

On the origin of present Neotropical biodiversity: a preliminary meta-analysis about speciation timing using molecular phylogenies

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Abstract

The evolutionary origin of extant species has been largely debated. The controversy is especially vivid in the Neotropics, one of the more biodiverse regions of the world. One hypothesis is that Neotropical species emerged primarily during the Quaternary (the last ~2 million years), favored by the alternating glacial/interglacial climates. An opposite view proposes an older Tertiary origin linked primarily to paleogeographic changes. Here, a thorough review of the available literature on DNA molecular dating shows that the Tertiary-Quaternary debate no longer makes sense. Indeed, the >1400 Neotropical species dated so far appeared in a continual fashion since the late Eocene/early Oligocene (~39 million years before present) to the Quaternary. Speciation rates maximized during the Plio-Pleistocene (the last ~5 million years), coinciding with a global climatic cooling. Paleogeographic mechanisms of speciation are relatively well known, but diversification processes linked to climate are still poorly understood. These results are important to understand the origin of present-day biodiversity patterns at both local and global scales, as well as the genetic and environmental mechanisms involved, two crucial aspects for suitable biodiversity conservation strategies.

Key words: biodiversity, climate change, molecular phylogenetics, Neotropics, paleogeography, Quaternary, speciation, Tertiary.

Resum. *Sobre l'origen de la biodiversitat neotropical actual: una metaanàlisi preliminar sobre el ritme d'especiació utilitzant filogènies moleculars*

L'origen evolutiu de les espècies actuals és un tema encara polèmic, especialment al neotòpic, que és una de les regions amb més biodiversitat del planeta. Una hipòtesi planteja que aquestes espècies s'han originat principalment durant el quaternari (els darrers ~2 milions d'anys), gràcies a l'alternança climàtica representada per les glaciacions i els interglaciars. Altres, en canvi, proposen que les espècies actuals són més antigues i que es van formar durant el terciari, degut principalment als canvis paleogeogràfics que hi van tenir lloc. En aquest article es revisen totes les evidències publicades que utilitzen filogènies moleculars d'ADN per esbrinar l'edat de les espècies neotropicals actuals. Es conclou que

la polèmica entre l'origen terciari o quaternari es pot considerar superada, ja que les >1.400 espècies documentades han anat apareixent gradualment des del límit eocè/oligocè (~39 milions d'anys abans del present) fins al quaternari. Les màximes taxes d'especiació han estat registrades al pliopleistocè (els darrers ~5 milions d'anys), coincidint amb un refredament global del planeta. Els mecanismes paleogeogràfics d'especiació són força ben coneguts, però no així aquells relatius als canvis climàtics. Aquests resultats són importants per comprendre l'origen de la biodiversitat actual, tant a nivell regional com global, així com dels mecanismes genètics i ambientals involucrats, que són dos aspectes fonamentals per al disseny d'estratègies de conservació de la biodiversitat adequades.

Praules clau: biodiversitat, canvi climàtic, especiació, filogènia molecular, neotròpic, paleogeografia, quaternari, terciari.

Introduction

The tempo and mode of origin of extant species and, therefore, of present-day biodiversity is still controversial. The debate has been largely focused on the potential influence of the dramatic climatic changes occurred during the last ~2 million years, known as the Quaternary or Pleistocene glacial cycles (Bennett, 2004). Some authors believe that Pleistocene glacial/interglacial alternation has been decisive in shaping the present-day biota, while others think that modern species originated mostly in the Tertiary or earlier, but before the Quaternary glaciations (Hewitt, 2000; Willis & Niklas, 2004). In either one or the other case, the evolutionary mechanisms and environmental forcing agents involved differ substantially (Coyne & Orr, 2004). Knowing speciation timing, genetic mechanisms and forcing agents involved would provide fundamental clues for biodiversity conservation (Moritz, 2002). Therefore, the research about the origin of present-day species is not only of intrinsic ecological and evolutionary interest, but is also needed for the development of suitable biodiversity conservation strategies.

The Neotropics (Fig. 1) is among the most biodiverse regions in the world and, as such, is a preferred target in the research about the origin of biological diversity. Some Neotropical areas are under manifest danger of biodiversity loss and have been identified as biodiversity hotspots, submitted to special conservation programs (Myers *et al.*, 2000). For long time, the most popular proposal on Neotropical diversification has been the refuge hypothesis, according to which the assumed aridity of Neotropical lowlands during the Quaternary glaciations favored forest fragmentation into islands in a sea of savannas and/or deserts, thus promoting allopatric speciation (Hooghiemstra & van der Hammen, 1998; Whitmore & Prance, 1987). The refuge hypothesis attracted the attention of many scientists, and was considered for long time the valid explanation for the evolutionary consequences of Quaternary climate change. However, further paleoecological evidence was controversial and this hypothesis is at present under serious criticism (Bush & de Oliveira, 2006; Colinvaux *et al.*, 2000). The discredit of the refuge proposal in the region led many researchers to abandon the idea of Quaternary speciation, and proposed that Neotropical species were older, in fact of Tertiary origin (e.g. Colinvaux & de Oliveira, 2001). In this case, the main forcing agents suggested were

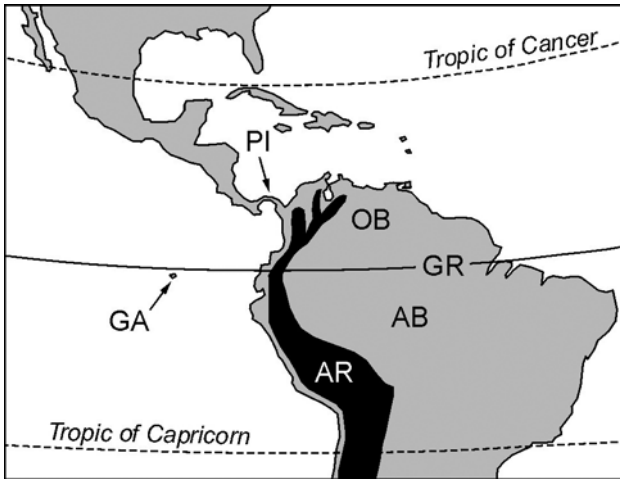


Figure 1. Sketch-map of the Neotropical region showing the main geographical features quoted in the text. AB = Amazon basin, AR = Andean range (in black), GA = Galápagos archipelago, GR = Guayana region, OB = Orinoco basin, PI = Panamá Isthmus.

related to paleogeographical reorganizations linked to continental drift, such as the Andean orogeny, the closure of the Panama Isthmus, or the flooding of the Orinoco and Amazon basins by epicontinental seas, among others (Nores, 2004). This generated a still ongoing debate about the Tertiary or Quaternary age of extant Neotropical species.

Until recently, both Tertiary and Quaternary hypotheses have been supported primarily by geological and paleoecological data, which provided indirect arguments in favor of either one or another. During the last decades, however, straightforward time measurements of diversification events have been possible thanks to the development of DNA-based molecular phylogenies that allow estimation of speciation timing (Harvey et al., 1994; Nee et al., 1992; Riddle, 1996). At the beginning, the method was criticized for methodological reasons (Ayala, 1999). Nevertheless, further improvements such as the use of neutral characters, mutation rate heterogeneity, and the calibration with radiometrically dated geological evidence have notably increased its reliability (Arbogast et al., 2002; Rutschmann, 2006). Recent reviews discuss the potentialities of the method and conclude that it is a very promising tool to investigate the historical construction of major biomes, especially those with high diversity (Pennington et al., 2004b; 2006). However, despite the advent of such new powerful dating methods, the Neotropical Tertiary-Quaternary controversy continues, due to the finding of contrasting diversification histories for different groups of organisms (e.g. Bush, 2005; Rull, 2006). The first attempt to gather phylogenetic data and draw a more or less general assessment was carried out by Moritz et al. (2000), who concluded that the diversification within 22 groups of rainforest fauna (amphibia, reptiles, small mam-

mals and birds) predates the Quaternary. Later, Pennington et al. (2004a) found higher Quaternary speciation rates in several tree genera from seasonally dry forests of South America, and both Quaternary and pre-Quaternary speciation in the same genera from Central America. More recently, Weir (2006) studied the data available for 27 avian taxa and observed higher Miocene rates of diversification for lowland species, and higher Quaternary speciation rates for highland taxa. Molecular phylogenetic studies of Neotropical organisms have flourished during the last two decades, but there is no any comprehensive review to provide solid support to the current hypotheses. This study attempts to fill the gap by providing a thorough analysis of the phylogenetic studies with quantitative dating of Neotropical species published so far.

Methods and terms used

This paper is based on all the literature dealing with phylogenetic analysis of living Neotropical species found until 2006 in widely recognized journals included in the ISI's Journal Citation Records. More than 300 references were analyzed in depth, and a selection was performed, based on the application of objective criteria. As the main objective is to know the time of origin of present-day species diversity, only studies dealing with species or lower taxonomic categories were used. The basic taxonomic unit considered is the Evolutionarily Significant Unit (ESU) (Ryder, 1986). It has been emphasized that species alone are not enough to fully account for actual biological diversity, due to the ecological and evolutionary significance of intraspecific genetic variability (Agapow et al., 2004). ESUs-including species and subspecific categories that are reciprocally monophyletic, with significant allelic divergences, and with manifest ecological distinctiveness-have been considered more realistic biodiversity descriptors (Crandall et al., 2000; Moritz, 1994). In this study, subspecific lineages have been treated as ESUs only if they are explicitly and unequivocally recognized as distinct genetic and ecological/geographical entities in the source studies. This includes subspecies and disjunct geographical clades, minor differentiation at population or metapopulation level has not been considered. On the other hand, only studies providing quantitative estimations for the age of origin of involved species have been employed; surveys with qualitative, vague or incomplete dating information have not been included. The age of origin of a given ESU is considered here as the time in which it diverged from its closest relative. Finally, only surveys with original estimations of diversification timing have been selected; revisions and re-calculations based on other's divergence rates were not considered. No any taxonomic criterion was used for the selection process, any kind of organism was included provided their study fitted with the above-mentioned criteria.

In the final selection, only raw data provided by the authors in the form of numerical tables, time-constrained phylogenetic trees and explicit in-text numerical values were used, no any additional calculation was performed. In studies comparing two or more genetic divergence rates, those recommended by the author(s) have been selected. In the absence of author's pronouncement, the total age range

derived from all calibrations considered has been used. When different authors subdivide the same species into different sets of geographical clades, the more parsimonious solution adopted has been to consider the option with less clades, in order to minimize the possibility of including non-significant genetic/ecological differences. In order to prevent taxonomical duplication, the following procedures have been applied. In the case of two studies about the same species or ESU, both are included together if the results coincide, or separately if there is some age disagreement or uncertainty. The quantitative analysis, however, only uses their divergence ages if they coincide. If they disagree they are not used, unless the disagreeing taxa have been studied by the same author or research team, in which case the results of the more recent publication have been adopted.

A critical point to decide whether a species was originated during the Quaternary or before it is the age of the Tertiary/Quaternary (or Pliocene/Pleistocene) boundary. According to classical lithological criteria, this boundary is placed at 1.8 million years before present (my BP), while using magnetostratigraphy, the limit is located at 2.6 my BP (Walsh, 2006). This would make a big difference in the context of the tempo of evolution of extant species, which is intimately related to the mechanisms and forcing factors involved. In this sense, Quaternary speciation is considered to be strongly linked to Pleistocene glaciations, hence, the age of initiation of these glacial cycles is the key point. Paleoclimatological studies on marine sediment cores have shown that the onset of Northern Hemisphere glacial cycles was around 2.6 my BP (Raymo, 1994), coinciding with the magnetostratigraphic criterion. In order to avoid unnecessary terminological controversies, this paper uses the informal terms 'Glacial' (G) for the last 2.6 my, and 'pre-Glacial' (pG) for earlier Tertiary times. This focuses the debate on the potential influence of glacial/interglacial alternation, rather than the stratigraphical concept of Quaternary, on speciation.

Results

The application of the conditions mentioned on the analyzed references resulted in a selection of 113 studies (Appendix 1), containing 105 taxonomic groups (mostly genera), and 1404 ESUs. Globally, around the half of ESUs studied so far were originated during the pre-Glacial and the other half in the Glacial (Fig. 2). Individually, amphibians and fishes emerged primarily in the pre-Glacial, whereas insects, plants and birds did it mainly during the Glacial. Others are intermediate, but mammals show a pre-Glacial preference, while reptiles have more Glacial species. Studies on echinoderms, arachnids and corals are still too scarce for a sound assessment. It could be argued that the amount of Glacial speciation has been exaggerated because of the inclusion of subspecific categories as ESUs. However, numbers are not significantly different if subspecies and geographical clades are removed. Indeed, from a total of 845 species left, 51% originated in the pre-Glacial, and the remaining 49% are of Glacial origin. Figure 3 shows that speciation leading to present-day ESUs has actually proceeded in a continual fashion since the late late Eocene-early Oligocene, with no bursts of diversification in any

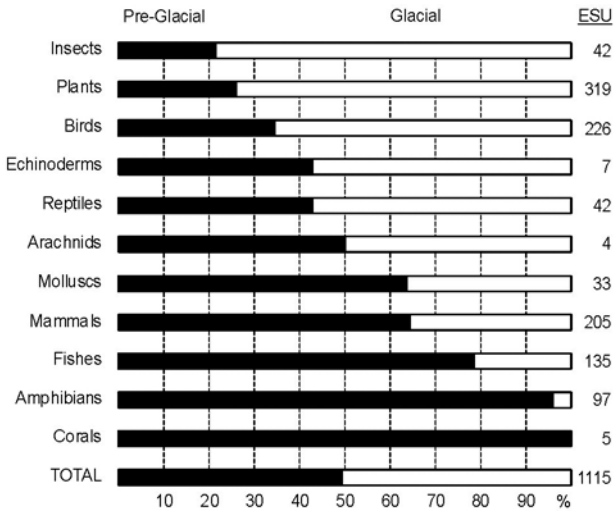


Figure 2. Percentage of ESUs originated either in the pre-Glacial (black bars) or in the Glacial (white bars) for each taxonomic group studied. The number of ESUs for each group is given in the right side. Note that the number of ESUs reported here (1115) is lower than the total number of ESUs analyzed (1404). This is due to the unavailability of quantitative age estimates for some of the ESUs considered.

time period, and no evident differences between Tertiary (or pre-Glacial) and Quaternary (or Glacial) phases. The major paleogeographic events documented have been superimposed for a tentative test of their possible influence on the general diversification process (Figure 3). However, due to the monotonous trend of the speciation process, none of them seems to have had any differential impact on diversification with respect to the others.

If we examine the initial diversification of each group studied, a continuous exponential trend can be observed (Fig. 3), with very few groups (<7%) diversifying before the middle Miocene (around 17 my BP), and a spectacular increase after that date. The maximum concentration of speciation is in the Plio-Pleistocene interval, starting around 5 my BP. Concerning rates, if we consider the whole time interval studied, the gross average rate is of 0.27 species per million years per group ($\text{sp my}^{-1} \text{gr}^{-1}$), or one species per group every 3.7 my. However, due to the exponential increase observed, there is a significant variability among the different time periods involved. For example, the rate is 0.14 $\text{sp my}^{-1} \text{gr}^{-1}$ (1 species per group every 7 my) for the Tertiary, and 2.10 $\text{sp my}^{-1} \text{gr}^{-1}$ (1 species per group every 0.5 my) for the Quaternary. The different duration of these periods makes the bulk Quaternary rates to be around 14 times higher than the Tertiary ones. The maximum rates of group speciation occur in the Pliocene, followed by the Pleistocene and the Miocene (Fig. 4). The Plio-Pleistocene acceleration coincides with a remarkable global cooling, as deduced from the oxygen isotope general curve (Fig. 3).

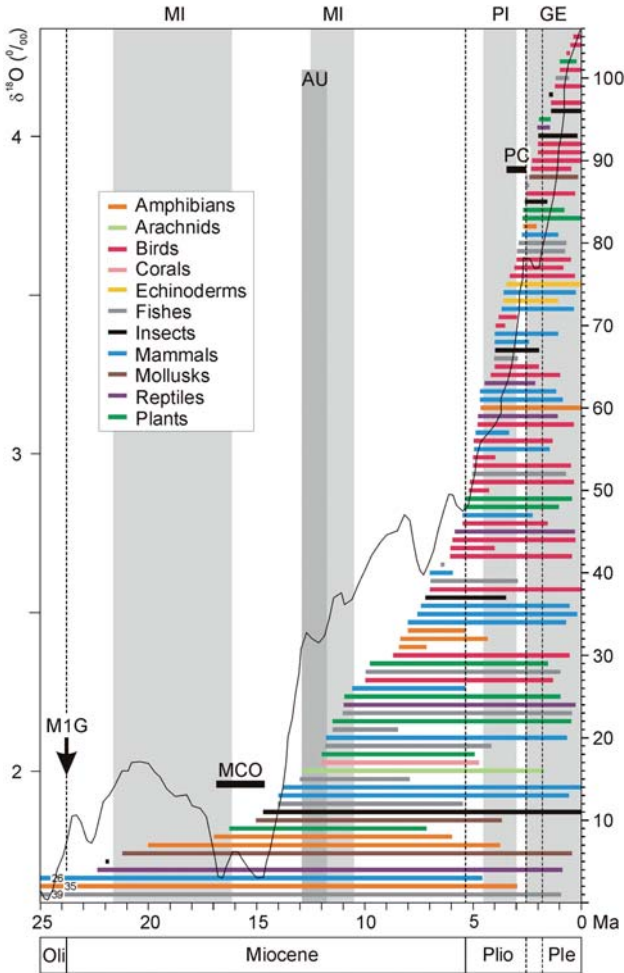


Figure 3. Time range of ESU's divergence for each group studied. Bars represent the time interval between the origin of the older (left) and the younger (right) ESU within each group, and are sorted chronologically according to the emergence of the older ESU. Time in million years before present (my BP). Geochronological units: Oli = Oligocene, Plio = Pliocene, Ple = Pleistocene (Berggren et al., 1995). The two possibilities for the Pliocene/Pleistocene boundary are depicted (Walsh, 2006). Singular periods and events are highlighted with grey areas: GE = Glacial Epoch, PI = formation of the Isthmus of Panamá (Bartoli et al., 2005), MI = Marine incursions into the Amazon basin (Lovejoy et al., 2006), AU = Major event of north-Andean uplift (Hoorn et al., 1995). The smoothed oxygen isotope deep-sea curve (solid black line) is represented in $\delta^{18}\text{O}$ units (Zachos et al., 2001). This parameter is largely (~70%) controlled by the ice volume of Antarctica and the Northern Hemisphere, hence, it is correlated with the intensity of continental glaciation and therefore with global cooling. M1G = Miocene-1 Glaciation, MCO = Miocene Climatic Optimum, and PC = Pliocene Cooling (Zachos et al., 2001).

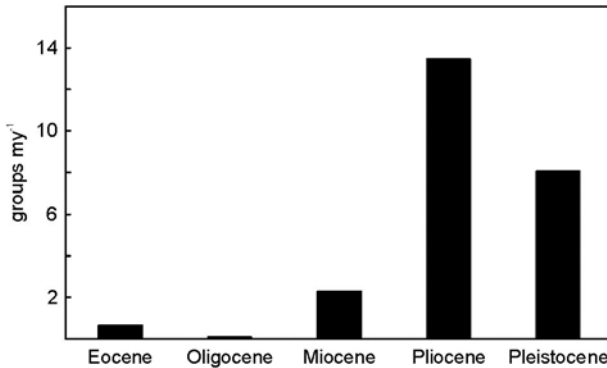


Figure 4. Speciation rates measured as the number of groups that began to diversify per million years, within each period.

Discussion and conclusions

The available molecular phylogenetic evidence shows that the extant Neotropical species and ESUs studied so far have originated in a continual manner since the late Eocene/early Oligocene until the Pleistocene, with no any peaks or out-breaks in speciation at any given time period. Speciation rates within the taxonomic groups reported show an exponential increase since the Eocene, with a middle Miocene intensification, and a maximum during the Plio-Pleistocene, when more than 60% of extant ESUs originated. The time of maximum speciation rates per group has been the Pliocene.

In this frame, the Tertiary-Quaternary debate loses relevance and should be replaced by a more realistic approach. The present-day Neotropical biodiversity can be viewed as a mixture of species of different ages, likely originated through diverse mechanisms. Indeed, timing and speciation mechanisms are closely linked, as the more significant paleogeographic reorganizations occurred in the Tertiary, whereas the climatic changes were the norm during the Quaternary. The effects of Miocene and Pliocene paleogeographic changes on speciation trends are relatively well-known, and are related to the building and vanishing of bridges and barriers, thus changing migrational and isolation patterns, and favoring vicariance (Coyne & Orr, 2004). There is little doubt that events such as the uplift of the Andes and the closure of the Panama Isthmus have played a significant role in shaping Neotropical biodiversity patterns (Bush & Hooghiemstra, 2005). The influence of climate, however, is still difficult to ascertain. So far, studies linking speciation with climate focused on the influence of Pleistocene glaciations, often through the questionable refuge hypothesis. New proposals are needed to account for Pleistocene diversification. One possibility is the disturbance-vicariance hypothesis (Noonan & Gaucher, 2006), according to which, a maintained but oscillating cooling trend can cause downward altitudinal migrations, thus favoring the spreading of cool-adapted species, colonization of new habitats, and frag-

mentation and isolation of initial populations, which may finally result in adaptive radiation and allopatric/parapatric speciation (Colinvaux, 1998; Rull, 2005). An elegant example of such mechanism can be found in the harlequin toads of the genus *Atelopus*. It has been suggested that the Guayanan species of this genus derive from a common ancestor that, thanks to the Pliocene cooling, migrated from the Andes and crossed the Amazon basin (Figure 1). Once in the Guayana region, the extant *Atelopus* species would have emerged by vicariance on isolated highland summits, favored by Pleistocene climatic changes (Noonan & Gaucher, 2005). Other mechanisms, as well as the coupling of two or more of them, are possible and this should be the target of future studies, especially in the case of aquatic organisms. The results shown here support the view of Neotropical diversification as a complex process, in which paleogeographic and paleoclimatic forcings have been constantly interacting (Bush, 1994). However, the surprisingly high amount of speciation found during the last 2.6 my, when climate changes have been the stronger environmental constrain, is remarkable.

As phylogenetic research is rapidly growing, and the dating methods constantly improving, the conclusions of this study should be periodically revised and updated with the new information available. It would be desirable to compare these results with other tropical regions of the world; unfortunately, the scarcity of molecular phylogenetic studies at the species level in African and Asian tropics is a handicap (Pennington et al., 2004b; Plana, 2004). The tempo and mode of speciation, and the Tertiary-Quaternary debate, is a common issue to other, extra-tropical regions, with important implications for conservation (Hewitt, 2004). A classical example is the continuing polemics about the origin of the North-American avifauna (Johnson & Cicero, 2004; Lovette, 2005; Zink & Klicka, 2006). It would be useful to establish a global database based on phylogenetic dating, to face the problem of biodiversity origin and conservation from a worldwide perspective, on the basis of real data about speciation timing.

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Appendix 1

Molecular phylogenetic studies selected as sources for raw data, according to the criteria settled in the methods section.

Aleixo, A. 2004. *Evolution* 58: 1303-1317.

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