a comprehensive theory of biogeography, using chironomid midges as the exemplar lineage.

- **Croizat, Léon, Gareth Nelson, and Donn Eric Rosen. 1974. Centers of origin and related concepts. *Systematic Biology* 23.2: 265–287.**

  The panbiogeographer Croizat teams up with phylogenetic biogeographers Nelson and Rosen to unite ideas from his generalized-tracks concept, sympatry, and phylogenetics, making conceptual advances to the biogeographic thinking of the time.

- **Hennig, Willi. 1966. *Phylogenetic systematics*. Urbana: Univ. of Illinois Press.**

  Rigorous methodology for reconstructing phylogenetic trees, a key driver in the development of vicariance biogeography. English version/reduction of the earlier German work.

- **Nelson, Gareth. 1974. Historical biogeography: An alternative formalization. *Systematic Zoology* 23.4: 555–558.**

  Rejects Hennig's progression rule in the context of rejecting dispersalist approaches, especially hypothesizing centers of origin; fully acknowledges the power of Croizat's approach using the geographic congruence of multiple lineages to interpret ancestral distributions. Notes in summary that vicariance is to be shown via cladistic analysis.

- **Nelson, Gareth. 1978. From Candolle to Croizat: Comments on the history of biogeography. *Journal of the History of Biology* 11.2: 269–305.**

  Reviews the debate on areas of endemism. Credits Augustin Pyramus de Candolle with posing this question: What explains areas of endemism? Contrasts Darwin and Wallace's answers, grounded in dispersal explanations with that of Croizat, who brought in tectonic ideas and thus vicariance explanations to historical biogeography.

- **Nelson, Gareth, and Norman I. Platnick. 1981. *Systematics and biogeography: Cladistics and vicariance*. New York: Columbia Univ. Press.**

  An important work uniting Hennig's phylogenetic systematics and Croizat's "Space, Time, Form: The Biological Synthesis" (1964) into a biogeographical theory. Highlights the lack of connection between the disciplines, and the authors who do not cite each other's work. Highlights that together these theories and philosophies yield a simple but powerful thesis: that geology and phylogeny—earth and life—evolve together, from global to local scales.

- **Platnick, Norman I., and Gareth Nelson. 1978. A method of analysis for historical biogeography. *Systematic Zoology* 27.1: 1–16.**

  A lucid presentation of the problems facing biogeographers attempting to distinguish vicariance from dispersal in historical biogeography, and the introduction of a cladistics-based analysis technique as a solution.

- **Rosen, Donn E. 1978. Vicariant patterns and historical explanation in biogeography. *Systematic Zoology* 27.2: 159–188.**

A rigorous representation of vicariance arguments depending on the congruence of biological and geological cladograms, with emphasis on the three-taxon clades central to the then-novel cladistics methods. Includes a statistical approach to testing using confidence intervals based on level of congruence.

- **Wiley, E. O. 1988a. Vicariance biogeography. *Annual Review of Ecology and Systematics* 19:513–542.**

  An accessible, systematic representation of the then-young discipline of vicariance biogeography, with an excellent description and comparison of the alternative methodological approaches then in use, with arguments for parsimony analysis of area relationships as the best.

- **Wiley, E. O. 1988b. Parsimony and vicariance biogeography. *Systematic Zoology* 37.3: 271–290.**

  A review of the then-new generation of techniques for testing vicariance hypotheses, with a strong advocacy for the parsimony-based approach, grounded in an analogy to the cladistics analysis of congruence between the evolution of parasites and that of their hosts.

Foundational Works and Collections

The foundational works of vicariance biogeography integrate fundamental developments in biogeographic theory, plate tectonics, and phylogenetic systematics. The defining guide to these works is the major compilation of Lomolino, et al. 2004. This excellent collection reproduces and annotates key publications spanning the period from pre-evolutionary thinking to the late 20th century, culminating in the development of plate tectonic theory and phylogeny-based vicariance biogeography. Lomolino and Field 2014 offers an exhaustive list of foundational monographs in historical biogeography, and several textbooks provide thorough summaries of the development and history of the field. Many renowned 18th- and 19th-century scientists (e.g., Carl Linnaeus, Alexander von Humboldt, Augustin Pyramus de Candolle, Charles Darwin, Alfred R. Wallace, Joseph D. Hooker) speculated on the role of geography in explaining disjunct distributions, and early ideas on continental drift were provided, for example, by Antonio Snider-Pellegrini in the 1850s and Frank B. Taylor in the early 1900s. However, Wegener 1924 presented a fully developed theory of continental drift that was ultimately to become groundbreaking. The later retooling of the theory as plate tectonics by a series of workers in the late 1960s (see Geology and Plate Tectonics) set the stage for the rapid development of vicariance biogeography as a discipline. Dewey 2015 provides an excellent summary of the discovery of various geophysical features (e.g., midocean ridges, deep-sea trenches, transform faults, mantle-plume hotspot trails, seismic zones, volcanic belts, continental rift systems, orogenic belts) associated with continental drift and plate tectonics and how they were melded into a coherent theory. Brundin 1966, among others, then integrated the emerging theory on the dynamic nature of Earth's surface with Hennig 1966—a new method of phylogenetic systematics—to yield a solid biogeographic theory and developed a conceptual approach to testing biogeographical hypotheses. Methodological approaches to vicariance biogeography were further developed in Croizat, et al. 1974; Wiley 1988; and others (summarized in Brief History of Vicariance Biogeography)—ably summarized in Morrone and Crisci 1995.

- **Brundin Lars. 1966. *Transantarctic relationships and their significance, as evidenced by Chironomid midges: With a monograph of the subfamilies Podonominae and Aphroteniinae and the Austral Heptagyiae*. Stockholm: Almqvist & Wiksell**

  The first thorough integration of the phylogenetic methodology in Hennig 1966 into the testing of vicariance-biogeographic hypotheses. In this work, Brundin developed the concept of vicariance as a null hypothesis in historical biogeography, to be rejected before dispersal hypotheses are proposed.

- **Croizat, Léon, Gareth Nelson, and Donn Eric Rosen. 1974. Centers of origin and related concepts. *Systematic Zoology* 23.2: 265–287.**

  An explicit, formal articulation of vicariance biogeography, incorporating at once the idea of building hypotheses for vicariance from congruent distribution patterns (Croizat's generalized tracks) and incorporating sympatry as evidence for dispersal confounding the vicariance history, with an exhaustive rejection of center-of-origin hypotheses as valid historical-biogeographic hypotheses.

- **Dewey, John F. 2015. A harbinger of plate tectonics: A commentary on Bullard, Everett and Smith (1965) "The fit of the continents around the Atlantic." *Philosophical Transactions of the Royal Society A* 373.2039: 1–19.**

  Provides an excellent summary of the discovery and development of continental drift and plate tectonic theory.

- **Hennig, Willi. 1966. *Phylogenetic systematics*. Urbana: Univ. of Illinois Press.**

  The English-language translation of the work that lays the foundation for modern phylogenetic systematics, which in turn became the most fundamental tool in historical biogeography.

- **Lomolino, Mark V., and Richard Field. 2014. Re-articulation and re-integration of publications: Monographs in biogeography. *Frontiers of Biogeography* 6.2: 57–59.**

A summary of foundational biogeographical monographs published in outlets other than mainstream biogeographical venues.

- **Lomolino, Mark V., Dov F. Sax, and James H. Brown, eds. 2004. *Foundations of biogeography*. Chicago: Univ. of Chicago Press.**

  An exhaustive collection of foundational papers on biogeography dating from 1761 to 1982, comprising an array of subtopics introduced with a commentary by prominent biogeographers. A comprehensive guide to, and reprints of, classic papers in biogeography.

- **Morrone, Juan J., and Jorge V. Crisci. 1995. Historical biogeography: Introduction to methods. *Annual Review of Ecology and Systematics* 26:373–401.**

  A lucid review of the history, salient characteristics, and methodology of deductive historical biogeography with vicariance biogeography at its center, focused on the period from the mid-1950s to the early 1990s. Includes a synthesis of three approaches into a suggestion for an integrated approach to analysis.

- **Wegener, Alfred. 1924. *The origin of continents and oceans*. 4th ed. Translated by J. G. A. Skerl. London: Methuen.**

  The first fully developed publication of a theory of continental drift and the idea that the world's landmasses had once formed a single body called Pangaea.

- **Wiley, Edward O. 1988. Parsimony analysis and vicariance biogeography. *Systematic Zoology* 37.3: 271–290.**

  A review of techniques for testing vicariance hypotheses. Advocates the parsimony-based approach, grounded in an analogy to the cladistics analysis of congruence between the evolution of parasites and that of their hosts, introduced by Daniel Brooks in his 1981 work on what was later termed Brooks Parsimony Analysis (BPA). BPA explicitly uses independent phylogenies to look for shared patterns in biogeographic relationships among areas, inspired by inferring coevolutionary relationships between parasite and host.

Current Practice in Vicariance Biogeography

The foundations for present-day molecular phylogenetic and statistical vicariance biogeography were laid by Ronquist 1997 (who developed a statistical model-based methodology), Avise 2000 (who introduced the field of phylogeography), and Knowles and Maddison 2002 (who inaugurated statistical phylogeography). Armed with statistical tools, the field is rapidly expanding beyond simply discussing patterns and their consistency with hypotheses toward explicit hypothesis testing. For example, the most-recent analytical advances have been in the increased sophistication of maximum likelihood and Bayesian statistical model testing (e.g., in Ree and Smith 2008; Landis, et al. 2013; and Matzke 2014). These provide a framework for hypotheses testing using phylogenetic structure, timing analyses, and simulated vicariance events; for example, using time-slice analyses to evaluate impacts of vicariance events. Furthermore, current development is concerned with ameliorating shortcomings of recently developed methods, integration of uncertainty into analyses, and an increased focus on explicit consideration of the biology of the organisms under study into biogeographical analyses. For example, classical models in biogeography lack a parameter for founder-event speciation, presumably an important factor especially in island biogeography. Matzke 2014 proposes a solution by integrating a "jump" dispersal parameter "J" into the widely used dispersal-extinction-cladogenesis (DEC) model and provides a test for the role of jump dispersal (fitting models with or without this parameter). While this advance was immediately adopted by the field, Ree and Sanmartín 2018 points to potential statistical and conceptual issues, debating whether "J" actually achieves its stated goal. Current Bayesian and likelihood methods readily account for phylogenetic uncertainty in model testing by running analyses across multiple trees, but further development is necessary to simultaneously and adequately account for uncertainty in phylogenetic dating, geological history, and actual (versus known) taxon distribution. Graham, et al. 2018 highlights the need for deeper consideration of phylogenetic scale in biogeographic analyses, especially in appropriately comparing different taxa and different levels of hierarchies across phylogenetic trees. Finally, as argued in Papadopoulou and Knowles 2016, the field, classically based just on abiotic factors, is ripe for renewed focus on the role of taxon-specific traits—biology, process—in explaining biogeographic patterns. For example, 2010s work increasingly includes niche modeling in the study of biogeography and vicariance. For example, Mairal, et al. 2015 shows how vicariance and niche evolution combine to explain disjunct distributions in the flowering plant *Canarina*. Software packages such as R rapidly adopt such advances and allow highly sophisticated and integrated hypothesis testing that can be fine-tuned to any particular study. Simpler platforms, such as the RASP program (Yu, et al. 2015), focus on making these tools available to a broad user base, still allowing quite elaborate analyses.

- **Avise, John C. 2000. *Phylogeography: The history and formation of species*. Cambridge, MA: Harvard Univ. Press.**

The landmark work by the founder of phylogeography; provides both a formal articulation of and introduction to a methodology for reconstructing the phylogenetic history of lineages, integrated with the geography of these lineages.

- **Graham, Catherine H., David Storch, and Antonin Machac. 2018. Phylogenetic scale in ecology and evolution. *Global Ecology and Biogeography* 27.2: 175–187.**

  Formalizes the concept of phylogenetic scale and its role in evolutionary hypothesis testing, emphasizing that patterns may be scale dependent, which is to say, not uniform from the root to the tip of trees. Comparison across taxa, taking into account phylogenetic scale (instead of, say, taxonomic ranks), can offer a more precise comparative framework and an increased appreciation for the interplay of multiple processes in shaping the distribution and diversity of life.

- **Knowles, L. Lacey, and Wayne P. Maddison. 2002. Statistical phylogeography. *Molecular Ecology* 11.12: 2623–2635.**

  Further develops the field of statistical phylogeography, aiming to objectively infer the history and processes underlying the genetic structure of populations.

- **Landis, Michael J., Nicholas J. Matzke, Brian R. Moore, and John P. Huelsenbeck. 2013. Bayesian analysis of biogeography when the number of areas is large. *Systematic Biology* 62.6: 789–804.**

  A major development in Bayesian biogeographical analyses, allowing the inclusion of multiple areas in a model-testing statistical software environment.

- **Mairal, Mario, Lisa Pokorny, Juan José Aldasoro, Marisa Alarcón, and Isabel Sanmartín. 2015. Ancient vicariance and climate-driven extinction explain continental-wide disjunctions in Africa: The case of the Rand Flora genus *Canarina* (Campanulaceae). *Molecular Ecology* 24.6: 1335–1354.**

  An excellent empirical example of the integration of niche modeling and biogeographical hypothesis testing in the study of vicariance.

- **Matzke, Nicholas J. 2014. Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. *Systematic Biology* 63.6: 951–970.**

  Introduces the dispersal-extinction-cladogenesis (DEC)+J model, where J is a parameter for “jump” dispersal, adding founder-event speciation to existing dispersal and vicariance models of biogeography, realized in the R package BioGeoBEARS.

- **Papadopoulou, Anna, and L. Lacey Knowles. 2016. Toward a paradigm shift in comparative phylogeography driven by trait-based hypotheses. *Proceedings of the National Academy of Sciences of the United States of America* 113.29: 8018–8024.**

  Discusses the role of taxon-specific traits (e.g., life history traits) in developing biogeographic hypotheses, potentially shifting the paradigm from focusing solely on concordance between phylogenies of multiple taxa and abiotic factors (geology, climate, etc.). Taking into account the biology of the taxa under study, specifically, can aid in understanding patterns of discordance—cases where similarly aged codistributed taxa display contrasting biogeographical patterns.

- **Ree, Richard H., and Isabel Sanmartín. 2018. Conceptual and statistical problems with the DEC+J model of founder-event speciation and its comparison with DEC via model selection. *Journal of Biogeography* 45.4: 741–749.**

  Offers a critique of DEC models including the “J” parameter, aiming to model the mode of speciation. Discusses shortcomings of such models in ignoring factors such as rate of speciation and time. Suggests that likelihood comparisons of DEC versus DEC+J models are not valid, nor necessary, and encourages a more critical approach to interpretation of results from such analyses that analyze patterns without regard to process.

- **Ree, Richard H., and Stephen A. Smith. 2008. Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology* 57.1: 4–14.**

  Proposes the DEC (Dispersal, Local Extinction, and Cladogenesis) model for historical changes in geographic range, using likelihood estimations of ancestral ranges for common ancestors.

- **Ronquist, Fredrik. 1997. Dispersal-vicariance analysis: A new approach to the quantification of historical biogeography. *Systematic Biology* 46.1: 195–203.**

  A major step in the development of current statistical model-based biogeographic analyses, introducing likelihood-based tests of dispersal and vicariance hypotheses (DIVA). The introduction of (1) an approach to inferring biogeographic history based in likelihood and (2) an approach to analyses that simultaneously address vicariance, dispersal, and extinction, rather than relegating the last two to being considered post hoc, when vicariance is rejected. The model allows for the possibility that barriers are not necessarily permanent.

- **Yu, Yan, A. J. Harris, Christopher Blair, and Xingjin He. 2015. RASP (Reconstruct Ancestral State in Phylogenies): A tool for historical biogeography. *Molecular Phylogenetics and Evolution* 87 (June): 46–49.**

Introduces the software packet RASP, a user-friendly platform for biogeographic analyses using mainstream models, simultaneously accounting for phylogenetic uncertainty.

Land Bridges, Land Movement, and Long-Distance Dispersal

In a letter to Charles Lyell, Charles Darwin succinctly, and with characteristic wit, expressed concerns regarding land bridges: “the geological strides, which many of your discipline are taking. . . . If you do not stop this, if there be a lower region of punishment of geologists, I believe, my great master, you will go there.” Historical explanations of disjunct distributions fall into three categories: (1) movement of organisms across barriers (dispersal), (2) movement of organisms over temporary connections among landmasses (land bridges), and (3) movement of organisms as the landmasses themselves divide (vicariance). Joseph D. Hooker (Hooker 1853), the “father” of vicariance biogeography, argues that “many of the peculiarities of each of [the] great areas of land in the southern latitudes . . . [are] not to be accounted for by any theory of transport or variation, but which is agreeable to the hypothesis of all being members of a once more extensive flora, which has been broken up by geological and climatic change.” However, absent a theory of continental drift, the debate focused primarily on stochastic dispersal versus dispersal across land bridges. Wallace 1876 espouses the land-bridge explanation: “the distribution of animals and plants . . . may indicate the existence of islands or continents now sunk beneath the ocean.” In contrast, Darwin (Darwin 1872) rejected most land-bridge hypotheses, appalled by how Hooker, Lyell, and other “extensionists” created land bridges “as easy as a cook does pancakes.” Instead, Darwin worked assiduously on gathering evidence for long-distance dispersal; for example, demonstrating the ability of organisms to survive lengthy immersion in salt water. Curiously, some hypothesized land bridges have in fact been revealed to be actual land connections (e.g., the land bridge proposed between Madagascar and India and Gondwana). Yet, as summarized in Agnarsson and Kuntner 2012, the biota of Madagascar are only in small part vicariant—supporting Darwin’s point of view. Some land-bridge hypotheses have gained support both from geological and biological evidence. Taiwan is a classic land-bridge island. The land-mass has only existed since about 5 Ma and due to it being separated from mainland Eurasia by shallow sea-bed, the regular sea-level falls that occurred over the last 700,000 years has seen it connect with the continent many times. Consequently, its land animals are mainly non-endemic species (Ali 2018). Yet other land bridges are still being debated, such as GAARlandia, which Iturralde-Vinent and MacPhee 1999 suggests facilitated overland colonization of the Caribbean archipelago. The explanatory power and testability of vicariance hypotheses marginalized dispersal biogeography for a long period, except for disjunctions involving remote volcanic ocean islands. However, with convincing evidence for dispersal in taxa generally considered to be vicariant, such as amphibians (discussed in Vences, et al. 2003) and chameleons (highlighted in Raxworthy, et al. 2002), dispersal biogeography was eventually “resurrected”—as dubbed in de Queiroz 2005. Dispersal hypotheses competing on even ground with vicariance hypotheses, in turn, led to current practice and model testing in historical biogeography.

- **Agnarsson, Ingi, and Matjaž Kuntner. 2012. The generation of a biodiversity hotspot: Biogeography and phylogeography of the western Indian Ocean islands. In *Current topics in phylogenetics and phylogeography of terrestrial and aquatic systems*. Edited by Kesara Anamthawat-Jónsson, 33–82. Rijeka, Croatia: InTech.**

  A thorough comparative review of biogeographic patterns of a large diversity of partially or wholly codistributed taxa across islands of the western Indian Ocean. Aims to summarize the broad strokes in western Indian Ocean biogeography and quantify the relative roles of vicariance and dispersal, and the direction of dispersal. Only 7 percent of the Malagasy lineages surveyed are supported as vicariant.

- **Ali, Jason R. 2018. Islands as biological substrates: Continental. *Journal of Biogeography* 45:1003–1018.**

  The work summarizes the nine different sorts of islands with continental basements, and their key biogeographical features. Taiwan is classified as an orogenic margin island. There, the continental shelf margin of eastern Eurasia has locally collided with Luzon Arc on the Philippine Sea Plate. The collision started about 5 Ma and has cause uplift to almost 4 km.

- **Darwin, Charles R. 1872. Geographical distribution. In *The origin of species by means of natural selection*. 6th ed. By Charles R. Darwin, 316–342. London: John Murray.**

  Darwin adopts a dispersalist approach to interpret historical biogeography, incorporating the progression rule as later promulgated by Willi Hennig. At the same time, he uses vicariance to explain disjunct distributions, evoking climate change and sea-level change, but he rejects the possibility that continents have shifted positions in recent-enough times to influence organic evolution.

- **de Queiroz, Alan. 2005. The resurrection of oceanic dispersal in historical biogeography. *Trends in Ecology & Evolution* 20.2: 68–73.**

  An influential paper arguing for the importance of dispersal during a period in the science of biogeography where dispersal hypotheses were marginalized and considered secondary to vicariance. Examines a broad array of case studies where disjunct distributions are better explained by dispersal than vicariance, notably due to current knowledge on clade ages.

- **Hallam, Anthony. 1967. The bearing of certain palaeozoogeographic data on continental drift. *Palaeogeography, Palaeoclimatology, Palaeoecology* 3:201–241.**

  A thorough investigation of the distribution of two highly different Triassic groups—land vertebrates and marine mollusks—and what these can tell about continental drift. Includes a discussion of several land-bridge hypotheses and their shortcomings.

- **Hooker, Joseph D. 1853. *The botany of the Antarctic voyage of H.M. discovery ships* Erebus *and* Terror *in the years 1839–1843*. Vol. 2, *Flora Novae Zelandiae*. London: Lovell and Reeve.**

  Offers a strong criticism of dispersal hypotheses. Claims that the plants of the Southern Ocean represent the "remains of a [southern latitude] flora that had once spread over a larger and more continuous tract of land than now exists in that ocean" and that they are "not to be accounted for by any theory of transport or variation, but which is agreeable to the hypothesis of all being members of a once more extensive flora, which has been broken up by geological and climatic change."

- **Iturralde-Vinent, Manuel A., and R. D. E. MacPhee. 1999. Paleogeography of the Caribbean region: Implications for Cenozoic biogeography. *Bulletin of the American Museum of Natural History* 238:1–95.**

  A detailed paleogeographical account on the Caribbean region, focusing on three time slices (35–33 million years ago [Ma], 27–25 Ma, and 16–14 Ma) that may have been influential in the biogeography of the Caribbean. Marshals geological evidence for a land bridge, the Greater Antilles-Aves Ridge, which the authors refer to as GAARlandia, existing as a potential route of overland colonization of the Greater Antilles 35–33 Ma. Discusses subsequent breakup and movement of landmasses as they start taking their current shape.

- **Raxworthy, Christopher J., Michael R. J. Forstner, and Ronald A. Nussbaum. 2002. Chameleon radiation by oceanic dispersal. *Nature* 415.6873: 784–787.**

  A commentary on the excessive focus on vicariance in historical biogeography, using novel evidence on chameleons. Traditionally considered vicariant, they are instead an example of out-of-Madagascar dispersal, including a "reverse colonization" of a continent (Africa) from an island. An important landmark study in the resurrection of dispersal biogeography.

- **Vences, Miguel, David R. Vieites, Frank Glaw, et al. 2003. Multiple overseas dispersal in amphibians. *Proceedings of the Royal Society of London Series B: Biological Sciences* 270.1532: 2435–2442.**

  Discusses the debate between vicariance and dispersal explanations in biogeography by using the distributions of amphibians, generally considered unable to cross oceanic barriers. Presents and discusses evidence for multiple transoceanic events in the groups while also highlighting the major role of vicariance in explaining the biogeography of amphibians as a whole.

- **Wallace, Alfred Russel. 1876. *The geographical distribution of animals*. Vol. 1. New York: Harper.**

  An encyclopedic review of living and fossil animal distributions, arguing that oceans and climate types are key isolating mechanisms, leading to an array of divergence hypotheses for the impact of past dispersal on modern distributions. Emphasizes the role of land bridges in explaining disjunct distribution, and rejects vicariance as a cause of disjunct distributions of lineages across the southern continents. Clearly values the reciprocal illumination that historical biogeography and geology can provide one another.

Geology and Plate Tectonics

The history and theory of plate tectonics and its supporting geological evidence are summarized in Fowler 2005 and Kearey, et al. 2009. The notion of Earth having a mobile surface has been around since it was observed that some of the landmasses on the opposite sides of the ocean basins had coasts that matched. In the early 20th century, Alfred Wegener published his theory of continental drift. The marshalled evidence included the jigsaw-like fit of the shorelines of the Atlantic-bordering landmasses; evidence for a Late Paleozoic glaciation that affected the southern continents, suggesting they were then in close proximity and implying that they were close to the South Pole; fossils of the same terrestrial animals and plants on widely separated landmasses; and sedimentary formations, for instance desert dunes, shallow-marine limestones, and coal accumulations that had to have formed in conditions (and hence, at latitudes) that were quite unlike the ones they currently occupied. However, a critical problem with the theory was the absence of a mechanism by which the quartz-rich continents could "float" across a denser olivine-rich basement, akin to oil tankers gliding across the ocean. Hence, although the hypothesis had several vocal advocates, its limitations prevented a paradigm shift. As summarized in Dewey 2015 (cited under Foundational Works and Collections), the theory was reformulated in the 1960s as plate tectonics, emerging from a period of exploration and discovery that followed World War II in which various phenomena associated with the earth's surface and inner regions, particularly its ocean basins, were revealed. The all-encompassing hypothesis not only explains continental drift but also accounts for sea-floor spreading, transform faults, mantle-plume hotspot tracks, the subduction of oceanic lithosphere at deep-sea trenches, earthquake belts, volcanic chains, mountain building, and the planet's internal structure. Consequently, the dynamic-earth model provided biologists with a conceptual framework to interpret disjunct biological distributions, and to also dismiss long-distance dispersal proposals. Paleogeographic maps and scenarios have since been presented that are of great value to vicariance biogeographers. For example, Smith, et al. 1994 provides coastline maps for various intervals back to about 250 million years ago (Ma); a further series of such maps is commercially available from Deep Time Maps (founded by Ron Blakey). Many studies are regional in outlook; for example, Hall 2013 offers a detailed history of the area around the Wallace Line, and O'Dea, et al. 2016 discusses the evidence for the formation and emergence of the Panama Isthmus, which connected North and South America.

- **Deep Time Maps.**

  Originally named Colorado Plateau Geosystems, founded in 2004 by Ron Blakey. A producer of an extensive library of detailed paleogeographic maps that depict the shorelines and inferred topography/bathymetry since the late Precambrian, 600 Ma. For a relatively small fee, individual images can be purchased online.

- **Fowler, C. M. R. 2005. *The solid earth: An introduction to global geophysics*. 2d ed. Cambridge, UK: Cambridge Univ. Press.**

  An introductory geophysics textbook that covers plate tectonics and a broad scope of geophysical research.

- **Hall, Robert. 2013. The palaeogeography of Sundaland and Wallacea since the Late Jurassic. *Journal of Limnology* 72.2: 1–17.**

  Presents a set of detailed paleogeographic maps of the Wallace Line region. These are a key resource for biogeographers working on the flora and fauna of offshore Southeast Asia and New Guinea (Malesia).

- **Kearey, Philip, Keith A. Klepeis, and Frederick J. Vine. 2009. *Global tectonics*. 3d ed. Chichester, UK: Wiley-Blackwell.**

  A textbook dedicated entirely to tectonics, presenting detailed descriptions of the various plate tectonic phenomena and the associated geological processes.

- **Le Pichon, Xavier. 1968. Sea-floor spreading and continental drift. *Journal of Geophysical Research* 73.12: 3661–3697.**

  One of the 1967–1968 synthesis papers that outlined how plate tectonics works. Le Pichon's global model uses six major plates. Reconstructions based on the marine magnetic-anomaly data were presented for the anomaly 5 Late Miocene (*c*. 10 Ma) and anomaly 31, what is now known to be the latest Cretaceous, 70 Ma, although at the time Le Pichon considered it to be the Paleocene.

- **McKenzie, Dan P., and Robert L. Parker. 1967. The North Pacific: An example of tectonics on a sphere. *Nature* 216.5122: 1276–1280.**

  One of the 1967–1968 synthesis papers on plate tectonics. Focusing on the North Pacific, the authors explained the vast area by the relative movements of the rigid Pacific, Juan de Fuca, and North American plates around poles of rotation. Importantly, the region includes the three main sorts of plate boundaries: midocean ridges, where oceanic lithosphere is generated; deep-sea trenches, where oceanic lithosphere is subducted into the mantle; and transform faults, where plates slide past one another.

- **Morgan, W. Jason. 1968. Rises, trenches, great faults, and crustal blocks. *Journal of Geophysical Research* 73.6: 159–182.**

  One of the 1967–1968 synthesis papers that outlined how plate tectonics works. Morgan proposed that the earth's surface comprises twelve rigid plates that move with respect to one another. Using various associated phenomena from around the globe, he explained how they could all be fitted into a coherent theoretical model. It is worth noting that Morgan's work was originally presented at a spring 1967 conference; McKenzie and Parker's publication appeared on 30 December 1967.

- **O'Dea, Aaron, Harilaos A. Lessios, Anthony G. Coates, et al. 2016. Formation of the Isthmus of Panama. *Scientific Advances* 2.8: e1600883.**

  Thorough explanation of the geological and biological evidence indicating that the land bridge between South and North America, the "Panama Isthmus," emerged just under three million years ago. More recently, a number of papers have been published arguing for an appreciably earlier opening (≥20 Ma), and this has created much confusion. This work clarifies key elements in the discussion.

- **Smith, Alan G., David G. Smith, and Brian M. Funnell. 1994. *Atlas of Mesozoic and Cenozoic coastlines*. Cambridge, UK: Cambridge Univ. Press.**

  Presents a series of coastline maps at various times back to 250 Ma that are very useful for assessing land connections between various areas at particular times. Unfortunately, the book does not incorporate land topography and marine bathymetry. With regard to the former, mountains are major barriers to the dispersal of animals and plants and thus need to be accommodated in any biogeographic interpretation.

Tests of Vicariance Hypotheses: Geological Data

Research aimed at establishing the presence of postulated former land bridges would ideally use a combination of geological and geophysical techniques. Geological dredging (cheap) and, better still, drilling (expensive) would be carried out. Evidence indicating past emergence would include “high-energy” sedimentary accumulations (e.g., cobble beds, cross-bedded strata, marginal marine sediments) and large amounts of plant debris, possibly in the form of coal beds. There should be sharp surface-to-marine depositional conditions, indicating past inundation; for example, coral reefs and limestone. Importantly, the oldest marine sediments constrain the causeway’s closure. Where there is land, subaerial erosion will lead to the rapid accumulation of detritus in the nearby offshore areas. This will be easily detectable from seismic lines, where distinctive packages of sediment will emanate from a “basement high.” Notably, the promontory will “cut through” the depositional units that have piled up alongside it. This sort of information was used in Bassias 2016 to demonstrate that sections of the Davie Ridge, which runs from just offshore southern Tanzania down the middle of the Mozambique Channel, were subaerial at various times in the Cretaceous and Cenozoic. However, the emergence of the Davie Ridge was discontinuous both temporally and spatially, and the approximately 600-kilometer-long feature should not be thought of as a long peninsula. Two research projects in which geophysical information has been used to test vicariance hypotheses come from work in the Galápagos Islands in the eastern equatorial Pacific. In 1905–1906 the California Academy of Sciences carried out a seventeen-month expedition to the archipelago to collect and record its biota. Subsequent studies of the reptiles were carried out principally by John Van Denburgh. Van Denburgh 1912 and Van Denburgh and Slevin 1913 identify common species of leaf-toed gecko (*Phyllodactylus*) and lava lizard (*Microlophus*) on the central and western Galápagos Islands, with congeners on peripheral islands. Racer snakes (*Pseudalsophis*) and land iguanas (*Conolophus*) displayed similar patterns. Van Denburgh proposed that the Galápagos had once formed a large landmass that had been connected to the Americas via a vast causeway (Wright 1983). Prior to its sundering, the conduit enabled the various reptile groups to walk out across the eastern Pacific. Later, their subpopulations were isolated due to differential subsidence sporadically drowning portions of the platform and thus creating isolated landmasses. As discussed in Ali and Aitchison 2014 the first part of Van Denburgh’s hypothesis can be dismissed because there is no geophysical evidence indicating that such a causeway ever existed; realistically, the only feasible explanation is that the colonizing ancestors arrived on the archipelago via overwater dispersal. However, the later phase of subsidence leading to island creation and hence species formation is compatible with an intra-archipelago vicariance model.

- **Ali, Jason R., and Jonathan C. Aitchison. 2014. Exploring the combined role of eustasy and oceanic island subsidence in shaping biodiversity on the Galápagos. *Journal of Biogeography* 41.7: 1227–1241.**

  This geophysics-based study argues that large oscillations in relative sea level, resulting from eustasy, subsidence, and isostasy (all geophysical processes) over the last several hundred thousand years, profoundly shaped the archipelago’s landlocked reptile suite. During sea-level lows, the islands in the central and western parts of the archipelago, which sit on a shallow platform, coalesce into a single landmass.

- **Bassias, Yannis. 2016. Was the Mozambique Channel once scattered with islands? *GEO ExPro Magazine* 13.5: 58–63.**

  Succinct summary of the geological and geophysical data demonstrating that parts of the Davie Ridge were subaerial at different times in the Cretaceous and Cenozoic. The former is based on an analysis of rock samples that have been dredged from the seabed of the Mozambique Channel. The latter is gleaned from seismic data, which provides a cross-sectional image of the upper levels of the earth’s crust.

- **Van Denburgh, John. 1912. Expedition of the California Academy of Sciences to the Galapagos Islands, 1905–1906: VI, The geckos of the Galapagos archipelago. *Proceedings of the California Academy of Science*, 4th ser. 1: 405–430.**

  This and Van Denburgh and Slevin 1913 are primarily concerned with taxonomy of the three groups, but they also outline a model for a land bridge to the Americas to explain the presence of the reptiles on the Galápagos.

- **Van Denburgh, John, and Joseph R. Slevin. 1913. Expedition of the California Academy of Sciences to the Galapagos Islands, 1905–1906: IX, The Galapagoan lizards of the genus *Tropidurus*; with notes on the iguanas of the genera *Conolophus* and *Amblyrhynchus*. *Proceedings of the California Academy of Science*, 4th ser. 2: 132–202.**

  Continues work of the prior paper in developing vicariance hypotheses for the Galápagos Islands, this time focusing on iguanas. Proposes that localized subsidence isolating parts of the (hypothesized) Galápagos platform explained diversification of reptiles on the islands.

- **Wright, John W. 1983. The evolution and biogeography of the lizards of the Galápagos archipelago: Evolutionary genetics of *Phyllodactylus* and *Tropidurus* populations. In *Patterns of evolution in Galápagos organisms*. Edited by Robert I. Bowman, Margaret Berson, and Alan E. Leviton, 123–155. San Francisco: Pacific Division of the American Association for the Advancement of Science.**

  An excellent summary of Van Denburgh’s “Galápagos Land” hypothesis that was presented in two early 1900s papers. The ancestral colonizers walked to the island group, which was thought to have formed a single landmass, via a ≥930-kilometer land bridge that was linked to northern South America. Later sinking of the causeway isolated the platform's land-reptile suite. Subsequent differential subsidence created the various islands and led to the separation of subpopulations.

Tests of Vicariance Hypotheses: Biological Data

Biological data provide tests of geological hypotheses in many ways. Geological hypotheses make predictions about the age, availability (e.g., emergence), and connectivity of landmasses. Geological changes are expected to directly influence key elements in the distribution of biotas, so that lack of evidence supporting, for example, a temporary connection between two currently isolated islands could be used to refute the geological hypothesis. Such data ideally come from a complete or random sample of lineages (the more the better) from the biota, since the biogeographical history of any given lineage reflects its unique history. This history may or may not be the same as the geological history, just as individual gene trees may not reflect the history of the biological vessels that carry them. Currently, testing vicariance hypotheses with biological data starts with a thorough geographic sampling of taxa and phylogenetic data, followed by a three-pronged phylogenetic approach: (1) phylogenetic reconstruction, (2) dating, and (3) explicit hypothesis testing. Vicariance hypotheses can be rejected at different stages in this approach. Agnarsson, et al. 2015, for example, finds that the global phylogeny of *Anelosimus* spiders is inconsistent with Earth's geological history, and the authors specifically reject a vicariant origin of Malagasy species as both lineages occurring in Madagascar nest sister to American taxa. Yoder and Nowak 2006 reviews a large sample of phylogenetic studies of Malagasy biota. While the majority of the studies that the authors reviewed found a sister relationship between Malagasy and African taxa, clade ages vary across taxa with disparate dispersal modes. Typically, the clade ages are much younger than the ancient separation of Madagascar from Africa. Similarly, Ricklefs and Bermingham 2008 is a comparative review of Caribbean biogeography, revealing a pattern of vicariant origins in some lineages, with dispersal dominating in others. Even when tree structure and clade ages are consistent with vicariance, some studies still reject vicariance hypotheses on the basis of explicit hypothesis-testing such as time-slice analyses. The rejection may be a consequence of phylogenetic and dating uncertainty, or better fit of competing hypotheses. For example, Uit de Weerd, et al. 2016 rejects vicariance incorporating the GAARlandia model in its analysis of uropectid land snails, instead finding support for an ancient dispersal model, both preceding and following the time span of the putative land bridge. Other studies find support for vicariance in all three stages. For example, Berger, et al. 2016, using time-slice model testing, finds strong support for a vicariant Gondwanan history of the plant order Myrtales.

- **Agnarsson, Ingi, Brian B. Jencik, Giselle M. Veve, et al. 2015. Systematics of the Madagascar *Anelosimus* spiders: Remarkable local richness and endemism, and dual colonization from the Americas. *ZooKeys* 509:13–52.**

  A straightforward study of the diversity and phylogeny of Malagasy *Anelosimus* spiders in a global context. With two lineages present on Madagascar, the authors found strong support for the sister relationships of each of these to New World congeners. These findings clearly favor dispersal over a vicariance hypothesis based merely on phylogenetic relationships.

- **Berger, Brent A., Ricardo Kriebel, Daniel Spalink, and Kenneth J. Sytsma. 2016. Divergence times, historical biogeography, and shifts in speciation rates of Myrtales. *Molecular Phylogenetics and Evolution* 95 (February): 116–136.**

  A biogeographic study of eudicot flowering plants in the order Myrtales distributed across historically Gondwanan landmasses. Employs a variety of approaches using dated phylogenies and explicit model testing, including time-slice analyses in BioGeoBEARS, and finds convincing evidence for a Gondwanan vicariant biogeography of the lineage.

- **Ricklefs, Robert, and Eldredge Bermingham. 2008. The West Indies as a laboratory of biogeography and evolution. *Philosophical Transactions of the Royal Society B: Biological Sciences* 363.1502: 2393–2413.**

  A comprehensive and highly approachable review of all aspects of Caribbean biogeography, with an excellent section on dispersal versus vicariance. In the discussion section of the paper, John W. Wright summarizes Van Denburgh's biogeographical model for the Galápagos reptiles. A useful associated graphic is also provided.

- **Uit de Weerd, Dennis R., David G. Robinson, and Gary Rosenberg. 2016. Evolutionary and biogeographical history of the land snail family Urocoptidae (Gastropoda: Pulmonata) across the Caribbean region. *Journal of Biogeography* 43.4: 763–777.**

  A study on the Caribbean biogeography of dispersal-limited land snails. While this group colonized the Caribbean early in the biogeographic history of the archipelago, this study does not support the GAARlandia ancient land-bridge hypothesis. It instead finds evidence for a colonization of the Caribbean predating that hypothetical land bridge, while later dispersal and vicariance events combine to explain the distribution of the snails across islands.

- **Yoder, Anne D., and Michael D. Nowak. 2006. Has vicariance or dispersal been the predominant biogeographic force in Madagascar? Only time will tell. *Annual Review of Ecology Evolution and Systematics* 37:405–431.**

  Reviews a large set of biogeographic studies on a large variety of Malagasy taxa, including many distantly related groups of plants, arthropods, and vertebrates, winged and wingless, representing diverse life histories and dispersal modes and propensities. The emerging pattern from this comparative biogeographic approach is that while most Malagasy lineages are sister to African relatives, almost all of the divergence ages post-date the separation of Madagascar and Africa.

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