

## DIVERSIFICATION IN THE NEOTROPICS: PHYLOGENETIC PATTERNS AND HISTORICAL PROCESSES

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**Resumen.** – **Diversificación en el Neotrópico: Patrones filogenéticos y procesos históricos.** – Resumimos los resultados de dos simposios que reunieron un amplio espectro de presentaciones sobre cómo los datos moleculares están aumentando nuestro conocimiento de los patrones y procesos de diversificación de las aves Neotropicales, y del momento en que esta diversificación tuvo lugar. Los expositores están asociados con museos de historia natural, lo que asegura que los datos moleculares estén asociados con especímenes de referencia. La sistemática molecular es un campo que avanza rápidamente, y que resulta muy promisorio para mejorar el entendimiento de los procesos evolutivos en los años venideros.

**Abstract.** – We summarize two symposia that brought together a broad spectrum of talks on how molecular data are expanding our understanding of the patterns, processes and timing of avian diversification in the Neotropics. Presenters are associated with natural history museums, which ensure that genetic data are associated with vouchered specimens. Molecular systematics is a rapidly evolving field which promises to bring new understandings of the evolutionary process in the years to come. *Accepted 21 December 2007.*

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The earliest naturalists working in the Neotropics contemplated the mechanisms that could have produced and maintained such a dazzling array of biological diversity. That glacial/interglacial cycles, mountain-building, riverine barriers, dispersal, and genetic differentiation were important in the diversification of Neotropical birds has been known for a long time (Wallace 1853, Chapman 1917, Chapman 1923), yet a detailed understanding of the role of these processes in generating

and maintaining biological diversity remains poor. This is in part because there are still few well-supported phylogenies available for Neotropical birds. In addition, historical diversification hypotheses have an inherently temporal component that is difficult to assess using phylogenies obtained from morphological data.

Our understanding of speciation patterns and processes in the Neotropics is rapidly progressing with the application of molecular

data to help address these questions (e.g., Omland *et al.* 1999, Burns & Naoki 2004, Bates *et al.* 2004, Pérez-Emán 2005, Aleixo *et al.* 2006, Ribas *et al.* 2005, 2006, Weir 2006, Barker 2007, Brumfield & Edwards 2007, Cadena *et al.* 2007). Over the last 30 years, the technologies to gather and study molecular data have been developed and improved at dramatic rates. The costs of performing PCR and DNA sequencing continue to decrease, making the acquisition of molecular data possible for a greater number of ornithologists. The growth of molecular studies of Neotropical birds has also been facilitated by the creation and ongoing maintenance of genetic resources collections (Edwards *et al.* 2005).

Although molecular data have some advantages over morphological data in the context of making inferences about genetic relationships, be they familial or phylogenetic, morphological data still play a vital role in evolutionary studies – phenotypic characters are shaped by evolution through direct interactions with the external environment. Referring to his desire for geneticists and systematists to cooperate, Chapman (1923) stated that, “After all, both are trying to discover real relationships and if the latter from the nature of their material, the limitation of their methods, and the classifiers’ necessity of always making some decision infrequently reach erroneous conclusions, their handicaps should win for them the assistance rather than the criticism of those who are discovering more certain means for the determination of affinities than are afforded by most museum specimens.”

Phylogenies generated from DNA sequences also have had an immediate impact on taxonomy (e.g., Braun *et al.* 2005, Isler *et al.* 2006). The dynamic nature of taxonomy is illustrated elegantly by the web page of the American Ornithologists’ Union’s South American Checklist Committee (Remsen *et al.* 2007), which is updated almost daily with tax-

onomic changes. Anyone can submit a proposal to the committee to be evaluated. As of 13 June, 2007, 291 proposals have been evaluated, with the last two “passing” proposals being decisions to transfer *Picooides mixtus* and *P. lignarius* to *Veniliornis* (Moore *et al.* 2006) and a revision of the linear sequence of *Tangara* tanagers (Burns & Naoki 2004), both based on recent molecular studies.

The two symposia we organized brought together a broad spectrum of talks that illustrate the influences of molecular data on our understanding of the patterns, processes and timing of avian diversification in the Neotropics. In addition, these symposia illustrated well that molecular data are being gathered by an increasing number of Latin American ornithologists, often working in Latin American laboratories. Many of these laboratories are associated with natural history museums, which ensure that genetic data are associated with vouchered specimens. The latter is important not only for identification purposes, but also to help us to understand the relationships between genotype and phenotype (Bates *et al.* 2004, Peterson *et al.* 2007).

Remsen, using a large molecular data set on hummingbirds (McGuire *et al.* 2007), one of the most diverse and taxonomically challenging Neotropical families, discussed the implications on the classification of hummingbirds at the generic level. New understandings of relationships from the molecular data include the grouping together of a previously unrecognized clade of hummingbirds characterized by “knife-like” bills.

No matter what species concept one favors, molecular data offer important new insights on speciation and species limits. Bates presented an overview of several molecular studies on Neotropical birds and discussed the patterns from these studies in the framework of “ecological and genetic exchangeability” (Crandall *et al.* 2000). Comparing data sets for groups including Galapa-

gos finches (Sato *et al.* 1999, Zink 2002), Galapagos mockingbirds (*Nesomimus*, Arbogast *et al.* 2006) and Wedge-billed Woodcreeper (*Glyphorhynchus spirurus*, Marks *et al.* 2002), he emphasized the importance of isolation in addition to exchangeability, citing Zink's (2002) assertion that *Geospiza* and *Camarhynchus* finches may best be considered singles species. In contrast, he argued that Galapagos mockingbirds, with reciprocal monophyly on each island sampled, comprise more than the currently recognized four species.

The pattern of high levels of intraspecific genetic variation in traditionally recognized species, particularly in Amazonian birds, was highlighted by Chesser for lineages of antwrens in the genus *Myrmotherula*, and by Aleixo for lineages of manakins and woodcreepers. Results of these studies illustrate the levels of complexity that exist in the history of population subdivision in Amazonian birds. Ribas presented data on patterns of divergence in parrots (Ribas *et al.* 2005, 2006, 2007), which included Amazonian and non-Azorian taxa. Her data illustrate that parrots display a complicated set of evolutionary exchanges with respect to the major biomes (e.g., Amazonia, Cerrado, the Andes). In lineages of suboscine birds (e.g., antbirds and ovenbirds), the majority of generic lineages have invaded another biome only once, but parrots appear to have had multiple lineages evolve across the Cerrado, Amazonia, and the Andes.

Areas of endemism are thought to represent biogeographic regions that were important historically in the diversification of birds. Vicariance biogeography (Platnick & Nelson 1978) has provided a conceptual framework for testing such biogeographic patterns in the Neotropics, by the prediction that biogeographic patterns shared by a diversity of unrelated taxa must reflect a common underlying vicariant history. While many studies have

corroborated the importance of large-scale vicariant events (e.g., Andean uplift) in Neotropical diversification (e.g., Bates *et al.* 1998, Ribas *et al.* 2007), it is becoming increasingly clear that dispersal across pre-existing barriers has also played an important role. Because dispersal propensity is species-specific, shared biogeographic patterns are not necessarily expected. Brumfield & Burney examined the role of the Andes in the diversification of 40 humid forest species that have populations isolated on opposite sides of the Andes. Their preliminary mitochondrial data illustrated that dispersal propensity of species influenced the level of genetic divergence across the Andes, a relationship not expected under a simple vicariance model.

Pérez-Emán & Cadena presented data on population structure in taxa that live in two major highland regions, the Tepuis and the Andes. Pérez-Emán has found major genetic breaks between populations from the eastern and western Tepui regions, including redstarts (*Myioborus*, Pérez-Emán 2005) as well as a relationship between central Andean and Pantepuian taxa. Cadena presented data on the complex evolutionary patterns in a number of Andean lineages, including tapaculos (*Scytalopus*), wood-wrens (*Henicorhina*) and brush-finches (*Atlapetes*). These studies demonstrate the exciting prospect of uncovering sets of lineages that have responded differently to the same historical events. Studies on both the Andes and the Tepuis reveal that the history of many lineages is complex, such that current patterns of distribution and differentiation are the result of an interplay of various events of dispersal, vicariance, and importantly, extinction.

One of the most intriguing prospects for molecular data is their value in dating divergences on evolutionary trees. Dating molecular data is controversial because it relies on the assumption of a comparable molecular clock across different lineages. Although new ana-

lytical methods allow one to relax this assumption, there is still the challenge of deciding what represents an appropriate calibration. For Neotropical birds, little is known about the fossil record of most lineages; thus, hypotheses based on molecular clocks are the first data-rich methods to look at the timing of splits, and they are challenging some traditional views, such as the Pleistocene being the primary period of divergence at the species level. Klicka *et al.* presented data on genetic structure from throughout the distribution of the House Wren (*Troglodytes aedon* complex) and their results provide evidence that extremely widespread taxa can be comprised of multiple lineages hypothesized to have diverged before the Pleistocene.

Tello and colleagues dated deep divergences throughout the New World suboscines, the lineage that contributes the most to the high levels of endemism in the Neotropics, using penalized likelihood (Sanderson 2002). In uncovering the temporal patterns of lineage diversification, they tested if the resulting pattern fits a model of gradual lineage accumulation. The results supported a global pattern of constant diversification with low extinction for the New World suboscines in the time between 60 to 10 MYA. However, when partitioned by families, the results showed a more complex pattern with cases of increase and decrease in diversification rates at different times. Their results will help our understanding of the history of suboscine diversification in the region beyond 5–10 MYA (i.e., the time when most intrageneric diversification is suggested to have occurred).

In a recent paper, Weir (2006) reviewed DNA sequence studies on a wide variety of Neotropical taxa and concluded that rates of lineage divergence (speciation) were greater in the Andes than in the lowlands. As interesting as this approach is, Ribas' analyses of multiple

lineages of lowland parrots suggests the overall patterns reported by Weir may be the result of a number of biases, including a lack of recognition of the degree of intraspecific genetic structure in the lowlands. Again, given that the fossil record is exceedingly sparse for Neotropical avian lineages, these data and the new analytical techniques being employed to analyze them are revolutionizing our understanding of the timing and patterns of Neotropical divergence. This new understanding has implications for all other aspects of avian biology.

Looking to the future, these symposia illustrate where the field is now, but we are only scratching the surface of what these data can ultimately tell us about avian diversity in the Neotropics and the processes that have shaped such diversity. Most taxa have yet to be included in any molecular study. Phylogeographic analyses are still in their infancy, and many more detailed studies are needed at both regional and local scales using multiple types of markers to understand the role of barriers to gene flow and the prevalence and influence of dispersal. To date, most of the studies on Neotropical birds have studied mitochondrial DNA sequences. The breadth of concordant, well supported results with analytically tractable and useful amounts of variation across a fairly broad evolutionary scale suggests that mtDNA genes continue to be the most broadly comparable type of sequence data, but it is still desirable to gather independent molecular data sets and to compare and contrast molecular results with other types of data. In the future, our ability to work with additional types of molecular sequence data from the nuclear genome will allow researchers to uncover the molecular underpinnings of phenotypic variation (Cheviron *et al.* 2006). While there is still much to learn, molecules are unraveling previously unassailable mysteries about Neotropical evolution.

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## REFERENCES

- Aleixo, A., T. Burlamaqui, E. Goncalves, & P. Schneider. 2006. Molecular systematics of the Ocellated Woodcreeper complex (Dendrocolaptidae) in tropical South America: Implications for taxonomy, conservation, and historical biogeography. *J. Ornithol.* 147: 125–126.
- Arbogast, B. S., S. V. Drovetski, R. L. Curry, P. T. Boag, G. Seutin, P. R. Grant, B. R. Grant, & D. J. Anderson. 2006. The origin and diversification of Galapagos mockingbirds. *Evolution* 60: 370–382.
- Barker, F. K. 2007. Avifaunal interchange across the Panamanian isthmus: insights from *Campylorhynchus* wrens. *Biol. J. Linn. Soc.* 90: 687–702.
- Bates, J. M., S. J. Hackett, & J. Cracraft. 1998. Area-relationships in the Neotropical lowlands: An hypothesis based on raw distributions of passerine birds. *J. Biogeogr.* 25: 783–793.
- Bates, J. M., J. Haffer, & E. Grismer. 2004. Avian mitochondrial DNA sequence divergence across a headwater stream of the Rio Tapajos, a major Amazonian river. *J. Ornithol.* 145: 199–205.
- Bates, J. M., R. C. K. Bowie, D. E. Willard, G. Voelker, & C. Kahindo. 2004. A need for continued collecting of avian voucher specimens in Africa, or: Why blood is not enough. *Ostrich* 75: 187–191.
- Braun, M. J., M. L. Isler, P. Isler, J. M. Bates, & M. B. Robbins. 2005. Avian speciation in the Pantepui: the case of *Percnostola* [*Schistocichla*] "*leucostigma*" *saturata*. *Condor* 107: 329–343.
- Brumfield, R. T., & S. V. Edwards. 2007. Evolution into and out of the Andes: a Bayesian analysis of historical diversification in *Thamnophilus* antshrikes. *Evolution* 61: 346–367.
- Burns, K. J., & K. Naoki. 2004. Molecular phylogenetics and biogeography of Neotropical tanagers in the genus *Tangara*. *Mol. Phylogenet. Evol.* 32: 838–854.
- Cadena, C. D., J. Klicka, & R. E. Ricklefs. 2007. Evolutionary differentiation in the Neotropical montane region: Molecular phylogenetics and phylogeography of *Buarremon* brush-finches (Aves, Emberizidae). *Mol. Phylogenet. Evol.* 44: 993–1016.
- Chapman, F. M. 1917. The distribution of bird-life in Colombia. *Bull. Am. Mus. Nat. Hist.* 36: 1–729.
- Chapman, F. M. 1923. Mutation among birds in the genus *Buarremon*. *Bull. Am. Mus. Nat. Hist.* 48: 243–278.
- Cheviron, Z. A., S. J. Hackett, & R. T. Brumfield. 2006. Sequence variation in the coding region of the melanocortin-1 receptor gene (MC1R) is not associated with plumage variation in the Blue-crowned Manakin (*Lepidothrix coronata*). *Proc. Roy. Soc. B-Biol. Sci.* 273: 1613–1618.
- Crandall, K. A., O. R. P. Bininda-Emonds, G. M. Mace, & R. K. Wayne. 2000. Considering evolutionary processes in conservation biology. *Trends Ecol. Evol.* 15: 290–295.
- Edwards, S. V., S. Birks, R. T. Brumfield, & R. Haner. 2005. The future of avian genetic resources collections: archives of evolutionary and environmental history. *Auk* 122: 979–984.
- Isler, M. L., D. R. Lacerda, P. R. Isler, S. J. Hackett, K. V. Rosenberg, & R. T. Brumfield. 2006. *Epinicrophylla*, a new genus of antwrens (Aves: Passeriformes: Thamnophilidae). *Proc. Biol. Soc. Wash.* 119: 522–527.
- Marks, B. D., S. J. Hackett, & A. P. Capparella. 2002. Historical relationships among Neotropical lowland forest areas of endemism as inferred from mitochondrial DNA sequence variation in the Wedge-billed Woodcreeper (Dendrocolaptidae: *Glyphorhynchus spirurus*). *Mol. Phylogenet. Evol.* 24: 155–167.
- McGuire, J. A., C. C. Witt, D. L. Altshuler, & J. V. Remsen, Jr. 2007. Phylogenetic systematics and biogeography of hummingbirds: Bayesian and maximum likelihood analyses of partitioned data and selection of an appropriate partitioning strategy. *Syst. Biol.* 56: 837–856.
- Moore W. S., A. C. Weibel, & A. Agius. 2006. Mitochondrial DNA phylogeny of the woodpecker genus *Veniliornis* (Picidae, Picinae) and related

- genera implies convergent evolution of plumage patterns. *Biol. J. Linn. Soc.* 87: 611–624.
- Omland, K. E., S. M. Lanyon, & S. J. Fritz. 1999. A molecular phylogeny of the New World orioles (*Icterus*): the importance of dense taxon sampling. *Mol. Phylogenet. Evol.* 12: 224–239.
- Pérez-Emán, J. L. 2005. Molecular phylogenetics and biogeography of the Neotropical redstarts (*Myioborus*; Aves, Parulinae). *Mol. Phylogenet. Evol.* 37: 511–528.
- Peterson, A.T., R. G. Moyle, A. S. Nyári, M. B. Robbins, R. T. Brumfield, & J. V. Remsen, Jr. 2007. The need for proper vouchering in phylogenetic studies of birds. *Mol. Phylogenet. Evol.* 45: 1042–1044.
- Platnick, N. J., & G. Nelson. 1978. A method of analysis for historical biogeography. *Syst. Zool.* 27: 1–16.
- Remsen, J. V., Jr., C. D. Cadena, A. Jaramillo, M. A. Nores, J. F. Pacheco, M. B. Robbins, T. S. Schulenberg, F. G. Stiles, D. F. Stotz, & K. J. Zimmer. 2007. A classification of the bird species of South America. American Ornithologists' Union, version 13 June 2007. Published online at <http://www.museum.lsu.edu/~Remsen/SACCBaseline.html>.
- Ribas, C.C., R. Gaban-Lima, C. Y. Miyaki, & J. L. Cracraft. 2005. Historical biogeography and diversification within the Neotropical parrotgenus *Pionopsitta* (Aves: Psittacidae). *J. Biogeography*: 32: 1409–1427.
- Ribas, C. C., L. Joseph, & C. Y. Miyaki. 2006. Molecular systematics and patterns of diversification in *Pyrrhura* (Psittacidae), with special reference to the *picta-leucotis* complex. *Auk* 123: 660–680.
- Ribas, C. C., R. G. Moyle, C. Y. Miyaki, & J. Cracraft. 2007. The assembly of montane biotas: linking Andean tectonics and climatic oscillations to independent regimes of diversification in *Pionus* parrots. *Proc. Roy. Soc. London B.* 274: 2399–2408.
- Sanderson, M. J. 2002. Estimating absolute rates of molecular evolution and divergence times: A penalized likelihood approach. *Mol. Biol. Evol.* 19: 101–109.
- Sato, A., C. O'Huigin, F. Figueroa, P. R. Grant, R. B. Grant, H. Tichy, & J. Klein. 1999. Phylogeny of Darwin's finches as revealed by mtDNA sequences. *Proc. Natl. Acad. Sci. USA.* 96: 5101–5106.
- Wallace, A. R. 1853. *A narrative of travels on the Amazon and Rio Negro*. Reeve and Co., London, UK.
- Weir, J. T. 2006. Divergent timing and patterns of species accumulation in lowland and highland neotropical birds. *Evolution* 60: 842–855.
- Zink, R. M. 2002. A new perspective on the evolutionary history of Darwin's finches. *Auk* 119: 864–871.