On the role of biogeography in the Extended Evolutionary Synthesis

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ABSTRACT

In the first half of the 20th century, the Modern Synthesis (MS) integrated Mendelian genetics, paleontology, systematics, natural history, common descent, and natural selection. Although the MS has been the guiding paradigm of evolutionary studies since 1950, by the beginning of the 21st century, a new synthesis incorporated themes such as evo-devo, phenotypic plasticity, and epigenetic inheritance. This research program, known as the Extended Evolutionary Synthesis (EES), emphasizes processes and mechanisms rather than pattern analysis, and the relevance of the spatial or geographic component for the origin and diversification of organisms is virtually absent. As Croizat argued in 1964, evolution means change over time and space. Thus, an EES encompassing an integrated view of the historical process of evolution should include biogeography. Here, we explore the role of biogeography in the EES. Our proposal is based on an integrative, pluralistic approach to biogeography that combines theories, models, methods, and data-collection techniques to best explain the complex phenomenon of life evolving in space and time. In this context, given biogeographical reciprocal illumination, we reinforce the importance of biogeographical consilience as an evaluation criterion for biogeographic hypotheses.

Keywords: consilience, Croizat, evolution, pattern analysis, reciprocal illumination.

1. Introduction

Biogeography describes patterns, processes, and mechanisms that shape the distribution of taxa and their attributes on Earth. It has a long and intricate intellectual heritage (for reviews, see Nelson and Platnick 1981; Humphries and Parenti 1999; Nelson and Ladiges 2001; Crisci et al. 2003; Ebach 2015; Morrone 2021, 2022a). The aim of biogeography is broad enough to encompass almost the whole field of comparative biology, given that life is a three-dimensional phenomenon of form changing through time and space (Croizat 1964).

Due to its intrinsic complexity, biogeography is still seeking its place among the biological sciences (Ebach 2015; Sluys 2021). The number of variables involved in a biogeographical analysis is vast, and the challenges of dealing with biological species, methods, computational tools, geological and geographical evidence, biodiversity data, and epistemological issues seem almost unmanageable. Therefore, integrative pluralism is appropriate for explaining complex biological phenomena, combining particular theories and models to produce a critical framework that allows the understanding of biotas and the dynamics of their assembly (Morrone 2009, 2020a, b).

As Wen et al. (2019) pointed out, nowadays biogeography incorporates data from phylogenetics, phylogenomics, ecology, paleobiology, population biology, and geology, using new approaches and analytical tools. Biogeography, however, has not been a significant presence at the core of either of the "grand syntheses" of evolutionary theory. The Modern Synthesis (MS, Huxley 1943) treats biogeography conservatively, whereas the Extended Evolutionary Synthesis (EES, Pigliucci and Müller 2010; Laland et al. 2015; Müller 2017) has not included biogeography among its main components to date.

There is room for deepening the role of biogeography in evolutionary theory. Here, our goal is to briefly review the history of the two significant syntheses and explore the role that biogeography might play in the EES based on pattern-based biogeography (Croizat 1964; Rosen 1978; Nelson and Platnick 1981) and the concepts of biogeographical consilience (Santos and Capellari 2009; Capellari and Santos 2012) and integrative pluralism (Morrone 2020a). An updated EES incorporating these concepts will allow us to better handle the patterns and processes that have shaped Earth's life since its beginning, billions of years ago.

2. Historical Background

According to the established history, from the 1920s onwards, geneticists, paleontologists, and naturalists combined their knowledge in a broad research program known as the Modern Synthesis of evolutionary theory (from now on, MS). Modern historiography has challenged the concept of the MS as a coherent and consensual set of ideas, being more a kaleidoscope of research interests than a unified movement (Deslile 2017; Shan, 2024).

The MS was based on gradualism, natural selection of preexisting varieties, and geographical speciation (Bowler 2003). It prioritized population thinking, in which evolution was considered the changing of gene frequencies over generations due to natural selection, with the advantageous varieties that increase both survival rates and reproductive chances being selected and fixed in subsequent generations. In organisms, a genetic program would run recursively from DNA to RNA to protein until advantageous mutations arise (Depew 2017).

In the MS, the view that evolution is an explanatory hypothesis for the Linnaean hierarchy grounded the systematic work (Mayr et al. 1953). Biological classifications were represented in evolutionary trees, in which ancestor-descendant relationships were evident, and differences in branch lengths reflected the amount of evolutionary variation accumulated. Especially important is the conservative view on Earth's geology, biotic distribution, and biogeography professed by the MS advocates. Mayr, Simpson, and colleagues disregarded continental drift and plate tectonics, although geophysicists and geologists discussed these models between the 1920s and 1940s (Oreskes and LeGrand 2001).

Research on evolution continued throughout the second half of the 20th century and the first two decades of the 21st century. Given the need to update the MS, a new synthesis emerged, often called the Extended Evolutionary Synthesis (EES) (Müller and Newman 2003; West-Eberhard 2003; Pigliucci 2009; Pigliucci and Müller 2010; Laland et al. 2015; Müller 2017, 2021). The EES is not a radical new theory of evolution. On the contrary, it enlarges the scope of evolutionary theory to increase its explanatory power, incorporating four main issues (Laland et al. 2015): evolutionary developmental biology (evo-devo), phenotypic plasticity, inclusive inheritance, and niche construction.

According to Müller (2021), one of the most significant contributions of evo-devo to the EES is the concept of developmental bias. It explains why some phenotypes are more readily generated than others: in some cases, the developmental system facilitates and constrains the production of variation.

Phenotypic plasticity is an organism's responsiveness to its environment during ontogeny, leading to the emergence of distinct forms without genetic alterations; hence, the environment acts as a selection pressure, enabling the expression of phenotypic variation (West-Eberhard 2003).

The EES advocates that non-DNA-based mechanisms –transgenerational epigenetics, behavior, and cultural processes– may influence gene expression in more than one generation (Müller 2021). These epigenetic inheritance systems may interfere with gene expression networks and are crucial to evolution. They vary from self-sustaining circuits to structural inheritance, chromatin labeling systems, and RNA interference (Bošković and Rando 2018).

Niche construction is how organisms' metabolism, activities, and life choices modify environmental states, affecting selection (Odling-Smee et al. 1996; Laland et al. 2016). For instance, the accumulation of environmental changes (such as alterations to soil or the atmosphere) caused by previous generations through niche-building activities may affect the evolutionary dynamics of descendants (Uller and Helanterä 2019). In this sense, non-genetic characters may become evolutionarily significant.

The issues above show clearly that the EES emphasizes evolutionary processes over patterns. The focus on processes shaping evolution is a trend influenced by experiment-based scientists since the first days of the MS. However, the concerns about patterns go back to the 19th century: the single figure in *On the Origin of Species* (Darwin 1859) is a schematic representation of the evolutionary pattern of descent with modification. This sketch inspired Haeckel's phylogenetics (Rieppel 2016; Morrone 2022b) and the whole field of biological systematics. The depiction of evolutionary patterns, showing the putative relationship among species (phylogenetic systematics) or the relationships among areas of endemism (evolutionary or historical biogeography), is central to understanding evolution.

In the MS, a broad comprehension of evolutionary history requires exploring and discovering new forms (Schwartz 2011) through identifying and describing the intermediate steps during evolution, including all of the adaptations naturally selected, paving the bridge between micro and macroevolution (Reznick and Ricklefs 2009) – noteworthy, discovering and describing new forms will hardly include every adaptation selected neither permit the identification of the series of morphological transformations that occurs during evolution. The MS also reshaped the definition of evolution, from Darwin's descent with modification from a common ancestor to a more practical definition of evolution as changes in the allelic frequency of populations. In a certain sense, the EES inherits from the MS the need to explain and describe molecular processes, genetic frameworks, and toolkits (Buskell 2020). Although there is concern about macroevolution, there is no similar concern about elucidating biogeographical patterns.

2.1 Biogeography in the MS and the EES

How does the EES differ from the MS in terms of biogeography? According to its official repository, hosted at https://extendedevolutionarysynthesis.com/, biogeography does not appear among the main topics of EES. Love (2010) discussed the role of biogeography in evolutionary theory from a philosophical perspective. There is indeed a concern about EES about the interface between geographic range and species selection, latitudinal diversity gradients, and diversity/disparity patterns, especially in paleontology (Lieberman et al. 2007; Jablonski 2017); however, Laland et al. (2015) did not include biogeography when describing the EES structure, assumptions, and predictions.

The EES increasingly prioritizes understanding the generative processes underlying evolution, such as developmental biology, phenotypic plasticity, and epigenetic mechanisms. Thus, while pattern analysis, systematics, and taxonomy remain integral components of evolutionary research, their prominence has diminished in light of the EES's expanded conceptual framework.

Although both patterns and processes are included among their core foundations, the MS and the EES are causal-mechanistic theories, with the former focusing on population dynamics and the latter on generative processes, organismal agency, and inclusive inheritance (Toepfer, 2023). Consequently, spatial components are not integrated into these mechanistic frameworks, even though biogeography may influence the organism-environment relationship, as formulated by the EES approach, which integrates niche construction, environmental induction, and natural selection. Evolutionary processes are insufficient to explain species' geographical distribution and, hence, to understand biological evolution. It is crucial to consider other factors, such as non-biological environmental variables and geology, that are not at the core of the MS's or the EES's. However, León Croizat had anticipated much of the complexity of the biogeographical problem since the 1950s, suggesting that his ideas could have been considered for both MS and EES.

2.2 Earth and life evolving together

Croizat was an Italian botanist who founded the field of panbiogeography (Croizat 1958, 1964). He understood biological evolution as the relation of life, space, and time. For him, understanding how organisms evolve in time depends on analyzing their spatial distribution. Hence, biogeography is pivotal for evolutionary theory.

Croizat's dictum "Earth and life evolve together" (Croizat 1964) relies intensely on geology, especially the notion that the planet and the organisms change over time. Any biota distributed in a geographical area corresponds to a picture of a time slice in a time-axis continuum. Space is as changeable in time as life. The same is true for the distribution of life across space: long-distance dispersal events, range expansions, geodispersal, vicariance, and extinction shape biogeographical patterns (Amorim et al. 2009). The idea of a dynamic Earth later underpinned the concept of vicariance (Croizat 1964; Morrone 2021).

Croizat's panbiogeography was an attempt to unify all the factors that influence biotic evolution into a single theoretical framework. The general procedure of panbiogeography is the identification of tracks – lines connecting two or more areas – summarizing different distribution patterns. These graphs show shared patterns across taxa and allow us to infer how they evolve in space, suggesting that the areas are connected by ancient vicariance events (Crisci et al., 2003). Generalized tracks are superimposed patterns of past disjunctions (Craw et al., 1999) and are the first steps in searching for the shared pattern's geological connections and common causes. Transoceanic generalized tracks suggest the occurrence of past continental disjunctions, thus anticipating plate tectonic models (Keast 1991).

The search for collective patterns is the core of Croizat's (1964) panbiogeography and contrasts with the process-oriented MS and EES. Nevertheless, Croizat was ahead of his time and became a *persona non grata* to the intellectual elite of evolutionary theory in the mid-20th century. During the 1950s and 1960s, the MS perspective on biogeography dominated the debates, and panbiogeography survived at the periphery of evolutionary theory until cladistic biogeography emerged in the 1980s.

As Croizat suggested, biogeography is inseparable from understanding Earth's influence on life. The similarities of continental coasts, particularly between South America and Africa, led researchers to infer that these continents were previously united (Davies 1965; Nelson and Platnick 1981; Milner 2009). Wegener (1912, 1915) assumed that if South America and Africa were once merged into a supercontinent, the Pangea fragmentation would explain the shared patterns of fossil distribution and glacial deposits, as well as the similarity of the coastlines of eastern South America and western Africa. The existence of an ancient Pangea would explain many animal and plant fossil distributions (Drake 1976)

In general, the biogeography of the MS relied on fixed landmasses with native biota evolving in these regions (Simpson 1943, 1953; Morrone 2022a). This permanentism focused on the species but neglected geology's role in generating biodiversity. Fortunately, the advances in geology after the 1940s led to increasing recognition of continental drift. As Croizat advocated, Earth is changing, and so is its biota. The continents move like "floating rafts," carrying species to form distribution patterns worldwide. In biogeography, dealing with historical distribution patterns on a moving surface is a reiteration of Wegener's observations.

Based on panbiogeography and continental drift, and further refined by the plate tectonics model, Rosen (1978) and Nelson and Platnick (1981) proposed a pattern-based biogeographical approach known as cladistic biogeography. In general, it assumes a direct correspondence between phylogenetic patterns and area relationships (Nelson and Platnick 1981; Wiley 1988; Morrone and Crisci 1995; Humphries and Parenti 1999; Crisci 2001; Ebach and Morrone 2005; Santos and Amorim 2007; Morrone 2009, 2021).

The first step of cladistic biogeographical analysis is to replace terminal taxa in cladograms with the areas they inhabit. The resulting taxon-area cladograms often present some biogeographical noise in the form of widespread taxa (multiple areas on a single terminal branch or MASTs), redundant distributions or paralogies (when the same taxon is present in different areas), and missing areas (when specific taxa are absent from certain areas) (Crisci et al. 2003; Morrone 2009, 2020b; Parenti and Ebach 2009; Santos et al. 2023). Since ambiguity blurs relationships among areas, discovering common biogeographical patterns through cladistic biogeography requires more than a single taxon cladogram.

Even if a method allows the construction of an entirely resolved general area cladogram, the question remains: Is the biogeographical pattern reliable as an evolutionary scenario? The answer demands comparing the obtained biogeographical hypothesis to additional data –patterns from other taxa, geological information, and area cladograms obtained through distinct methods– in a comprehensive research program that deals with multiple approaches (Morrone 2009, 2020a).

3. Integrating biogeography into EES through consilience

Space is no less complex than life. Earth's surface constantly changes, erodes, rises, fuses, and splits (Jordan and Grotzinger 2008). As space is a mosaic of multiple layers of different evolutionary histories, framing the areas of a study takes work (Morrone 1994; Hausdorf 2002). Frequently, areas can mix, leading to composite areas valid for some taxa but not others. It is not uncommon, for example, to find endemism within endemism (Fachin et al. 2020), where areas of endemism exist nested within larger ones.

Before biogeographical analyses, the dynamism of the areas should be taken into account, or the resulting patterns will be poorly informative or even unreliable (Amorim and Santos 2018). A roadmap to address biogeographical complexity and handle different spatial and temporal scales should prioritize seeking congruence among biogeographical patterns.

Congruence is the target of historical or evolutionary biogeography (Donoghue and Moore 2003; Ebach and Williams 2004; Morrone 2009). In cladistic biogeography, a general-area cladogram is a hypothesis derived from the congruence among individual-area cladograms (Morrone and Crisci 1995). Such a hypothesis is, in turn, illuminated when compared with hypotheses based on other classes of evidence. This procedure aims to turn the pattern into a general biogeographical theory with greater explanatory power (Santos and Capellari 2009). Still, congruence among individual biogeographical hypotheses is not guaranteed (Morrone and Carpenter 1994; Donoghue and Moore 2003). There are cases when a general pattern does not emerge even after rechecking and reevaluation. In these situations, the biogeographical discrepancies may explain long-distance dispersal, failures in vicariance, geodispersal, secondary distributional expansion, and extinctions.

Both dispersal and vicariance are processes related to biotic assembly (Morrone 2020a) that depend on the nature of the biological groups, the areas involved, and the spatial and temporal scales. Dispersal events, often considered *ad hoc* hypotheses when vicariance scenarios failed to explain biogeographical patterns, have been viewed differently since the publication of model-based inference techniques. They examine the dispersal history of species over millions of years and have shown that some organismal traits reveal that long-distance dispersal plays a decisive role in shaping biotic distributions (van Dam and Matzke 2016).

Incongruence among area cladograms is especially relevant when we treat problems using different analytical methods. According to Santos and Capellari (2009), the application of biogeographical methods is often challenging due to the plethora of ambiguities in real data sets, the difficulties of delimiting biogeographical unities (the areas of endemism), and how past and present events affect the distributional patterns of life, as well as the presence of widespread taxa, redundancy, and missing areas.

Evolutionary biogeography generally integrates phylogenetic patterns, areas of endemism, delimitation of area relationships, processes and mechanisms (both short- and long-term), and geological evidence (Morrone 2009, 2020a, b). Thus, to be considered a reliable evolutionary scenario, every biogeographical hypothesis should be tested under different classes of evidence in Hennig's (1966) reciprocal illumination sense. This test is necessary to construct hypotheses that explain how life changes over space and time. Here, we consider biogeographical consilience (Santos and Capellari 2009) to build hypotheses that can explain their original evidence concurrently with other phenomena.

3.1 A protocol for biogeographical consilience

According to Whewell (1840, p. XXXIX), "The Consilience of Inductions takes place when an Induction, obtained from one class of facts, coincides with an Induction obtained from another class. This Consilience is a test of the truth of the Theory in which it occurs." Thus, consilience occurs when a causal explanatory theory successfully explains phenomena beyond those considered during its construction (Whewell 1847). In the words of Laudan (1971, p. 371): "Given that induction is the formulation of a hypothesis which will explain (or 'express') a class of known facts, it follows that a consilience of inductions occurs when we discover that the same hypothesis explains (or expresses) two (or more) classes of facts." Consilience is thus a criterion of the reality or reliability of a scientific theory (Snyder 2005).

Santos and Capellari (2009) highlighted the difference between consilient-like and consilient processes. In a consilient-like process, a scientific hypothesis simultaneously addresses unrelated generalizations. In a genuine consilient case, the initial hypothesis explains a single set of generalizations, but it also explains other sets equally well. A consilient process would reveal the *vera causa*, or natural affinity, underlying a natural phenomenon, since it would be unlikely that a false theory could casually unify diverse phenomena (Snyder 2011). Santos and Capellari (2009) proposed the concept of biogeographical consilience based on this premise. A consilient general biogeographical hypothesis explains phenomena not contemplated in the first place, such as the distribution of other than the original taxa or the phylogenetic relationships within other taxa sharing distributional patterns in the areas under scrutiny.

Santos and Capellari (2009) and Capellari and Santos (2012) suggested a sequence of steps to apply biogeographical consilience as an evaluation criterion for biogeography, which we used as the basis for the following protocol (Fig. 1): (1) defining the taxon sampling and phylogeny, (2) identifying spatial units (areas of endemism), (3) choosing a method, and (4) searching for biogeographical reciprocal illumination and consilience.

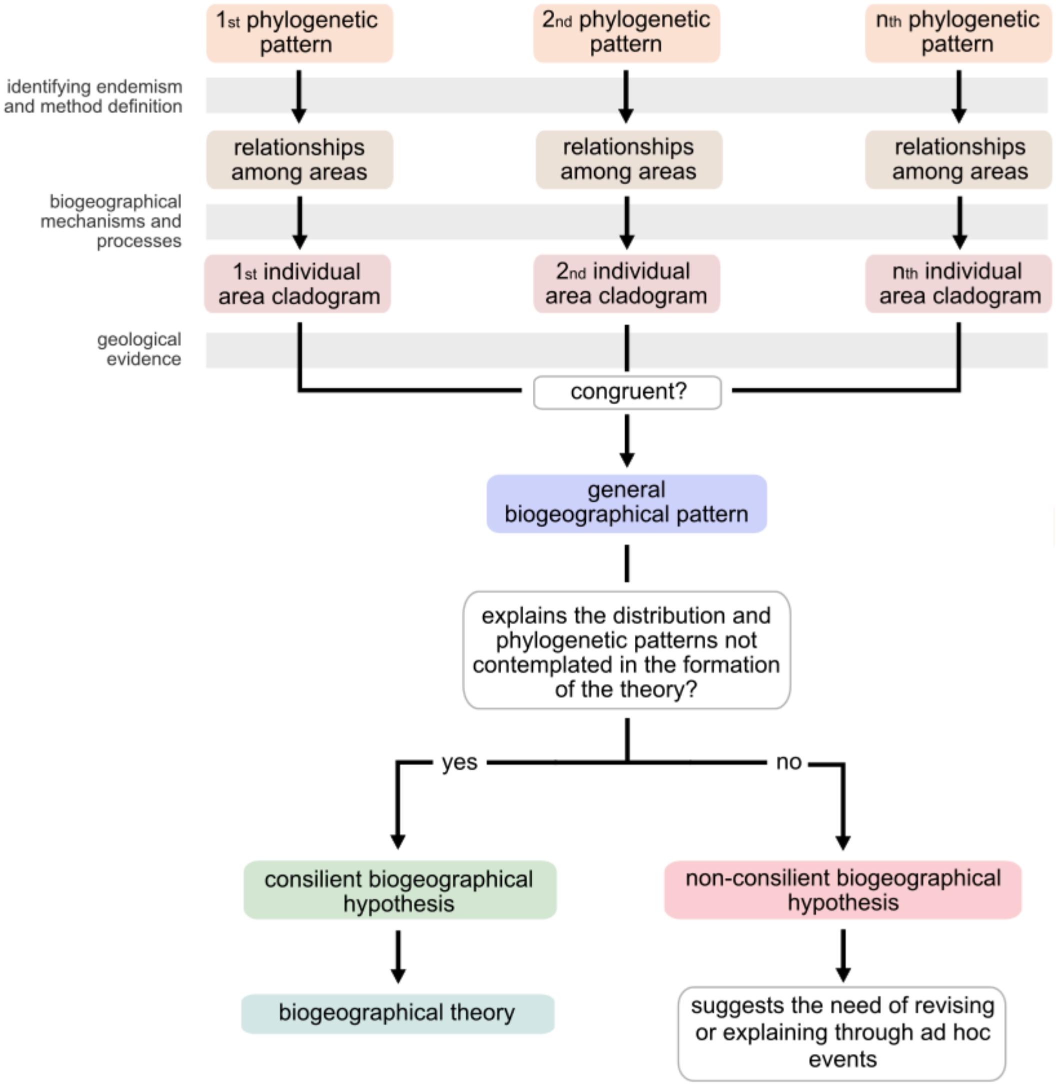

FIGURE 1. Flowchart showing a protocol for historical biogeographical analysis based on the concept of consilience (modified from Santos and Capellari 2009).

1. Taxon sampling

The first step in every biogeographical study is defining which taxon or taxa will be analyzed. As the underlying concept of evolutionary studies is common descent, we should rely on monophyletic groups. Hence, regardless of the chosen method, phylogenetic reasoning is critical for a biogeographical analysis (Santos and Amorim 2007). The importance of phylogenies seems evident for historical but not ecological biogeography, although this dichotomy does not accurately reflect the complexity of biotic evolution (Lieberman 2003; Wiens and Donoghue 2004; Morrone 2020b).

2. Areas of endemism

Harold and Mooi's (1994, p. 43) definition offers a general framework for understanding the concept of area of endemism: "(...) a geographic region comprising the distributions of two or more monophyletic taxa that exhibit a phylogenetic and distributional congruence and have their respective relatives occurring in other such defined regions".

Based on the identification of general distributional patterns, the hypothesis of an area of endemism demands a distributional-level analysis of monophyletic taxa, followed by hypothesis testing. Morrone (2009) and Amorim and Santos (2018) pointed out that the congruence among areas of endemism defined by different monophyletic taxa suggests a common historical cause. Morrone (2001) called primary biogeographical homology the hypothesis of an area of endemism or a generalized track before testing its reliability. Hence, the primary biogeographical homology should be checked for congruence through a process of reciprocal illumination to uncover general, wide-scale patterns (Sigrist and Carvalho 2008). Methods to identify primary biogeographical homology include Parsimony Analysis of Endemicity (PAE; Rosen 1988; Morrone 1994), NDM/VNDM (Szumik and Goloboff 2007), and Topographic-Unit Parsimony Analysis (TUPA; Amorim and Santos 2018).

3. Methods and congruence

As discussed, biogeography is rich in methods (Morrone and Crisci 1995; Humphries and Parenti 1999; Morrone 2009; Parenti and Ebach 2009; Sluys 2021). In pattern-based biogeography analysis, phylogenetic hypotheses are the basis for information on the spatial evolution of taxa. Based on the fundamentals of cladistic biogeography, every biogeographical analysis derived from phylogeny results in an individual taxon-area cladogram (Humphries and Parenti 1999). The initial result is not collective, even in other biogeographical methods, such as phylogeography. Hence, a comparison among individual taxon-area cladograms is needed to obtain a comprehensive pattern.

After dealing with noise, general biogeographical hypotheses emerge from the common grounds identified among individual taxon-area cladograms. Different methods solve MASTs, paralogies, and missing areas in particular ways, often based on various assumptions. Some of them rely on matrix construction and parsimony analysis, e.g., Primary and Secondary BPA (Brooks et al. 2001) and Modified BPA (Santos et al. 2021); others rely on topology comparison, e.g., Component Analysis (Nelson and Platnick 1981; Page 1988); and others are a mix of both approaches, e.g., SAMBA (Santos et al. 2023). The comparison among individual area cladograms focuses on recognizing "historical signals in a sea of geographic homoplasy" (Humphries and Parenti 1999, p. 87). This search for distributional patterns across disjunct areas converges with Croizat's panbiogeography; however, current methods of cladistic biogeography are more refined in interpreting mechanisms and processes.

Each method can handle only some of the complexities of the spatial-temporal history of organismal distribution. Therefore, it is not necessary to identify the ultimate method. Morrone's (2009) approach to evolutionary biogeography considers the results of distinct methods to be equally valid, to varying degrees, during the analysis. Furthermore, biogeographical consilience (cf. Santos and Capellari 2009) can be key to evaluating the generality and robustness of a general-area cladogram. That is the core of our proposal to include biogeographical pattern analysis in the EES.

4. Biogeographical reciprocal illumination and consilience

The final step in the biogeographical analysis includes reciprocal illumination and the search for consilience. Considering biogeographical reciprocal illumination, we reinforce the need to compare the general-area cladograms resulting from the analysis with external hypotheses, such as geological patterns. Since Earth and life evolve in tandem (Croizat 1964), a pattern of spatial fragmentation, as revealed by a general area cladogram, is proposed as a scenario that occurred in nature, indicating that geology and biogeography are intertwined. Similarly, because biogeographical patterns are collective, we should also seek congruence with area cladograms derived from analyses of taxa other than those used in our initial taxon sampling.

Santos and Capellari (2009) discussed consilience as an evaluation criterion for a hypothesis in biogeography. A consilient biogeographical pattern can explain taxon distributions and phylogenetic patterns that were not considered in developing the biogeographical theory. Given a biogeographical theory, finding correspondence between the area cladogram (derived from a phylogeny of a given taxonomic group) and a consilient biogeographical hypothesis means finding supporting evidence that the phylogeny shares a causal relationship with Earth's history. Therefore, the congruence of a phylogeny with a consilient biogeographical hypothesis suggests that "the phylogenetic pattern is not just the result of a well-conducted algorithmic protocol for phylogenetic analysis (...) but depicts a meaningful evolutionary scenario" (Capellari and Santos 2021, p. 173).

4. Extending the Extended Synthesis a step further

Considering an integrative approach to biogeography based on biogeographical consilience and reciprocal illumination is a way to deal with the multiple aspects of biological diversity that are not accepted in the current version of the EES. It is worth remembering that biogeography, rather than a single unified field, is a diverse array of fragmented disciplines practiced by individuals from different scientific backgrounds. Ebach (2015, p. 153) suggested that biogeography is "(...) effectively an eclectic field that is unifying in name only" and attempts to encompass all of its goals, methods, theories, and practices in a single theoretical and methodological corpus, which will probably disconsider some clusters of practitioners that call themselves "biogeographers". Still, our proposal does not depend on a unified view of biogeography. We advocate adopting an analytical methodology grounded in panbiogeographical reasoning and pattern-based biogeographical methods to further expand our understanding of evolution.

A genuinely integrative biogeography should go beyond the separate compartments of evolutionary and ecological biogeography (Lieberman 2003; Crisci and Katinas 2009; Morrone 2009, 2020b; Weeks et al. 2016; Jørgensen et al., 2024). Instead of the orthodox distinction between ecological and historical biogeography, Morrone (2020b) suggested that any biogeographical analysis may consider a taxon-biota versus an ecological-evolutionary axis. As examples of biogeographical analyses, we may cite niche modeling of a species (taxon/ecological axis), diversification history of a lineage (taxon/evolutionary axis), macroecological analysis (biota/ecological axis), and reconstruction of the biotic history of an area (biota/evolutionary axis).

In this context, the search for biogeographical consilience implies that any biogeographical hypothesis should be tested or "illuminated" by others. Thus, it would be possible to bring together evolutionary and ecological analyses and examine whether their deductions agree (Morrone 2020b). If discrepancies are evident, we may consider misinterpretations, flaws, or missing information.

Integrative pluralism is the general philosophical approach that allows the EES to include both pattern and process analyses (Morrone 2020a). Combining theories, models, methods, and data collection techniques best explains a complex phenomenon (Mitchell, 2003). In contrast to reductionism, integrative pluralism aims to provide a broad framework for understanding complex phenomena. According to Mitchell (2002, 2003) and Mitchell and Dietrich (2006), complexity involves three issues: constitutive complexity (the phenomenon is a structurally complex system), dynamic complexity (diverse processes are involved), and evolved complexity (the phenomenon evolves over time). A pluralistic approach is especially pertinent in biogeography, a field marked by its intricate nature (Morrone 2020a), to help bridge the gap between biogeography and the EES.

The EES is a work in progress that continuously seeks to expand the frontiers of biological knowledge. The EES needs to discuss, in both philosophical and empirical/observational terms, issues related to processes (such as epigenetics, phenotypic plasticity, and genomic evolution) and patterns (phylogenetics and biogeography). The diagram in Fig. 2 synthesizes the main aspects of a broader evolutionary theory centered on Darwin's original ideas of common descent, variation, and natural selection, rounded out by the key concepts established since the MS.

Integrating biogeographical concepts such as consilience and congruence with core evolutionary theory enriches understanding of evolutionary dynamics through spatial and historical perspectives. Biogeographical consilience (cf. Santos and Capellari 2009), emphasizing the unity of knowledge around the spatial component of evolution, aligns with the interdisciplinary nature of a broad conceptual framework such as the EES. In this sense, biogeography – especially pattern-based biogeographical analysis – can provide the very basis of cohesive and robust evolutionary narratives.

Combining EES concepts such as developmental bias, niche construction, and inclusive inheritance with integrative biogeography and consilience is necessary. We should acknowledge the mutual influence between organisms and their environments over evolutionary timescales. Developmental bias can be influenced by historical biogeographical events, shaping the availability and selection of phenotypic variations. Niche construction and ecosystem engineering by organisms (Jones 2010), the process by which organisms modify their own and each other's niches, can be seen as a dynamic interaction between biogeographical settings and evolutionary processes, influencing and being influenced by the distribution and diversification of species. Thus, understanding the evolution of endemism and biotic assembly will inform discussions of niche construction scenarios. Inclusive inheritance, encompassing genetic, epigenetic, behavioral, and cultural factors, can be integrated with biogeographical concepts by considering how these mechanisms affect and contribute to geographical distribution and speciation patterns.

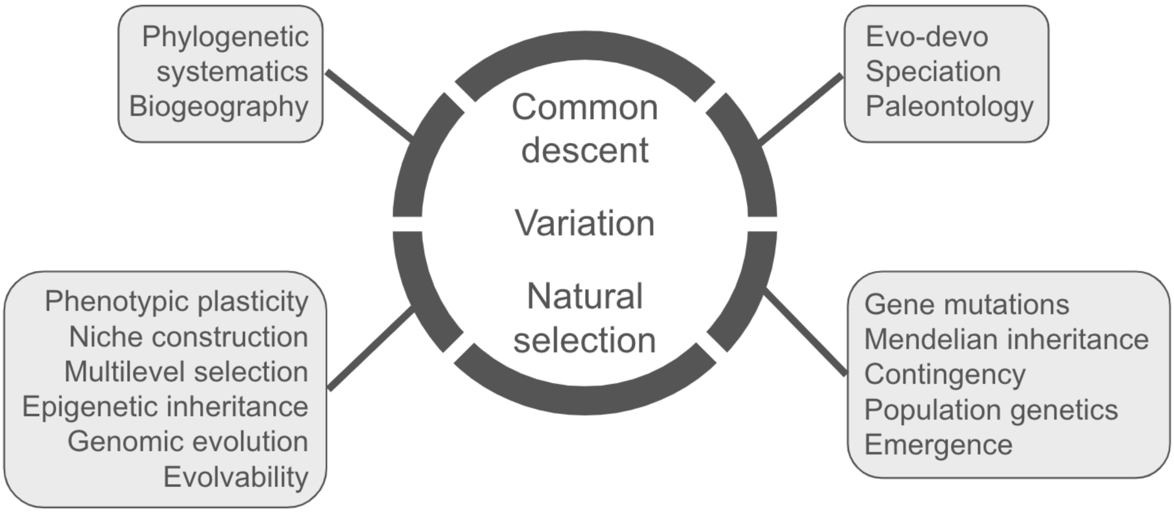

FIGURE 2. Schematic representation of a broader evolutionary theory including the key concepts of Darwinism, the Modern Synthesis, the Extended Evolutionary Synthesis, and pattern-based analysis (phylogenetic systematics and biogeography).

5. Conclusion

Incorporating biogeographical concepts into the EES offers a comprehensive understanding of evolutionary processes, emphasizing the significance of spatial and historical contexts in shaping life's diversity. This integration may broaden the EES's explanatory power by highlighting the interconnectedness of evolutionary dynamics across scales and disciplines.

A conceptual expansion of evolutionary theory seems inevitable. Claims that the MS requires only minor modifications fail to recognize the transformative nature of the EES. To effectively depict the historical patterns and mechanisms underlying biological diversity, the theory of evolution must prioritize the use of the most substantial evidence. This includes an examination of genetic and non-genetic processes, as well as the interplay between taxa, biotas, and the Earth. Additionally, historical phenomena like vicariance and dispersal, intertwined with Earth's dynamic changes, should be considered. A twenty-first-century evolutionary biologist should have a broader perspective on the study of evolution and biological organization. An updated EES, as discussed here, has the potential to provide a more robust view of the diversification of life on our planet.

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