Biotic assembly in evolutionary biogeography: A case for integrative pluralism

Juan J. Morrone
Museo de Zoología “Alfonso L. Herrera”, Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México (UNAM), 04510 Mexico City, Mexico.
Correspondence: Juan J. Morrone: morrone@ciencias.unam.mx

Abstract
The emphasis on vicariance or dispersal has led to alternative and competing approaches to analyze biotic assembly, but both processes should be considered in an evolutionary integrative analysis. I define some relevant concepts (biotas, horobiotas, cenocrons, dispersal, vicariance and extinction) and discuss the differences between the dispersal-vicariance model and the center of origin-dispersal-vicariance (CODA) and vicariance models. I use the philosophical framework of integrative pluralism to justify an integrative evolutionary biogeographic approach, not implying an eclectic or “anything goes” perspective, but that different methods are compatible because they give partial solutions, when answering particular questions. This approach allows for the integration of the results of different analyses to explain biotic assembly.

Highlights
• Key evolutionary biogeographic concepts and methods are revised and their relevance for biotic assembly is discussed.
• The center of origin-dispersal-vicariance (CODA), vicariance and dispersal-vicariance models are briefly compared.
• To provide a way forward in studying biotic assembly, a step-wise protocol encompassing different questions and methods is outlined.
• The philosophical framework of integrative pluralism is used to justify this perspective.

Keywords: Biotic assembly, cenocron, dispersal, evolution, extinction, historical biogeography, horobiota, vicariance.

Introduction
A biota corresponds to the flora and fauna of a region (Merriam-Webster 2020). The use of different terms to refer to biotas (e.g., chronofaunas, areas of endemism, nuclear areas, centers of endemism, generalized tracks, biogeographical assemblages, and species assemblages, among others; see Morrone 2014, Passalacqua 2015, Fattorini 2016, Ferrari 2017) has promoted disagreements among different biogeographic approaches and traditions and impeded a transparent and productive communication among biogeographers.

Biotic assembly is a complex phenomenon, which has been analyzed from ecological and historical perspectives. An example of an ecological perspective is island biogeography (e.g., MacArthur & Wilson 1967), although more recent treatments have incorporated evolutionary concepts (Whittaker & Fernández-Palacios 2007). From the historical biogeographic perspective, the emphasis on different processes has led to alternative and competing approaches to explain biotic assembly. Classical dispersal
biogeographers, in the tradition of Darwin (1859) and Wallace (1876), have emphasized long-distance dispersal from restricted centers of origin. In contrast, panbiogeographers (e.g., Croizat 1958, 1964, Craw et al. 1999) and cladistic biogeographers (e.g., Nelson & Platnick 1981, Parenti & Ebach 2009) have emphasized vicariance to explain biotic differentiation due to the appearance of geographic barriers. Other authors have considered it appropriate to integrate alternating periods of dispersal and vicariance (e.g., Reig 1981, Savage 1982). More recent approaches, such as phylogeography (Avise 2000) and event-based and parametric biogeography (Sanmartín 2012, 2016), have implemented methods incorporating both dispersal and vicariance but are commonly aimed at the analysis of particular taxa, not of biotas as a whole. On the other hand, connections between historical and ecological biogeography have been noted by some authors. For example, Reig (1962) coined the term “cenogenesis” (meaning the origin of communities) to highlight the relevance of investigating the historical development of communities, not isolated taxa; and Halffter (1987) considered that when elucidating biogeographic patterns, special consideration should be given to taxa with similar evolutionary and macroecological trends.

My perspective of evolutionary biogeography (Morrone 2009, 2020) incorporates both dispersal and vicariance to the analysis of biotic assembly, following a step-wise protocol. In this sense, a biota represents a complex assemblage of taxa where we try to analyze a diverse array of ecologically and phylogenetically different taxa that belong to it. This protocol is aimed at identifying particular questions, choosing the most appropriate methods to answer them, and finally integrating them within a coherent theoretical framework explaining how a biota has been assembled. When addressing such questions, we choose those taxa from the analyzed biota that best address a given question. Similar integrative protocols have been proposed by Andersson (1996), Riddle & Haffner (2006), Santos & Amorim (2007), and Weeks et al. (2016).

Integrative pluralism is a philosophical approach aimed at providing the best explanation of a complex phenomenon by combining particular theories and models (Mitchell 2003). In contrast to reductionism, which tries to reduce the diversity of explanations, integrative pluralism is intended to produce a critical framework for understanding complex biological phenomena. According to Mitchell (2002, 2003), complexity involves three different issues: constitutive complexity (the phenomenon is a structurally complex system), dynamic complexity (there are diverse processes involved), and evolved complexity (the phenomenon evolves through time). I find that biotic assembly represents a complex phenomenon that may benefit from an integrative approach.

My objective is to contribute to an evolutionary integrative perspective of biotic assembly. I review some basic concepts of the patterns and processes involved, the models proposed, and some of the methods that have been used. I also provide a justification for this approach within the philosophical framework of integrative pluralism.

**Biogeographic patterns**

Biogeographic patterns refer to nonrandom repetitive elements, which include endemism, biogeographic homology, diversity, and taxonomic replacement gradients, among others (Morrone & Escalante 2016). In evolutionary biogeography, I find it useful to recognize basically two entities that are based on the patterns of endemism and biogeographic homology: biotas and cenocrons.

**Biotas:** They correspond to all the organisms from an area or the organismic community (Andersson 1996). We may use the term horobiota to represent a snapshot of a biota at a particular time. It represents the assemblage of taxa that coexist and diversify in a given area during a time period, thus representing an enduring biogeographic unit (Reig 1981). I consider that this term is useful to describe
the biotic assemblage that characterizes a biota at a given time, providing the opportunity to analyze different stages of biotic assembly. From an ontological perspective, I think that biotas represent “natural kinds”, meaning that they exist as real natural entities. Thus, when it comes to their circumscription or identifying the taxa that diagnose them, we should “carve nature at its joints” (Slater & Borghini 2011).

_Cenocrons_: A cenocron refers to a set of taxa that share the same biogeographic history, constituting an identifiable subset within a biota by their common biotic origin and evolutionary history (Morrone 2009). This term is used explicitly to refer to the dispersal and subsequent relatively synchronic implantation of a group of taxa in a biota (Reig 1981). Cenocrons constitute testable hypotheses and further studies allow the possibility of falsifying them, for example, by dating selected lineages and examining their phylogenetic placement and the distribution of their related taxa, and it is also possible to discover new cenocrons (Lobo 2007, Halffter & Morrone 2017). The relevance of cenocrons lies in the identification of geodispersal events that led communities to become incorporated into a biota, producing a new horobiota. Additionally, the deconstruction of biotas into their constituting cenocrons may be beneficial in order to address further evolutionary and ecological questions.

**Biogeographic processes**

There are three basic processes recognized in historical biogeography: dispersal, vicariance, and extinction (Fig. 1). A major emphasis in either dispersal or vicariance, or a combination of both, has led to alternative biogeographic models.

**Dispersal**: This general term refers to the expansion of the distributional area of a taxon (Myers & Giller 1988). For classical dispersalists (e.g., Darwin 1859, Wallace 1876, Matthew 1915), it meant the movement, by active migration or passive transfer, of a species from its center of origin, usually crossing a preexisting barrier, and allowing it to colonize a new area and eventually differentiate into new taxa. Dispersal as commonly used encompasses various mechanisms acting on different temporal scales, like the routine transport of propagules in a short-term or biological time scale, the chance crossing of barriers in short to long term scales, and the change of the distributional area of a species in short to evolutionary time scales (Morrone 2009).

Several authors (e.g., Platnick 1981, Andersson 1996, MacDonald 2003, Lieberman 2004, De Queiroz 2004, Cowie & Holland 2006) have considered it useful and important to distinguish between “dispersal” and “dispersion”. “Dispersal”, also known as “long-distance dispersal” or “jump dispersal”, refers to the colonization across a geographical barrier that allows the successful establishment of the species in distant areas (Fig. 1a). “Dispersion”, also known as “range expansion”, refers to the continuous expansion of the distributional area of a species, crossing adjacent suitable habitats, during several generations (Fig. 1b). A third process, “geodispersal” or “biotic dispersal”, concerns the simultaneous movement of several taxa (a community) due to the loss of a barrier (Fig. 1c). Confusion concerning these terms has been the cause of much misunderstanding between different biogeographic approaches, so it is important to understand when we are referring to dispersal in general or only to one of its varieties.

Both panbiogeographers (Croizat 1958, 1964, Craw et al. 1999, Heads 2014) and cladistic biogeographers (Nelson & Platnick 1981, Parenti & Ebach 2009) consider that only dispersion previous to the vicariant event is acceptable and that long-distance dispersal and geodispersal are rare phenomena, with no relevance in the establishment of biotic patterns. Other authors consider that the relevance of long-distance dispersal has been underestimated (Wilkinson 2003, De Queiroz 2004, 2014
2016, McDowall 2004). Wilkinson (2003) and McDowall (2004) have emphasized the relevance of long-distance dispersal in biotic assembly.

*Vicariance:* Refers to the appearance of a barrier that allows the fragmentation of the distribution of an ancestral species, after which the descendant species may evolve in isolation (Morrone 2009). The appearance of the barrier causes the disjunction, so they both have the same age (Fig. 1d). After barriers disappear, secondary sympatry may occur due to dispersal (dispersion), and also some species may overcome the barrier (long-distance dispersal), resulting in complex patterns layered one on top of another (Weeks et al. 2016). De Queiroz (2014, 2016) considered that molecular evidence has shifted current evolutionary biogeography to a more balanced view, where vicariance is not assumed to be the default explanation for disjunct distributions. Although I basically agree with de Queiroz’s view, I think that biotic disjunct patterns involving different taxa should have vicariance as the default explanation.

*Extinction:* This term refers to the local extirpation or total disappearance of a species or supraspecific taxon (Morain 1994). In rare cases, even biotas may disappear (“mass extinction”). Extinction (Fig. 1e) has the potential to obscure biogeographic patterns because biotas may appear to be different simply because one region has experienced differential extinction (Lieberman 2003, 2005). Although extinction is a fact, mechanisms explaining it usually do not concern biogeographers because it does not form patterns; however, we should be aware of the potential relevance of extinction for reconstructing patterns of biotic assembly.
Biogeographic models
Based on the emphasis on different types of dispersal or vicariance, three different biogeographic models have been proposed (Morrone 2015).

Center of origin-dispersal-vicariance (CODA) model: This model assumes a restricted origin of the ancestor of a group, followed by long-distance dispersal, arrival to new areas and adaptation to new conditions. This model has been adopted by dispersalism, and its origins can be traced to Darwin (1859) and Wallace (1876). In intraspecific phylogeography (e.g., Avise 2000) it is the implicitly assumed model.
**Vicariance model:** Vicariance assumes a widespread ancestor, which differentiates due to the appearance of barriers that isolate the populations. This model assumes that dispersion (the only type of dispersal that is accepted) before the vicariance event has allowed the ancestor to be widely distributed. Both panbiogeography (Croizat 1958, 1964) and cladistic biogeography (Nelson & Platnick 1981) are based on this model. In comparative phylogeography (e.g., Taberlet et al. 1998, Abogast & Kenagy 2001, Zink 2002, Riddle & Hafner 2006) instances of “geographic structure” are considered to result from vicariance.

**Dispersal-vicariance model:** This model assumes that geographic distributions evolve in two steps (Morrone 2009): (1) dispersal (encompassing all types of dispersal): when climatic and geographic factors are favorable, organisms expand actively their geographic distribution according to their dispersal capabilities or vagility and acquire their ancestral distribution; and (2) vicariance: when organisms have occupied all the available geographic or ecologic space, their distribution may stabilize, allowing the isolation of populations in different sectors and the differentiation of new species through the appearance of geographic barriers. After vicariance events, geographic barriers may disappear and dispersal of individual species or cenocrons may contribute to the biota. This model allows biogeographers to consider that both vicariance and dispersal (including dispersion and jump-dispersal of particular species as well as geodispersal of communities) contribute to biotic assembly (Fig. 2), not discarding any process a priori, as they are not mutually exclusive (Crisci & Katinas 2009, Sanmartin 2012).
Evolutionary biogeographic methods
There are many biogeographic methods that have been proposed in historical biogeography (see Morrone & Crisci 1995, Crisci et al. 2003). Some of these methods have been considered appropriate for an integrative biogeographic approach (Morrone 2009).

Track analysis: Croizat’s (1958, 1964) panbiogeography emphasizes the spatial or geographic dimension of biodiversity to allow a better understanding of evolutionary patterns and processes (Craw et al. 1999). Its main objective is to identify generalized tracks, which result from the significant superposition of different individual tracks and are typically interpreted as indicating the pre-existence of ancestral biotas that were fragmented by geological or climatic events. Additionally, nodes are detected in the areas where two or more generalized tracks intersect and allow us to speculate on the existence of compound or transition areas (Morrone 2015). A track analysis comprises three successive steps: (1) constructing individual tracks for two or more different taxa by connecting the localities of each taxon according to their geographical proximity; (2) obtaining generalized tracks based on the superposition of two or more individual tracks; and (3) identifying nodes in the areas where two or more generalized tracks intersect. There are several methods that can be applied in track analyses (Crisci et al. 2003, Morrone 2009, 2015).

In evolutionary biogeography, track analysis contributes by identifying generalized tracks, which correspond to ancestral biotas or horobiotas. On the other hand, the identification of nodes allows us to hypothesize on biogeographic convergence due to geodispersal.

Identification of areas of endemism: Areas of endemism are defined as areas of non-random distributional congruence among different species or supraspecific taxa (Morrone 1994). Both historical and ecological factors are invoked when explaining endemism: historical events (usually vicariance) explain how taxa are confined to the areas of endemism, whereas ecological explanations (biotic and abiotic factors) deal with their present limits. There are several methods that can be applied to identify areas of endemism (Crisci et al. 2003, Morrone 2009, Noguera-Urbano 2016).

In evolutionary biogeography, areas of endemism (similarly to generalized tracks) correspond to biotas. In the case where different areas of endemism show partial overlap, they may allow the identification of past events of dispersion or geodispersal.

Cladistic biogeography: This method assumes that there is a correspondence between the phylogenetic relationships of the taxa and the relationships between the areas that they inhabit, considering that if several taxa show the same pattern, such congruence is evidence of a common history (Nelson & Platnick 1981). 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.

There are many cladistic biogeographic methods (Morrone 2009, Ronquist & Sanmartín 2011, Sanmartín 2012, 2016, Arias 2017). These methods are based fundamentally on three different
strategies: (1) methods aimed at finding general patterns: the first classic methods, e.g., component analysis and Brooks parsimony analysis (BPA); (2) event-based methods: those that use deterministic procedures in which the different biogeographic processes are assigned costs; and (3) parametric methods: those that incorporate statistical models, treating the different processes as parameters (Sanmartín 2012, 2016). Preference for either of these strategies is a complex issue that is beyond the scope of this essay.

Identification of cenocrons: After a cladistic biogeographic analysis is done, a temporal perspective may allow the provision of a time framework for the dispersal of cenocrons to a biota (Morrone 2009). This time perspective is based on the information provided by time-slicing, intraspecific phylogeography and molecular dating, in addition to the current distribution of each taxon, the current geographical distribution of its sister-taxon (or related taxa, in case of unresolved phylogenies) and the phylogenetic relationships of the higher taxon to which it belongs (Halffter & Morrone 2017, Roig-Juñent et al. 2018, Morrone 2020).

In evolutionary biogeography, when hypotheses on cenocrons are available for a given area, it is possible to undertake a time-sliced cladistic biogeographic analysis (Corral-Rosas & Morrone 2017). For example, in a case where two cenocrons were incorporated into the biota distributed in a given area, three different time-slices (each corresponding to a different horobiota) may be identified. The oldest time-slice would correspond to the original horobiota. The intermediate time-slice corresponds to the horobiota resulted from the dispersal of the first cenocron and its incorporation along with the original horobiota. The last and most recent time-slice corresponds to the horobiota encompassing the taxa of the original horobiota and the two cenocrons that dispersed to join it. Separate cladistic biogeographic analyses for the different time-slices may help understand how different vicariance events have affected the successive horobiotas.

Identification of long-distance dispersal events: Molecular dating of lineage divergence has allowed the identification of instances where long-distance dispersal is the most plausible explanation (Crisci & Katinas 2009). De Queiroz (2004, 2014) has provided numerous examples of molecular phylogenetic studies that support long-distance dispersal, by showing that the estimated minimum age of a divergence is more recent than the vicariance event, although there are some critics of this assumption (e.g., Heads 2010, 2014, 2017). In evolutionary biogeography, identification of long-distance dispersal events is fundamental to identify the taxa that have achieved their distribution through this process instead of vicariance.

Construction of a geobiotic scenario: Once we have identified the biotas and their cenocrons, as well as the species that dispersed across barriers, we may be able to construct a geobiotic scenario by accounting biological data (means of dispersal, etc.) and non-biological data (past continental configurations, dated geological and paleoclimatic events, etc.). These data allow the biogeographer to integrate a plausible scenario to explain the different episodes of vicariance and dispersal that have shaped biotic assembly (Morrone 2009).

Integrative pluralism
The constitutive complexity of biotas and the complex dynamics of their assembly can benefit from an integrative approach. Current biogeographic patterns are the result of vicariance, dispersal, and extinction, as well as ecological interactions. No single approach can resolve this complexity. Integrative pluralism (Mitchell 2002, 2003) does not imply an eclectic or “anything goes” approach, but that


**Acknowledgements**

I thank Rob Whittaker for inviting me to contribute with this personal perspective and Tim Böhner and Brett Riddle for constructive criticisms of the manuscript.

**References**

Abogast, B.S. & Kenagy, G.J. (2001) Comparative phylogeography as an integrative approach to historical biogeography. Journal of Biogeography, 28, 819-825.
Andersson, L. (1996) An ontological dilemma: epistemology and methodology of historical biogeography. Journal of Biogeography, 23, 269–277.
Arias, J.S. (2017) An event model for phylogenetic biogeography using explicitly geographical ranges. Journal of Biogeography, 44, 2225–2235.
Avise, J.C. (2000) Phylogeography: the history and formation of species. Harvard University Press, Cambridge, Massachusetts, USA.
Corral-Rosas, V. & Morrone, J.J. (2017) Analyzing the assembly of cenocrons in the Mexican Transition Zone through a time-sliced cladistic biogeographic analysis. Australian Systematic Botany, 29, 489–501.
Cowie, R.W. & Holland, B.S. (2006) Dispersal is fundamental to biogeography and the evolution of biodiversity on oceanic islands. Journal of Biogeography, 33, 193–198.
Craw, R.C., Grehan, J.R. & Heads, M.J. (1999) Panbiogeography: tracking the history of life. Oxford Biogeography Series 11, Oxford University Press, New York, USA.
Crisci, J.V., & Katinas, L. (2009) Darwin, historical biogeography, and the importance of overcoming binary opposites. Journal of Biogeography, 36, 1027–1032.
Crisci, J.V., Katinas, L. & Posadas, P. (2003) Historical biogeography: an introduction. Harvard University Press, Cambridge, MA, USA.
Croizat, L. (1958) Panbiogeography or an introductory synthesis of zoogeography, phytogeography and geology: with notes on evolution, systematics, ecology, anthropology, etc. Vol. I - The New World and Vols. IIA and IIB – The Old World. Published by the author, Caracas.
Croizat, L. (1964) Space, time, form: the biological synthesis. Published by the author, Caracas.
Darwin, C.R. (1859) The origin of species by means of natural selection, or, the preservation of favoured races in the struggle for life. John Murray, London, UK.
de Queiroz, A. (2004) The resurrection of oceanic dispersal in historical biogeography. Trends in Ecology and Evolution, 20, 68–73.
de Queiroz, A. (2014) The monkey’s voyage: how improbable journeys shaped the history of life. Basic Books, New York, USA.
de Queiroz, A. (2016) Jurassic primates, immobile ducks and other oddities: a reply to Heads’ review of The monkey’s voyage. Australian Systematic Botany, 29, 403–423.
Fattorini, S. (2016) A history of chorological categories. History and Philosophy of Life Sciences, 38, 1–21.
Ferrari, A. (2017) Biogeographical units matter. Australian Systematic Botany, 30, 391–402.
Ferro, I., Navarro-Sigüenza, A.G. & Morrone, J.J. (2017) Biogeographic transitions in the Sierra Madre Oriental, Mexico, shown by chorological and evolutionary biogeographic affinities of passerine birds (Aves: Passeriformes). Journal of Biogeography, 44, 2145–2160.
Halffter, G. (1987) Biogeography of the montane entomofauna of Mexico and Central America. Annual Review of Entomology, 32, 95–114.
Halffter, G. & Morrone, J.J. (2017) An analytical review of Halffter's Mexican transition zone, and its relevance for evolutionary biogeography, ecology and biogeographical regionalization. Zootaxa, 4226, 1–46.
Halffter, G., Verdú, J.R., Márquez, J. & Moreno, C.E. (2008). Biogeographical analysis of Scarabaeinae and Geotrupinae along a transect in central Mexico (Coleoptera, Scarabaeoidea). Fragmenta Entomologica, 40, 273–322.
Heads, M.J. (2010) Evolution and biogeography of primates: a new model based on molecular phylogenetics, vicariance and plate tectonics. Zoologica Scripta, 39, 107–127.
Heads, M.J. (2014) Biogeography by revelation: investigating a world shaped by miracles. Australian Systematic Botany, 27, 282–304.
Heads, M.J. (2017) Biogeography and evolution in New Zealand. CRC Press, Taylor and Francis Group, Boca Raton, USA.
Lieberman, B.S. (2003) Paleobiogeography: the relevance of fossils to biogeography. Annual Review of Ecology and Systematics, 34, 51–69.
Lieberman, B.S. (2004) Range expansion, extinction, and biogeographic congruence: a deep time perspective. In: Lomolino, M. V. & Heaney, L.R. (eds.), Frontiers of biogeography: new directions in the geography of nature. Sinauer Associates Inc., Sunderland, Massachusetts, pp. 111–124.
Lieberman, B.S. (2005) Geobiology and paleobiogeography: tracking the coevolution of the Earth and its biota. Palaeobiogeography, Palaeoclimatology, Palaeoecology, 219, 23–33.
Lobo, J.M. (1999) Individualismo y adaptación espacial: Un nuevo enfoque para explicar la distribución geográfica de las especies. Boletín de la Sociedad Entomológica Aragonesa, 26, 561–572.
Lobo, J.M. (2007) Los "patrones de dispersión" de la fauna ibérica de Scarabaeinae (Coleoptera). In: Zunino M. & Melic A. (eds.), Escarabajos, diversidad y conservación biológica: Ensayos en homenaje a Gonzalo Halffter, Sociedad Entomológica Aragonesa, Monografías 3er. Milenio M3M, Zaragoza, pp. 159–177.
Lobo, J. M. & Halffter, G. (2000). Biogeographical and ecological factors affecting the altitudinal variation of mountainous communities of coprophagous beetles (Coleoptera: Scarabaeoidea): A comparative study. Annals of the Entomological Society of America, 93, 115–126.
MacArthur, R.H. & Wilson, E.O. (1967). The theory of island biogeography. Princeton University Press, Princeton.
MacDonald, G.M. (2003) Biogeography: space, time, and life. John Wiley & Sons, New York, USA.
McDowall, R.M. (2004) What biogeography is: a place for process. Journal of Biogeography, 31, 345–351.
Merriam-Webster (2020) Merriam-Webster online dictionary. Available from: http://www.merriam-webster.com.
Mitchell, S.D. (2002) Integrative pluralism. Biology and Philosophy, 17, 55–70.
Mitchell, S.D. (2003) Biological complexity and integrative pluralism. Cambridge University Press, Cambridge, UK.
Mitchell, S.D. & Dietrich, M.R. (2006) Integration without unification: an argument for pluralism in the biological sciences. American Naturalist, 168, 573–579.
Morain, S.A. (1984) Systematic and regional biogeography. Van Nostrand Reinhold Company, New York, USA.
Morrone, J.J. (1994) On the identification of areas of endemism. Systematic Biology, 43, 438–441.
Morrone, J.J. (2009) Evolutionary biogeography: an integrative approach with case studies. Columbia University Press, New York, USA.
Morrone, J.J. (2014) On biotas and their names. Systematics and Biodiversity, 12, 386–392.
Morrone, J.J. (2015) Track analysis beyond panbiogeography. Journal of Biogeography, 42, 413–425.
Morrone, J.J. (2020) The Mexican Transition Zone: A natural biogeographic laboratory to study biotic assembly. Springer, Cham.
Morrone, J.J. & Crisci, J.V. (1995) Historical biogeography: introduction to methods. Annual Review of Ecology and Systematics, 26, 373–401.
Morrone, J. J. & Escalante, T. (2016) Introducción a la biogeografía. Las Prensas de Ciencias, UNAM, Mexico City, Mexico.
Myers, A.A. & Giller, P.S. (1988) Biogeographic patterns. In: Myers, A.A. & Giller, P.S. (eds.), Analytical biogeography: An integrated approach to the study of animal and plant distributions, Chapman and Hall, London and New York, pp. 15–21.

Nelson, G. & Platnick, N.I. (1981) Systematics and biogeography: cladistics and vicariance. Columbia University Press, New York, USA.

Noguera-Urbano, E. A. (2016) Areas of endemism: travelling through space and the unexplored dimension. Systematics and Biodiversity, 14, 131–139.

Parenti, L.R. & Ebach, M.C. (2009) Comparative biogeography: discovering and classifying biogeographical patterns of a dynamic Earth. University of California Press, Berkeley and Los Angeles, USA.

Passalacqua, N.G. (2015) On the definition of element, chorotype and component in biogeography. Journal of Biogeography, 42, 611–618.

Platnick, N.I. (1981) Widespread taxa and biogeographic congruence. In: Funk, V.A. & Brooks, D.R. (eds.), Advances in cladistics: Proceedings of the First Meeting of the Willi Hennig Society. New York Botanical Garden, Bronx, New York, USA pp. 223–227.

Reig, O.A. (1962) Las integraciones cenogenéticas en el desarrollo de la fauna de vertebrados tetrápodos de América del Sur. Ameghiniana, 2, 131–140.

Reig, O.A. (1981) Teoría del origen y desarrollo de la fauna de mamíferos de América del Sur. Museo Municipal de Ciencias Naturales Lorenzo Scaglia, Mar del Plata, Argentina.

Riddle, B.R. (2005) Is biogeography emerging from its identity crisis? Journal of Biogeography, 32, 185–186.

Riddle, B.R. & Hafner, D.J. (2006) A step-wise approach to integrating phylogeographic and phylogenetic biogeographic perspectives on the history of a core North American warm deserts biota. Journal of Arid Environments, 66, 435–461.

Roig-Juñent, S.A., Griotti, M., Domínguez, M.C., Agrain, F.A., Campos-Soldini, P., Carrara, R., Cheli, G., Fernández-Campón, F., Flores, G.E., Katinas, L., Muzón, J.R., Neita-Moreno, J.C., Pessacq, P., San Blas, G., Scheibler, E.E. & Crisci, J.V. (2018) The Patagonian Steppe biogeographic province: Andean region or South American transition zone? Zoologica Scripta, 47, 623–629.

Ronquist, F. & Sanmartín, I. (2011) Phylogenetic methods in biogeography. Annual Review of Ecology, Evolution and Systematics, 42, 441–464.

Sanmartín, I. (2012) Historical biogeography: evolution in time and space. Evolutionary Education Outreach, 5, 555–568.

Sanmartín, I. (2016) Breaking the chains of parsimony: the development of parametric methods in historical biogeography. In: Cox, C.B., Moore, P.D. & Ladle, R.J. Biogeography: an ecological and evolutionary approach, 9th ed. John Wiley and Sons, Ltd., Chichester, UK, pp. 241–245.

Santos, C.M.D. & Amorim, D.S.. (2007) Why biogeographical hypotheses need a well-supported phylogenetic framework: a conceptual evaluation. Papéis Avulsos de Zoologia, 47, 63–73.

Savage, J.M. (1982) The enigma of the Central American herpetofauna: dispersals or vicariance? Annals of the Missouri Botanical Garden, 69, 464–547.

Slater, M.H. & Borghini, A. (2011) Introduction: lessons from the scientific butchery. In: Campbell, J.K., O’Rourke, M. & Slater, M.H. (eds.), Carving nature at its joints: natural kinds on metaphysics and science, The MIT Press, Cambridge, Massachusetts, USA, pp. 1–31.

Taberlet, P., Fumagalli, L., Wust-Saucy, A.G. & Cossin, J.F. (1998). Comparative phylogeography and postglacial colonization routes in Europe. Molecular Ecology, 7, 453-464.

Wallace, A.R. (1876) The geographical distribution of animals, with a study of the relations of living
and extinct faunas as elucidating the past changes of the Earth’s surface. Macmillan and Company, London, UK.

Weeks, B.C., Claramunt, S. & Cracraft, J. (2016) Integrating systematics and biogeography to disentangle the roles of history and ecology in biotic assembly. Journal of Biogeography, 43, 1546–1559.

Whittaker, R.J. & Fernández-Palacios, J.M. (2007) Island biogeography: ecology, evolution, and conservation, 2nd edn. Oxford University Press, Oxford, UK.

Wilkinson, D.M. (2003) Dispersal, cladistics and the nature of biogeography. Journal of Biogeography, 30, 1779–1780.

Zink, R.M. (2002) Methods in comparative phylogeography, and their application to studying evolution in the North American aridlands. Integrative and Comparative Biology, 42, 953-959.

Submitted: 19 June 2020
First decision: 20 July 2020
Accepted: 23 July 2020

Edited by Robert J. Whittaker