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REVIEW

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Revisiting Amazonian phylogeography: insights into diversification hypotheses and novel perspectives

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Abstract The Amazon Basin harbors one of the richest biotas on Earth, such that a number of diversification hypotheses have been formulated to explain patterns of Amazonian biodiversity and biogeography. For nearly two decades, phylogeographic approaches have been applied to better understand the underlying causes of genetic differentiation and geographic structure among Amazonian organisms. Although this research program has made progress in elucidating several aspects of species diversification in the region, recent methodological and theoretical developments in the discipline of phylogeography will provide new perspectives through more robust hypothesis testing. Herein, we outline central aspects of Amazonian geology and landscape evolution as well as climate and vegetation dynamics through the Neogene and Quaternary to contextualize the historical settings considered by major hypotheses of diversification. We address each of these hypotheses by reviewing key phylogeographic papers and by expanding their respective predictions. We also propose future directions for devising and testing hypotheses. Specifically, combining the exploratory power of phylogeography with the statistical rigor of coalescent methods will greatly expand analytical inferences on the evolutionary history of Amazonian biota. Incorporation of non-genetic data from Earth science disciplines into the phylogeographic approach is key to a better understanding of the influence of climatic and geophysical events on patterns of Amazonian biodiversity and biogeography. In addition, achieving such an integrative enterprise must involve overcoming issues such as limited geographic and taxonomic sampling. These future challenges likely will be accomplished by a combination of extensive collaborative research and incentives for conducting basic inventories.

Keywords Amazonia · Terrestrial vertebrates · Biogeography · Evolutionary history · Phylogeography · Diversification hypothesis · Predictions · Coalescent

Introduction

The Amazon drainage basin is a major component of the Neotropical region that includes an area of over 8 million km^2 comprised mainly of lowland rainforest habitats (Sioli 1984). It extends across South America from the eastern Andean slopes towards the Atlantic coast and across the Brazilian and Guiana plateaus. There is large horizontal variation in relief across the basin (Bigarella and Ferreira 1985), and the overall warm and humid Amazonian climate also exhibits regional differences in precipitation and rainfall distribution (Salati 1985). Moreover, patterns of biotic composition and distribution have been influenced by a number of interrelated environmental features that have shaped the landscape development of Amazonia throughout its geological history (Hoorn et al. 2010c).

The analysis and interpretation of species evolution forms a strong basis for sustainable use and conservation planning strategies of species-rich regions such as Amazonia (Moritz 2002; Moritz and Faith 1998). Why Amazonia is so diverse relative to other regions on Earth is an important question in

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the discussion of large-scale species richness patterns. Time and variation in diversification rates are seen as major drivers of species richness patterns across different clades and regions, but this topic has been explored elsewhere (e.g., Mittelbach et al. 2007; Wiens 2011; Wiens et al. 2006). Nevertheless, understanding the link between Amazonia's intricate history and the mechanisms promoting and maintaining its high levels of species diversity remains a daunting task for evolutionary biologists (Moritz et al. 2000). Many alternative hypotheses have been proposed to explain species diversification in the Amazon Basin (reviewed in Haffer 1997). However, there is no agreement about the generality of any of these explanations, nor are they mutually exclusive (Hall and Harvey 2002; Patton and da Silva 1998). Difficulties exist in devising tests for competing hypotheses that lack temporal and spatial hierarchical division, as well as from the fact that organisms with inherently different life histories likely respond differentially to the same historical events (Moritz et al. 2000).

The integrative field of phylogeography plays a central role in elucidating the processes underlying patterns of genetic diversity at the species level (Avise 2000). Ever since its establishment as a discipline over two decades ago (Avise et al. 1987), phylogeographic methods have been employed to evaluate gene genealogies in a geographic context, and to infer biogeographic and demographic scenarios of interest (Avise 2009). More recently, advances based on the coalescent theory and technical developments have enhanced phylogeographic research (Knowles 2009) by establishing a rigorous statistical framework for the testing of explicit alternative models (Hey and Machado 2003; Hickerson et al. 2010). The coalescent is a retrospective approach that predicts the ancestry of DNA sequence samples (i.e., gene genealogies) under a mathematical model (Wakeley 2008). This theoretical approach forms the basis for a number of methodologies with varying assumptions that are implemented in different programs (Knowles 2004). Moreover, these methods are being applied to an increasing body of DNA sequence data derived from multiple loci (Brito and Edwards 2009) and from next-generation sequencing (Carstens et al. 2012; McCormack et al. 2012; Puritz et al. 2012). Therefore, the field of phylogeography is now equipped with innovative methods that will revolutionize the manner in which empirical data are evaluated. These new perspectives promise valuable insights for empirical studies concerned with species diversification in Amazonia.

Unfortunately, tropical countries lack many of the resources and infrastructure necessary to fully evaluate the mechanisms responsible for the formation and maintenance of their megadiverse biotas (Cracraft 2001). As a result, species-rich regions in the Southern Hemisphere such as Amazonia have been understudied relative to temperate regions of the world (Beheregaray 2008). Additionally, there are a number of practical challenges involved in studying evolutionary processes governing Amazonia's biodiversity. These include insufficient biological inventories scattered over a vast area coupled with relatively high rates of habitat loss (Garda et al. 2010; Peres et al. 2010; Silva et al. 2005). Lastly, although terrestrial vertebrates comprise the majority of phylogeographic studies (Beheregaray 2008), only a small percentage of Amazonian mammals, birds, reptiles and amphibians has been evaluated.

In this context, we present a paleoenvironmental overview of the Amazon Basin to serve as a brief background of the historical settings considered in the formulation of Amazonian diversification hypotheses. We then proceed by reviewing major hypotheses of biotic diversification in light of the phylogeographic research achieved in Amazonia. We expand genetic and genealogical predictions derived from these major diversification hypotheses, and provide a synthesis of the current status of Amazonian phylogeography, focusing on terrestrial vertebrates. We also summarize information about the number of studies, their choice of genetic markers and analyses, as well as the distribution of targeted taxa in areas of endemism. Finally, we include an empirical example to illustrate how hypothesis-driven approaches can be used to discern alternative biogeographic scenarios and infer evolutionary processes involved in species diversification in the Amazon Basin. We discuss the prospects for future investigations with regard to phylogeographic approaches and suggest areas for new biological inventories in Amazonia. We anticipate that this review will improve the basis for the interpretation of the historical evolution underlying species diversity and distribution in Amazonia.

Historical setting

Geological processes have had great influence over the development of the Amazon Basin and its ecosystems. The modern drainage is the result of relatively recent geological events that caused drastic changes in the Amazonian landscape (Hoorn et al. 2010c), and account for much of the biotic diversification patterns seen today (Rull 2011, 2008). The debate on the geological history of Amazonia is as yet contentious; however, it gains momentum as geological studies present new data and insights into depositional patterns, drainage formation, edaphic variation, and past climate dynamics emerge (Hoorn and Wesselingh 2010). Linking both geological and biological data, as well as those derived from interdisciplinary subareas, is key to interpreting patterns of biodiversity and biogeography (Riddle et al. 2008).

Several authors recently have emphasized the utility of placing inferences of the historical evolution of Amazonian organisms derived from molecular data within a geological context (e.g., Aleixo and Rossetti 2007; Antonelli et al. 2010; Pennington and Dick 2010). However, using a geological perspective for the design and testing of hypotheses of biological diversification in the Amazon Basin remains largely unexplored. This is complicated because geoscientific information over broad temporal and spatial scales is lacking due to difficult access to the terrain (Hoorn and Wesselingh 2010). As a result, geological frameworks attempting to resolve large-scale aspects of the history of the landscape in Amazonia (e.g., Campbell 2010; Figueiredo et al. 2009; Irion et al. 2005; Rossetti et al. 2005) often are subject to criticism and alternative interpretations of the data. Therefore, careful assessment of the historical settings should be made before any hypothesis can be applied as a working model to explain patterns of species diversity and distribution in the Amazon Basin. Nevertheless, the scarcity of solid paleoenvironmental data should not preclude Amazonian phylogeographic studies from exploring a priori hypotheses in experimental designs that seek to objectively integrate relevant information from biological and Earth sciences. Indeed, ad hoc explanations are potentially more misleading. Below, we summarize key aspects of the debate on geological history of the Amazon Basin and present alternative views of landscape evolution that are useful for interpreting species differentiation in a phylogeographic context.

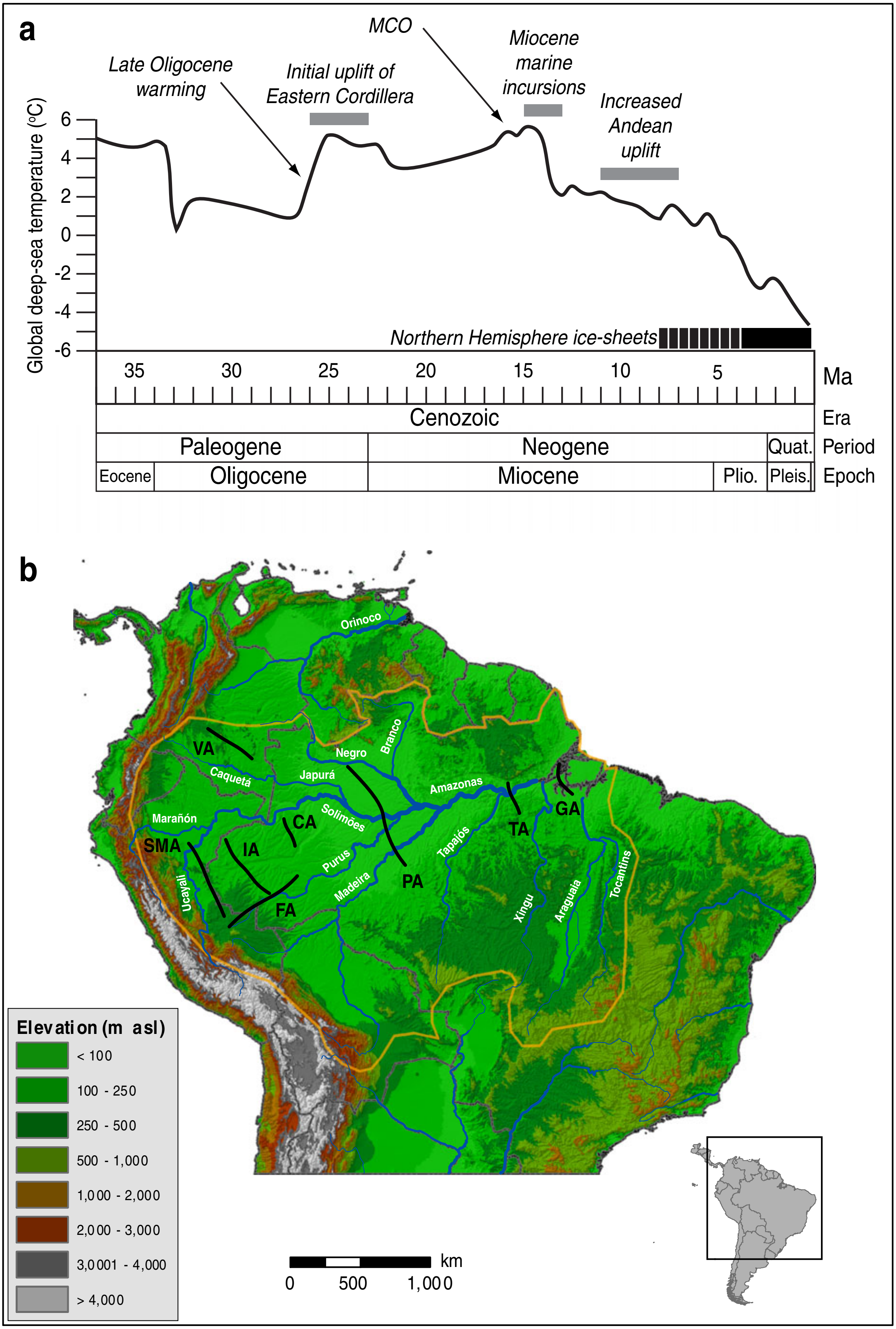
Geology and landscape evolution

The modern Amazon Basin is composed of several sedimentary units that can be distinguished based on their distribution, age and composition (Bigarella and Ferreira 1985). However, the interplay of sedimentary processes, tectonics, and climate and sea level fluctuations controlling the geological history of Amazonia has been complex (Irion and Kalliola 2010). Perhaps one of the most striking characteristics of Amazonian geology is the dichotomy between eastern and western Amazonia (Aleixo and Rossetti 2007). To the east of Manaus, the Amazon drainage divides the Precambrian basement of the Amazonian Craton into the Guiana Shield to the north, and the Brazilian Shield to the south. These two regions constitute the source of most of the sediments of the intracratonic basins, with distinct fingerprints from sediments of Andean provenance (Kroonenberg and de Roever 2010). The sedimentary fill of the east–west trend rift separating the two shields was deposited during the Paleozoic, with renewed subsidence in the Cretaceous and Cenozoic, although much less significant (Wanderley-Filho et al. 2010).

In contrast to eastern Amazonia, which remained mostly stable and had limited sediment deposition after the Late Cretaceous, western Amazonia experienced a much more recent and dynamic geological history (Aleixo and Rossetti 2007; Rossetti et al. 2005). This region is composed of numerous sedimentary units deposited during the Late Cenozoic (Hoorn 1994, 1993; Vonhof et al. 1998). Between Early and Middle Miocene, a distinct sedimentary record derived from the Andes is registered in western intracratonic and pericratonic basins, which marked the transition from craton-dominated fluvial systems to Andean-driven fluvio-lacustrine and lacustrine depositional environments (Hoorn et al. 2010a). The uplift of the Andes through the Late Miocene favored the development of a complex mega-wetland system with marginal marine influence, and the reversal of rivers flowing toward the west (Hoorn et al. 2010b; Hovikoski et al. 2010). Thus, throughout the Neogene, numerous geological transformations occurred in the western Amazon region and culminated with the establishment of modern landscape patterns (Fig. 1).

Detailed correlations between episodes of Andean uplift and drainage development remain to be described (Horton et al. 2010; Mora et al. 2010). However, tectonism in the northeastern Andes has played a major role in the genesis of the Amazon Basin, and an increased Andean deformation since the Late Miocene (Fig. 1a), presumably triggered the initial development of the transcontinental Amazon River (Figueiredo et al. 2009; Hoorn 1993; Hoorn et al. 1995). It was hypothesized that when the eastern margin of the Andes reached a critical elevation it became an orographic barrier that trapped moisture and supplied the western lowlands with greater sediment deposition. Then, overfilling of the foreland basin redirected the drainage towards the Atlantic and prompted the development of the transcontinental Amazonian network (Mora et al. 2010). In this context, the Amazon drainage basin acquired its modern configuration in the Pliocene, from ~7 Ma onwards, with the aid of global sea level changes (Figueiredo et al. 2009; Wesselingh et al. 2010). Support for the Late Miocene onset hypothesis comes from the initial buildup of the Amazon Fan at ~11 Ma, due to accumulation of Andean sediments in the Foz do Amazonas Basin (Figueiredo et al. 2009), and from the Ceará Rise, which increasingly received terrigenous sediments from the Andes off the Atlantic coast (Dobson et al. 2001).

Although Andean tectonism has been linked with the formation of major unconformities and depositional events throughout western Amazonia in the Miocene, Campbell et al. (2006) credited the establishment of the transcontinental drainage to terrain development within an erosional regime beginning in the Late Pliocene (~2.5 Ma). Under this scenario the Amazon River acquired its eastward flow by breaching the eastern rim of the


a
Late Oligocene warming
Initial uplift of Eastern Cordillera
MCO
Miocene marine incursions
Increased Andean uplift
Global deep-sea temperature (°C)
6
4
2
0
-2
-4
-6
Northern Hemisphere ice-sheets
35
30
25
20
15
10
5
Ma
Cenozoic
Era
Paleogene
Neogene
Quat.
Period
Eocene
Oligocene
Miocene
Plio.
Pleis.
Epoch
b
Orinoco
Branco
Negro
VA
Caquetá
Japurá
Amazonas
Marañón
Solimões
CA
TA
GA
SMA
IA
Purus
Tapajós
Ucayali
Madeira
PA
FA
Xingu
Araguaia
Tocantins
Elevation (m asl)
< 100
100 - 250
250 - 500
500 - 1,000
1,000 - 2,000
2,000 - 3,000
3,0001 - 4,000
> 4,000
km
0
500
1,000

◀**Fig. 1** **a** Schematic timeline of paleoclimate (adapted from Fig. 2 of Zachos et al. 2001) and major geological events in the course of Amazonian landscape development (based on Hoorn and Wesselingh 2010, and references therein). Ice coverage is represented by *dark dashed* (≤ 50%) and *full bars* (> 50% of present). **b** Present-day configuration of the Amazon drainage basin (*yellow outline*) depicting main rivers and presumed location of structural arches. *MCO* Miocene climate optimum, *Ma* mega-annum, *Quat.* Quaternary, *Plio.* Pliocene, *Pleis.* Pleistocene *GA* Gurupá Arch, *TA* Tapajós Arch (=Monte Alegre Arch), *PA* Purus Arch, *CA* Carauari Arch, *IA* Iquitos Arch, *SMA* Serra do Moa Arch (=Serra do Divisor Arch), *FA* Fitzcarrald Arch, *VA* Vaupés Arch (=Vaupés Swell)

sedimentary basin via overfilling, headward erosion of the proto-Amazon River, or both. Alternatively, Rossetti et al. (2005) proposed that the onset of the transcontinental Amazon did not take place until the Late Pleistocene. They postulated that Plio-Pleistocene fault reactivation caused subsidence of western Amazonia. After a period of stability and dominance of erosional processes, subsequent episodes of deposition resumed in the Late Pleistocene, which culminated in the development of the modern Amazonian drainage due to eastward fault reorientation, at ~32 ka (27,130±200 ^{14}C yr BP).

The limit between eastern and western Amazonian basins prior to the onset of the Amazon River also is contentious. Some authors suggest the site of this divide is contiguous with the Purus Arch (Rossetti et al. 2005) or that this feature conforms with the Purus Arch itself (Figueiredo et al. 2009), whereas its location can also be inferred further east on the Lower Tapajós Arch area (Campbell et al. 2006; Costa et al. 2001) (Fig. 1b). Most of these structural arches are buried under Cretaceous and Cenozoic sediments (Caputo 1991; Wesselingh and Salo 2006), and apparently have had no effect on deposition of Late Neogene–Quaternary sedimentary units of lowland Amazonia (Campbell et al. 2006; Rossetti et al. 2005). Conversely, distribution of the Solimões Formation, which is restricted to western lowlands, may suggest reactivation of the Purus Arch during deposition in the Miocene (Figueiredo et al. 2010).

Paleoclimate and paleovegetation dynamics

It is generally recognized that Amazonian plant diversity developed primarily during the Early–Middle Tertiary, when the climate was mostly warmer than today (Hooghiemstra and van der Hammen 1998; van der Hammen and Hooghiemstra 2000). Palynological records of the northwestern Neotropics dating from the early Cenozoic suggest that plant diversity increased between the Middle Miocene and Pleistocene to reach its present-day levels (Jaramillo et al. 2006). Although the precise timing of this increase in floral diversity is unknown, seasonal rainfall patterns of Amazonia during the Miocene indicate that humid climatic conditions sufficient to sustain a rainforest existed as early as the Miocene Climate Optimum (MCO), at ~16 Ma (Kaandorp et al. 2005) (Fig. 1a). Pollen records also support the existence of a *várzea* environment during Middle–Late Miocene. This type of rainforest seems to have persisted in the upper Amazon area despite a global cooling phase subsequent to the MCO (Hoorn 1994). Moreover, fossil trees dated from the Middle Miocene to the Pliocene demonstrate that the paleofloristic assemblage is comparable to the modern flora typical of terra firme lowland rainforests (Pons and De Franceschi 2007).

Despite important geological events, such as the Andean uplift and closure of the Panama seaway, and Milankovitch-driven climate cycles taking place in Neogene Amazonia, these potential influences on atmospheric circulation did not alter rainfall patterns in the Amazon Basin sufficiently to depart from a wet and warm tropical climate with monsoonal dynamics (Vonhof and Kaandorp 2010). Recent modeling of the effects of a lower relief during Andean uplift indicates that total precipitation remained fairly similar for the most part of the Amazon Basin, but because the Andes act as a moisture barrier for atmospheric circulation and influence zonal patterns of rainfall distribution, Amazonian climate likely experienced enhanced seasonality (Sepulchre et al. 2010).

Climatic alterations may have driven large-scale changes in the vegetation cover of Amazonia throughout the Cenozoic, with replacement of rainforests by relatively dry and open formations during cooler cycles, especially in the Pleistocene and early Holocene (Prance 1985). Records from the Ceará Rise support basin-wide Pleistocene climate variability (Harris and Mix 1999) and ice core paleoclimatic data (Thompson et al. 2000) reveal conditions of lower atmospheric humidity and precipitation at glacial stages, which suggest that rainforest cover was somewhat less extensive.

Paleoenvironmental interpretations, mostly of pollen records, assume that mean temperatures in Amazonian lowlands were at least 4 °C cooler at the Last Glacial Maximum (LGM) than today, which, coupled with an approximate reduction in precipitation of 30–50%, may have resulted in widespread aridity and savanna expansion relative to lowland rainforests (van der Hammen and Hooghiemstra 2000). However, the relationship between cooling and reduced precipitation is difficult to interpret from the available palynological records (Colinvaux et al. 2000; Hooghiemstra and van der Hammen 1998). Fossil Poaceae pollen is often used as a proxy for paleoclimate, and these data are subject to specific settings of local habitat conditions that can be misleading (Bush 2002). Moreover, Amazonian rainforests apparently have remained quite resilient to climatic conditions significantly drier than today since the LGM (Mayle et al. 2004; Mayle and Power 2008)

Likewise, reinterpretation of geomorphologic evidence linking glacial cycles with rainforest contraction due to increased aridity refute this hypothesis as a viable scenario for the vegetation dynamics of Cenozoic Amazonia (Colinvaux and De Oliveira 2001; Colinvaux et al. 2000). Despite some reduction in precipitation during ice-age conditions in northwestern Amazonia, decreases in rainfall apparently were most evident in wet season precipitation (Bush et al. 2004), supporting the continuous presence of mesic vegetation throughout the Late Pleistocene. Pollen and organic matter composition of the Amazon deep sea fan also indicates relatively mesic conditions at the LGM (Haberle and Maslin 1999; Kastner and Goñi 2003). Moreover, paleodistribution modeling do not indicate significant expansion of South American dry biomes into the core of the Amazon Basin (Werneck et al. 2011, 2012b).

These lines of evidence favor the alternate explanation that lowland forest assemblages changed in composition as a result of invasions of heat-intolerant montane taxa during cooler and relatively drier periods, albeit with localized peripheral displacements of savanna/forest ecotones in the southwestern portion of the basin (Bush 1994; Colinvaux et al. 1996, 2000). Yet, such views are not necessarily exclusive, and climatic changes mirroring both hypotheses may have occurred in distinct areas of the Amazon Basin and at different times, depending on climate constraints related to local environments (Hooghiemstra and van der Hammen 1998; van der Hammen and Hooghiemstra 2000).

Diversification hypotheses

Since the nineteenth century, a series of hypotheses has been proposed to explain the unprecedented levels of biodiversity and biogeographic patterns present in Amazonia (Hall and Harvey 2002). These models typically invoke historical or ecological processes promoting species diversification, and generally are associated with environmental shifts in a geographic context. Nevertheless, unambiguous temporal and/or spatial hierarchical explanations often are missing, and such omissions can hamper an objective testing of alternative hypotheses (Moritz et al. 2000). In part, this is due to the overall incompleteness of supporting evidence, particularly paleoenvironmental data (Aleixo and Rossetti 2007), necessary to formulate explicit models of population structure and species differentiation (Carstens and Richards 2007; Hickerson et al. 2010; Richards et al. 2007). Indeed, the majority of studies addressing Amazonian biogeography and speciation have based their conclusions on occurrence data or descriptive phylogenetics, and only a few have derived genetic or genealogical predictions from testable hypotheses.

In this section, we briefly review the main hypotheses of Amazonian diversification, followed by a synopsis of the literature that includes findings relevant to our discussion. Objective hypothesis testing is a key step for thoroughly characterizing the phylogeographic history of any particular organism or, in a comparative context, the historical evolution of entire communities (Knowles 2009). In fact, this theme is central to our review paper, and hence we elaborate on the distinct evolutionary signatures derived from these major diversification models. Despite previous attempts to generalize such expectations within the context of Amazonia's biotic evolution (e.g., Aleixo 2004; Antonelli et al. 2010; Bonvicino and Weksler 2012; Haffer 1997; Noonan and Wray 2006), former compilations were limited with regard to genetic and genealogical predictions especially at the phylogeographic level (i.e., intraspecific), which we now formally underscore in light of the recent advances of phylogeography (Table 1).

Riverine barriers

The earliest hypothesis to explain patterns of animal distribution in Amazonia was advanced by Wallace in 1852 (Wallace 1852). Based on observations of primate species separated by major Amazonian rivers, he divided the basin into four biogeographic areas dissected by the Amazon-Solimões, Negro and Madeira rivers. The riverine barrier hypothesis postulates that large ancestral populations become fragmented into subpopulations upon the formation of major rivers in a once continuous forested region (Sick 1967). The river then acts as a barrier to gene flow, and thus favors differentiation between populations isolated by rivers (Gascon et al. 1998).

Under this vicariance model, populations from opposite riverbanks form sister lineages that share a most recent common ancestor (MRCA) across major river intersections, in contrast with descendent populations that would otherwise coalesce within the same interfluve. Moreover, the genetic divergence between sister populations along margins is reduced towards the headwaters, as the width and flow rate of a river decrease, allowing for gene flow and ultimately cases of admixture in contact zones (Haffer 1997; Lougheed et al. 1999; Patton et al. 1994). Accordingly, the riverine hypothesis is not a strictly allopatric model because of nonzero migration rates, especially in the headwaters (Table 1).

Therefore, the effect of a river as a barrier is dependent largely on whether the focal organism has low vagility, resulting in relatively high levels of genetic differentiation. Likewise, it is conditional on the geography and formation history of the drainage system. For instance, rivers whose headwaters are located in open-vegetation formations, such as the *cerrados* of central Brazil (e.g., Tapajós, Xingu and Araguaia rivers), are expected to limit gene flow between populations from opposite banks conditional on the degree to which the area of contact reduced to gallery forests may have an effect of restricting the range of forest-dwellers. Also, river channels that undergo fluvial disturbance may passively transfer populations from one bank to the other due to meander cutoffs, especially carved into soft molasse beds, or

Table 1 Summary of major hypotheses of diversification in the Amazon Basin and their evolutionary implications

Hypothesis	Geographic barrier (divergence mode)	Timing	Differentiation mechanism	Genetic predictions	Genealogical effects
Riverine barriers	Amazonian rivers (allopatric)	From Late Miocene onwards depending on which river is considered	Development of major rivers separates populations into opposite banks—isolating effect is less pronounced in the headwaters as the river width and flow rate decrease	Population divergence is higher between opposite banks near the mouth of the river and decreases gradually towards the headwaters. Rivers whose headwaters extend into dry regions are expected to show higher levels of genetic variation between opposite margins. Rivers with meandering cut-offs are expected to have little or no differentiation between banks	Lineages from opposite banks coalesce with each other and form sister relationships before finding the most recent common ancestor (MRCA) of the gene copies from within the same interfluve—that is, assuming a small to moderate migrant exchange with each margin. There is some haplotype sharing between opposite banks in the headwaters owing to nonzero rates of migration.
Refugia	Savannas and/or dry forests (allopatric)	Cenozoic	Climatic cycles oscillating between arid and mesic conditions fragment populations in areas of favorable relief (refugia) during cooler periods, with subsequent rainforest reconnection during warmer periods	Bottlenecks during episodes of refugium contraction may affect populations with small effective sizes and lower their genetic diversity. Reduced variability is expected given rapid demographic growth following rainforest reconnection in postglacial periods—especially for long distance dispersers, and due to founder events in areas newly colonized by expanding populations. Relatively higher genetic diversity is expected in stable (refugia) versus non-stable areas, and in older (Late Tertiary) versus more recent (Pleistocene) refugia	At the time of a severe bottleneck most gene copies coalesce, and the topology has short terminal branches if the bottleneck was a recent event, whereas it resembles the topology of an expanding population if the event was older. The genealogical effect of a moderate bottleneck is similar to that of a subdivided population. A genealogy under exponential growth has relatively shorter branches closer to the root than one under a constant coalescent process. A genealogy that diverged more recently in the past has shallower terminal branches with relatively shorter time until MRCA
Gradients	None—environmental gradients (parapatric)	Quaternary	Contiguous populations differentiate along (steep) ecogeographic clines driven by selective adaptation to habitat variation and isolation by distance	Genetic differentiation increases with distance along the gradient due to local drift. Greater genetic diversity is expected towards the center rather than at the extremes of a gradient. Heterogeneous habitats at the middle of gradients may favor balancing selection and retention of polymorphisms. Homogeneous habitats at the opposite ends of gradients may promote directional selection and the fixation of adaptive traits	Sister lineages are expected along a gradient in adjacent but distinct habitats. Time to the MRCA increases with geographic distance separating sampled genes and lineage-split times (backward in time) are greater towards the center than near the ends of the gradient. Selected loci have a local effect on genealogies. When there is balancing selection and low mutation rate most genes coalesce within each allelic type before finding the MRCA, resembling the genealogy of a subdivided population with limited gene flow. When a favorable allele

Table 1 (continued)

Hypothesis	Geographic barrier (divergence mode)	Timing	Differentiation mechanism	Genetic predictions	Genealogical effects
					becomes fixed due to strong positive directional selection the genealogy resembles one of rapid population growth
Disturbance–vicariance	Unsuitable cold-related rainforest conditions (allopatric)	Cenozoic	Temperature oscillations affect vertical distribution ranges and fragment populations into suitable rainforest patches according to fine-scale habitat heterogeneity—cooling promotes downslope invasions of cold-adapted organisms	Genetic differentiation is higher at the perimeter of the Amazon Basin (particularly where both montane and lowland taxa shift their distributional ranges vertically) than at the core. Genetic diversity is expected to be lower towards central Amazonia since rainforest invasion decreases. Given the presence of a central dry corridor during Pleistocene glaciations, rainforest taxa adapted to warmer conditions show relatively higher genetic exchange between western and eastern populations (especially during interglacial periods) as compared to cold-adapted taxa	Sampled genes coalesce within the proximity of major mountain ranges before finding a MRCA in adjacent lowlands located further away in the core of the basin. The genealogy fits into a model of ancient subdivision where ancestral polymorphisms are retained between western and eastern Amazonia. Ecological disturbance may have an effect on the adaptation of selective traits associated with distinct habitat requirements
Marine incursions	High eustatic sea level (allopatric)	Middle Miocene	Marine embayments isolate populations in large landmasses above high sea level stand	Genetic diversity in western Amazonia is lower than in other regions not submerged by marine incursions. Levels of differentiation within the eastern Andean slopes, the Brazilian Shield, or the Guiana Shield are higher than within the western Amazonian lowlands. Demographic decline and exponential growth may also be predicted—but their effect (if any) may be detected only for western lineages	Coalescent events within western Amazonia occur more rapidly and lineages have short branches. Western lineages descend from the eastern Andean slopes, the Brazilian Shield, or the Guiana Shield, and coalesce within each of those ancestral lineages until ultimately finding their MRCA. The genealogy has long internal branches characteristic of an ancestral subdivision between three major landmasses
Structural arches	Intracratonic and foreland geologic arches (allopatric)	Pliocene and older depending on which arch is considered	Uplifting structural arches divide rainforest habitats into different drainage compartments and fragment populations	Levels of population divergence within drainages separated by arches are expected to be lower than between-drainage levels of differentiation	A large ancestral population is broken up into two daughter lineages connected by long branches

tectonics (Cheviron et al. 2005; Haffer 1997; Patton et al. 1994; Räsänen et al. 1987; Salo et al. 1986).

Early studies of allozyme variation in understory birds of the Peruvian Amazon support the notion that rivers preclude the exchange of alleles between populations on opposite banks, with considerably higher between-population differentiation than within (Capparella 1988, 1992). Similar conclusions based on mitochondrial DNA (mtDNA) sequence distances of nonpassarine taxa also indicate that the Amazon, Solimões and Ucayali rivers function as barriers to gene flow (Armenta et al. 2005). In addition, analyses of passerine distributions revealed limited dispersal across the lower Amazon for forest species restricted to upland (*terra firme*) habitats (Hayes and Sewlal 2004). Upland woodcreepers showed evidence of genetic divergence among populations from opposite margins of clear-water rivers, namely the Xingu and Tapajós, situated in crystalline rocks of the Brazilian Shield (Aleixo 2004). Furthermore, the temporal framework for the establishment of major Amazonian rivers has been linked with patterns of cladogenesis in trumpeter birds (Ribas et al. 2012). Regional primate assemblages also were correlated significantly with river attributes such as width and flow rate (Ayres and Clutton-Brock 1992). Likewise, patterns of haplotype networks for tamarin subspecies were consistent with distinct pelage color on opposite banks and intermediate phenotypes in the headwaters of the Juruá River (Peres et al. 1996).

Nevertheless, studies in support of the riverine hypothesis are equivocal. For example, ten bird species representing diverse guilds across a headwater tributary of the Tapajós exhibit varied levels of genetic differentiation without obvious correlation between their morphology-based taxonomy and ecology (Bates et al. 2004), and two floodplain-specialist birds along the Amazon and its main tributaries lack a geographic structuring consistent with river barriers (Aleixo 2006). In a *terra firme* frog, spanning the Juruá, Napo and Madre de Dios rivers, there is support for population divergence in the last intervening river, but evidence of population expansion is indicative only of a secondary contact area (Funk et al. 2007). Moreover, phylogenetic analyses of tamarin species recovered non-sister relationships between taxa from opposite margins of the Juruá (Jacobs et al. 1995), suggesting that this river is not the primary diversification driver in these primates. Genealogical relationships of an arboreal echimyid rodent along the Juruá revealed closer affinities between mouth and headwater areas, and greater haplotype sharing across banks of the mouth than the headwaters (Patton et al. 1994). Similarly, allozyme variation and mtDNA sequence data of frog populations found in *várzea* (floodplain) and *terra firme* are at odds with the riverine barrier hypothesis (Gascon et al. 1996, 1998; Lougheed et al. 1999; Symula et al. 2003). It is important to note, however, that the Late Tertiary to Quaternary sediments that shape most of today's river valleys in western Amazonia are prone to the long-term fluvial disturbance typical of meandering rivers (Räsänen et al. 1987), as opposed to the crystalline beds of eastern Amazonian rivers.

Refugia

The refugia hypothesis invokes vicariant processes (Haffer 1982, 1969), and is by far the most widely discussed model of diversification in Amazonia (Moritz et al. 2000; Prance 1982, 1985; Whitmore and Prance 1987). Following Haffer's (1969) initial observations that closely related species of birds typically exhibit parapatric distributions in the Amazon Basin, core areas of endemism were inferred as regions of past climatic stability, the so-called refugia. Haffer proposed that alternating climate conditions during the Pleistocene led to cycles of rainforest fragmentation and reconnection, such that savanna or dry forest formations expanded at the expense of lowland rainforests under the assumption that cooler glacial phases accompanied a significant increase in aridity. Forest patches restricted to areas where surface relief favored mesic conditions then formed refugia. Isolation of populations into different refugia promoted allopatric differentiation, with high levels of species diversity resulting from repeated fluctuations (Haffer 1997, 1982, 1969). More recently, Haffer's original refugia model has been modified to accommodate not only Pleistocene events but also climatic oscillations driven by Milankovitch cycles throughout the Cenozoic (Haffer 1997, 1993; Haffer and Prance 2001).

First assessments of the validity of refugia for several groups of vertebrates, invertebrates and plants were based on distribution ranges and secondary contact zones between closely related taxa, below or above the species level, and often combining present-day rainfall patterns or other geoscientific data (Whitmore and Prance 1987, and references therein). However, there is no solid evidence to support the notion that cooler temperatures during glacial times reduced precipitation to the point where dry vegetation surrounded rainforest blocks (see section on Paleoclimate and paleovegetation dynamics). Lack of temporal and spatial hierarchical structure among refugia also precludes a more objective testing of this model due to particularly intractable lineage divisions linked with different refugia (Patton and da Silva 1998). Moreover, the location of putative refugia and secondary contact zones are uncertain and may be discordant depending on the set of taxa investigated (Lynch 1988; Moritz et al. 2000).

Aside from these drawbacks, much progress has been made with regard to deriving and testing genetic predictions of the refugia hypothesis (Table 1). Episodes of refugium contraction are expected to inflict demographic bottlenecks on isolated populations (Aleixo 2004; Moritz et al. 2000). These can also be associated with founder effects, which reduce the genetic diversity in areas colonized by expanding populations (Hewitt 2000). Another expectation of the refugia hypothesis is demographic growth following postglacial rainforest reconnection (Lessa et al. 2003; Moritz et al. 2000). Typically, a genealogy experiencing exponential growth has relatively shorter branches closer to the root than one with constant size. Also, the genealogical effect of a bottleneck depends on how long ago it occurred as well as its severity and length (Hein et al. 2005). The impact of genetic drift during climate instability is expected to be stronger on very small effective population sizes, which can drastically impoverish the gene pool, and most gene copies likely will coalesce at that time. If samples diverged more recently in the past (perhaps during the Pleistocene as opposed to the Tertiary), then coalescence time until the MRCA (TMRCA) is shorter with relatively shallower coalescent events.

Variance in dispersal abilities also produces differences in the genetic variability of postglacial recolonization, such that range expansion of long-distance dispersers exhibit relatively large areas with low genetic diversity (Hewitt 1996; Ibrahim et al. 1996). As in a strict allopatric model, migration between local populations is null or negligible owing to an inhospitable matrix of open dry vegetation separating refugia. Clearly though, the level of genetic structure corresponding to the geographic structure of a species depends on assumptions made about the ecology, physiology and behavior of organisms, and our ability to model those overall effects in a tractable and biologically realistic framework (Wakeley 2008).

Lack of support for the refugia hypothesis is derived primarily from estimates of divergence times predating Pleistocene differentiation for the majority of taxa evaluated (Antonelli et al. 2010; Moritz et al. 2000). However, rejecting long-term paleoclimatic fluctuations (driven by orbital forcing cycles; see above discussion) is more challenging (Patton and da Silva 2001). Moreover, studies dealing with Amazonian refugia typically restrict their inferences to the Quaternary.

Lessa et al. (2003) implemented coalescent-based estimates of the growth rate parameter to examine the demographic histories of both Neotropical and Boreal mammals during favorable environmental conditions. These authors showed that lowland Amazonia taxa had genetic signatures consistent with limited signs of population expansion. Likewise, there was support for ancient divergence without gene flow among lineages of frogs in the upper Amazon, but distinct clades exhibit somewhat weak and conflicting evidences of recent population expansion (Elmer et al. 2007; Funk et al. 2007). Thus, rather discordant signatures of sudden demographic growth seem to be the norm for forest taxa, as was also suggested for populations from different refugial areas of geographically widespread leafcutter ants (Solomon et al. 2008) and a *terra firme* bird (Aleixo 2004).

Phylogeographic studies of nonforest taxa, with disjunct distribution in open formations across the intervening Amazonian rainforest, are equally important because they can provide novel perspectives on the role of past vegetation dynamics and climatic oscillations. For example, a contentious but appealing work about the Neotropical rattlesnake proposed a dispersal route between northern and southern populations via a trans-Amazonian central corridor of dry forest or savanna habitats, which supposedly fragmented the rainforest in the Early–Middle Pleistocene (Gosling and Bush 2005; Quijada-Mascareñas et al. 2007; Wüster et al. 2005). Divergence and karyologic variation of cane mice in northern Amazonian savannas also rest on the influence of climate-driven fluctuations during the Middle–Late Pleistocene (Bonvicino et al. 2009). In addition, the patchy distribution and genetic subdivision of the red-footed tortoise—an inhabitant of savannas and adjacent forests—were attributed to dispersal during episodes of rainforest contraction and later differentiation in isolation, despite predating the Pleistocene (Vargas-Ramírez et al. 2010).

Gradients

The gradient hypothesis differs fundamentally from other models because allopatric isolation is not required. It postulates that centers of endemism occur in areas of relatively uniform environment—or habitat conformities—between contact zones formed by ecogeographic clines. Thus, contiguous populations differentiate along one (sharp) environmental continuum, and adaptation to selective habitat conformities may lead to parapatric divergence in spite of gene flow (Endler 1977, 1982). The extent of habitat variation and environmental stress balance the rates of adaptive divergence and levels of genetic exchange and phenotypic diversity (Ogden and Thorpe 2002; Orr and Smith 1998; Smith et al. 2001; Smith et al. 1997).

The gradient hypothesis essentially is a model of isolation by distance (Endler 1982), in which sister lineages are expected along a gradient in adjacent but distinct habitats (Moritz et al. 2000; Patton and Smith 1992). Accordingly, geographically distant individuals show higher genetic differentiation due to localized genetic drift such that TMRCA increases with separating distance and time is greater towards the center than near the ends of a continuous range (Wilkins and Wakeley 2002). Geographic structure will arise with limited gene flow across the habitat space, resulting in a greater genetic diversity along the gradient's core than at more uniform opposite extremes. In addition, adaptive selection can often be incorporated into environmental gradient scenarios (Table 1). Therefore, it is important to understand how different patterns of selection may affect the underlying population structure, albeit selected loci have a local effect on genealogies (Nordborg 2001).

In the case of balancing selection, which favors polymorphisms, most genes will coalesce within each allelic type before finding the MRCA if mutation is rare. This situation resembles the topological effect of a subdivided population when the migration rate is small. Thus, coalescence events occurring more rapidly within types (or *patches*) give rise to many short terminal branches, whereas long branches connect the ancestral lineages after sufficient time has passed to allow mutation (or *migration*) between types (Hein et al. 2005; Nordborg 2001). On the other hand, when a favorable allele becomes fixed due to strong positive directional selection (also termed a selective sweep) the genealogy of the selected locus will look like one of rapid population growth (Nordborg 2001). Moreover, linked neutral variation can be fixed each time a selectively favored substitution sweeps through a population (also termed genetic hitchhiking), such that repeated selective sweeps tend to decrease the genetic variability in a particular genomic region unless the local rate of recombination is large (Kaplan et al. 1989).

The gradient hypothesis (in its original formulation) lacks any explicit spatial configuration except for the vague presence of ecotones between the rainforest and adjacent habitats. It also assumes that population divergence is driven by contemporary ecogeography, thus over a relatively short period despite having no definite time boundaries. However, understanding how past climate oscillations influenced the dynamics of environmental clines becomes more difficult the deeper we extend them into the past. In addition, adaptation of selective traits and differentiation patterns among taxa depend on how different ecophysiologic and behavioral organismal requirements correlate with habitat attributes across the gradient. Therefore, choosing an appropriate framework for testing predictions of the gradient hypothesis ultimately involves a critical assessment of the range and ecological steepness of a cline, as well as resource availability for the organism under study.

The role of environmental clines in promoting differentiation among Amazonian taxa was assessed along the eastern slope of the Andes (Antonelli et al. 2010). Insectivorous mice across a steep elevational gradient in the Andean valleys of Peru showed closer affinities between taxa from the same altitude rather than vertically within drainages (Patton and Smith 1992). Additional observations contrary to expectations of a parapatric model of isolation were also found in birds (Dingle et al. 2006) and an upland frog (Funk et al. 2007). Nevertheless, support for the gradient hypothesis is suggested by paraphyly among lineages of mountain and lowland tapirs (de Thoisy et al. 2010), although this branching pattern could result from incomplete lineage sorting due to recent diversification. However, the application of geographic information system (GIS) to model niche distributions in Ecuadorian dendrobatid frogs demonstrated that parapatric speciation is facilitated across environmental gradients because of divergent selection and those lineages have a symmetric and substantial overlap in their range (Graham et al. 2004). In addition, genetic and phenotypic variation in montane versus lowland poison frogs from northwestern Amazonia suggested a rapid selective divergence in coloration across transition zones (Roberts et al. 2006, 2007).

Disturbance–vicariance

The disturbance–vicariance hypothesis counters the Pleistocene refugia in explaining Amazonian diversification on the basis of temperature fluctuations per se, rather than forest fragmentation due to increased aridity (Bush 1994; Colinvaux 1993). It proposes that past climatic shifts caused repeated lowland invasions by montane lineages during cooling phases and retraction into elevated areas in subsequent warmer periods. Regions of local higher precipitation and relief, likewise refugia, promoted allopatric differentiation and acted as centers of endemism, albeit as a result of population maximal disturbance rather than environmental stability (Colinvaux 1993; Haffer 1997; Patton and da Silva 1998).

This hypothesis was further elaborated by Bush (1994), who acknowledged that a southeast-to-northwest corridor below 1,500 mm of annual rainfall might have facilitated dry forest expansion given a moderate rainfall reduction (~20 %) during Northern Hemisphere glaciations (Fig. 1a). However, most of the lowlands persisted as two large forested blocks, with dispersal routes for cold-adapted taxa limited along the western and southern Amazonian flanks. Hence, cooling primarily facilitated a reassortment of rainforest communities without modern analogues, while unsuitable fine-scale habitat conditions and local competitive exclusion throughout the Late Cenozoic climate oscillations promoted allopatric divergence (Bush 1994).

Under this scenario, differentiation is expected to be greater at the perimeter of the Amazon Basin than at its core, particularly in the Andean forelands and the Guianan highlands, where both montane and lowland taxa shift their distribution ranges vertically. In addition, genetic diversity is expected to decrease towards central Amazonia since the rate of rainforest invasion is less intense. Genes will therefore coalesce within the proximity of major mountain ranges nearby western or eastern Amazonia before finding their MRCA, so that ancestral polymorphisms are retained. A model of ancient subdivision may also incorporate episodes of population bottleneck and demographic growth, and ecological disturbance may have an effect on the adaptation of selective traits in populations with distinct habitat requirements (Table 1).

Additional predictions of the disturbance–vicariance hypothesis were derived from a niche modeling approach to cold-adapted species of Andean origin. According to Lötters et al. (2010), the Late Miocene cooling allowed Andean lineages to disperse through the Amazonian lowlands and reach the Guiana Shield. However, during the subsequent Pliocene warming, cold-adapted species became isolated by the intervening lowlands and differentiated while isolated in montane habitats on either side of the Amazon Basin. Because the range of vertical displacement for populations in upland areas of the Guianas was more limited than for western populations in the Andes, Lötters and colleagues postulated that eastern lineages have shifted their climate envelopes as a means to survive warmer periods. Moreover, western and eastern lineages continued to diverge during the Pleistocene glacial phases as a result of a postulated barrier of dry forests in central Amazonia which prevented the exchange of migrants between Andean and Guianan populations.

Phylogeographic studies have generally overlooked the context of past climatic oscillations under the disturbance–vicariance hypothesis, but a few recent examples are available from studies of anurans distributed in the Guiana Shield. Harlequin toads and dyeing poison frogs (Noonan and Gaucher 2005, 2006) represent cold-adapted lineages descendants of Andean invaders from the Late Tertiary. Diversification occurred within rainforest patches across a mountainous relief during the Quaternary, which resulted in significant genetic divergence and structure among populations despite geographically proximate and undisturbed regions. Evidence for multiple Quaternary refugia isolated by unsuitable (dry forest/savanna) habitats and a concordant phylogeographic break among 11 other lowland frog species also provide support for the disturbance–vicariance hypothesis (Fouquet et al. 2012).

Marine incursions

Periodic marine incursions caused by eustatic sea level fluctuations throughout the Tertiary (Haq et al. 1987; Miller et al. 2005) were responsible for the formation of an interior seaway in the Amazon Basin (Räsänen et al. 1995). These marine embayments affected the patterns of Amazonian diversification as the lowlands were flooded extensively during high sea stands (Webb 1995) via maritime connections with the Caribbean and perhaps southern South America. The marine incursion hypothesis postulates that sea level rise isolated three large blocks of land corresponding to elevated areas in the eastern slope of the Andes, the Guiana Shield, and the Brazilian Shield, which, as a result, favored allopatric differentiation (Aleixo 2004). The Middle Miocene is typically used as the temporal predictor for assessing the eustatically (and tectonically) controlled marine influence in Amazonia (see Hovikoski et al. 2010) (Fig. 1a). However, there is another episode of marine incursion during the Late Miocene predominantly controlled by tectonic loading of the Eastern Cordillera fold-and-thrust belt (Hernández et al. 2005). There is still some uncertainty associated with the timing, duration and magnitude of these incursions (Haq et al. 1987; Miller et al. 2005).

Nores (1999) traced a contour line of 100 m above modern sea level to map endemic bird taxa in the context of marine incursions, assuming that the relief of Mio-Pliocene Amazonia did not greatly differ from present-day topography (at least with regard to his mapping procedure, which left the southern and westernmost parts of the basin out). He identified areas of endemism congruent with two large islands to the north of the Amazon River as well as several smaller islands and archipelagos along the coast of Guiana and at the periphery of the basin. However, its core region would have been completely below sea level and surrounded by islands and archipelagos. Thus, numerous opportunities for population divergence and speciation would have existed. Once the sea level retracted, viable populations occurring in high water-free areas were able to disperse and establish in the interior lowlands. Consequently, the expected genealogical outcome of the marine incursions is that western lineages will coalesce more rapidly, prior to the coalescence within each ancestral lineage descending from one of the major landmasses, until ultimately finding their MRCA after some time has passed. Long internal branches conforming to an ancestral subdivision are expected unless there is sufficient gene flow to prevent the retention of ancient polymorphisms (Table 1). Predictions of the marine incursion hypothesis may also incorporate episodes of population bottleneck and expansion (Solomon et al. 2008). Nevertheless, signatures of demographic decline or exponential growth will likely not be as apparent (if at all) for the long lasting lineages distributed in the eastern Andean slopes, the Brazilian Shield, or the Guiana Shield, compared to the more recent western lineages. In addition, the genetic diversity in the Amazonian core is expected to be lower in comparison to other regions of the basin.

Only a few studies have addressed some predictions of the marine incursion hypothesis, perhaps because this requires extensive geographic sampling. It is uncertain whether

Miocene marine incursions may have contributed to differentiation in leafcutter ants despite the fact that the timing of population divergence falls within that period range (Solomon et al. 2008). Nevertheless, upland passerine woodcreepers diversified mainly from ancestral populations known to the Brazilian Shield inasmuch as its endemics form basal clades relative to samples from western Amazonia (Aleixo 2004). On the other hand, the geographic patterns observed in riverine habitat specialists differ strikingly in that there are no marked genetic structures associated with their presumed high dispersal rates (Aleixo 2006; Cadena et al. 2011). In addition, floodplain woodcreepers represent relict lineages whose hypothesized mode of diversification is consistent with episodes of population bottlenecks (during low sea level stands in glacial periods) and recent expansion since the establishment of floodplain forests in eastern Amazonia in the Holocene (Aleixo 2006).

Structural arches

Structural arches constitute major geological features present in the basement of intracratonic and foreland basins of Amazonia (Cunha et al. 2007; Räsänen et al. 1990; Wanderley-Filho et al. 2007) (Fig. 1b). By and large, arches played a role as drainage dividers and in the shaping of habitat heterogeneity, and despite encompassing different origins and a variety of features (Wesselingh and Salo 2006), they reputedly have been considered important barriers in explaining allopatric differentiation (Lougheed et al. 1999; Patton and da Silva 1998). Their direct influence, as an uplifting structure, on the biotic diversification of Amazonia is nonetheless questioned in favor of a long-term edaphic control and mosaicism of the forest bed (Wesselingh and Salo 2006; see above discussion).

It seems that some arches remained inactive deep in the subsurface after deposition of Early Tertiary and older overlaying formations (e.g., Gurupá Arch and Lower Tapajós Arch) (Caputo 1991; Costa et al. 2001), whereas orogenic events in the Andean front during the Neogene accounted for a more dynamic role of other arches in reorganizing the Amazonian forelands (Räsänen et al. 1987; Räsänen et al. 1990). For example, uplift and dissection of the Vaupés Arch (Late Miocene–Pliocene) and the Fitzcarrald Arch (Pliocene) apparently confined rivers flowing parallel to the Andes during an underfilled stage and changed respective paleocurrent directions (Espurt et al. 2010; Roddaz et al. 2010), which in turn rearranged drainage divides and catchment areas creating dynamic mosaics of the forest bed (Mora et al. 2010) for the associated biota. Also, the relief of the Carauari and Iquitos arches seem to have exerted some control on the development of transverse megafans in the Late Miocene–Pliocene (Wilkinson et al. 2010).

Although largely undescribed, the timing and spatial configuration of the various geological arches present in the Amazon region, along with knowledge about their development and control patterns, are key elements for devising realistic hypothesis tests that relate to lineage splitting events and geographic structuring. Predictions of the structural arches are derived from a classical model of vicariance, wherein a large ancestral population is broken up into two sister populations and the specified arch forms the isolating barrier between them (Table 1).

The role of arches in promoting population differentiation was assessed for small mammal assemblages in western Amazonia, where deep phylogeographic breaks across the central section of the Juruá River, concordant with the hypothesized location and orogenesis of the Iquitos Arch, were identified for a number of rodents and marsupials (Patton and da Silva 1998; Patton et al. 2000). Similar conclusions were proposed for a dart-poison frog that also occurs along the Juruá (Lougheed et al. 1999). Finally, the location of several structural arches is generally consistent with the differentiation patterns of another group of poison frogs throughout most of the Amazon Basin, although the error associated with divergence time estimates were too broad to distinguish between vicariance due to the formation of geological archers or Miocene marine incursions (Symula et al. 2003).

Advances in Amazonian phylogeography

A series of studies have used a phylogeographic approach to explore hypotheses concerning the biogeography and evolution of terrestrial vertebrates distributed in the Amazon Basin and surrounding regions (e.g., Aleixo 2004; Cheviron et al. 2005; Noonan and Gaucher 2005; Patton et al. 2000; Quijada-Mascareñas et al. 2007; Vargas-Ramírez et al. 2010). These analyses provided valuable insights into the evolutionary processes underlying Amazonian diversification (Aleixo and Rossetti 2007; Antonelli et al. 2010; Moritz et al. 2000). However, phylogeographic inferences can attain a greater appreciation of the forces that govern population structure and divergence by incorporating the latest theoretical and methodological developments of phylogeography (Emerson and Hewitt 2005; Hickerson et al. 2010). As knowledge about Amazonia's paleoenvironmental history as a whole is still being compiled (Hoorn and Wesselingh 2010), such an integrative phylogeographic approach could aid in the formulation of an overall framework tying landscape and species evolution in Amazonia.

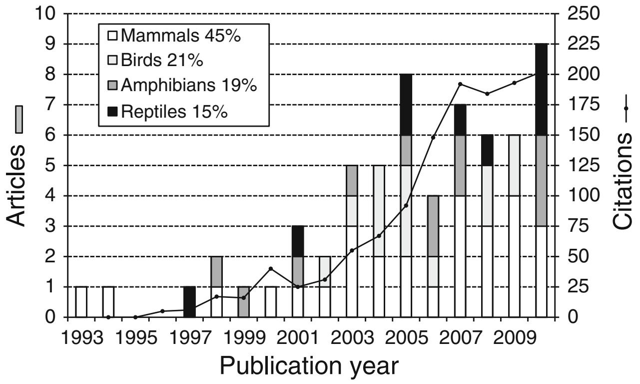


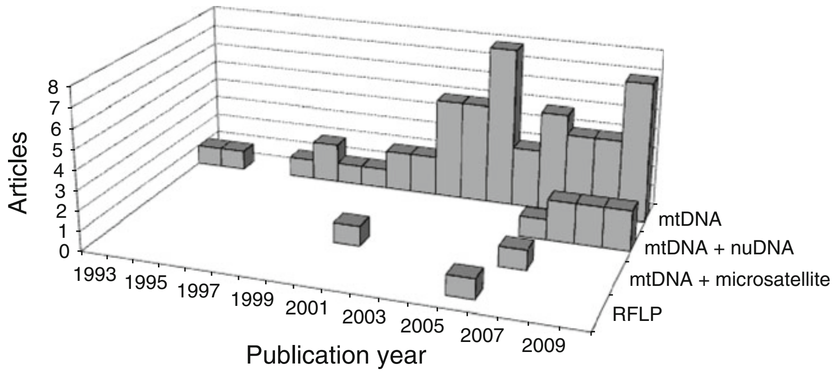
Fig. 2 Number of articles on Amazonian phylogeography sorted by major group of terrestrial vertebrates with corresponding number of citations; published from 1993 to 2010

To help illustrate trends of studies dealing with phylogeography of the Amazon region, we searched for scientific articles in the Web of Science^{SM} and Zoological Record$^{®}$ databases. Details of how we performed queries and treated records are available at the Appendix S1 in the Supporting Information. Although the results of our search are limited to articles from online databases, they serve as a general proxy for phylogeographic investigations focusing on Amazonian terrestrial vertebrates. Moreover, our discussion about current progress and future perspectives of Amazonian phylogeography encompasses a broader view of the field since it is not constrained by the records retrieved from those databases.

The first Amazonian phylogeographic study dealt with arboreal echimyid rodents as inferred from mtDNA haplotypes (da Silva and Patton 1993). This benchmark paper was followed by other contributions involving mainly small mammals, anurans, and lizards. A decade passed before there was a conspicuous increase in the number of articles, including bird papers, and citations associated with this topic (Fig. 2). In the course of the nearly 20 years since da Silva and Patton's pioneering publication, studies dealing with mammals and birds, respectively, have comprised the majority of papers, which altogether correspond to two-thirds of all articles. The proportion of studies per taxonomic group is only a rough indication of the existing bias towards specific vertebrate taxa in Amazonia, as it does not reflect previous compilations of species richness for those groups (see Silva et al. 2005). It is also important to note that the current taxonomic knowledge of Neotropical biodiversity is changing. For example, the rate of mammalian species descriptions greatly exceeds that of birds in the Neotropics (Patterson 2000), and the number of reptile (Rodrigues 2005) and amphibian (Funk et al. 2012) species in Amazonia is grossly underestimated. This suggests that a greater deal of attention should be paid to such understudied taxa, but at the same time it does not mean that "well-studied" groups deserves lesser consideration in future phylogeographic studies. Indeed, there are sampling discrepancies even within "well-studied" groups and many collection gaps for virtually all species in the Amazon region that otherwise hamper any direct geographic and taxonomic comparisons.

The bulk of Amazonian phylogeographic papers have employed analyses of mtDNA sequences; used in 86% of the studies, followed by 10% and 3% of articles that also used nuclear sequence data (nuDNA) or microsatellites, respectively (Fig. 3). Of course, mtDNA offers some advantages for intraspecific studies over the use of nuclear markers because haploid mitochondrial genes have relatively high levels of informative polymorphisms due to shorter coalescent times as a result of smaller effective population sizes (Moore 1995). Moreover, mtDNA sequence data are relatively easy to generate, and there is no need for haplotype phase determination of heterozygous sites or testing for recombination. However, inferring population history based

Fig. 3 Number of Amazonian phylogeographic studies sorted by the types of molecular markers used; published from 1993 to 2010



solely on this class of marker can be misleading, because the mitochondrial genome is inherited maternally as a single-linkage unit (Ballard and Whitlock 2004). The acquisition of nuclear data typically is more labor-intensive, but it can greatly extend the phylogeographic inferential approach with genealogical comparisons across unlinked loci (Brito and Edwards 2009; Edwards and Beerli 2000; Hare 2001). More recently, nuclear markers have been incorporated into phylogeographic inferences in Amazonia (Fig. 3), although these efforts are as yet modest.

Traditionally, phylogeographic studies have made historical inferences by describing hypotheses that underlie patterns of genetic diversity embedded on gene trees (Carstens et al. 2005; Garrick et al. 2010). This qualitative approach typically is combined with some measure of genetic variance within and among populations (see Pearse and Crandall 2004). Another common practice is to utilize molecular dating methods that do not take into account the stochastic variance of coalescence times in gene trees and assume equivalence between the timing of gene divergences and speciation events in the population history (see Knowles and Maddison 2002; McCormack et al. 2011). Recent meta-analyses lumping together various estimates of gene divergences for Neotropical biodiversity at the species-level (Rull 2011, 2008), disregard that gene trees contained in population trees produce dates that are overestimates of the population divergences (Arbogast et al. 2002; Edwards and Beerli 2000).

Descriptive assessments of topological relationships reconstructed via phylogenetic methods are routinely applied in studies of Amazonian phylogeography using varied taxonomic and geographic sampling. In this context, ad hoc explanations are devised to fit a posteriori hypotheses dealing with aspects of species diversification, such as population structure, historical biogeography or systematics. Exploratory analyses are important because they aid in the delineation of key evolutionary processes and provide a basic understanding of putative barriers or geological events and paleoenvironmental scenarios that are of interest in phylogeographic inferences (Garrick et al. 2010). Although, the majority of these studies lack a rigorous statistical framework of model-based inferences, integration of exploratory and model-driven approaches is what makes phylogeography a fundamental discipline for expanding research on Amazonian diversification. As a result, this discipline plays a central role in both testing existing hypotheses and generating new ones, the latter of which should be explored in more depth during the upcoming years.

Recently, studies also have combined several different analytical methods to examine questions about the evolutionary history of Amazonian organisms. Depending on the scope of the study and the set of assumptions regarding relevant biological properties of the target group, these analyses include (but are not limited to) topological tests, nested clade phylogeographic analyses, tests of neutrality and demographic equilibrium, as well as coalescent-based simulations and estimates of demographic parameters. Despite potential problems associated with the latter as to model misspecification and violation of underlying assumptions (Garrick et al. 2010; Nielsen and Beaumont 2009), model-based coalescent methods offer a robust statistical framework upon which alternative evolutionary scenarios and multiple genetic processes can be accommodated in models of population history (Knowles 2004, 2009). Moreover, coalescent methods explicitly consider the inherent variation in mutation rates and the stochasticity of genealogical processes (Knowles and Maddison 2002). Therefore, this model-driven approach has enabled testing of a priori hypotheses and estimation of biologically relevant demographic parameters useful for making phylogeographic inferences (Beaumont et al. 2010).

Phylogeographic studies in the Amazon Basin just have begun to explore some advantages of coalescent-based inferences, mostly by employing coalescent software for parameter estimation; also called genealogy samplers (see Kuhner 2008). These programs, which are available under different coalescent models and assumptions, calculate posterior probabilities or maximum likelihood estimates of various demographic parameters such as effective population sizes, migration rates and divergence times. Some findings that illustrate the application of coalescent-based estimates of demographic parameters on Amazonian phylogeographic studies include scenarios of recent (Quaternary) divergence coupled with negligible migration rates among populations of harlequin frogs (Noonan and Gaucher 2005), highly variable lineage-split times in several butterfly taxa distributed across a suture-zone (Dasmahapatra et al. 2010), and lack of substantial evidence for population growth in western small mammals (Lessa et al. 2003). In addition, DNA sequence data simulated along constrained gene trees under neutral coalescence were used to generate null distributions and test the fit of empirical data against a priori hypotheses concerned with the population history of dyeing poison frogs and lowland tapirs (de Thoisy et al. 2010; Noonan and Gaucher 2006). More recently, Fouquet et al. (2012) employed approximate Bayesian computation to test the synchrony of lineage-splits across 12 leaf-litter frog species codistributed in eastern Guiana lowlands. We provide an empirical illustration of how to explicitly design and test alternative models of Amazonian diversification under a coalescent-based approach in Box 1. Additional non-Amazonian examples on the use of coalescent-based analyses as well as complementary analytical methods to phylogeographic inference are reviewed in Garrick et al. (2010).

Box 1. Empirical example of how to design and test alternative hypotheses of Amazonian diversification within an explicit biogeographic context

Herein, we illustrate how competing models of population divergence in the Amazon Basin can be formulated and tested using a coalescent-based framework. Geological and paleoecological evidences (Salgado-Laboriau 1997; Costa et al. 2001; Rossetti and Valeriano 2007; Valente and Latrubesse 2012) suggest that neotectonics and climate fluctuations have played a role on the landscape formation of southeastern Amazonia. Specifically, such events were key for the configuration of modern drainage systems (e.g., Xingu and Araguaia/Tocantins sub-basins) and establishment of the ecotonal area between the Amazonia and Cerrado biomes, thereby shaping the phylogeographic history of forest-dwelling taxa found both in southeastern Amazon rainforests and Cerrado gallery forests. In this example, populations of the terrestrial spiny-rat *Proechimys roberti* (Fig. 4) are structured geographically at three divergent mitochondrial clades distributed, from west to east, in plateau (*orange*) or fluvial depression (*light blue*) areas of the Xingu–Araguaia/Tocantins interfluve, or east (*pink*) of the Araguaia/Tocantins drainage system (Fig. 5a), whereas there is substantial haplotype sharing across populations at multiple independent nuclear loci (Fig. 5b–f), indicating that elapsed time has been insufficient for complete lineage sorting since population divergence due to landscape rearrangements.

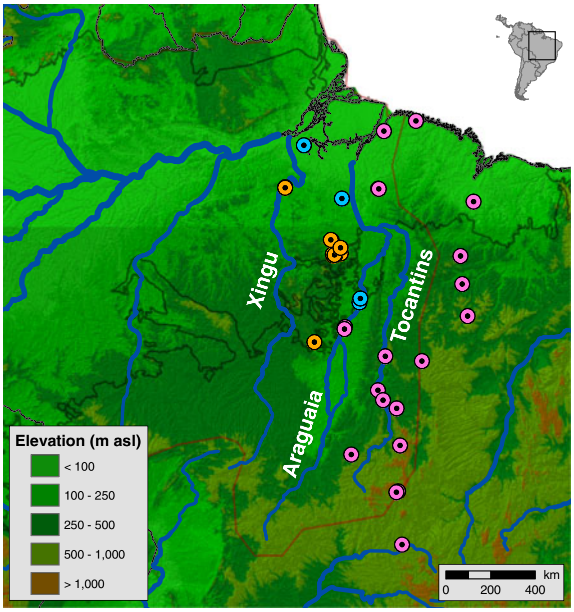


Fig. 4 Distribution of *Proechimys roberti* in plateau (*orange*), fluvial depression (*light blue*), and eastern (*pink*) populations. Major rivers are depicted in blue. Contour lines represent limits of the Amazon drainage basin (*red*) and Amazonian biome (*dark gray*)

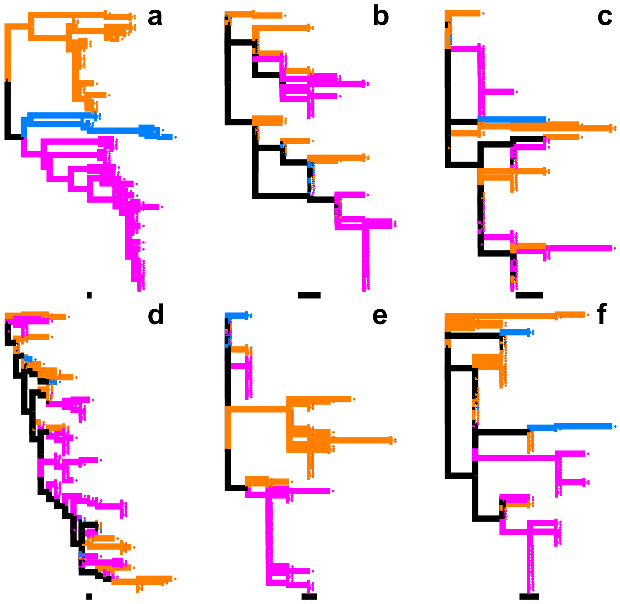


Fig. 5 Gene genealogies estimated for samples of *Proechimys roberti* from **a** one mitochondrial and five nuclear loci **b**–**f**. Colors correspond to plateau (*orange*), fluvial depression (*light blue*), and eastern (*pink*) populations, as referred in the text and map. *Scale bars* are drawn to proportion and equal 0.001 substitutions/site

Two competing hypotheses can be formulated according to this scenario: (1) establishment of the paleo-Tocantins River (Costa et al. 2001; Rossetti and Valeriano 2007) in the Plio-Pleistocene may have isolated *P. roberti* ancestral population within the interfluve region bounded on the west by the Xingu and on the east by the present-day Araguaia and lower Tocantins rivers (Fig. 4). More recently, formation of the fluvial depression of the Araguaia/Tocantins drainage basin in the Middle Pleistocene (e.g., Valente and Latrubesse 2012) may have prompted the differentiation of *P. roberti* into plateau and depression populations (LIM: late interfluve model). Capture of the lower Tocantins, due to fault reactivation with abandonment of the paleovalley (Rossetti and Valeriano 2007), and development of the Amazonia-Cerrado ecotone (e.g., Salgado-Laboriau 1997) during the Late Pleistocene may have promoted eastward expansion via the lower Tocantins or through gallery forests in the Araguaia/Tocantins headwaters, with subsequent differentiation between depression and eastern populations (Fig. 6a); (2) Alternatively, *P. roberti* ancestral population may have differentiated into western and eastern populations upon the formation of the paleo-Tocantins River (ERM: early riverine model), while development of the Araguaia/Tocantins fluvial depression may have driven divergence between western counterparts into plateau and depression populations (Fig. 6b). Establishment of the ecotonal region and reorganization of the lower Tocantins may have facilitated gene flow between these areas, but no significant population expansion would be expected. This historical scenario, which is currently under investigation involving a comprehensive sampling (R.N. Leite et al., manuscript in preparation), has broader implications for Amazonian phylogeography as it illustrates the type of questions that can be considered within a testable hypothesis-driven framework.

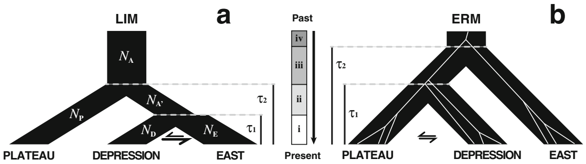


Fig. 6 Two competing hypotheses of population divergence for *Proechimys roberti* in southeastern Amazonia: **a** Late Interfluve Model, LIM; and **b** Early Riverine Model, ERM. Distinct divergence times (τ) and migration rates (*horizontal arrows*) are represented in schematic models **a** and **b**. Effective population sizes (*N*) also are shown in **a**—note the expanded size in eastern population, and a hypothetical gene genealogy is depicted in **b**. Letters in vertical timeline correspond to: (i) Late Pleistocene; (ii) Middle Pleistocene; (iii) Early Pleistocene; and (iv) Pliocene

Biogeographic hypotheses such as above—for example, derived from paleogeographic information—imply alternative population structures that can be modeled explicitly to reflect relevant attributes of the population history (i.e., population tree), and which can be tested statistically using a coalescent-based approach (see Hickerson et al. 2010, and references therein). The goal is to build simple yet biologically realistic models that are able to discriminate among alternative hypotheses. Gene genealogies mirroring demographic conditions of the organism's history are simulated by a neutral coalescent process within each model of population structure, and sequence data are simulated on these genealogies. Each of the simulated data set is then used to calculate a summary statistic that characterizes the data and a large number of replicates provides a null distribution for the summary statistic. The expected patterns of genetic variation corresponding to each hypothesis are evaluated by the fit of the observed data to the null distributions generated from these coalescent simulations, that is, the ability to reject or fail to reject the respective population model.

Historical scenarios may also be investigated using fully probabilistic methods that calculate from the molecular data demographic parameters under a specific coalescent model. Combined with a simulation approach and after careful consideration of the different underlying assumptions of these coalescent-based methods, parameter estimates provide an opportunity to understand in more detail evolutionary processes governing population structure. For example, estimates of effective population size and growth rate may reveal episodes of bottleneck or population expansion, whereas migration rate estimates are useful for distinguishing patterns of gene flow. Moreover, divergence time estimates offer not only a quantitative framework for evaluating the timing of differentiation between populations, but also a means to assess the appropriateness of external sources (e.g., geological events) of divergence time used in simulations. Specifically, for *P. roberti* this means asking whether there is a significant signature of population expansion towards the east; whether migration between depression and eastern populations vs plateau and depression populations is appreciable considering both direction and magnitude of gene exchange; and whether divergence times support a model of late interfluve vs early riverine history of population differentiation (Fig. 6).

The Amazon region is not a homogeneous biogeographic unit. Rather, species distributions tend to form clusters arranged in a mosaic of different areas of endemism. Given that each harbors unique biotic assemblages (López-Osorio and Miranda-Esquivel 2010; Silva et al. 2005), these areas are useful for a basic understanding of Amazonian diversity and historical evolution. Hence, we counted how many times each area of endemism was covered by the taxon sampling in articles included in our survey. Although we recognize this is a very simplistic evaluation of the geographic complementarity of empirical studies in Amazonia, an exhaustive spatial analysis (see Kress et al. 1998) is beyond the scope of this review. Nevertheless, our assessment serves as an indication of how phylogeographic sampling efforts have been distributed in terms of the Amazonian areas of endemism, which seems appropriate since information about these areas can be used in conservation planning (e.g., López-Osorio and Miranda-Esquivel 2010).

The percentage of papers published among the eight Amazonian areas of endemism (according to Silva et al. 2005) illustrates obvious regional differences resulting from skewed taxon sampling (Fig. 7). More importantly, it demonstrates which areas have received less attention. Although some studies directed their efforts towards the Guiana and southwestern Amazonian areas (i.e., Napo, Inambari and Rondônia), fewer studies sampled the Imeri and other areas of endemism to the southeast (i.e., Xingu, Tapajós and Belém).

Remarkably, the former areas of endemism also were identified as the most valuable for conservation according to various diversity metrics based on evolutionary information (López-Osorio and Miranda-Esquivel 2010; Silva et al. 2005). However, areas ranked with the highest conservation priorities generally correspond to areas with ample collecting efforts (Kress et al. 1998; Nelson et al. 1990). Few areas in Amazonia have been inventoried in a fashion to permit definite conservation recommendations (Laurance 2005), but the disproportionate number of phylogeographic studies illustrated in Fig. 7

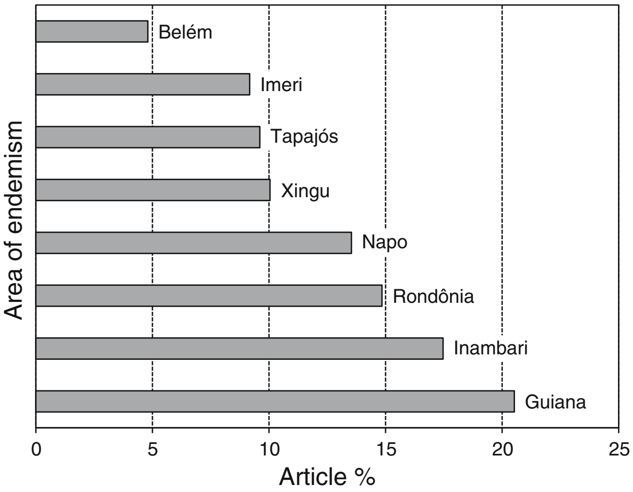


Fig. 7 Percentage of phylogeographic studies in each Amazonian area of endemism (according to Silva et al. 2005); published from 1993 to 2010

emphasizes that some of the least sampled areas, such as Xingu and Belém, also are among the most vulnerable and unprotected (see Silva et al. 2005). In addition, the Xingu figures as the second most critical area of endemism to preserve for complementary purposes (López-Osorio and Miranda-Esquivel 2010).

Future perspectives

It is clear that questions about the historical evolution of Amazonia's vertebrate biota, including the role of putative barriers and the relative influence of climatic and geological events for shaping present-day patterns of species diversity and distribution, have been refined by means of a phylogeographic approach. Based on our review of major diversification hypotheses and the emphasis given to an explicit hypothesis testing approach, together with our empirical example of how coalescent-based inferences can shed light into current trends of Amazonian phylogeography, we evaluate which directions investigators should consider in future research. We agree with Bush's assertion (1994) that no single model can indisputably explain the complex evolutionary history of the Amazon Basin and its biota. Indeed, the available hypotheses account for non-exclusive and simplified views of a handful of differentiation mechanisms (Moritz et al. 2000). Although a lack of consensus regarding geological and paleoclimatic events preclude an elaborate scheme to explain the history of Amazonian landscape and ecosystems, phylogeographers need to make the most of the existing data to aid in the analysis of population divergence and demographic histories, especially when trying to discriminate among alternative evolutionary scenarios. Nevertheless, the fortune of Amazonian phylogeography largely depends on implementing hypothesis-driven designs that are appropriate in terms of geographic sampling, target taxa, and molecular markers for the biological questions being considered.

At present, collection efforts are distributed unevenly among various taxonomic groups and account for sharp sampling disparities. This situation is probably due to the synergy between localized specimen collecting and an insufficient number of investigators working in the Amazon region. Moreover, research centers often undertake the challenge of accessing pristine areas to do fieldwork without collaboration from other institutions. All things considered, Amazonian phylogeography needs to expand its human resources, both in numbers and extent, across a diverse array of taxonomic expertise if we want to overcome intrinsic sampling biases and gain a detailed historical perspective.

Although mtDNA likely will continue to be the workhorse of future phylogeographic investigations (Zink and Barrowclough 2008), the potential utility of nuclear markers remains largely unexplored in Amazonian studies. Clearly, datasets incorporating nuDNA sequences, single nucleotide polymorphisms or microsatellites are better suited for inferring population genetic processes when based on genomic regions that offer informative variation at the population level (Brito and Edwards 2009; Hare 2001; Sunnucks 2000; Thomson et al. 2010), such as introns, anonymous nuclear loci, and highly polymorphic microsatellites (e.g., Bowcock et al. 1994; Lee and Edwards 2008). Nevertheless, assaying nuclear loci is not as straightforward as using markers from haploid genes, which can ultimately impact the number of populations screened and sample sizes evaluated (Garrick et al. 2010). However, advances in genomic technologies are expected to appreciably expand the cost-efficiency of sequencing multilocus datasets for use in phylogeographic studies with multiple individuals per population (Brito and Edwards 2009).

Spurious interpretations of the underlying population history may arise if discordance among reconstructed gene trees is ignored (Maddison 1997). However, when heterogeneity in topology and coalescent times from gene trees is taken into account appropriately, model inferences and demographic parameter estimates plus associated confidence intervals show improved accuracy overall (Carling and Brumfield 2007; Edwards and Beerli 2000; Felsenstein 2006). There is increased opportunity for Amazonian phylogeographers to add multiple independent loci that can capture a clearer view of the evolutionary processes shaping species diversity in the region. Variable nuclear markers are becoming more widely available for non-model species, and analytical methods are expected to improve on sophistication and flexibility to accommodate large amounts of data assembled via next-generation sequencing (Wakeley 2004). Nevertheless, research groups will have to consolidate the necessary laboratorial and computational infrastructure for widespread use of multiple loci and genome-wide datasets, which can be particularly challenging for the scientific community of developing Amazonian countries. Brazil has shown increased albeit incipient interest in scientific and technological innovation through investments in infrastructure and education (Lemos 2012; Massarani 2012), an example to be adopted by and fully integrated among those nations.

In the meantime, phylogeographic studies based on single-locus datasets can be used as a "first pass" in making historical inferences about Amazonia's intricate ecosystems and biotic communities. For the same reason, exploratory methods will continue to contribute with de novo working hypotheses that form the basis for a detailed analytical framework (Garrick et al. 2010). However, assessing genealogical concordance of a collection of gene trees with tree-based approaches is rather cumbersome, particularly when attempting to account for complex historical scenarios because these methods disregard the inherent stochasticity of genetic processes (Brito and Edwards 2009).

In this context, coalescent theory provides a powerful mathematical framework in deriving common patterns of population ancestry drawn from a set of gene trees (Hey and Machado 2003), while offering statistical discrimination among alternative models (Nielsen and Beaumont 2009). The so-called statistical phylogeography posits a shift in how historical inferences are made by explicitly considering the stochastic variance of mutation and coalescence of gene lineages, as well as the processes generating genetic structure (Knowles 2004; Knowles and Maddison 2002). Hence, there are many possible historical scenarios in Amazonia amenable to testing via a coalescent-based approach (Table 1).

Although coalescent methods represent novel prospects for thoroughly evaluating genetic structure and population divergence, the decision on which analyses to use should be based on careful consideration of the underlying assumptions of each method. Otherwise, inferences may not capture any signal from the data or render incongruous results (Garrick et al. 2010). Moreover, the ability to formulate an objective experimental design ultimately rests on the researcher's ingenuity in translating plausible historical scenarios into a hypothesis-testing framework (Knowles 2009). For this reason, phylogeographic studies need not to be constrained by long-held biogeographic hypotheses in explaining Amazonian diversification. To the contrary, development of novel models will be required, or some combination of portions of available models may be appropriate for the study system under investigation (see Box 1 for an example). Nevertheless, such a decision depends on the manner in which historical scenarios may have affected target organisms. Therefore, acquaintance with the particulars of the paleogeographic setting is critical for devising and testing meaningful evolutionary hypotheses. With a good grasp of the study system, and given adequate taxon and geographic sampling, phylogeographers can put forward biologically realistic models that are readily testable.

There may be some occasions when plausible a priori hypotheses will comprise a variety of alternative candidate models, and researchers will be unable to differentiate among fail-to-reject null models (Anderson et al. 2000). This can be the case for phylogeographic studies dealing with complex evolutionary histories in Amazonia. However, information-theoretic methods provide a means of measuring the fit of candidate models relative to one another, and so the ranking of alternative hypotheses can be used to scrutinize the influence of demographic processes or historical events shaping population structure (Carstens et al. 2009). In any case, informed methods of analysis should make comprehensive use of the historical features that might be relevant in the evolutionary context of any particular organism or biotic community while delimiting phylogeographic hypothesis (Buckley 2009).

For example, testing of riverine barriers entails discerning how surface relief, seasonal and long-term disturbances or the distribution of depositional units specifically affect river dynamics and relate to organismal idiosyncrasies (e.g., dispersal rates, mating systems, ecological requirements). Likewise, past climatic oscillations apparently provided different opportunities for species during Amazonian ice ages, whether or not aridity was ubiquitous. Amazonian phylogeographers need to pay greater attention to non-forest taxa because climate changes are expected to affect their evolutionary histories in ways that differ from their forest counterparts. This approach should shed additional light on overall patterns of forest cover dynamics from the perspective of open-habitat dwellers. Geological data are useful sources of external evidence while formulating alternative historical scenarios. However, there may be situations in which the available information is insufficient to outline the historical context of species diversification. In those instances, GIS-based environmental niche modeling (ENM) approaches have proven useful in delineating phylogeographic inferences (see Hickerson et al. 2010; Richards et al. 2007).

In the Brazilian Atlantic Forest, ecological niche models under different paleoclimate regimes revealed climatically stable areas and predicted patterns of genetic diversity (Carnaval et al. 2009). Likewise, paleodistribution modeling of Seasonally Dry Tropical Forests (Werneck et al. 2011) and the Cerrado (Werneck et al. 2012b) were used to identify areas of climatic stability during the Quaternary and further elaborate biogeographic hypotheses and identify research priorities for South American open vegetation biomes (Werneck 2011; Werneck et al. 2012a). ENM of Amazonian birds, woody plants and leafcutter ants projected onto LGM conditions also illustrated how paleodistribution limits may vary among taxa (Bonaccorso et al. 2006; Solomon et al. 2008). Moreover, phylogeographic inferential approaches based on information from ENM have key implications for the purpose of identifying cryptic refugia (Provan and Bennett 2008). Finally, GIS-based spatial analyses using Shuttle Radar Topography Mission (SRTM) data and floristic composition in western and central Amazonia verified that geological formations partition forest assemblages into large-area units due to edaphic control (Higgins et al. 2011). SRTM data in combination with regional geological information also provided a detailed geomorphologic characterization of the lowest Amazon drainage basin, which formed the basis for reconstructing the geological history of this area during the Late Tertiary–Quaternary (Rossetti and Valeriano 2007).

Various unique types of transitional zones in the Amazon Basin await detailed phylogeographic study. Specifically, quantifying molecular and phenotypic variation in concert with key ecological attributes may reveal how adaptive selection and population divergence operate with respect to vertical gradients typical of mountainous regions, as well as horizontal contact zones between upland and floodplain forests or in savanna–forest interfaces. The consequences of disturbance–vicariance have been evaluated only for amphibians, which are known to exhibit restricted ecological requirements, and mostly within the Guiana Shield. Additional research focusing on whether or not other taxonomic groups with distinct or broader climatic regimes display similar phylogeographic patterns across the Guianas as well as other regions of the basin will improve our understanding of climatic events in the history of Amazonian biota. Finally, phylogeographic studies focusing on the extent and frequency of marine embayments, in addition to the tempo and mode of formation of different arches and the presumed location of paleo-channels, will be able to trace important pieces of Amazonian history.

It is clear, however, that the Amazon region constitutes an open laboratory for experimenting with the exploratory power of phylogeographic inference and hypothesis testing. As Amazonian phylogeographers engage in an active research program that integrates emerging analytical inferences with tools borrowed from related disciplines, new perspectives about the evolutionary histories of Amazonian organisms will be addressed in ways never envisioned before. To examine the evolution of Amazonian ecosystems as a whole, comparative phylogeography establishes the link between population processes and regional biodiversity patterns (e.g., areas of endemism) through comparison of multiple codistributed taxa within the geographic scale of entire communities (see Hickerson et al. 2010). This comparative approach provides a means to better understand the relationship between shared mechanisms driving biotic diversification and landscape formation despite the idiosyncratic variation of organisms' attributes in response to historical events (Arbogast and Kenagy 2001; Bermingham and Moritz 1998). Moreover, coalescent-based inferences can substantially extend the application of comparative studies by considering life-history parameters that are so important when testing for genealogical concordance among distinct organisms (Carstens et al. 2005).

The mapping of previous collection efforts is one of the first steps towards a precise identification of patterns of diversity and biogeography in the Amazon region. Although sampling gaps will exist for virtually all Amazonian taxa, this mapping procedure will facilitate new collecting efforts by indicating underrepresented areas. Natural history museums have a fundamental role in coordinating these efforts effectively not only by serving as the final repositories of biological, geographic and genomic data of focal organisms and granting specimen loans whenever necessary, but also by providing information accessibility to these types of data (i.e., via online database systems, see Antonelli et al. 2010).

The Amazon region is contained within nine South American countries and borders three other major biogeographic units in the Neotropics (namely the Caribbean, Chacoan and Paranean regions). Its value in terms of environmental and biodiversity services are undeniable within a global context (Fearnside 1997), despite alarming conservation threats (Kirby et al. 2006). Due to its size, extensive regional and international collaborations are of utmost importance should we aspire to enhance biological inventories across political boundaries and benefit from recent theoretical and methodological advances (Barlow et al. 2011; Beheregaray 2008). At the same time, governmental and non-governmental agencies must work in concert with the scientific community to facilitate inventory programs by avoiding bureaucratic pitfalls that for instance delay issuance of scientific collecting permits (see Antonelli and Rodriguez 2009; Renner et al. 2012). Brazil, as the leading country in terms of Amazonian territory, has a central role in the integration of a conservation plan involving private sectors and public policies devoted to the sustainable social-economic development of the Amazon Basin, and that should also contemplate scientific research efforts within regional and international arenas.

Conclusions

The biotic diversification of Amazonia involves complex historical scenarios encompassing a range of temporal and spatial scales. Although generalizations are hard to make, emerging lines of geological and biological evidence indicate that landscape development, past-climate dynamics and biotic evolution in Amazonia shared some broad-spectrum attributes. In devising and testing meaningful models of Amazonian diversification, such commonalities need to be discerned on the basis of the requirements of each taxon or assemblage of interest and their resilience to potential environmental pressures through time. Relatively recent climatic oscillations apparently have had a more pronounced effect on taxa with narrower ecological and physiological requirements (i.e., within lineages), whose responses often are associated with shifts in distribution or niche envelopes. On the other hand, major geological events and long-term landscape changes played an important role for the geographic structuring of genetic diversity, especially at deeper hierarchical levels (i.e., among lineages).

Phylogeography has changed the way many questions concerned with the history of Amazonia's ecosystems and its biota can be examined. However, in spite of an increasing number of empirical contributions, our appreciation of the diversification patterns as well as the evolutionary and geophysical processes shaping Amazonian diversity and biogeography is still far from complete. The exploratory yardstick of Amazonian phylogeographic inferences can now take advantage of the robustness offered by statistical discrimination of a priori models of organismal history applied to complementary multilocus datasets. The potential of these latest advances to assist Amazonian research also will depend on the ability to integrate reliable external information and overcome practical issues such as limited geographic and taxonomic sampling. Nevertheless, as we revisit major diversification hypotheses and consider future challenges for those studying Amazonian organisms, we also can anticipate that this renewed phylogeographic agenda will offer valuable insights into the evolution of Amazonian biota, and hopefully will help determine long-term conservation priorities for safeguarding the richest biota on Earth.

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