

Phylogeny, biodiversity, and macroevolution: a qualitative approach

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Abstract

Biodiversity is the product of a unique and non-reproducible historical process. To understand biological diversity and the history responsible for the formation of present biotas, it is fundamental to understand the relationships among recent biotas. The study of changes that occurred above the traditional population level becomes important to reconstruct history in its full time scale. Biological classifications resulting from phylogenetic analyses represent direct tools for the comprehension of present biodiversity, because they organize all organisms, present and extinct, around a single central parameter (evolution). This systemic approach has been considered the only compatible theoretical perspective for a macroevolutionary view of biological diversity. Phylogenetic systematics may be seen as the central cogwheel for connecting macroevolutionary theory to the science of biodiversity.

Key words: historical biology, history of biodiversity, phylogenetic methods, systematics.

Resumo

FILOGENIA, BIODIVERSIDADE E MACROEVOLUÇÃO: UMA ABORDAGEM QUALITATIVA. A biodiversidade é o produto de um processo histórico único e irreproduzível. Compreender as modificações que conduziram esse processo em um nível acima do nível populacional, tradicionalmente abordado, é fundamental para entender a origem das relações existentes entre as entidades que formam a diversidade biológica e a própria história que culminou na formação das biotas atuais. Nessa perspectiva, classificações resultantes de análises filogenéticas são ferramentas diretas para a compreensão da biodiversidade atual, organizando todos os organismos, atuais e extintos, em torno de um único eixo central (evolução), de forma sistêmica e compatível com uma visão macroevolutiva da diversidade biológica. Uma sistemática filogenética plenamente estabelecida e com uma base teórica sólida é fundamental para alcançar esse objetivo, podendo ser vista como uma engrenagem central, capaz de proporcionar uma ligação direta entre a teoria macroevolutiva e as ciências da biodiversidade.

Palavras-chave: biologia histórica, história da biodiversidade, métodos filogenéticos, sistemática.

Introduction

The central aim of systematics is to comprehend and organize biodiversity knowledge (Cracraft, 2002). When evolution is seen as the central paradigm uniting species, this same process becomes the only biological model capable of promoting cohesion among all organisms, extant and extinct, and of organizing this diversity into a single hierarchy. Evolution is responsible for generating the observed diversity of living beings through history. Thus we are only capable of understanding all the structural changes that we observe in the light of evolution. These changes directly influence the patterns of environmental occupation, the formation of biotas, the establishment of ecological relationships, the physiological adaptations, the behavioral traits, the co-evolutionary bonds, and the history of the successive biotas which dominated our landscapes through time, resulting in our present evolutionary time slice. Knowledge of the history and origin of biological entities

that form biodiversity (phylogeny) is just as important as establishing these relations (Hastings et al., 2007). Classifications that result from phylogenetic analyses may be used as critical tools for evolutionary studies. They are based on a philosophical foundation which is much more adequate for viewing nature than the pre-evolutionary typological perspective. The systemic foundation of phylogenetic systematics makes this approach more successful for answering questions and for resolving problems dealing with the origin and evolution of ecological relations among organisms (Wiley, 1981). Phylogenetic systematics synthesizes the vision of Darwin (1859), of uniting all life by genealogical relations, with the systemic model of Hennig (1950), of recovering the hierarchical patterns that reflect in an explicit way the genealogical relationships existing among species and higher taxa.

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Following the principles of Hennig (1950), it is necessary to obtain phylogenies that reflect with high fidelity the historical relationships existing among groups and that may serve as references for the systematization of organisms into a single genealogical arrangement. Unfortunately, during this year of 2009, in which the world commemorates 150 years of the acceptance of the theory of evolution of species, we still do not have a phylogenetic practice that is totally agreed upon and which is guaranteed to produce congruent cladograms for the same set of terminal taxa derived from different classes of characters (Wägele, 1999; Christoffersen et al., 2004). Although dozens of cladistic methods are available, the theoretical bases of modern cladistics are still fragile (Sober, 1988; Christoffersen, 2007). Basic problems, such as which characters are evolutionarily informative, or how to identify the informative characters in an efficient way, avoiding the interference of phylogenetic noise produced by homoplasies and plesiomorphies in the final results of the analyses, have still not been resolved in a consensual way.

Our aim in this paper is to discuss biodiversity from the perspective of historical biology, going beyond the organismic and populational levels traditionally stressed by the followers of the neodarwinistic evolutionary synthesis.

Darwin (1859) and Hennig (1950): a new vision for biodiversity

Darwin (1859) and Hennig (1950) may be seen as the main references in the development of modern biology and of our understanding of biological diversity. Darwin (1859) proposed that the observed diversity on our planet is the result of a simple and continuous process that acted throughout history. This process has been referred to as "descent with modifications". Characters which are shared among living beings should thus reflect their genealogical origin. According to Darwin (*op cit.*), present diversity is descended from a single ancestor, that along millions of years of change, lineage diversification, and extinctions, originated all life forms on our planet. In his landmark book "On the origin of the species", Darwin (1859) concluded that the best way to understand and organize diversity is to use the same process that created this diversity, evolution. A taxonomic model that reflects genealogical relationships among living species and among higher taxa, producing hierarchical and systemic interrelationships among each other, necessitates the acceptance of evolution as the process directly responsible for this diversity. The obvious difficulty for the implementation of Darwin's vision was the absence of a tool capable of producing consistent, stable and testable cladograms reflecting the historical reality. Such a methodological tool was developed nearly

a century later, after the publication and discussion of the ideas of Hennig (1966).

The Hennigian movement, similar to the Darwinian movement of the nineteenth century, did not remain restricted to systematics, but influenced all historical disciplines (Christoffersen, 2007), including the humanities and social sciences, such as anthropology, archeology, and sociology. Hennig (1950, 1966) provided the philosophical framework for modern systematic phylogenetics, and was the first to present an objective and explicit method for recovering kinship relationships among groups. The phylogenetic principles established by Hennig permitted the substantiation of a dream, the possibility of constructing a single genealogical tree for all living beings. Phylogenetic trees proposed before Hennig (e.g., Haeckel, 1866; Hyman, 1951; Hanson, 1958; Remane, 1958) lacked objective scientific criteria to sustain the proposed hypotheses, and almost always failed in recognizing monophyletic groups. The method of Hennig (1950) represented a great advance because he perceived that, although all similarities may be useful for identifying monophyletic groups, they are only informative at that hierarchical level in which they appear as evolutionary novelties, producing incorrect groupings if used at any other evolutionary levels. With a broad evolutionary context, it is possible to hypothesize nested sets of generalities for many informative characters, but this qualitative assessment of characters was largely abandoned in present quantitative cladistic procedures, as we will further discuss below.

The acceptance of the theory of evolution of species resulted in immediate practical changes in the way the scientific community viewed biodiversity. Darwin's ideas, later complemented by the views of Hennig, end a period of creationist explanations for biodiversity. This change in perspective generates important consequences for the management and exploitation of biodiversity. From this moment on, biological diversity and the world cease to be seen as the result of a superior power, created for the sole satisfaction of human beings, previously considered to represent central creatures in the universe. They are finally recognized as products of a unique, irreversible, and un-reproducible historical process, and immediately gain an immeasurable value. Science becomes responsible for unraveling diversity, protecting the biological resources and establishing goals for their sustainable exploration, given that they were no longer believed to be instantly recreated (Wilson & Peter, 1988). Man becomes but another historical lineage among myriads of populations, species and monophyla, ceasing to be seen as the divine heir of all natural resources. This certainly represents the initial step for all conservationist actions being developed in our days, making humanity aware of what now represents our largest endowment, biodiversity.

Our typological inheritance persists in modern systematics

One hundred and fifty years after the acceptance of the theory of evolution of species by the scientific community, and more than 40 years after the mature views of Hennig (1966), little has been gained regarding the production of the longed-for "tree of life". Great philosophical insights are being systematically abandoned and lost among the methodological positions that have gained prestige during the last decades. Depressingly, systematics continues to be based on a typological foundation.

We perceive that phylogenetic systematics is fulfilling a role much below its true potential as a historical science, functioning as a sheer method for the reconstruction of cladograms. Notwithstanding, phylogenetics represents our best tool for the understanding of the evolution of species and of other biological entities that participated in the historical construction of biodiversity (Wiley, 1981). A better use of this potential, however, will not be possible as long as characters continue to be used as a basis for forming taxonomic groups instead of as a basis for the identification of monophyletic groups, as proposed by Hennig (1950). A particular taxonomic group does not form a natural unit simply for sharing "n" characters, but because its members descend from a common and exclusive ancestor. To infer this kinship relationship in a consistent manner depends on an analysis of the available evidence (characters), and of their variability along all related groups, taking into account all forms that these characters may take in more inclusive taxa. A quantitative analysis fails to identify monophyletic groups when homologous characters are codified as independent structures, and this error is committed whenever distinct structures are coded as different characters for the simple typological reason that they look different. One of the most evident consequences of the phylogenetic world-view is that biological diversity changes as a whole through history, not only the component species, but also the morphological structures that belong to these species, and the functions that these structures fulfill. The famous dichotomy Protostomia x Deuterostomia represents a classical example of persistent typological thinking. The two groups are based, respectively, on the presence of schizocoely or enterocoely, spiral or radial cleavage, blastopore originating mouth or anus, etc. These characters continue to be coded as independent characters in many numerical cladistic analyses, even against biological arguments that sustain the hypotheses that these particular pairs of structures represent different states of the same characters. Thus Protostomia (and all derivative descriptive names such as Spiralia, Trochozoa, etc.) should only be considered monophyletic when including the Deuterostomia (including Radialia, etc.) as descendant

and subordinate clades of protostomes (Christoffersen & Araújo-de-Almeida, 1994; Almeida et al., 2003). The persistence of this typological outlook conflicts with the phylogenetic model based on ancestry. Only a qualitative and biologically contextualized approach is able to avoid these common methodological misunderstandings.

The typological inheritance resulting from Linnean classification is not the only obstacle for the adoption of a fully systemic model of classification. There is also a dominant reductionist culture coming from classical microevolutionist Neodarwinism that minimizes the importance of evolutionary processes above the populational level of diversity. Finally, the incorporation of concepts and practices originating with the defenders of evolutionary and phenetic taxonomy into the now dominant paradigm of cladistics, although certainly developing the phylogenetic paradigm, also introduced ideas incompatible with the original Hennigian principles. All these conflicts within present macroevolutionary theory produce distorted evolutionary patterns that do not adequately reflect the historical reality that needs to be reconstructed and that molded biodiversity through time. Computer programs, initially conceived to run analyses of phenetic similarity, have been incorporated into cladistic methodologies. Because they unquestionably increase resolution power and speed in quantitative analyses of large databases, they have been amply utilized. On the other hand, they are responsible for the present situation, in which character quality is neglected in favor of the quantity of characters incorporated into phylogenetic analyses. Large data matrices based on total evidence, containing numerous plesiomorphies and homoplasies, as well as unidentified apomorphies, feed programs that are frequently not able to correctly identify these three classes of similarities. The search for a strictly objective, mechanistic, cladistic method, with a minimum participation of the researcher in the understanding of the evolutionary process, is affecting the comprehension of the fundamental Hennigian principle, which is the previous identification of apomorphies as the sole characters able to recognize monophyletic clades. Computerized algorithms presently in use in numerical analyses are mostly based on total character congruence (Patterson, 1988). They are thus highly affected by the unfavorable proportion of phylogenetic noise in relation to the phylogenetic signal provided exclusively by eventual apomorphies contained in the data matrices. This unfavorable proportion of noise to signal is compounded in molecular analyses, where decisions as to character polarities are rarely made by the researcher, either prior or after a cladistic analysis (Hillis & Huelsenbeck, 1992; Flook & Rowell, 1997). We are thus witnessing in practice a return to the pre-Hennigian paradigm, where the sole basis for the formation of taxonomic groups is the quantity of shared similarities between these groups.

Objectivity and subjectivity in phylogenetic research

Many central tenets pertaining to the systematization philosophy of Hennig (1950, 1966) have been abandoned by cladists, to the point that modern cladistics differs markedly from the original phylogenetic systematics (Padian, 2004). One of the main changes refers to an inversion of the qualitative principle, the detriment of complex and evolutionary contextualized characters in favor of an inclusion of the largest number possible of characters into the analysis. In name of objectivity, no previous evaluation of character quality is made, all character polarizations being established quantitatively and *a posteriori* by the parsimony algorithm, with no decisions by the researcher.

Character polarizations used in Hennigian analyses were strongly criticized by the scientific community, the main objection being that the subjective nature of the procedure could permit the insertion of preconceived evolutionary ideas into the analysis. However, Hennig (1950) defended objective and explicit phylogenetic procedures, without preventing the influence of the subjective previous experience of the researcher for a better comprehension of character transformations. The necessity of providing strong and convincing biological arguments for the inferences reached by the researcher certainly minimizes the proposal of biased hypotheses.

Despite this extreme tendency for the production of objective cladistic methods, this goal of maximum objectivity has never been attained. The choice of a computational program among numerous available options (e.g., PAUP, Hennig86, MrBayes, MacClade), the configuration of the program in order to optimize the analysis, the choice among several methods of tree construction (e.g., parsimony, likelihood, Bayesian inference, neighbor-joining), the choice of existing character class (e.g., morphological, behavioral, ecological, mtDNA, 18S rDNA, 28S, 12S, cytochrome b, nuclear DNA, sequences of aminoacids), determining which taxa will be sampled, which taxa will be used as outgroups, which characters will be used or discarded from the data matrix, how characters will be treated (binary, multistate, ordered, etc.), are all very subjective and arbitrary decisions. These decisions appear to be as subjective, or even more subjective, than the sound and sensible Hennigian suggestion of determining the direction of evolution of a transformation series on the basis of all available information accumulated by past generations of comparative biologists and processed by the best judgment of the experienced researcher. On the other hand, in cladistic analysis the subjective decisions enumerated above are almost never supported by biological arguments derived from a comparative analysis of the groups of interest. Decisions are simply taken on authority,

convenience, consensus opinions, research fads and latest bandwagons, very much in the way of the vituperated traditional taxonomists. Methodological tools for cladistic analyses seem now to be selected solely by their chances of surviving the peer-review process and gate-keeping preferences of the editors of our main journals.

Systematics is a historical science dealing with unique events which are impossible to analyze in a strictly quantitative way. The judgment and previous experience of the researcher becomes a valuable tool for the understanding the events of anagenesis and cladogenesis which affect lineages through time. These historical processes are shaped by stochastic geological and ecological events, all of which influence the final biodiversity. The knowledge accumulated along 200 years of comparative studies represents a powerful tool for the reconstruction of phylogenies and obviously cannot be discarded. It is clearly not necessary or advantageous to return to the times in which phylogenies were inferred in a completely subjective and non-retrievable fashion. But the critical eye of the experienced researcher over the totality of knowledge available on the evolution and morphology of the main groups of organisms is fundamental for the advancement of this knowledge at a macroevolutionary scale. This understanding must permeate the construction of data matrices and should be independent of any tree construction method. Objectivity is certainly very important for any scientific study, but the present anxiety for "automatic" and "instantaneous" phylogenies, inherited from a numerical taxonomy ideal, should not continue to substitute the human potential for analyzing historical facts.

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