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Biotic assembly in evolutionary biogeography: a case for integrative pluralism

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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 (Avice 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

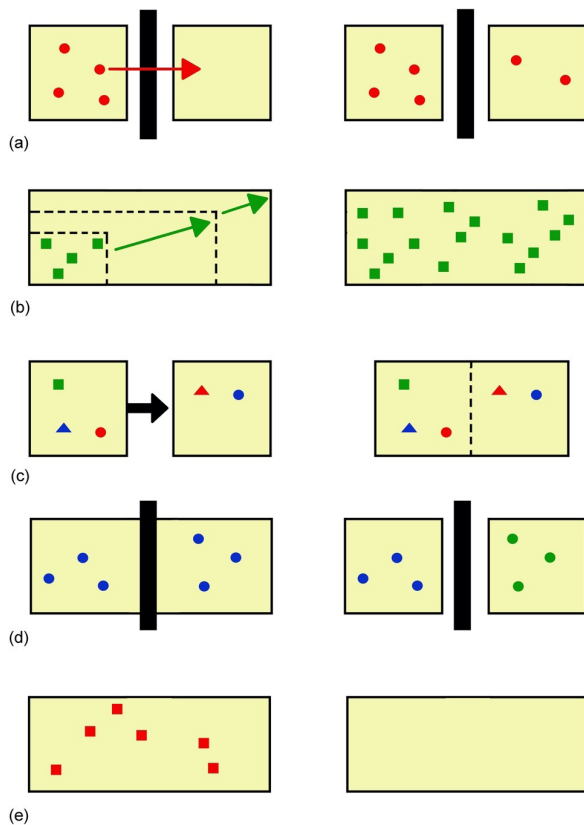


Fig. 1. Biogeographic processes: dispersal, vicariance and extinction. (a) Long-distance dispersal; (b) dispersion or range expansion; (c) geodispersal or biotic dispersal; (d) vicariance; (e) extinction.

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 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, Sanmartín 2012).

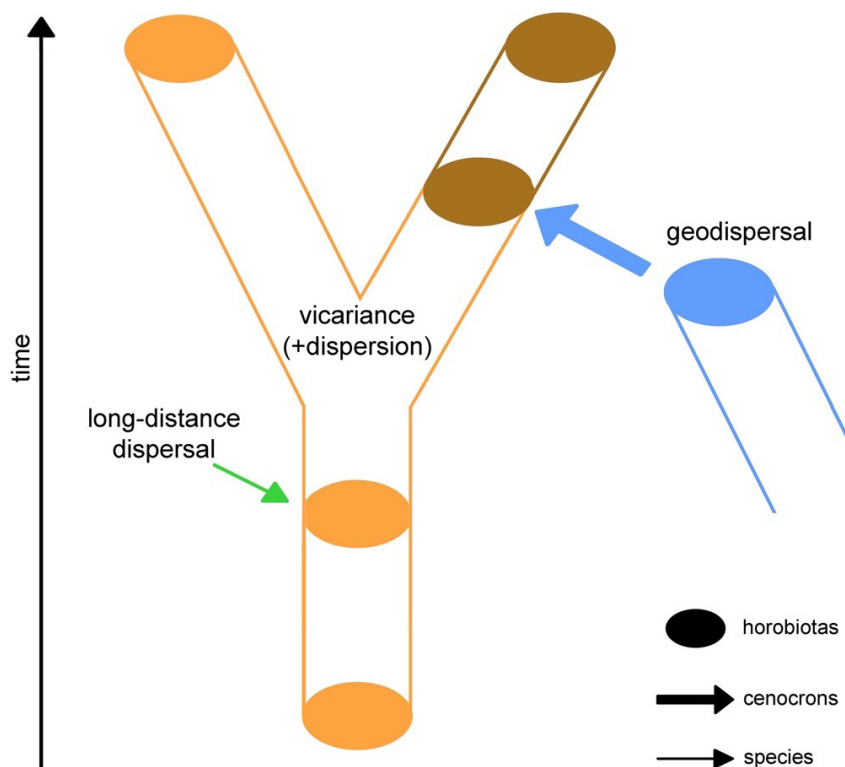


Fig. 2. Graphical representation of biotic assembly under a dispersal-vicariance model. Horobiotas are shaped by dispersal and vicariance, where dispersal includes long-distance dispersal of particular species and geodispersal of cenocrons, and dispersion is implicit in vicariance.

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 different methods may be compatible because they give partial solutions when answering particular questions. This perspective allows for integration to explain a complex phenomenon such as biotic assembly, without the need for unification on a large scale (Mitchell & Dietrich 2006). This means that different biogeographic traditions or approaches can fruitfully collaborate, each one addressing particular questions and applying its methods, without being unified into a single synthetic approach. Santos & Amorim (2007) have already noted that a synthetic “recipe” is not a solution for analyzing these complex phenomena, and that integrating different approaches and methods is most appropriate. Crisci & Katinas (2009) have concluded that both the practice and philosophy of historical biogeography depend on a coherent conceptual framework. I think that integrating diverse processes and concepts in a step-wise evolutionary biogeographic approach provides such a framework.

De Queiroz (2016) recently postulated that biotic assembly of islands is more complex than what simplistic models have previously assumed. The biotas of ancient continental islands, such as New Zealand and Madagascar, typically include some lineages that reflect ancient vicariance events, although they seem to be dominated by lineages that arrived by long-distance over-water dispersal, and that several oceanic island radiations seem to predate the current islands, indicating the colonization of prior land in the area. Also, he highlighted that some bird taxa seem to be more constrained by ocean barriers than one might expect and their disjunctions are often a result of vicariance, whereas amphibians have been unexpectedly effective at crossing sea barriers, and some reptiles have apparently crossed oceans on numerous occasions. De Queiroz (2016) concluded that plausible explanations for the distributions of widespread groups involve a combination of vicariance and long-distance dispersal, which are difficult to explain by either a pure vicariance or a pure long-distance dispersal scenario.

In addition to evolutionary biogeography, an integrative perspective may also be applied to analyze ecological biogeographic aspects of biotic assembly (Lobo 1999, 2007, Halffter & Morrone 2017). It is increasingly recognized that the dichotomy between ecological and historical biogeography does not track all the patterns and processes that are relevant for biogeography (Riddle, 2005). For example, studies of elevational variation in richness and composition in mountain biotas show different biotic assemblages at different elevations, and when these assemblages are deconstructed into their cenocrons, the patterns become clearer than when all species are analyzed together (Lobo & Halffter 2000, Halffter et al. 2008, Ferro et al. 2017). Some authors have suggested that some adaptations of the taxa belonging to a cenocron may have been acquired by their ancestors in the areas where they originally evolved, and some of these adaptations may be relevant when explaining their current distribution (Lobo 1999, Halffter & Morrone 2017).

I hope that in the future this step towards an integrative biogeography is followed by other authors. As I have tried to show empirically with the analysis of the biotic assembly of the Mexican Transition Zone (Morrone 2020), different biogeographic approaches or traditions can be brought together when addressing complex biogeographic problems. I sincerely feel that restricting our analyses to simplistic models is not an adequate strategy to solve complex issues as biotic assembly, and I urge biogeographers to consider the possibilities of collaborating in integrative biogeographic projects.

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