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The "Atlantis Forest hypothesis" does not explain Atlantic Forest phylogeography

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Leite et al. (1) conclude that isolation according to the forest refuge hypothesis (FRH) may have had a minor, if any, role on Atlantic Forest (AF) biotic evolution based on genetic data from five mammal species. Their evidence comes from signatures of population expansion during both glacial and interglacial periods, and fragmentation of reconstructed distributions during interglacial periods. Despite its novelty (i.e., the influence of sea-level changes in AF phylogeography), Leite et al.'s study presents many issues that need a critical appraisal.

First, analyses based on a single locus are prone to stochastic error and often lack sufficient variation for detecting historical processes, such as bottlenecks and shallow population structure, which are key in contrasting refugium vs. nonrefugium hypotheses. Leite et al.'s (1) conclusion that their study models lack the expected signals of refugial isolation-namely population structure and bottlenecksmay simply reflect poor resolution of the genetic marker, discordance between gene and population history, or even natural selection, issues that commonly plague mitochondrial DNA studies (2). Second, Leite et al. (1) do not explain how AF studies demonstrating population expansion and phylogeographic structure within appropriate time frames in accordance to FRH (e.g., ref. 3), including their own work (e.g., ref. 4) and many with wider geographical and genetic sampling, can be reconciled with their interpretations. Third, it is difficult to accept that a study including only five mammal species, lacking a description of their ecology and distributions, and utilizing geographically unbalanced and restricted genetic sampling, would explain the history of the AF with its diverse forest types (e.g., semideciduous and evergreen) and organisms (e.g., montane vs. lowland, volant vs. nonvolant), all of which likely respond differently to the same historical events. Subtropical organisms, for example, should expand during glacial phases according to the FRH (3). Similarly, potentially suitable habitat on the emerged continental shelf does not equal accessible habitat, and colonization could depend on specific ecological requirements. Additional complexity ignored by Leite et al. (1) involves distinct climate history among AF's regions (5). Finally, Leite et al. (1) present no evidence that the Brazilian continental shelf itself and forest fragmentation during interglacial periods underlie population subdivision and species formation. In addition, because the continental shelf is currently underwater, the "Atlantis Forest hypothesis" is not amenable to falsification from a genetic standpoint. The authors fail to offer unambiguous predictions on these grounds. Thus, Leite et al. lack solid data to conclude that "forest refuges played only a minor role, if any, in this biodiversity hotspot during glacial periods" (1).

We should abandon the simplistic idea that one or two diversification models explain AF evolution. Inference of processes in AF phylogeography should ideally be based on sufficiently sized nuclear datasets obtained from ecologically and taxonomically diverse species and well-designed geographic sampling, instead of inconclusive single-locus analyses from a handful of species that do not represent the ecological diversity and the histories that, together, explain the evolution of this hyperdiverse biome.

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- 1 Leite YLR, et al. (2016) Neotropical forest expansion during the last glacial period challenges refuge hypothesis. Proc Natl Acad Sci USA 113(4):1008–1013.
- 2 Edwards S, Bensch S (2009) Looking forwards or looking backwards in avian phylogeography? A comment on Zink and Barrowclough 2008. *Mol Ecol* 18(14): 2930–2933, discussion 2934–2936.

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³ Carnaval AC, et al. (2014) Prediction of phylogeographic endemism in an environmentally complex biome. Proc Biol Sci 281(1792):20141461.

⁴ Batalha-Filho H, Miyaki CY (2016) Late Pleistocene divergence and postglacial expansion in the Brazilian Atlantic Forest: Multilocus phylogeography of *Rhopias* gularis (Aves: Passeriformes). J Zoological Syst Evol Res, 10.1111/jzs.12118.

⁵ Cheng H, et al. (2013) Climate change patterns in Amazonia and biodiversity. *Nat Commun* 4:1411.