Dynamic endemism and ‘general’ biogeographic patterns

By Silvio Shigueo Nihei

This paper deals with some theoretical aspects of areas of endemism. I do not intended to make a contribution toward an innovative methodology but, in fact, my major concern is toward understanding and approaching areas of endemism under a dynamic view, which I am terming ‘dynamic endemism’. Following my initial argumentation on dynamic view of areas of endemism, I will thereafter exemplify my discussion with two case studies (Amazonia and the Mexican Transition Zone).

Areas of distribution and areas of endemism are understood as basic elements in biogeography. Area of distribution can be defined as the whole spatial range occupied by a taxon at a given time (Roig-Juñent et al. 2002) or a region occupied by a monophyletic taxon (Humphries and Parenti 1999). Basic information in biogeography are the localities of occurrence known for a given taxa, and gathering of localities is the starting point for the inference of areas of distribution. As it is virtually impossible to have all the localities of occurrence known and recorded for any taxon, some manual methods have been applied by authors to estimate area of distribution by extrapolation (see Roig-Juñent et al. 2002 for a review). On the other hand, definition of areas of endemism is considerably more complex. Many authors have approached the subject with both theoretical and operational discussions (Nelson and Platnick 1981, Cracraft 1985, Harold and Mooi 1994, Morrone 1994, Linder 2001, Roig-Juñent et al. 2002, Hausdorf 2002, Szumik and Goloboff 2004). Nevertheless, some common points can be traced among the several authors and, despite differences and controversies, in a general way, areas of endemism can be defined in terms of spatial coincidence among areas of distribution of different taxa. For a comprehensive definition we can refer to that of Harold and Mooi (1994), by which areas of endemism should be recognized after phylogenetic and distributional congruence: “…area of endemism as a geographic region comprising the distributions of two or more monophyletic taxa that exhibit a phylogenetic and distributional congruence and having their respective relatives occurring in other such-defined regions” (Harold and Mooi, 1994 p. 262).

Coincidence on biotic history (phylogeny) and on their distribution in space should thus be regarded as the main components assumed as relevant and essential to recognize areas of endemism. The complexity on dealing with areas of endemism is that identification (delimitation) of areas of endemism and the area relationships reconstruction are two inextricable steps. Morrone (2001b) defined this as being a two-stage analysis comprised first by the recognition of areas of endemism (primary biogeographic homology) and then a cladistic test of the previously recognized areas (secondary biogeographic homology). That is a rational procedure intended to integrate panbiogeography (to identify primary spatial homologies) and cladistic biogeographic methods (to evaluate and legitimate the previously identified homologies). Since areas of endemism are hierarchically linked (nestedness) and scale-dependent (Cracraft 1985), when defining area relationships one is also delimiting the areas of endemism in a given scale. Therefore, an area may be a set of localities on southeastern Brazil at one end to the Neotropical region at the other end, or even Gondwana and Pangaea, if going back to past areas. This reciprocal dependence raises another problem towards a reliable delimitation of areas of endemism, because the cladistic test (sensu Morrone 2001b) results in relationships among areas of endemism and therefore secondary biogeographic homologies are recognized and evaluated in a given hierarchical level (above-terminals) but without considering the monophyly of those terminals.

An area of endemism is a biological concept of space that contemplates processes and pattern. Processes related to the recognisability of areas of endemism are of two basic kinds, *geological* spatio-temporal processes (plate tectonics, climate change, sea water level change, etc.) and *biological* spatio-temporal processes (vicariance and extinction). Exemplification of this argument follows as ‘Stage 1’ (the processes): areas of endemism should exist due to intrinsic response of an ancestral taxon affected by the presence of a geological/ abiotic barrier splitting its original distribution, and the response (vicariance) being the isolation of that ancestral and subsequent differentiation into two derived sister-taxa. And 'Stage 2' (the pattern): when there is coincidence of several different taxa presenting the same vicariant response to that exactly same geological/ abiotic barrier, so there is a biogeographic pattern recognizing areas of endemism and their relationship. Similar responses from different taxa to the same geological events generate a congruent pattern of area relationships (spatial and temporal congruence, *sensu* Donoghue and Moore 2003). In a higher-level perspective, we might observe nestedness of restricted areas of endemism (districts and provinces) into large-scale areas of endemism (subregions, regions and realms) as Amazonia, the Atlantic Forest and the Neotropical region. Morrone (2001b) pointed out this as a "natural hierarchy of the biogeographical system".

Within a given time range (Δt between –10 and –7, assuming t=0 as the present time), a given area will involve a series of geological/ abiotic events. Similar responses from different taxa at this Δt will generate a general biogeographic pattern X. In another time range (Δt between –6 and –3), the same area will involve another series of geological events, and again, similar responses from different taxa at this Δt will generate another general biogeographic pattern Y. Patterns X and Y might be similar or not in terms of area relationships. Even in case of similarity, they are not congruent, as they were resulting from different series of geological events, thus temporally incongruent. Assuming that in the pattern X the areas A-B-C-D-E have resulted with the relationship (A(B(C(D,E)))), and in pattern Y related as (A((C,E)(B,D))). Based on this, one may conclude that DE is an area of endemism (monophyletic) in X, but not in Y. This illustrates how areas of endemism have their 'existence' affected along time scale and the floating dynamics of endemism across temporal dimension. This hypothetical explanation and my initial argumentation on dynamic endemism could be exemplified by some study-cases but herein I will discuss two important and relatively well-studied areas: Amazonia and the Mexican Transition Zone.

Amazonia is a spatial unit traditionally regarded as a historical unit (Fig. 1A), which means that biotic elements from all the small inclusive units of Amazonia share a common history. Several studies have supported Amazonia as a biogeographical unit: on Reduviidae bugs (Morrone and Coscarón 1998), primates (Da Silva and Oren 1996), passerines (Bates et al. 1998), several plant and animal taxa (Morrone 2000, 2001a), and many others. On the other hand, there are also several studies with favourable evidence on the hypothesis that Amazonia is a composite area (Fig. 1B): on primates and Nematoceran flies (Amorim and Pires 1996, Roig-Juñent and Coscarón 2001), Brachyceran flies (De Carvalho 1999, De Carvalho et al. 2003, Nihei and De Carvalho, 2007), Meliponini bees (Camargo 1996, Camargo and Moure 1996, Camargo and Pedro 2003), Pentatomiidae bugs (Grazia 1997), Cercopidae homopterans (Goldani and Carvalho 2003), Curculionidae beetles (Morrone 2002), Riodinidae butterflies (Hall and Harvey 2002), Trichodactylidae decapods (Morrone 2003), Felidae mammals (Eizirik et al. 1998), Aves (Cracraft and Prum 1988, Prum 1988, Marks et al. 2002), *Cecropia* plants (Franco and Berg 1997), several plant families (Cortés and Franco 1997), and several plant and animal taxa (Morrone 2000).

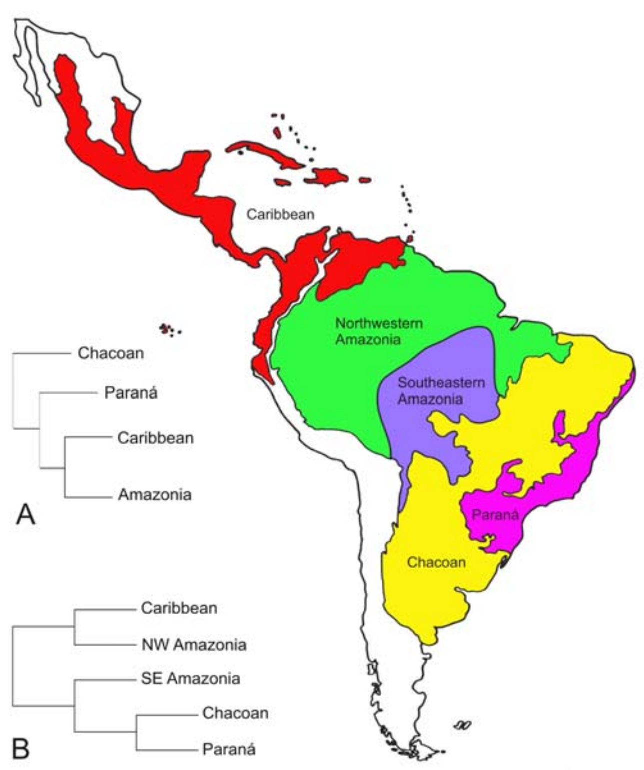

Fig. 1. Biogeographical classification of the Neotropics into subregions as suggested by Nihei & De Carvalho (2007), with area relationships proposed by: A, Morrone and Coscarón (1998); B, Nihei and De Carvalho (2007).

Not all of these individual patterns can be gathered within the same general pattern, however, because these patterns are not temporally congruent (Nihei and De Carvalho 2007). Ages provided by authors were Cretaceous (Amorim and Pires 1996, Grazia 1997, De Carvalho 1999), Quaternary (Manfrin et al. 2001), Cenozoic (Cracraft and Prum 1988), and Plio-Pleistocene (Eizirik et al. 1998). Furthermore, the Platyrrhini monkeys included in the pattern of Amorim and Pires (1996), besides the Nematoceran dipterous, have been dated to Oligocene (35 mya) (Schrago and Russo 2003). The hypothesis of composite Amazon was first developed by Dalton Amorim and Maria Rita Pires (Amorim and Pires 1996, Amorim 2001) and the main geological event responsible for generating that pattern is the lacustric formation in Amazon basin along the Amazonas-Madeira-Mamoré rivers caused by marine water transgression during Late Cretaceous. Nevertheless, several studies have reinforced that marine water transgression into the South American continent has taken place several times in the past (Hoorn 1993, Räsänen et al. 1995, Frailey 2002, Nores 2004, etc.), not only during the Late Cretaceous as pointed out in the model. And that is why this same pattern could be observed repeatedly in different groups on different time periods, leading some authors to equivocally determine a general biogeographic pattern, when in fact they are dealing with "pieces of different puzzles" (Nihei & Carvalho 2007).

Part of the discordance on the status of Amazonia as a unit or a composite area might be related to this temporal dynamism on the existence of a vicariance event dividing the Amazon. Organisms that did not respond or were not affected by the marine water transgression forming an epicontinental sea in Amazon do have corroborated a biogeographical pattern showing Amazon unity, as corroborated by the references aforementioned. While the organisms affected by this epicontinental sea, whenever it have occurred, have corroborated a pattern with Amazon as a composite area.

My second example is the Mexican Transition Zone (Fig. 2). This transitional area interfaces Neotropical and Nearctic regions and was firstly recognized and discussed by Gonzalo Halffter (1962, 1976, 1978, 1987). Besides, several studies have undertaken biogeographic analysis of this area (Liebherr 1994, Hernández-Baños et al. 1995, Luna-Vega et al. 1999, Marshall and Liebherr 2000, Morrone and Márquez 2001, Escalante et al. 2007, and several others; see Morrone 2005 for a review). Despite differences on the delimitation of areas of endemism and discordances on the areas relationships, we can synthesize a common finding recognized by the different authors. A number of the proposed area relationships converge so that Mexico is divided along the Transmexican Volcanic Belt into one northern and other southern portions (*e.g.*, Liebherr 1994, Marshall and Liebherr 2000, Morrone and Márquez 2001) (Fig. 2A). A recent study (Escalante et al. 2007), however, has revealed an opposite hypothesis with a division into eastern and western portions partially delimited, at the present time, by the mountain range of Sierra Madre Oriental (Fig. 2B). Escalante et al. (2007) distinguish both divisions by the age and nature of the major geological event responsible for generating each pattern: the north-south division due to North and South American plates convergence on Miocene period, whereas the east-west division associated to the Caribbean plate eastward migration in the Paleocene.

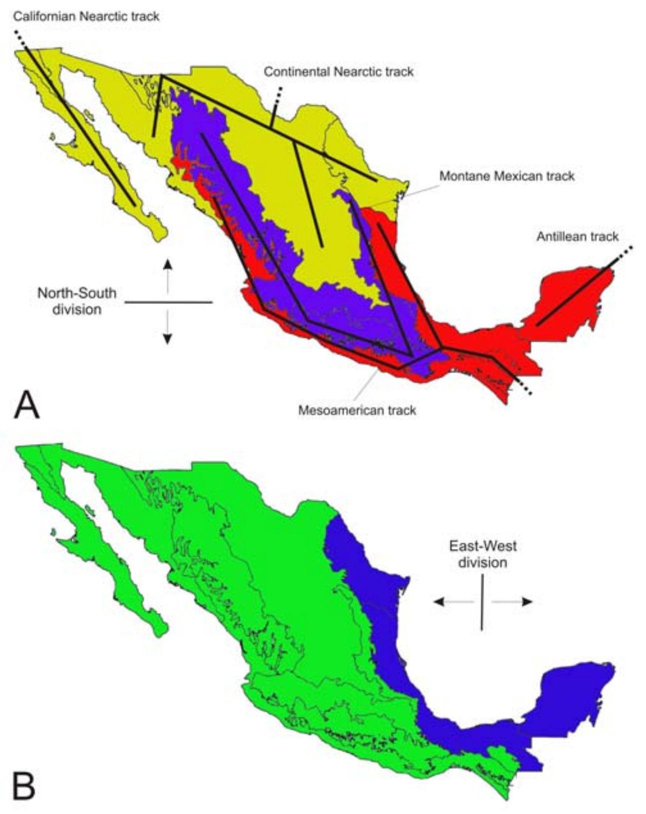

Fig. 2. Biogeographical classification of Mexico into provinces based on Morrone (2001a, 2004) (modified from Morrone 2005), with indication of: A, North-South division (Morrone and Márquez 2003); B, East-West division (Escalante et al. 2007).

The Mexican Transition Zone is widely and unquestionably recognized as a complex area with composite biotic nature, with not only Nearctic, Mesoamerican and South American affinities of its inhabiting biota, but also particular endemism. With regards to the attributes and differences between each area, some parallels can be made by extending the discussion on the dynamism of Amazonian biogeography to the Mexican Transition Zone. In this second case, we also observe dynamic patterns of endemism, with dual area cladograms recognizing relationships differing according to the temporal dimension (Paleocene or Miocene). Escalante et al. (2007) have assumed that former studies have not detected these two opposite patterns on the area, perhaps some of them comparing (and even constraining) the distributional patterns obtained onto the existing hypothesis of north-south division. The authors correctly warn that "previous biotic diversification studies of the Nearctic and Neotropical regions need to be revised".

By assuming this view, one should define and delimit spatial homologies (areas of endemism) also incorporating temporality. For this reason, methods available to identify primary spatial homologies (*e.g.*, panbiogeography, PAE, NDM) are not questioned herein, except that their users must be aware of the temporal dynamics of areas of endemism. Additionally, general biogeographic patterns for any area should incorporate temporal dimension and be interpreted as age-based patterns and not only form and space-based patterns. Area-relationships might differ along the time and obviously patterns also should be different and interpreted as differing for any time interval. Under this perspective, we should understand biogeographic general patterns as general hypothesis associated to a given time interval and not as an atemporal general hypothesis.

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