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Are Historical Biogeographical Events Able to Promote Biological Diversification?

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<http://dx.doi.org/10.5772/intechopen.69516>

Abstract

One of the goals of evolutionary biology is understanding how biological diversification change across spatial and temporal scales. Theoretically, it has been established that external (i.e., dispersals) and internal (i.e., origin of a key innovations) factors can modulate shifts in rates of species diversification. However, the role of historical events as trigger of species diversification rates have not been well understood in empirical studies. I reviewed the literature linking historical biogeographic events and species diversification in many groups. Many of studies conclude that dispersals can be associated with exceptional changes in species diversification rates in insular and mainland areas. I discuss the limitations of some approaches used to discover the link between historical biogeography and macroevolution. I propose some predictions under biogeographic scenarios to gain understanding in how historical events promote biological diversification. I suggest that future studies linking biogeography and macroevolution should incorporate ecologically-relevant traits to discern the mechanisms underlying these historical associations. Although new developments in phylogenetic comparative methods have been done, still is necessary more traditional field-based ecological and evolutionary research. The link between biogeography and diversification still remains narrative and a comprehensive approach is necessary to establish how diversification was triggered by historical events.

Keywords: dispersal, vicariance, ecological opportunity, macroevolution, event-based biogeography

1. Introduction

One the main goals of evolutionary biology is to understand why lineages exhibit differences in species diversification, understood as the difference between speciation and extinction rates

in a clade. Three competing hypotheses explain differences in species between clades and geographic regions [10, 51, 69]. The first hypothesis, known as the unbounded hypothesis, proposes that speciation and extinction processes are controlled only by time and diversity is not limited by any ecological process [69]. The second hypothesis, known as the bounded hypothesis, states that diversity reaches a limit imposed by the number of competing coexisting species [51, 52]. And a third recently proposed hypothesis, known as the damped hypothesis [10], states that diversity increases without limit and ecological factors constrain speciation and extinction rates.

The understanding of the historical and ecological circumstances where diversification dynamics occur is key to establish whether diversity is limited or not. Therefore, historical events as dispersals can be associated with shifts in species diversification [40]. However, the mechanisms underlying this association remains elusive for many taxa. For instance, for plant clade Dipsacales, it was found that some increases in species diversification rates were associated with dispersal to new geographic areas [40, 41]. Similarly, in Caribbean Anole lizards, it was found that diversification increases occurred after a lineage colonized an island above a certain island size [30, 50]. These two examples show how diversification dynamics can be linked with historical events and suggest also that macroevolutionary dynamics should be explicitly tested in a historical biogeography context.

With the aim to have a comprehensive understanding of the link between historical biogeography and species diversification, it is necessary to consider which ecological or evolutionary mechanisms were involved in this association. Ecological mechanisms can explain how diversification dynamics take place in a region after a biogeographical event. They also offer a conceptual bridge between historical and ecological biogeography. I assert that historical biogeography events (dispersal and vicariance) can promote biological diversification under some specific ecological and evolutionary mechanisms. For instances, some studies have found that some clades diversified through ecological opportunity [28, 33], biotic interactions [63], and/or climate change [26, 65]). The integration of ecological, phylogenetic, and biogeographic approaches in a comprehensive framework is key to understand why some clades diversify extensively when reach some regions and not others.

Here, I conduct a review of studies evaluating the link between biogeographical events and biological diversification. For biogeographical events, I refer mainly to dispersal and vicariance, which have been considered as competing hypotheses in historical biogeography for many years [45, 60]. Dispersal refers to movements of a lineage to a new region across a geographical (or ecological) barrier. Vicariance refers to the fragmentation of an ancestral geographical range and the emergence of geographical (or ecological) barriers. Here, I first discuss how these two biogeographical events can promote shifts in species diversification (e.g., increases in speciation rates or decreases in extinction rates) or diversification dynamics (from time-dependent to density-dependent cladogenesis). Also, I discuss some limitations of methods used to discover this historical link. I establish some basic specific predictions about the expected evolutionary trajectories of ecologically relevant traits under a dispersal or vicariance scenario and how these predictions might be tested using phylogenetic comparative methods. Finally, I provide some possible avenues for an integration of

ecological and evolutionary studies with historical biogeography within an explicit modern phylogenetic comparative framework.

2. Materials and methods

I conducted a literature search in Web of Science using the keywords as *dispersal*, *vicariance*, *species diversification*, and *biogeography* during the last 14 years (2002–2016). I selected only those studies that used statistical biogeographical methods to reconstruct ancestral areas in an explicit phylogenetic context (~80 studies). I select those studies where (or at least it was tested) a historical link between past biogeographical events and shifts in diversification dynamics was explicit. Although this review is not exhaustive, my aim here is to discuss some limitations and opportunities of current methods used to study biogeography and diversification.

3. Results and discussion

3.1. Historical associations between biogeography and diversification

Many studies identified that past biogeographic movements (i.e., dispersals) between regions acted as a trigger for species diversification. This recent tendency to identify dispersals as drivers of biological diversification have increased with time (**Figure 1**). This tendency is related with the growing recognition of dispersal not only as a process able to generate congruent distributional patterns [11, 49, 61, 72], but also as a driver of species diversification [41]. It seems that the traditional and senseless dispute about whether vicariance or dispersal explains biotic distribution is a thing of the past [34, 49]. Both biogeographical events contribute to explain current and past geographic distributions and explain how biodiversity evolved in some regions. Accordingly, it is necessary to evaluate simultaneously which of these events were more prevalent through the biogeographic history of a taxa.

Theoretically, dispersal can promote exceptional shifts in species diversification by ecological opportunity (e.g., absence of related competitors) in a new colonized region or climate regime [1, 32, 33, 71, 73]. When lineages disperse to these new selective regimes they are likely to experience ecological release that can promote increases in speciation rates [33, 73]. Ecological opportunity can facilitate changes in diversification dynamics after a dispersal event [33, 73]. This is partially supported by evidence showing that dispersal events did not occur randomly across geography, and for some groups colonizing islands it was a notable increase in speciation rates after that events [4, 16, 21, 56, 57, 61]. For instance, dispersal of the palm tribe Trachycarpeae to different island systems promoted parallel diversifications connected with climatic and geological changes [4]. For bird clades distributed in the Indo-Pacific archipelago, species diversification rates increased on islands where few dispersal events were inferred, whereas clades occupying islands with high immigration rates exhibited constancy in diversification rates [16]. In the case

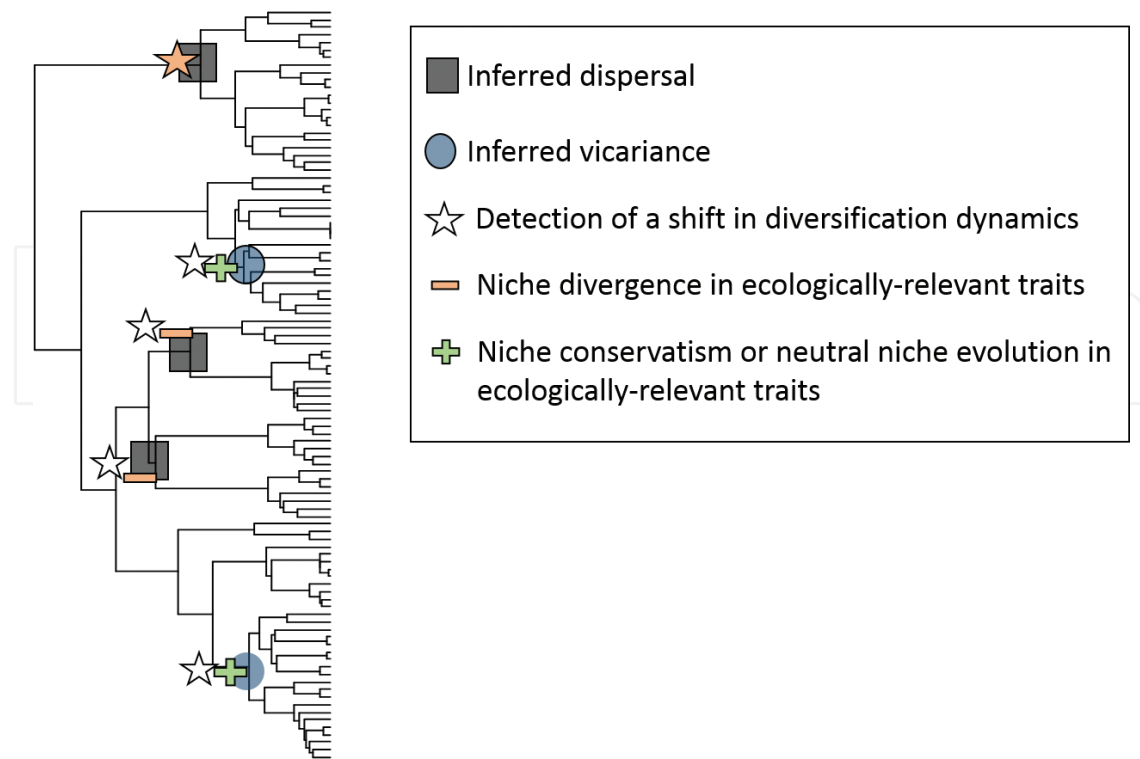


Figure 1. A hypothetical example showing inference of dispersal and vicariance and shifts in diversification dynamics across the phylogenetic diversification of a taxa. Nodes labeled with circles denote the position in the tree where it was inferred a dispersal (square) or a vicariance event (circles). Nodes labeled with stars denote where shifts in macroevolutionary regimes occurred. These shifts might involve increase in speciation rates or decrease in extinction rates or shifts in diversification dynamics from a time-dependent process to diversity-dependent cladogenesis (star). Under a dispersal scenario, where a lineage colonizes a new region with ecological opportunity, it is expected that ecologically relevant traits evolved through a pattern of niche divergence (dash). Whether all dispersal events promote speciation through ecological opportunity, it is expected that all events generated the same pattern of niche-trait divergence. By contrast, in a vicariance event, where the emergence of geographical barriers (e.g., a mountain uplift) promotes allopatric speciation, it is expected that ecologically relevant traits evolved little (i.e., phylogenetic niche conservatism) or under a neutral (drift) process in response to the changing environment (cross). Similarly, it is expected that all vicariant events generated the same pattern of niche conservatism or neutral evolution. Many other dispersal or vicariance events can be nested in the phylogeny; therefore, the inference of an event does not preclude that subsequent speciation events occur in sympatry or allopatry.

of Malagasy vangids, early dispersal from Africa to Madagascar promoted an increase in species diversification rates by ecological opportunity followed by a decline through time suggesting an ecological limit for this adaptive radiation [57].

Although these studies suggest a historical association between one or several dispersal events and shifts in net species diversification rates, it is still not clear which mechanisms were involved in this link between biogeography and macroevolution. Even more, it is not clear exactly how these past biogeographic events facilitate speciation in some regions and not in others or the mode of speciation involved in each event.

In contrast to the role of dispersal, vicariance has been associated as the only valid explanation for current distributional patterns and speciation for traditional biogeographers (e.g., Refs. [23, 45, 46]). However, few studies reviewed identified a vicariance event as a trigger of species diversification. Although these associations are congruent with the hypothesis of speciation

by vicariance [38], it is still unknown whether the emergence of geographical barriers promoted habitat and reproductive isolation in taxa examined. For instance, rapid Andean uplift during the Miocene, with the concomitant climate changes, likely promoted allopatric speciation in *Heliotropium* plant lineages, which adapted to new arid conditions in southern South America [31]. Similarly, the Miocene uplift of the Qinghai-Tibetan plateau promoted allopatric speciation in Asteraceae clades plants [27] and *Rheum* plants [66]. These two clades of plants evolved as a response of temperature changes and the apparition of dry habitat conditions. It is likely that climate changes facilitated bursts of diversification [19, 27, 66]. Again, although these studies show an association between vicariance and species diversification, likely mediated through climate change or emergence of new barriers, it is not clear which mechanisms were involved here. All these studies suggest that we lack the ecological and evolutionary processes in these narrative biogeographic studies and we should look forward to identify at least which main processes underlying these historical associations.

It is evident that dispersal and vicariance events can be associated, either in a narrative or quantitative way, with shifts in species diversification. The link can be inferred directly in some cases [4, 41]; however, again the mechanisms operating behind these events are unknown. Although it is necessary to identify these evolutionary or ecological mechanisms, it is still not clear how these mechanisms can be disentangled. I consider that a full integration of current phylogenetic comparative methods with modern parametrical biogeographical methods and incorporation of ecologically relevant traits might offer new avenues to understand how biodiversity was generated after dispersal or vicariance events.

3.2. Limitations of current methods to link historical events with biological diversification

Some studies only provide a weak evidence of a consistent link between historical biogeographical events and shifts in species diversification rates. In particular, these few studies did not test whether dispersal or vicariance events effectively generated increases in net species diversification rates (e.g., Refs. [4, 7, 9, 68]). For instance, Chaves et al. [9] suggested that Andean uplift promoted increases in species diversification in the *Adelomyia* hummingbird genus. However, they only provide a correlation between divergence times for *Adelomyia* clades with some phases of the Andean uplift. Here, it is necessary to test whether Andean clades diversified more than other clades or the entire group. Accordingly, it is possible to suggest with higher confidence that dispersal to the Andes promoted posterior cladogenesis likely through allopatric speciation.

The link between historical biogeography and species diversification need to be explicitly tested using a two-step framework. First, it is necessary to infer historical biogeographic events with a higher confidence using powerful statistical methods [34]. These methods are ideal to identify rare dispersal events (founder-event speciation; [34]) and allow us to incorporate explicit geological information (e.g., timing of emergence of island landmasses; see Ref. [48] for an example using Caribbean *Anolis* lizards). Many empirical datasets show that founder-event speciation have left a strong imprint on distributional patterns of many taxa [34]. However, it is necessary to develop more complex models allowing the possibility to incorporate life-history traits and how these traits can affect rates of dispersal between regions (e.g., Ref. [35]). After the historical inference is conducted, it is crucial to identify

whether these same nodes where a dispersal or vicariance event was inferred exhibit a notable shift in diversification dynamics [2, 3, 66].

Several methods allow to detect specific shifts in diversification dynamics in phylogenies, particularly increases in diversification rates [36, 37, 43, 53, 54]. These methods can be divided into temporal or topological methods, depending on the phylogenetic dataset at hand [43]. These methods also allow us to identify shifts in macroevolutionary regimes (i.e., shifts in diversification process; e.g., bayesian analysis of macroevolutionary mixtures (BAMM) approach developed by [53]; but see Ref. [42] for a criticism about the statistical power). However, these phylogenetic methods are not integrated fully with methods of historical biogeographic inference. Therefore, the association between dispersal or vicariance events and notable shifts in species diversification or diversification dynamics remains narrative [23]. Therefore, new methodologies are necessary to establish with more confidence whether these biogeographical events promote changes in biological diversification. Even more, it is possible that unmeasured traits (e.g., a “hidden” key innovation) affecting speciation and/or extinction rates evolve in the same nodes of a phylogenetic tree where a dispersal or vicariance event was inferred. In these cases, it might be very hard to distinguish whether diversification was affected by the presence (or absence) of a trait or by the movement to a new region (see Ref. [75]).

More robust methods to link historical biogeography and macroevolution are necessary. However, these new phylogenetic methods only can detect these historical associations, but these are very limited to establish the potential ecological or evolutionary process underlying this association. I consider that an integration of ecological studies (including testable predictions of trait-niche evolution) with a historical biogeographic approach will be useful to discern these mechanisms promoting speciation. The association between a biogeographic event and shifts in macroevolutionary dynamics is not enough to understand how biodiversity was generated in many regions. For instance, it has been found in warblers (*Phylloscopus*) that habitat isolation was the first form of niche differentiation to evolve in sympatry, followed by prey-size selection and feeding strategies [74]. It will be important to evaluate whether lineages diversifying after a dispersal event exhibit more niche differentiation [47] than lineages diversifying after a vicariant event. This can help to establish whether the initial trigger of speciation in a lineage was the colonization of a new region and the subsequent habitat isolation in sympatry [12, 13].

3.3. Is it possible to predict some ecological scenarios after a historical biogeographic event?

The ecological and evolutionary processes underlying the historical association between biogeography and diversification have been seldom discussed in the literature. Here, I propose that these contrasting historical events have left different imprints on the lineage diversification of taxa through its evolutionary history.

In a dispersal scenario, some lineages exposed to new ecological conditions (or ecological opportunity) likely experienced rapid diversification and rapid ecological divergence [18, 62, 64, 73]. In these cases, it is assumed that lineages evolved quickly by mechanisms of divergent selection due to ecological release and therefore occurs an increase in species diversification rates with ecological divergence. However, it is still not clear whether

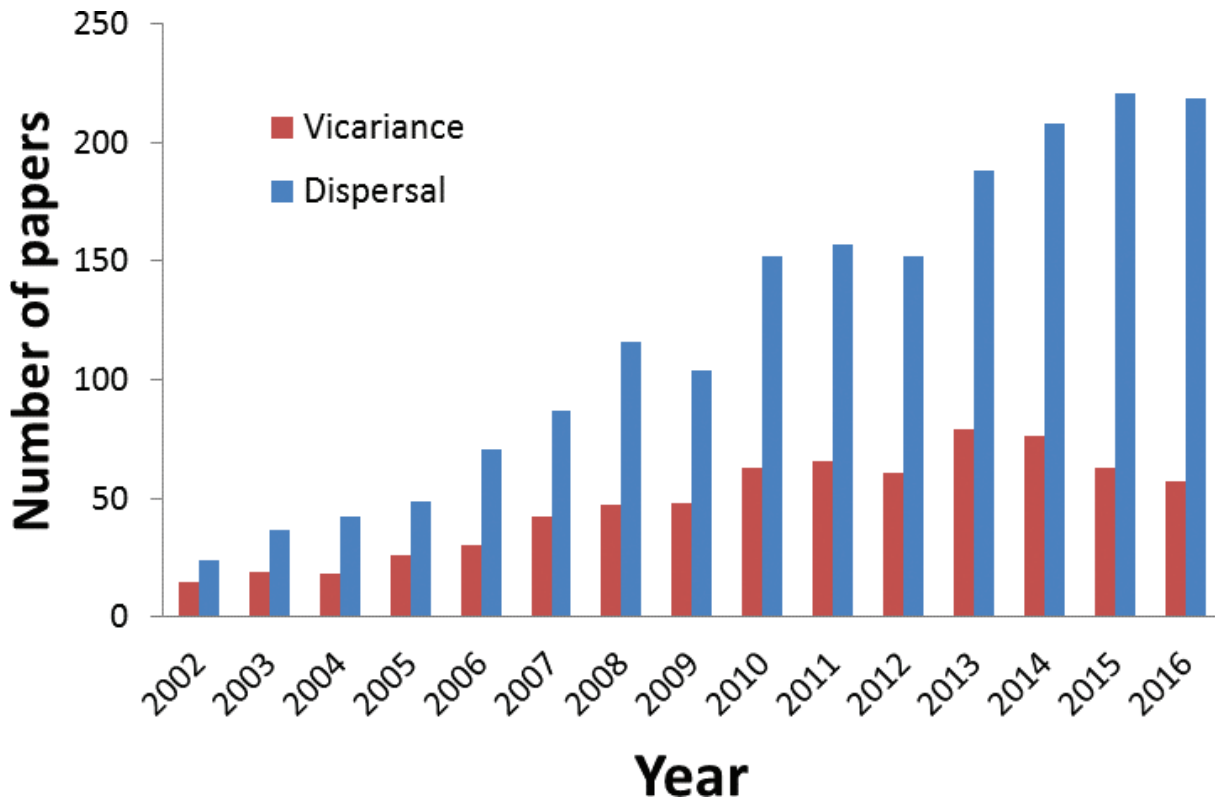


Figure 2. Number of papers published by year identifying dispersal or vicariance events as drivers of species diversification.

ecological or behavioral isolation occurred after the first lineage dispersed to a new region or speciation is driven by vicariance in the new colonized region (e.g., posterior mountain uplift in some islands or regions). Here, it is necessary to test whether a dispersal scenario promotes diversification in a similar fashion and therefore it is crucial to evaluate how species niche-traits evolved after a dispersal event. The colonization of a new region could not be the initial precursor of a change in macroevolutionary dynamics (e.g., increases in speciation rates) and other processes might be obscured here (e.g., reproductive isolation between ecologically diverging subpopulations inhabiting in sympatry [76]) (**Figure 2**).

By contrast, in a vicariance scenario I expected that all species diversification processes occur through allopatric divergence. In this scenario, new species emerge through geographical isolation of populations of a widespread ancestral species [12, 39]. Some studies reviewed here suggest that mountain uplift can generate a spatial gradient of climatic or ecological conditions that promote range subdivision and therefore allopatric speciation [5, 31]. However, still we do not know whether the mechanisms involved here will be different from a dispersal scenario. For instance, it is very well-known that ecological divergence between subpopulations is not a prerequisite for allopatric speciation. Therefore, species might acquire ecological niche differentiation by a pure genetic drift process [6] or species can exhibit strong niche stasis through time [26, 70]. Therefore, to establish whether vicariance effectively promote species diversification, it is crucial to test whether species evolved trait-niches through a pure drift process or maintain ancestral trait-niches due to stabilizing selection [6, 26, 70] (**Figure 2**).

In addition to this, climate change might act as a trigger of species diversification after a dispersal or vicariance event. For instance, many Neotropical diversification have been attributed to quaternary climatic cycles [77], where cooling phases in the Amazon basin facilitated geographic spread of highland species toward lowlands with subsequent range fragmentation and isolation during warm phases [77–79]. In the context of studies linking biogeographical events and diversification, very few studies have been able to detect a positive correlation between past climatic changes and species (or phenotypic) diversification after a given dispersal or vicariance event. For instance, Gamble et al. [80] suggested that main events of cladogenesis in *Gonatodes* geckos coincided with a phase of climate cooling in the late Eocene and Oligocene. In addition, Antonelli et al. [81] suggested that speciation in an orchid South American group was accelerated by climate cooling after the Middle Miocene Climatic Optimum, 15 million years ago. However, these two studies did not evaluate whether specific shifts in net diversification rates matched temporally with significant decreases in temperature (i.e., cooling) in each region. Although these two studies suggest that climate change might be a trigger of species diversification, they did not mention how cladogenesis can be affected by climate changes, particularly cooling phases. The link between climate change and diversification is still narrative and more research is necessary to establish first whether there is possibility to find a positive association between both phenomena and then to establish the mechanisms driving speciation by climate change oscillations. For the first part, some recently developed models are able to detect whether paleo-environmental variations (e.g., temperature fluctuations through Cenozoic; [82]) had a significant effect on speciation and extinction rates [43, 83, 84]. These new models allow to establish whether the association is strong and how effectively climate can influence speciation and extinction rates for many groups [85].

Summarizing, both dispersal and vicariance scenarios can promote shifts in net species diversification rates in contrasting ways. In dispersal scenarios, it is expected as an early ecological niche differentiation through the lineage diversification of co-occurring species, as has been the case in Caribbean *Anolis* lizards [29] and Hawaiian spiders [17]. In vicariance scenarios, it is expected, that co-occurring species exhibit ecological niche conservatism in trait-niche axes, either in coarse-grain or fine-grain scales, or that these trait-niches likely evolved by a purely drift process. If ecological niche conservatism prevails after allopatric speciation, it is merely a by-product of the ancestral range fragmentation and therefore it is not possible that it promotes speciation (*contra* [25]). Otherwise, if there is some degree of niche differentiation between species this is likely due to either neutral evolution [6] or adaptation to a slowly changing environment [22]. The distinction between these two patterns (i.e., neutral versus adaptive niche evolution) will be crucial although it can be difficult to be detected using only phylogenetic comparative methods [44]. Furthermore, it is very likely that other ecological or non-ecological processes facilitating speciation occur in each one of these biogeographic scenarios [12]. This suggests that reproductive isolation between subpopulations as by-product of these processes (e.g., polyploidization, hybridization, and genetic drift) is not necessarily driven by historical dispersal or vicariance events. In addition, it is important to remember that inferring an early dispersal event (or vicariance) does not preclude that subsequent cladogenesis occurred by a successive series of vicariance events (or dispersals). For instance,

a lineage colonized an oceanic island early in its evolutionary history, but the cladogenetic process that generated *in situ* diversity was driven by successive mountain uplifts.

3.4. Integration of a historical biogeography perspective with modern phylogenetic approaches and ecological studies

An integration of evidence from multiple study fields is necessary to get a deep understanding about the underlying mechanisms of the link between historical biogeography and diversification. Therefore, it will be crucial to develop and integrate new methodological approaches to generate sound evidence of a link between historical biogeographic events and changes in macroevolutionary dynamics. I consider that the first step necessary is to adopt a phylogenetic perspective to study the historical biogeography of a taxa and infer dispersal or vicariance events through its evolutionary history. Many studies reviewed have adopted such perspective, particularly implementing more complex event-based methods [60, 61]. New statistical biogeographical methods incorporating increasingly complex models of range evolution are being developed [34, 58]. The next step is to develop increasingly statistical robust methods to detect shifts in diversification dynamics and evaluate whether these shifts coincide with past dispersal or vicariance events and are not confounded by the emergence of hidden innovation key traits [53, 75]. Although there is a current debate about the power of these methods to detect these shifts [42, 53, 55], the BAMM approach ([53]) seems promising to detect these shifts in diversification dynamics across a phylogenetic tree with high confidence. BAMM allows us not only to detect shifts in speciation rates but shifts in the diversification dynamics itself. For instance, BAMM could allow us to detect in which nodes the diversification dynamics follows a time-dependent process, where only the time for speciation influences speciation rates [69]; or whether it follows a density-dependent cladogenetic process, where the clade diversity is limited by a carrying capacity [51]. Even more, using BAMM we could establish whether a macroevolutionary regime is more prone to occur.

In addition to the statistical detection of these historical associations, I suggest that it is necessary to test the specific predictions that might emerge from each biogeographical scenario. I outlined two specific predictions for phenotypic trait evolutionary trajectories after a dispersal or vicariance event (see above). In that case, it is necessary to collect information about ecologically relevant traits for species to test these predictions. This information can be collected from museum specimens (e.g., morphological traits) or field-based studies (e.g., habitat use, diet or foraging strategy). Using model-based phylogenetic comparative methods, it is possible to evaluate whether these traits evolved following a Brownian motion or Ornstein-Uhlenbeck model [20] or whether traits evolved under a pure drift process lacking its phylogenetic signal (e.g., a white-noise process [20]). Furthermore, recently developed methods allow to identify shifts in phenotypic trait diversification in nodes of a phylogenetic tree [14, 15, 53, 59, 67]. In these cases, it is possible to evaluate simultaneously whether specific shifts in species or trait diversification evolved as a response to a dispersal or vicariance event. I consider that testing these predictions allows us to establish potential ecological and evolutionary mechanisms driving biological diversity. Some recent studies have begun to adopt a combination of these new methodologies (e.g., Ref. [24]), but still more research is necessary.

Finally, studies undoubtedly need to include detailed research from the field of the genetics of the adaptation to new environments [8, 22]. These studies are useful to understand why some clades diversified extensively after a dispersal or vicariance events and others not. For instance, species widely distributed in archipelagos or species with disjunct distributions will be good candidates for these detailed studies. Information about mechanisms maintaining or disrupting genetic cohesion between populations or lineages is crucial to understand the role of biogeographical events in the generation of biodiversity.

4. Conclusions

There is a growing interest in establishing the historical causes of biological diversification phenomena. However, we are still far behind to understand the process and mechanisms generating this realized diversification. In this chapter, I discussed some limitations of current methodologies employed to infer how biogeographical events as dispersal and vicariance can promote biological diversification shifts across the evolutionary history of lineages. The majority of studies reviewed here only were able to detect a historical association between a given biogeographic event and shifts in species (or phenotypic) diversification. Although we have established that spatial and temporal changes in diversification rates are modulated by abiotic (e.g., geography and climate) and biotic factors (e.g., food availability, predator presences, and intensity), still there is a lack of understanding about specific mechanisms underlying these historical associations and what factors were important. Furthermore, I have showed that the inference of these historical associations is not a trivial matter and more robust methodologies are necessary to establish a joint inference of biogeographical events and shifts in species diversification. In addition, I outlined specific predictions for evolutionary outcomes after a given biogeographical event which can be tested using current phylogenetic comparative methods and ecologically relevant traits. However, the adoption of phylogenetic methodological approaches will not be sufficient to generate a complete understanding of how species radiated after a given dispersal or vicariance event. Accordingly, traditional ecological and genetic field-based approaches used in speciation studies will be important here.

Acknowledgements

Funding was provided by a graduate scholarship grant from CONACYT and a postdoctoral research grant from DGAPA at Universidad Nacional Autónoma de México (UNAM). My ideas about biogeography and diversification were greatly benefited from discussions with Enrique Martinez Meyer, Oscar Flores Villela, Luna Sanchez Reyes and Mark. E. Olson. Thanks to Mark E. Olson to read several draft versions of this manuscript and for his continuous thoughtful comments. All remaining errors are my own.

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