

Neotropical biodiversity: timing and potential drivers

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The origin of extant neotropical biodiversity has been a controversial topic since the time of Darwin. In this review, I discuss the timing of, and potential driving factors associated with, diversification using recent evidence from molecular phylogenetics. Although these studies provide new insights into the subject, they are sensitive to dating approaches and targets, and can eventually lead to biased conclusions. A careful analysis suggests that the origin of extant neotropical biodiversity cannot be attributed to the action of one or few events during key time intervals. Rather, it is the result of complex ecological and evolutionary trends initiated by Neogene tectonic events and palaeogeographical reorganisations, and maintained by the action of Pleistocene climatic changes.

The Neotropics and the latitudinal diversity gradient

The amazing biodiversity of the Neotropics had already been noted during the 19th century by naturalists such as Alexander von Humboldt and Charles Darwin [1]. Today, the decline of biodiversity with latitude is a well-established biogeographical pattern known as the Latitudinal Diversity Gradient (LDG) [2]. Several potential causes of the LDG have been proposed, all with more or less factual support. However, the problem remains unsolved. The topic has tremendous significance for the understanding of the present-day biosphere of the Earth, an interest that is more than intellectual curiosity. Without this knowledge, it is almost impossible to understand the effect of external and internal ecological and evolutionary drivers on the biosphere, which further hinders capacity to deal with eventual future environmental changes and their potential ecological consequences [3]. Here, I discuss current hypotheses about the origin of the high extant neotropical biodiversity, in terms of generation time and the more probable diversification agents.

Theoretical and empirical approaches

To date, the topic of neotropical biodiversity has been addressed from two main perspectives, one theoretical and the other empirical. The theoretical approach has centred on the potential ecological and evolutionary mechanisms favouring the development of the present-day LDG, and has focused primarily on short-term ecological knowledge and modelling. The initial idea that high tropical diversity was a consequence of extended environmental stability over time, favouring niche partitioning, was

questioned in the face of the realisation that the tropics have experienced environmental shifts similar to those occurring in extra-tropical regions [4,5]. Since then, a proliferation of ecological models has sought to explain the coexistence of more interacting species in the tropics, mainly as a function of niche differentiation, area, climate and energy availability, and biotic interactions [6–12]. Spatial scaling and environmental heterogeneity have been recognised as fundamental aspects important to a full understanding of global biodiversity patterns [13,14]. From a theoretical perspective, three general types of models have been proposed to explain the extant LDG. According to the ‘tropics as a cradle’ model, species origination is higher in tropical areas and extinction rates do not vary latitudinally. In the ‘tropics as a museum’ model, origination rates are constant but extinction rates are lower in the tropics. The ‘out of the tropics’ model proposes that origination is higher and extinction is lower in the tropics than in extra-tropical areas [8]. To test ecological models properly, however, empirical evidence is mandatory [15].

The empirical approach has traditionally relied upon modern biogeographical patterns and the fossil record, including palaeoecological and palaeoclimatic reconstructions. Based on this type of evidence, hypotheses emphasising the importance of Quaternary climatic changes on

Glossary

Chronostratigraphic correlation chart: a graphic display summarising the stratigraphy of a particular area. The vertical scale represents geological time, the horizontal scale represents distance, and the time range and geographical extent of known stratigraphic units are plotted against these two variables [72].

Crown group: a monophyletic clade that contains all extant members of the clade in addition to its last common ancestor and all of its descendants, both living and extinct. The extinct taxa that lie between the crown group and the nearest living relatives of that clade are called the ‘stem group’ [55].

Gauss–Matuyama palaeomagnetic reversal: geological boundary dated to 2.6 Ma, characterised by the reversal of the magnetic field of the Earth, from the normal polarity (i.e. as in the present) of the Gauss chron (3.6–2.6 Ma) to the inverted polarity of the Matuyama chron (2.6–0.8 Ma) [72].

International Commission on Stratigraphy: Commission of the International Union of Geological Sciences (IUGS), whose primary objective is to define precisely global units (systems, series and stages) of the International Chronostratigraphic Chart that, in turn, are the basis for the units (periods, epochs and ages) of the International Geologic Time Scale; thus setting global standards for the fundamental scale for expressing the history of the Earth (<http://www.stratigraphy.org>)

Lithostratigraphy: branch of stratigraphy concerned with the description of rock units in terms of their lithological features. It deals with the spatial relations of such rock units, but does not take into consideration the evolution of the organisms contained within the units (biostratigraphy) or geological time (chronostratigraphy) [72].

Neogene: geological period starting 23 Ma and ending 2.6 Ma. The Neogene Period follows the Palaeogene Period as the second period within the Cenozoic Era and is succeeded by the Quaternary Period [73].

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speciation have flourished. Over the past few decades, the development of molecular phylogenetic methods has provided crucial evidence, mainly in relation to the age of extant species and clades. As a result, a shift has occurred towards a paradigm involving a pre-Quaternary (mainly Neogene) origin for neotropical species. Here, the more recent molecular phylogenetic evidence, and the available meta-analyses based on it, used thus far to support either one or another paradigm is critically analysed, with the conclusion that: (i) neotropical diversification is a complex topic that cannot simply be restricted to a particular time interval and one or a few mechanisms; and (ii) both Neogene tectonic and palaeogeographical reorganisations, and Quaternary climatic cycles seem to have been equally important drivers of the origin of neotropical biodiversity. Emphasis is on the origin of extant neotropical species; biodiversity trends through geological history are beyond the scope of this paper.

The Quaternary and the Pleistocene

The definition of Quaternary is a crucial issue in this debate. Until a couple of years ago, the onset of the Quaternary, which corresponds with the boundary between the Pliocene (the last Neogene stage) and the Pleistocene, was set at ~1.8 million years before present (Ma), on the basis of lithostratigraphic criteria (see Glossary). However, the last version of the global chronostratigraphical correlation chart approved by the International Commission on Stratigraphy, which is the organisation responsible for this matter, places the Pliocene–Pleistocene boundary at ~2.6 Ma, coinciding with the Gauss–Matuyama palaeomagnetic reversal and the onset of glaciations [16]. This makes a big difference where the timing of speciation is concerned. Indeed, in the old framework, all species that emerged between 1.8 and 2.6 Ma were considered to be Neogene species; however, according to the new scheme, they should be considered of Quaternary origin. The Quaternary embraces the Pleistocene and the Holocene series, with the boundary at 11 500 years before present (y BP). The Holocene could be considered the interglacial following the last glaciation and, hence, part of the Pleistocene variability. This is why the terms ‘Quaternary’ and ‘Pleistocene’ are sometimes used interchangeably, although they are not synonyms. The Pleistocene is now defined mostly in palaeoclimatic terms, as the epoch in which the glaciations occurred. Therefore, the Pleistocene versus pre-Pleistocene (or pre-Quaternary) debate in relation to speciation turns out to be a debate on the influence of either climatic or other factors on diversification [17].

Neotropical diversification drivers

Beyond a merely chronological debate, causal mechanisms and their drivers would have been very different if diversification occurred either during or before the Pleistocene. Quaternary geographical and topographical patterns in the Neotropics have remained largely unchanged, relative to those observed during the Neogene [18]. The main Quaternary environmental shifts have been linked to the glacial–interglacial alternation and their potential evolutionary impacts, whereas the Neogene has been characterised by significant tectonic and palaeogeographical

reorganisations, leading to the creation of new pathways and barriers for biotic evolution [18].

The refuge hypothesis: rise and fall

A milestone in this debate was the finding, approximately 30 years ago, of palaeoecological evidence for extensive aridity that was assumed to have characterised the neotropical lowlands during the Last Glacial Maximum (LGM), approximately 21 000 yr BP. This, together with some animal endemism patterns, led to the proposal of the refuge hypothesis, thus reinforcing the Pleistocene paradigm, which dominated the discussion until recently. According to this hypothesis, neotropical speciation would have been determined chiefly by the alternation of vicariance and gene flow cycles linked to glacial contractions and interglacial expansions of lowland rainforests patches (or refugia), controlled by recurrent aridity–humidity oscillations. Evidence in support of this concept has been sought from the present biogeographical patterns of the Amazon basin, under the assumption that the former hypothetical refugia persist and can be identified with modern regions having higher biodiversity and endemism [19].

Further palaeoecological evidence, however, has led to serious questions about the validity of the refuge hypothesis. Critics have dismissed the assumed glacial aridity and proposed instead that cooling and atmospheric CO₂ depletion could have caused biotic reorganisations in the Amazon rainforests without compromising its continuity [20]. At present, this view is widespread. For many, the refuge hypothesis is considered valid mostly for the temperate zones but not for the Neotropics [21]. This position has, in turn, sparked a strong reaction, against not only this particular speciation mode, but also the Pleistocene paradigm itself. The outcome has been a shift towards the prevalence of Neogene diversification, an idea supported by several molecular phylogenetic dating studies. Key Neogene events have been emphasised in this context, including the closure of the Panama Isthmus (completely disrupting the connection–disconnection patterns in both continental and marine biomes), the Andean uplift (by creating a major continental barrier and a multitude of new mountain habitats and opportunities for colonisation, allopatry and adaptive radiation), or the cessation of marine incursions into the Amazon basin, with dramatic consequences for drainage patterns and, as a consequence, for spatial biotic features at local and regional scales [22–26]. It should be stressed, however, that the only one of these events with a well-bracketed age is the closure of the Panama Isthmus, whereas the age of Andean uplift and the occurrence of epicontinental seas are still controversial. According to some defenders of this view, the Quaternary was a time of distribution shifts, and probably of increased extinction, and can no longer be considered a time for diversification in the region [27]. Other diversification mechanisms that might have acted during both the Neogene and the Quaternary are: special edaphic adaptations, biotic interactions (especially pollination and plant–animal relationships), dispersal ability, niche conservatism, climate–area synergies, and major hydrological changes in the palaeo-Orinoco fluvial system [28].

Alternative Quaternary speciation hypotheses

These findings, however, do not invalidate the existence of Quaternary diversification because the refuge hypothesis is not the only proposed speciation model [19,29]. For example, recurrent altitudinal migrations during the Pleistocene glacial cycles have been considered crucial for biotic diversification in the Andes. These migrations would serve to drive successive connections and disconnections of high-mountain biomes. In the Amazon basin, low temperatures and atmospheric CO₂ depletion could have led to downward migrations in the biota of surrounding mountains. The resulting heterogeneous spatial patterns would have promoted vicariance [30,31]. The disturbance–vicariance hypothesis proposes a pre-Quaternary downward biotic migration from the Andes to the Amazon lowlands, followed by Pleistocene migration and speciation through the lowlands. When the migration ultimately reached the easternmost Guayana mountains, a new sequence of speciation events occurred on their summits during the past million years [32]. Neotropical mountains thus seem to have been decisive for Quaternary evolution, as they could have acted as ‘species pumps’ for the surrounding midlands and lowlands [33,34].

Molecular phylogenetic evidence

Biogeographical and palaeoecological evidence has been able to furnish testable hypotheses but has failed to provide dates for the origin of extant species. The fossil record can help but its biased and fragmentary nature is a constraint. The recent development of molecular phylogenetic methods has provided more chronological and explanatory power. These methods still have room for improvement, especially in relation to assumptions on rates of evolution, appropriate calibration, and incomplete taxonomic and genetic sampling [35–38], but available data already provide a sound and extensive basis for comparison. After dismissal of the refuge hypothesis, phylogenetic evidence on pre-Quaternary diversification flourished [23,39–41], but the same type of evidence also supported Quaternary diversification [42–44].

When the evidence from molecular phylogenies published up to 2006 was gathered to obtain a thorough picture, it was realised that the neotropical species dated by this method did not show any overall chronological trend. Indeed, 49% of the > 1400 species whose origin has been estimated in this way were shown to have originated during the Quaternary, whereas the other half had originated during the Neogene or earlier [17]. Timing among different types of organism differed, with insects, plants, birds and reptiles having more Quaternary species; and molluscs, mammals, fishes and amphibians having more Neogene representatives. By contrast, a more recent review concluded that most (87.5%) of the 169 genera studied in the Amazon basin [mainly birds (81) but also plants (34), mammals (22), amphibians (13), insects (12), fishes (3), reptiles (3) and arachnids (1)] diversified during the Neogene [40] (Figure 1). These differences can arise from dating procedures. In this case, the difference is the dating target. The targets of the first meta-analysis were the extant species [17], whereas the targets of the second were the crown groups [40].

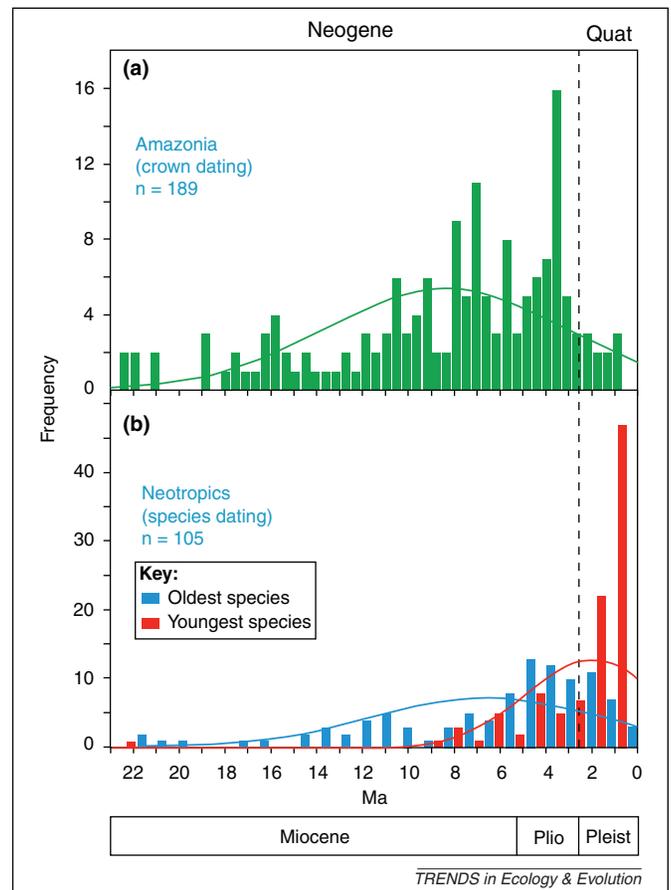


Figure 1. Timing of neotropical speciation. (a) Histogram and normalised density function of the ages of initial diversification events (crown nodes) leading to present-day species in the Amazon basin [40]. (b) Histograms and normalised density functions of the ages of oldest (blue) and youngest (red) extant species of each dated clade in the Neotropics [17]. The age of the oldest species often coincides with the crown age of the corresponding clade, the only exception being the case in which the oldest species is extinct (Figure 2). These ages follow a pattern similar to (a), but most youngest species originated during the Quaternary (Table 1).

In a phylogeny, a crown group can include some extant species (in fact, the older ones), some extinct ancestors that have further led to one or more extant species, and other species that have become extinct without leaving any descendant (Figure 2). In other words, a crown group accounts for the sub-recent evolutionary history of a given clade, but is not necessarily representative of either the origin of present-day extant species or, consequently, the extant biodiversity patterns. Crown dating would be useful when trying to elucidate the impact of a significant past event, for example the closure of Panama Isthmus [45] or the Andean uplift [23], on the diversification of neotropical biota. It has also been suggested that it avoids problems related to extinction rates [46]. However, this approach could be misleading when assessment of the origin of extant species is in question. For example, it has been estimated that the jewelweeds (*Impatiens*, Balsaminaceae) would have only contained one-fifth of its nearly 1000 species without the Pleistocene climatic changes [47]. Similarly, a recent study on neotropical *Adelpha* butterflies concluded that clade (crown) ages did not explain their high diversity, which is linked more to recent rapid diversification events [48]. By contrast, an approach that involved dating only of extant species would tend to mask

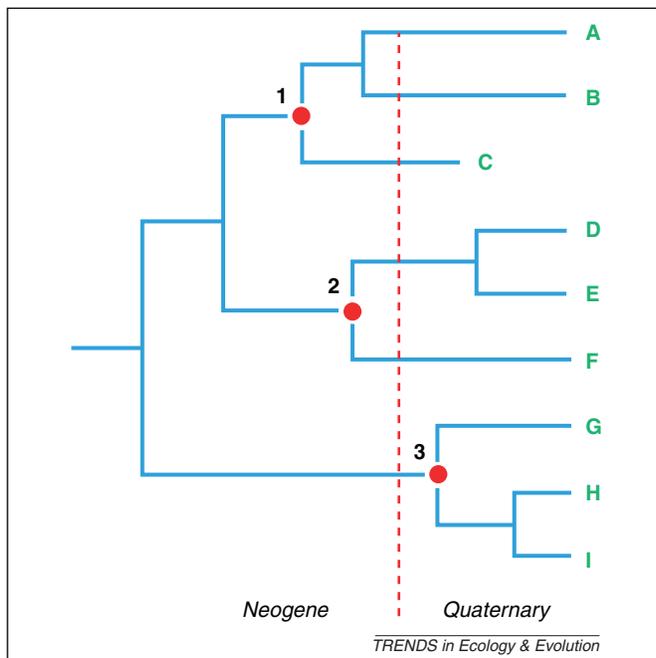


Figure 2. Hypothetical phylogeny illustrating common situations encountered in the study of neotropical species. Crown nodes are highlighted by red dots. Crown group 1 attained its present diversity in the Neogene and has one extinct species (C); group 2 initiated its diversification in the Neogene and lasted during the Quaternary, whereas group 3 diversified during the Quaternary. Of the eight hypothetical extant species represented, three (A, B, F) originated during the Neogene and five (D, E, G, H, I) during the Quaternary. However, the main diversification event of groups 1 and 2 (containing five extant species) occurred during the Neogene and only one initiated its diversification during the Quaternary (group 3).

previous diversification events that could have been important to the development of neotropical biota and community assembly; for example, singular Neogene events initiating key diversification trends without which many extant species would have not emerged. A coupled evaluation of the dating of crown and extant species would serve to provide a clearer picture of emergence of neotropical biodiversity [49].

A meta-analysis including both crown and species dating is available for the Neotropics [17]. This investigation shows that, of the 105 genera and species clades studied, 19.0% initiated and attained their present diversity during the Quaternary (Table 1). Of the 78.1% that initiated their speciation during the Neogene, only a quarter (24.8%) attained their present diversity in the same period, and more than a half (53.3%) continued to diversify during the

Table 1. Chronological diversification patterns of clades of neotropical genera and species^{a,b}

	Oldest species	Youngest species	
		Neogene	Quaternary
Quaternary	20	0	20
Neogene	82	26	56
Palaeogene (>23 Ma)	3	2	1
Total	105	28	77

^aBased on [17].

^bThe first column indicates the number of genera initiating their diversification in each geological period, as deduced from the age of their oldest extant species. The other two columns show the number of genera that ended their diversification in each period, as represented by the age of their corresponding youngest species.

Quaternary. Globally, most genera (78.1%) started to diversify in the Neogene and most (73.3%) ended their diversification during in the Quaternary (Figure 1). Noteworthy, the number of groups whose origin is exclusively Neogene (24.8%) or exclusively Quaternary (19.0%) is similar.

The role of extinction

Biodiversity is a balance between species input (speciation and immigration) and output (extinction and emigration), acting on a pre-existing species pool [50]. Extinction is poorly addressed, probably because of the difficulty of measuring it [51]. Differential Quaternary extinction patterns documented in the fossil record have been proposed as one of the causes of present-day LDGs [43,52]. Empirical approaches commonly ask why the tropics are so diverse, but the reverse question of why extra-tropical regions are so impoverished has also been formulated. The fossil record and some molecular phylogenetic studies provide contrasting insights into this question. For example, both significant extinctions and high diversification rates have been documented for Europe during the Pleistocene [53,54]. Unfortunately, evidence for extinction still relies on the fragmentary fossil record [55], and its significance is difficult to address. Climate change has been viewed as a primary influence on extinction, except during the last ten millennia, when humans seem to have had a role [56]. Synergistic effects among different drivers leading to amplifying feedbacks should not be neglected [57]. The study of extinction patterns through time is still in its infancy in the Neotropics. Despite some claims that, during the Quaternary, extinction has been more intense than speciation [27], empirical data are still insufficient to provide sound conclusions.

Conclusions, final comments and lessons for the future

The modern biodiversity patterns on Earth are the result of a long and complex history of evolutionary trends, mediated by, and intermingled with, ecological processes, and governed by external environmental forces. Such complexity is evident even within single clades, where significant Neogene and Pleistocene speciation co-occur [58–60]. Therefore, proposals emphasising the relevance of one or another factor (e.g. as for Pleistocene climatic changes or Neogene tectonic events) at the expense of others, would provide an incomplete perspective. The relevance of these and other events to diversification seems unquestionable, but the explanation of present-day biodiversity patterns requires not only the synergy of several scientific disciplines, but also a wide range of spatial and temporal scales. In the Neotropics, floral diversity has been favoured by the combination of mature as well as rapid and recent radiations, as it contains relatively stable environments and more dynamic landscapes. Thus, environmental heterogeneity, in both time and space, and evolutionary history seems to be crucial to understanding the origin of extant biodiversity patterns [61,62]. Differences among organism groups should also be considered. For example, amphibians show different features compared with endothermic taxa, owing to their strong dependence on water supply and climate. In this group, the magnitude of richness is

strongly determined by regional history, whereas within-region patterns are consistently linked to water and temperature [63].

Dating, a crucial tool for hypothesis testing, has been empowered by the recent development of molecular phylogenetics. The dating target is a decisive choice and depends on the type of study to be addressed. If the objective is to identify the more significant events that initiated the diversification of extant species groups, then crown dating is a suitable procedure. If the aim is to know the age of origin of extant species, individual dating would be preferred. However, to understanding fully the origin of present-day biodiversity patterns, both approaches should be combined. Extinction patterns should also be considered, although they cannot be derived from phylogenies and the fossil record is the only option available to date. In the case of the Neotropics, the evidence suggests that many extant clades initiated their diversification during the Neogene (probably through the action of events such as the closure of the Panama Isthmus or the Andean uplift) and attained their present biodiversity during the Quaternary, when the younger species originated, under the dominant climatic instability. Other groups attained their present diversity during the Neogene, whereas a third group fully diversified during the Quaternary. Future work should consider that different neotropical biomes seem to have distinct underlying geological and biological drivers and, therefore, contrasting evolutionary history and timing of species origin is an expected outcome [64]. Another methodological issue that should be considered for future work is increased taxonomic and genetic sampling, for more robust interpretations [28,38].

Anticipating potential biotic responses to future environmental changes is crucial for biodiversity conservation. A crucial question is whether species would be able to: (i) tolerate, as a result of phenotypic plasticity, the projected global warming; (ii) migrate to more favourable habitats; or (iii) quickly evolve and adapt to the new conditions [65,66]. If not, they would become extinct. Given the rapidity of the ongoing climate change, evolution seems the most problematic option. However, rapid evolution under environmental pressure has been documented in the past, especially in the Quaternary, during which the genetic structure of present-day species and their populations was shaped [67]. Therefore, the study of Quaternary evolutionary trends would be helpful to obtain past analogues for potential future situations. A valuable outcome would be the identification of the 'evolutionarily significant units' as conservation targets [68], and their evolutionary potential, which depends, in turn, on levels of intra-specific genetic variability [69]. Studies of this kind are making advances in some northern temperate areas [70,71], and similar surveys should also be encouraged in the Neotropics.

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