

Avian gene trees, landscape evolution, and geology: towards a modern synthesis of Amazonian historical biogeography?

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Abstract Recent studies have improved our understanding of Amazonian geological history during the late Tertiary and Quaternary, two periods regarded as critical for the recent diversification of the Amazonian avifauna. The notion that geologically older and more stable areas of Amazonia (such as the Brazilian and Guianan shields) functioned as “species-pumps”, whereas geologically more dynamic areas (such as the western Amazonian lowlands) mostly “captured” part of the diversity generated nearby, was supported by a recent phylogeographic study focusing on a species complex of the genus *Xiphorhynchus* (Dendrocolaptidae). Here, we review several additional molecular datasets to assess whether this historical scenario can be extended to other lineages of Amazonian birds as well. The datasets reviewed indicated that most lineages of upland forest species found nowadays in western Amazonia are associated with more basal lineages from the Brazilian shield, Guianan shield, and the Andes, indicating a more recent history in this geologically dynamic region. Conversely, lineages associated with seasonally flooded forests seem to have an ancient history in western Amazonia, apparently expanding over the geologically more stable areas only recently. Most sister taxa of the lineages

reviewed exhibited levels of pairwise sequence divergence consistent with splitting events dating back to a time frame stretching from the late Miocene to the early Pleistocene, a period when significant physiographic and landscape changes took place in Amazonia. When interpreted together, all the studies reviewed provide evidence that geology and landscape evolution are tightly linked with the timing and mode of differentiation of Amazonian birds.

Keywords Amazonia · Avifauna · Geology · Historical biogeography · Molecular systematics

Introduction

The bird fauna of the Amazon lowlands in South America is the richest in the world, with over 1,000 species, of which about 265 are endemic (Stotz et al. 1996; Mittermeier et al. 2003). This unparalleled ornithological diversity has intrigued naturalists since the early days of Amazonian exploration. As early as 1852, the British naturalist Alfred Russell Wallace put forward an evolutionary hypothesis to explain the history of diversification of Amazonian vertebrates (Wallace 1852), and, since then, several alternative hypotheses have been proposed (Haffer 1969, 1993; Endler 1977; Colinvaux 1993; Bush 1994; Marroig and Cerqueira 1997; Roy et al. 1997). Few testable predictions, however, could be derived from many of these hypotheses of diversification (Patton and Silva 1998); the biggest hurdle is the lack of specific temporal and geographic contexts in the formulation of most of the proposed hypotheses, making them hard to falsify by phylogenetic methods (Patton and Silva 1998; Moritz et al. 2000). For example, although the refuge hypothesis has been widely applied to tropical forest ecosystems around the globe

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(Haffer and Prance 2001), it is nearly impossible to be falsified in a phylogenetic context (Patton and Silva 1998).

To distinguish effectively among competing hypotheses of species diversification, several researchers have attempted to adopt a phylogeographic approach to the study of the diversification of the Amazonian biota (Patton and Silva 1998; Silva and Patton 1998; Lougheed et al. 1999; Moritz et al. 2000). The phylogeographic approach is the combined assessment of the phyletic (genealogical) and geographic components of allele distributions among populations and closely related species (Harrison 1991). These distributions can be contrasted with explicit expectations of geographical relationships among ancestral populations prior to divergence under the three main models of species formation available: allopatric, parapatric, and sympatric (Harrison 1991). Furthermore, phylogeographies can also be used to infer the timing of speciation for groups with poor or no fossil data, as is the case for most terrestrial tropical vertebrates (Moritz et al. 2000).

The use of the phylogeographic approach in Amazonian biogeography started in the 1990s, when Patton et al. (1994) initiated a series of papers aimed at testing predictions of the riverine barrier hypothesis of diversification based on gene trees of several rodent and marsupial species (Patton and Silva 1998; Patton et al. 1994, 1996, 2000; Silva and Patton 1998); however, most of those seminal papers were restricted in geographic scope to the Juruá river valley in western Brazilian Amazonia, and phylogeographic studies with broader geographic coverages in Amazonia were still lacking in the late twentieth century. This situation changed a few years later, when the first studies with broader sampling regimes in Amazonia appeared (Hall and Harvey 2002; Marks et al. 2002; Symula et al. 2003; Ribas and Miyaki 2004; Armenta et al. 2005; Cheviron et al. 2005; Ribas et al. 2005, 2006). Those studies contributed significantly to an overall re-evaluation of the models of diversification proposed earlier, supporting, among other things, the conclusion that recent Quaternary glacial cycles of forest change played a minor role in the origination of most species currently inhabiting Amazonia.

The pivotal role of recent studies of phylogeographic and population genetics in the critical evaluation of hypotheses of Amazonian diversification was further demonstrated by the series of papers on the avian genus *Xiphorhynchus* (Dendrocolaptidae); those studies tested predictions of four different hypotheses of Amazonian diversification with a broad, trans-Amazonian sampling regime (Aleixo 2002, 2004, 2006). Under the phylogeographic and population genetics frameworks, a test of the gradient (Endler 1982), riverine barrier (Gascon et al. 2000), refuge (Haffer 1969), and Miocene marine incursion

(Bates 2001) hypotheses of diversification would require a group of organisms with three main characteristics: high species richness, high ecological diversity, and widespread distribution. The genus *Xiphorhynchus* fulfilled all the requirements above and provided an excellent model to investigate the historical diversification of Amazonian organisms: nine of the 14 currently recognized species of *Xiphorhynchus* occur throughout Amazonia, where they show remarkable levels of ecological as well as population differentiation (Marantz et al. 2003). Therefore, phylogenetic and population genetics analyses of species in this genus provided important insights into the validity and generality of the four hypotheses of Amazonian diversification outlined above (Aleixo 2002, 2004, 2006).

Of the four hypotheses of Amazonian diversification tested with species of the genus *Xiphorhynchus*, two had some of their important predictions supported: the riverine barrier and the Miocene marine incursion hypotheses (Aleixo 2002, 2004, 2006). Hence, these two hypotheses appeared not to be mutually exclusive and may together account for the diversification of the genus *Xiphorhynchus* in Amazonia at different temporal and geographical scales. Nevertheless, as discussed in Aleixo (2006), these two hypotheses of diversification were readily applicable to upland forest species (*X. spixii* and *X. elegans*) but not to floodplain forest species (*X. kienerii* and *X. obsoletus*).

How these distinct supported predictions, derived from very different hypotheses of diversification, are integrated into a more general model of evolution depends directly on the level of resolution of Amazonian geological history. Below, a synopsis of Amazonian geology and landscape evolution is presented and later contrasted with phylogeographic data obtained for the genus *Xiphorhynchus* and several other avian taxa.

Amazonian geology revisited: implications for avian historical biogeography

Despite numerous publications on Tertiary and Quaternary deposits found in Amazonia (e.g., Rüegg and Rosenzweig 1949; Irion 1984; Hoorn 1994a; Irion et al. 1995; Räsänen et al. 1987, 1990, 1995; Hoorn et al. 1995; Campbell 1990; Campbell et al. 2006), there are still many questions open to debate concerning the reconstruction of Amazonian geological history. In particular, the available documentation is still inadequate to provide robust models of the depositional systems and their evolution through time. This is a result mainly of the overall large size of the area, absence of a greater volume of systematic studies, difficult access, and limited and discontinuous exposures that include mostly riverbank outcrops. Despite those limitations, the reconstruction of the evolution of Tertiary and Quaternary

deposits in Amazonia is of great relevance. This is because this time frame is thought to have witnessed the evolution of most of the modern Amazonian biodiversity, as indicated by several phylogeographic studies (Silva and Patton 1998; Hall and Harvey 2002; Marks et al. 2002; Aleixo 2004, 2006; Armenta et al. 2005; Cheviron et al. 2005; Ribas et al. 2005, 2006).

Amazonia has a complex geological history, with formations of different ages, compositions and histories distributed in different parts of the basin (Oliveira and Leonardos 1943). Essentially, the Brazilian and Guianan shields (distributed in southeastern and northeastern Amazonia, respectively), are composed of old Paleozoic and Precambrian rocks, whereas a huge and more recent composite sedimentary basin has developed in western Amazonia (Costa and Hasui 1997).

Recently, Rossetti et al. (2005) proposed a new geological mapping of sedimentary successions of Amazonia, where several late Pleistocene to Holocene depositional successions, previously considered as part of a Plio–Pleistocene unit called Içá Formation, were included. On the basis of this mapping, these authors provided a model summarizing the evolution of the depositional systems in this area. Essentially, while the eastern portions of the Brazilian and Guianan shields (from the city of Manaus eastward) have remained mostly stable since the Late Cretaceous (with erosion, but limited sediment deposition), western Amazonia experienced a more dynamic sedimentary history. It is well known that an extensive lake system was established in western Amazonia during the Miocene, as recorded by the Solimões/Pebas formation (e.g., Weseligh et al. 2001; Nuttal 1990; Vonhof et al. 1998). This lake setting evolved into a braided fluvial system, as recorded by the Plio–Pleistocene Içá Formation. This unit, together with four other late Quaternary to Holocene thin fluvial (mostly meandering) sedimentary successions, mantles most of the western Brazilian Amazonia, which is covered today by a complex mosaic of vegetation types. Tectonism is inferred as the major player behind landscape changes in western Amazonia, causing several episodes of subsidence that prompted the closure of the lake system in the Miocene and the establishment of the fluvial system, which probably acquired its modern characteristics (an eastward flow) only in the late Pleistocene (Rossetti et al. 2005). In central and eastern Amazonia, impacts of these major landscape changes were concentrated along the old Amazonian intracratonic basin, where the modern lower Amazon river floodplain developed. Therefore, the available data support the notion that different areas of Amazonia experienced distinct rates of landscape change, with the western Amazonia being the most dynamic area (Hoorn 1994b; Hoorn et al. 1995; Campbell et al. 2001; Rossetti et al. 2005).

This essentially dichotomous geological scenario, where the Brazilian and Guianan shields are more stable than the western dynamic sedimentary basins, can generate new predictions about phylogeographic relationships among related taxa distributed today in Amazonia (Fig. 1).

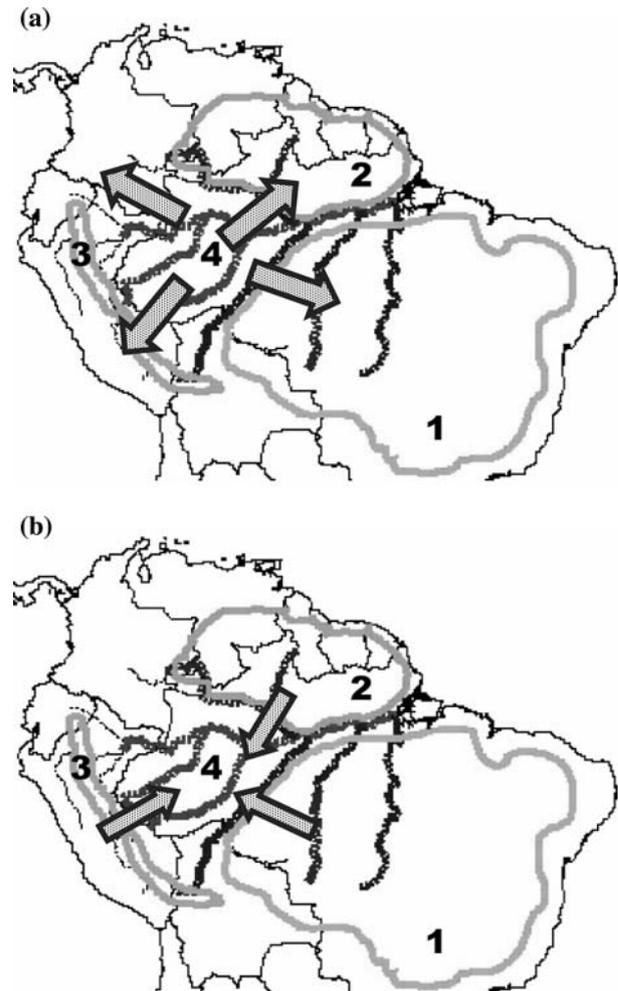


Fig. 1 Scenarios hypothesized for the evolution of avian lineages in response to regional landscape changes in Amazonia since the Miocene (Aleixo 2004, 2006; Rossetti et al. 2005). *Numbers* refer to the following geological areas: (1) Brazilian shield, (2) Guianan shield, (3) Eastern foothills of the Andes, and (4) western Amazonian lowlands. Main rivers are shown as *dashed black lines*. *Arrow tips* indicate the postulated direction of lineage colonization between neighboring areas. **a** Scenario for floodplain forest species: lineages with their distributions centered on the western Amazonian lowlands (coincidental with the so-called Lake Pebas) expanded demographically and colonized other parts of the region during the late Pleistocene and throughout the Holocene, following an increase in the area occupied by seasonally flooded forest due to a period of increasing, high, global sea levels and humidity. **b** Scenario for upland forest species: lineages with their distributions centered on the Brazilian and Guianan shields and foothill of the Andes began to colonize the western Amazonian lowlands after the extensive “Lake Pebas” dried out (late Miocene), and the modern upland forest became established in this area

However, as shown for species of the genus *Xiphorhynchus*, floodplain and upland species are expected to have differed profoundly in their responses to landscape change in Amazonia since the Miocene, and therefore, in their phylogeographic predictions as well (Aleixo 2004, 2006).

When phylogenetic and population genetics data available for floodplain species of *Xiphorhynchus* are interpreted in the context of modern Amazonian geology, it becomes suggestive that the extensive fluvio-lacustrine environment developed in western Amazonia since the early Miocene probably represented the center of evolution and source area for cyclical episodes of colonization of the entire Amazon basin by floodplain species (Aleixo 2006); the overall lack of phylogeographic structure detected for floodplain species of *Xiphorhynchus* was correlated with a recent episode of rapid population expansion following an increase in the area occupied by seasonally flooded forest due to a period of increasing high global sea levels and humidity (Behling and Costa 2000; Rossetti et al. 2005; Aleixo 2006; Fig. 1a). Because the distribution and dynamics of flooded forest types in Amazonia is not conducive to population subdivision, even at large time scales, it has been suggested that extant lineages of floodplain species might have comparatively little population subdivision and small rates of cladogenesis, being “relicts” of early radiations of widespread Neotropical lineages (Aleixo 2002, 2006).

On the other hand, the geologically dynamic western Amazonian floodplains probably constituted an inhospitable habitat to upland species, until at least the late Miocene, when the extensive “Lake Pebas” dried out, and organisms associated with upland forest probably began to colonize this immense area (Rossetti et al. 2005). However, the subsequent development of the western Amazonian sedimentary basins in response to large-scale river channel migration and re-orientation (Rossetti et al. 2005) might have created an extremely dynamic environment with rapid vegetation turnover and a continuous alternation between flooded and unflooded forest types. Therefore, as suggested by the genus *Xiphorhynchus*, lineages of upland forest species inhabiting western Amazonia might have colonized this area more recently (Pliocene and Pleistocene) from one of the three neighboring areas thought to be continuously inhabited by lineages of upland species: the Brazilian shield, the Guianan shield, and the eastern foothills of the Andes (Bates 2001; Aleixo 2004; Fig. 1b). Furthermore, as suggested previously by Bates (2001), those three areas probably functioned as centers of vicariance for lineages of upland species, since they were reciprocally isolated for different periods of time. While the Brazilian and Guianan shields have been separated from each other by the intracratonic Amazon basin since the Paleozoic, the eastern Andean foothills were isolated from both Brazilian and Guianan shields by epicontinental seas and Lake Pebas

until at least the late Miocene (Lundberg et al. 1998; Campbell et al. 2001; Rossetti et al. 2005).

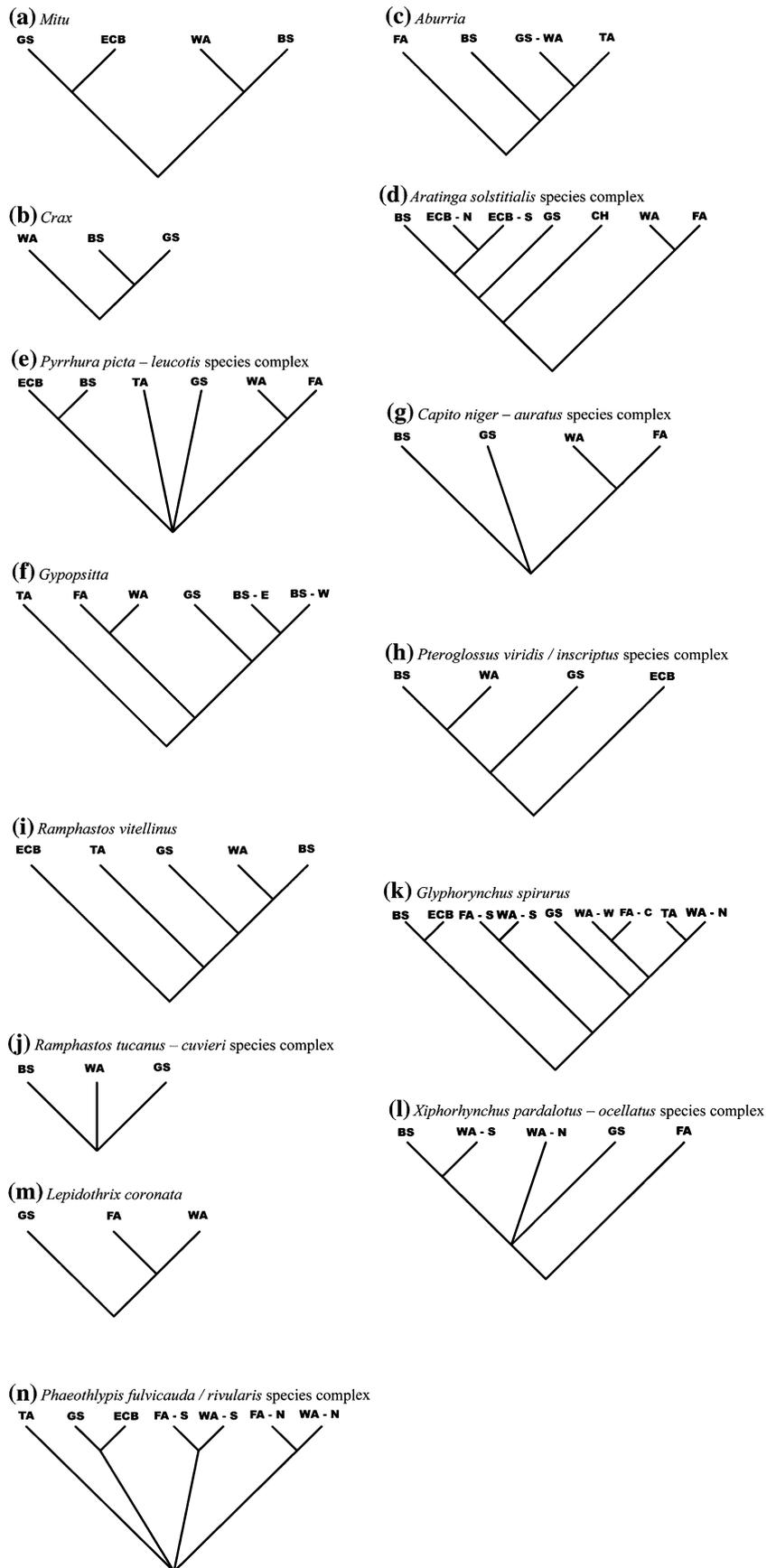
Can the inferred correlation between the diversification scenario proposed for some species of the genus *Xiphorhynchus* and that postulated by landscape changes in Amazonia since the late Tertiary be extended to other lineages of floodplain and upland species in Amazonia as well? Below, we provide a comprehensive review of recent phylogeographic data presented for several lineages of Amazonian birds and evaluate to what extent they fit the landscape evolution scenario proposed by Rossetti et al. (2005). When not stated otherwise, the translation of genetic distances into divergence times assumed a mtDNA substitution rate of 2% per million years (Klicka and Zink 1997; references below), which was the most frequently used calibration among the studies reviewed (see Garcia-Moreno (2004) and Lovette (2004a) for discussions on the problems associated with the 2% per million years’ calibration).

The genera *Crax*, *Mitu*, and *Nothocrax* (Cracidae)

Molecular phylogenies obtained for the monophyletic curassow genera *Crax*, *Mitu*, and *Nothocrax* revealed that species of these lineages occurring nowadays in upland and seasonally flooded forests in western Amazonia (*Crax globulosa*, *Mitu salvini*, and *Nothocrax urumutum*) represent independent radiations in their respective groups (Pereira and Baker 2004). While the monotypic genus *Nothocrax* consists of one of the earliest divergences among the curassows [estimated as dating back to 9.5 million years ago (Ma)], diversification in the genus *Mitu* began with the isolation between Guianan shield/eastern Brazilian and southern Amazonian populations (5.5 Ma), being followed by the split between Guianan shield (*M. tomentosum*) and Atlantic forest (*M. mitu*) populations, and between Brazilian shield (*M. tuberosum*) and western Amazonian taxa (*M. salvini*; 3.4 Ma; Fig. 2a; the placement of *Pauxi unicornis* as sister to *M. tuberosum* is very likely an experimental error, given that its sole and similar congener, *P. pauxi*, consistently appeared as the sister taxon of all *Mitu* species). As for *Crax*, a distinct pattern emerges, whereby Amazonian populations first diversified through a split between Guianan/Brazilian shield (*C. alectorifasciolata*) and western Amazonian populations (*C. globulosa*; 6.1 Ma; Fig. 2b), with a subsequent split occurring between Brazilian and Guianan shield populations (1.6 Ma).

Therefore, the time frame stretching from the late Miocene to the Pleistocene (late Tertiary and early Quaternary) consisted of a period of intensive differentiation among populations of Amazonian curassows, with the Brazilian/Guianan shields and western Amazonian functioning as important areas of vicariance and evolution.

Fig. 2 Summary of area relationships among main Amazonian geological areas and other extra-Amazonian regions as indicated by some of the avian lineages reviewed in this study. The following are the main Amazonian geological areas: *BS* Brazilian shield, *FA* eastern foothills of the Andes, *GS* Guianan shield, *WA* western Amazonian lowlands and extra-Amazonian regions, *ECB* eastern/central Brazil, *CH* Chaco/Pantanal, and *TA* trans-Andes. Area codes followed by *N*, *S*, *C*, *E*, and *W* refer, respectively, to those areas' northern, southern, central, eastern, and western parts. See text for details



The genus *Aburria* (Cracidae)

Molecular phylogenies obtained for the piping-guans (genus *Aburria*), birds predominantly associated with river-edge forest, showed that the Amazonian and Trinidad taxa (*A. kujubi*, *A. cumanensis*, and *A. pipile*) are monophyletic and sister to the eastern Andean species (*A. aburri*), from which they became evolutionarily independent by about 3 Ma (middle Pliocene; Fig. 2c; Grau et al. 2005). Further diversification within the former group occurred with the split between Brazilian (*A. kujubi*) and Guianan shields (*A. cumanensis*) populations, estimated to date back to about 1.7 Ma, followed by the separation of the Guianan shield and the Trinidad populations (*A. pipile*), which is thought to have been completed by 0.9 Ma (Fig. 2c).

Thus, the eastern Andean foothills, as well as the Brazilian and Guianan shields, were important centers of evolution for *Aburria* species; nonetheless, when compared with other avian lineages, diversification among Amazonian populations of *Aburria* is limited and fairly recent, being mostly restricted to the Quaternary (early and middle Pleistocene).

The *Aratinga solstitialis* (Psittacidae) species complex

Molecular phylogenies presented for the *A. solstitialis* species complex revealed a complex evolutionary history, where Amazonian taxa are not monophyletic and, in some cases, are sister to some extra-Amazonian lineages (Fig. 2d; Ribas and Miyaki 2004). The first split among populations of this complex was between populations of western Amazonia and Andean foothills (*A. weddelli*) and those from the Guianan and the eastern part of the Brazilian shields (remaining taxa); this event was dated back to about 4.9 Ma (Pliocene). Subsequent diversification of the complex took place during the Pleistocene in the following steps: (1) split between the Chaco/Pantanal populations (*A. nenday*) and those from the eastern Brazilian/Guianan shields (completed by 1.8 Ma); (2) split between Guianan (*A. solstitialis*) and remaining Brazilian shield populations (0.7 Ma); and (3) split between northern (*A. jandaya*) and southern (*A. auricapilla*) eastern Brazilian shield populations (Fig. 2d).

When contrasted to other lineages of Amazonian birds, the diversification of the *Aratinga solstitialis* species complex occurred predominantly in open rather than forested landscapes (only *A. weddelli* is found in upland forest edge). This fact probably explains why physiographic events of the Late Tertiary are thought to be responsible just for the initial burst of diversification in this species complex, while Pleistocene climatic changes linked to cyclical interplays between open and forest landscapes might be associated with the more recent speciation events.

The *Pyrrhura picta-leucotis* (Psittacidae) species complex

Molecular phylogenies available for the *P. picta-leucotis* species complex, a parakeet lineage distributed in different forest types through most of the Neotropics, revealed the existence of four main clades whose relationships were not entirely resolved: (1) a Guianan shield (*P. picta*), (2) a trans-Andean (*P. emma* and *P. eisenmanii*), (3) a Brazilian shield/central/eastern Brazilian (*P. snethlageae*, *P. amazonum*, *P. griseipectus*, and *P. leucotis*), and (4) an Andean foothill/western Amazonian (*P. peruviana* and *P. roseifrons*; Fig. 2e). A fourth lineage (*P. pfrimeri*, not shown in Fig. 2e), from central Brazil, could not be placed with a reasonable degree of certainty within or as sister to any of those three clades (Ribas et al. 2006). Fairly low genetic distances among members of this species complex indicated that most of its diversification occurred during the Pleistocene, probably starting at about 1.3 Ma. Therefore, molecular phylogenies support the division of Amazonian populations of the *Pyrrhura picta-leucotis* species complex into groups associated with each of the three main areas postulated to have acted as centers of vicariance for the avifauna in this region: Guianan shield, Brazilian shield, and foothills of the Andes.

The genus *Gypopsitta* (Psittacidae)

Molecular data available for the parrot genus *Gypopsitta* showed that Amazonian and Andean species are monophyletic (Ribas et al. 2005). The earliest episode of diversification within Amazonia involved the split between eastern (probably isolated on the Guianan and Brazilian shields) and western (probably isolated on the eastern slope of the Andes) populations, and was tentatively dated back to about 5 Ma (early Pliocene; Fig. 2f). Further splits in Amazonia involved: (1) populations of the Guianan and Brazilian shields (ca. 3 Ma; middle Pliocene), and (2) populations of the eastern and western parts of the Brazilian shield (about 0.5 Ma; Pleistocene; Fig. 2f). Under this scenario, the taxon currently inhabiting western Amazonia (*G. barrabandi*) is, in fact, derived from an ancient but apparently limited radiation of this genus in the Andes, whereas the remaining Amazonian species diversified on the Brazilian and Guianan shields during the Pliocene and Pleistocene.

The genus *Capito* (Ramphastidae)

Molecular phylogenetics data available for the genus *Capito* indicate that Amazonian species in this genus are not monophyletic (Armenta et al. 2005). While the southwestern Brazilian shield endemic *C. dayi* is sister to an

Andean taxon, the floodplain forest specialist *C. aurovirens* belongs to an independent lineage with no closely related living relatives. On the other hand, the so-called *C. niger/auratus* species complex, distributed through most of Amazonia, includes three monophyletic taxa: *C. brunneipectus* (northwestern corner of the Brazilian shield), *C. niger* (Guianan shield), and *C. auratus* (western Amazonian lowlands; Fig. 2g). These three major groups diverge from each other by over 6% of uncorrected pairwise sequence divergence, indicating that their separation was complete by at least 3 Ma (late Pliocene). While the Guianan and Brazilian shield populations (*C. niger* and *C. brunneipectus*) split early on and roughly at the same time (3 Ma), the western Amazonian radiation (*C. auratus*) is more recent (dating back to roughly 2.5 Ma). The phylogeography of *C. auratus* suggests that populations closer to the Andes are more genetically diverse and structured, and they probably represented the source of a widespread radiation into the western Amazonian lowlands; currently, the Amazon and Ucayali rivers bound two clades of *C. auratus*, indicating that they comprise important barriers preventing gene flow between populations from opposite river banks.

The genus *Pteroglossus* (Ramphastidae)

Molecular data published for the Amazonian *Pteroglossus viridis/inscriptus* and *Pteroglossus bitorquatus/flaviviridis* species complexes showed that these two groups have distinct evolutionary histories (Eberhard and Bermingham 2005). In the former group, the first split occurred between eastern Brazilian and Amazonian populations, followed by the separation between Guianan shield (*P. viridis*) and southern Amazonian populations (estimated as being completed by 1.5 Ma); the subsequent split involved Brazilian shield (*P. inscriptus*) and western Amazonian populations (*P. I. humboldti*) and is thought to have been completed by 1 Ma (Fig. 2h). In the *Pteroglossus bitorquatus/flaviviridis* species complex (not distributed on the Guianan shield), the first main split occurred between Brazilian shield/southwestern Amazonian and western/northwestern Amazonian populations (not shown in Fig. 2h); further splits separated the former and latter populations into two groups, respectively: *P. bitorquatus/P. beauharnesii* and *P. flaviviridis/mariae*. Essentially, these phylogenies and those of the *Pteroglossus aracari* species group are consistent with the recognition of three main areas of diversification for this genus in Amazonia: (1) the Brazilian shield, (2) Guianan shield, and (3) the western Amazonian lowlands. Furthermore, most of the splitting events in *Pteroglossus* were concentrated around 1 Ma, thus within the Pleistocene.

The genus *Ramphastos* (Ramphastidae)

Molecular data published for the toucan genus *Ramphastos* showed an interesting pattern, where populations of the exclusively or predominantly Amazonian species (*R. vitellinus* and *R. tucanus*) are poorly differentiated genetically throughout the basin (Weckstein 2005). In fact, many of the described subspecies of those two species are paraphyletic, and levels of sequence divergence among them are comparatively low (0.1–0.8%), indicating high levels of historical and current gene flow, consistent with the recognition of wide zones of morphological intergradation as described previously by Haffer (1974). Nevertheless, the dataset for both *Ramphastos* lineages contained the following strong phylogenetic signal: Amazonian populations were monophyletic and those of the Guianan shield were grouped in a separate clade from those of the remaining areas (Brazilian shield and western Amazonian; Fig. 2i, j).

The wedge-billed woodcreeper (*Glyphorhynchus spirurus*: Dendrocolaptidae)

A phylogeographic study on the widespread wedge-billed woodcreeper (*G. spirurus*) recovered essentially four distinct clades associated with the following areas: (1) Brazilian shield/eastern Brazil; (2) foothills of the Bolivian and southeastern Peruvian Andes/southwestern Amazonian lowlands; (3) Guianan shield; (4) foothills of the Central Peruvian and Ecuadorian Andes/western Amazonian lowlands; and (5) northwestern Amazonian/trans-Andean populations (Fig. 2k). Ancestral populations from the first three areas became completely isolated from each other at roughly the same time (estimated as 3 Ma, corresponding to an uncorrected average pairwise sequence divergence of about 6%), whereas those from the western Amazonian lowlands began to evolve independently about 2.5 Ma (Marks et al. 2002).

While populations from the Brazilian and Guianan shields are monophyletic, those from western Amazonia descend from at least three independent lineages associated with Andean and trans-Andean populations. The molecular data available for *Glyphorhynchus* also allow the conclusion that most of the diversification in this lineage occurred during the late Pliocene and early Pleistocene.

The *Xiphorhynchus pardalotus/ocellatus* (Dendrocolaptidae) species complex

Phylogeographic and population genetics analyses of the *X. pardalotus/ocellatus* species complex, a lineage inhabiting most of Amazonia and the foothills of the Andes, revealed that the initial split among its members occurred between the Andean and Guianan/Brazilian shields populations

(tentatively dated to about 4 Ma), with subsequent subdivision separating populations inhabiting the Guianan shield from those of the Brazilian shield (inferred to be completed about 3 Ma) (Aleixo et al. 2006). Populations from western Amazonia south of the Amazon river are related to those of the Brazilian shield (the major split within this clade is dated to about 1.7 Ma), whereas those north of the same river could not be placed robustly as sister to any other lineage, but they have been evolving separately since at least about 2.5 Ma (Fig. 2l). Thus, the late Tertiary and early Pleistocene were periods of intense population subdivision and speciation among members of the *X. pardalotus/locellatus* species complex, with the eastern Andean foothills and the Guianan/Brazilian shields harboring ancient monophyletic populations. On the other hand, populations from the western Amazonian sedimentary basins are paraphyletic and probably became established in this area following distinct colonization episodes (Fig. 2l).

The warbling (*Hypocnemis cantator*) and the striated (*Drymophila devillei*) antbirds (Thamnophilidae)

Molecular data available for these two lineages of antbirds indicated that their populations are highly divergent throughout Amazonia, probably consisting of separate species in some cases (Bates et al. 1999).

Data obtained for *D. devillei* revealed that populations of the western part of the Brazilian shield differ by about 3% of uncorrected pairwise sequence divergence from those of the eastern slopes of the Bolivian Andes and adjacent Amazonian lowlands (which translates into a split dating back to about 1.5 Ma); furthermore, Andean populations are far more diverse genetically than those of the Brazilian shield, suggesting a more recent colonization of the latter area.

A more limited sampling of *H. cantator* showed that populations separated by the Amazon river differ by up to 6% of pairwise uncorrected sequence divergence; interestingly, as found for several other lineages, the western part of the Brazilian shield is inhabited by very divergent populations of this species, with up to 4.5% of pairwise sequence divergence.

The blue-crowned Manakin (*Lepidothrix coronata*: Pipridae)

A detailed phylogeographic study on the upland forest manakin *Lepidothrix coronata* revealed that foothill Andean and western Amazonian populations of this species are monophyletic and sister to populations occurring on the western part of the Guianan shield (Venezuela), from which they had split completely by 2 ± 0.9 Ma (late Pliocene/early Pleistocene; Fig. 2m) (Cheverson et al. 2005). Subsequent

diversification in the Amazon took place through a split between foothill Andean/northern Amazonian and southern Amazonian populations (dated to 1.4 ± 0.6 Ma); while northern populations were in a mutation/drift equilibrium (usually associated with demographic stability), the southern populations have expanded continuously since they became separated. This scenario supports the notion that western Amazonian lowland populations of *L. coronata* might have colonized most of this area from ancestral populations associated with the Andean foothills in northern Peru and Ecuador during the past 1 Ma or so.

The *Phaeothlypis fulvicauda/rivularis* species complex (Parulidae)

A phylogeography proposed for the Neotropical wood-warblers of the *Phaeothlypis* species complex recovered four main clades whose basal relationships were not entirely resolved: (1) trans-Andean; (2) Guianan shield/eastern Brazil (Atlantic forest); (3) southwestern Amazonia/foothills of the Andes; and (4) northwestern Amazonia/foothills of the Andes (Fig. 2n) (Lovette 2004b). Amazonian populations, therefore, descend from three of those separate lineages (Guianan shield, southwestern Amazonia/Andes, and northwestern Amazonia/Andes), which became completely separated from each other between 3.4 and 3.6 Ma (assuming a clock-like substitution rate of 1.6% per million years).

The genus *Tangara* (Emberizidae)

Molecular phylogenetics data available for most species of this incredibly diverse genus showed that Amazonian species of *Tangara* are polyphyletic, with many species representing lowland Amazonian radiations of predominantly Andean and northern South American lineages (Burns and Naoki 2004). In fact, the genus as a whole is thought to be of northern Andean origin, and several subsequent episodes of dispersal into the Amazonian lowlands can be inferred, based on the phylogeny. In the genus *Tangara*, species began diverging from each other by about 6 Ma, with most splits occurring between 3.5 and 5.5 Ma, thus during a time frame stretching from the late Miocene to the Pliocene.

Towards a modern synthesis of Amazonian biogeography?

Of the 18 different Amazonian avian lineages for which molecular systematics and phylogeographic data were reviewed, half (nine, or 50%) diversified predominantly during the Late Tertiary (Pliocene): *Mitu*, *Crax*,

Gypopsitta, *Capito*, *G. spirurus*, *X. pardalotus/ocellatus*, *Hypocnemis cantator*, *P. fulvicauda/rivularis*, and *Tangara*. While the other half lineages (*Aburria*, *Aratinga*, *Pyrrhura*, *Pteroglossus*, *Ramphastos*, *Drymophila devillei*, and *Lepidothrix coronata*) began to diversify during the Pliocene, most of their cladogenesis took place during the early and middle Pleistocene. In one case (*Nothocrax*), the split between this isolated lineage and the remaining curassows dates back to the Miocene. Even though divergence estimates based on the molecular clock theory are widely open to criticism (Van Tuinen and Hadly 2004; Lovette 2004a), it is impressive that in such a wide range of taxa sampled (with distinct life-history attributes and evolutionary histories), divergence estimates of cladogenesis episodes overlap on a time frame stretching from the late Miocene to the early Pleistocene (late Tertiary and early Quaternary periods; see also Weir 2006). As discussed before, this time frame matches exactly the dynamic scenario of landscape evolution reconstructed for Amazonia, particularly the western Amazonian lowlands (Rossetti et al. 2005). Much geological research remains to be done in Amazonia to allow more accurate correlations between particular episodes of landscape change and lineage splitting, but it is now clear that late Tertiary and early Quaternary Amazonian geology can provide important clues as to the proximate causes of the incredible diversification experienced by avian as well as primate lineages in this unique region (Silva et al. 2005).

Another important pattern revealed by the molecular studies reviewed is that while the Brazilian and Guianan shields are often inhabited by monophyletic populations with no closest single relatives (suggesting in-site vicariance and long-term evolution), the western Amazonian sedimentary basins are frequently inhabited by paraphyletic or polyphyletic lineages with distinct evolutionary histories (e.g., *Glyphorhynchus spirurus*, *X. pardalotus/ocellatus*, and *P. rivularis/fulvicauda*). Thus, many lineages occurring nowadays in the western Amazonian lowlands have close relatives or populations living in the foothills of the Andes (*Aratinga*, *Pyrrhura*, *Gypopsitta*, *Capito*, *Pteroglossus bitorquatus* complex, *Glyphorhynchus spirurus*, *Drymophila devillei*, *Lepidothrix coronata*, *P. rivularis/fulvicauda*, and *Tangara*). Particularly in the cases where more detailed phylogeographic data are available (*Glyphorhynchus spirurus*, *Drymophila devillei*, and *Lepidothrix coronata*), a scenario of more recent colonization of the lowlands by foothill populations is supported (Bates et al. 1999; Marks et al. 2002; Cheviron et al. 2005). In other cases, however, taxa from the western sedimentary basins are more closely related to lineages of the Guianan and/or Brazilian shields (*Mitu*, *Aburria*, *Pteroglossus viridis/inscriptus* complex, *Ramphastos vitellinus* and *X. pardalotus/ocellatus* complex).

This biogeographic pattern is also in agreement with the geological history of the western Amazonian sedimentary basins, which have witnessed more drastic physiographic and landscape changes during the Tertiary and Quaternary than the adjacent Brazilian and Guianan shields (Rossetti et al. 2005). Particularly, the fact that most of the western Amazonian lowlands were covered by a huge lake system (called Lake Pebas), until at least the late Miocene, suggests that lineages strictly associated with upland forest could not have become established in this area before that period; thus, it is likely that they have colonized the western lowlands from neighboring areas which were inhabited by upland forest species, namely the Brazilian and Guianan shields and the foothills of the Andes.

Species not strictly associated with upland forest habitats, or those occurring mostly in seasonally flooded forests, might have more ancient histories in the western Amazonian sedimentary basins, as molecular phylogenetics data available for *Capito aurovirens* (Armenta et al. 2005), and *X. kienerii* and *X. obsoletus* seem to imply (Aleixo 2002, 2006). These lineages are very divergent from their nearest living relatives, and little phylogeographic structure and morphological polymorphism has been documented for their populations. Similarly, lineages with more generalized habitat requirements and higher dispersal capabilities (such as the genera *Aburria*, *Pteroglossus*, and *Ramphastos*) are more likely to have more ancient and complex histories in the western Amazonian sedimentary basins (Eberhard and Bermingham 2005; Grau et al. 2005; Weckstein 2005).

Nevertheless, in spite of this overall agreement between late Tertiary/early Quaternary geological history and avian molecular phylogenetics data, there is already some indication that more intricate evolutionary scenarios can be expected in particular areas of Amazonia. Many of the avian lineages reviewed in this paper have distinct or highly divergent taxa/populations replacing each other across a latitudinal gradient on the western part of the Brazilian shield, along the Madeira river basin (*Capito dayi/C. brunneipectus*, *Gypopsitta barrabandi/G. vulturina/G. aurantiocephala*, *G. spirurus*, *X. elegans*, *X. ocellatus*, and *Hypocnemis cantator*); in some cases, these lineages are not even monophyletic, with distinct subgroups having closer phylogenetic affinities with disparate lineages, such as those from other parts of the Brazilian shield, the Andes or the western Amazonian lowlands (Bates et al. 1999; Marks et al. 2002; Aleixo 2004; Aleixo et al. 2006; Armenta et al. 2005; Ribas et al. 2005). Coincidentally, the geological history of this area is currently under study, and it is now clear that the western fringe of the Brazilian shield in Amazonia is bordered by more recent sedimentary deposits, which have not yet been

characterized or dated (Rossetti et al. 2005). Therefore, the ancient Brazilian shield and the more recent western Amazonian sedimentary basins are separated by a yet distinct geological formation, which, as some of the reviewed data suggest, has also influenced patterns of diversification of several avian lineages.

In conclusion, the phylogeographic data reviewed here indicate that the diversification scenario proposed for Amazonia based on data for some species of the genus *Xiphorhynchus* (Aleixo 2004, 2006) can be extended to other lineages of floodplain and upland species as well. However, a more rigorous test of the influence of Tertiary and Quaternary Amazonian geology on the concordant phylogeographic patterns discussed here awaits a more detailed analysis, where molecular divergences obtained for all taxa considered can be reliably calibrated and contrasted directly with each other.

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