

The Amazon *Várzea*

The Decade Past and the Decade Ahead

Editors

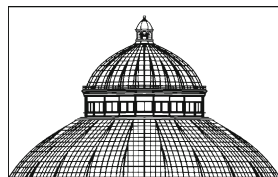
Miguel Pinedo-Vasquez

Mauro L. Ruffino

Christine Padoch

Eduardo S. Brondízio

 Springer



Editors

Dr. Miguel Pinedo-Vasquez
Center for Environmental Research
and Conservation
Columbia University
1200 Amsterdam Avenue, MC 5557
New York, NY 10027-7054
USA
map57@columbia.edu

Dr. Mauro L. Ruffino
Ministério da Pesca e Aquicultura - MPA
Esplanada dos Ministérios, Bloco D
Edifício Sede, 2º andar, sala 238
Cep. 70043-900
Brasília, DF
Brazil
mauro.ruffino@mpa.gov.br

Dr. Christine Padoch
The New York Botanical Garden
200th Street and Kazimiroff Boulevard
Bronx, NY 10458-5126
USA
cpadoch@nybg.org

Dr. Eduardo S. Brondízio
Indiana University
Department of Anthropology
701 E. Kirkwood Avenue
Student Building 130
Bloomington, IN 47405-7100
USA
ebrondiz@indiana.edu

ISBN 978-94-007-0145-8 e-ISBN 978-94-007-0146-5

DOI 10.1007/978-94-007-0146-5

Springer Dordrecht Heidelberg London New York

© Springer Science+Business Media B.V. 2011

No part of this work may be reproduced, stored in a retrieval system, or transmitted in any form or by any means, electronic, mechanical, photocopying, microfilming, recording or otherwise, without written permission from the Publisher, with the exception of any material supplied specifically for the purpose of being entered and executed on a computer system, for exclusive use by the purchaser of the work.

This book is a co-publication with The New York Botanical Garden Press and appears as volume 17 in the series “Advances in Economic Botany”, Charles M. Peters, Editor.

Printed on acid-free paper

Springer is part of Springer Science+Business Media (www.springer.com)

The River-Refuge Hypothesis and Other Contributions of Márcio Ayres to Conservation Science

Miguel A. Pinedo-Vasquez and Liliana M. Dávalos

Abstract For more than a century, biogeographers have sought to explain the large number of species found in Amazonian forests. The role of rivers as barriers to dispersal was recognized early on and this was the first evolutionary hypothesis to explain Amazonian diversity. Most of the recent debate on speciation in the Amazon has focused on the role of Pleistocene refugia. The methods of refuge biogeography helped shape early conservation priorities in Amazonia, although actual plans did not directly depend on the conceptual strengths or weaknesses of refugia biogeography. These approaches viewed people mostly as threats, though not always explicitly. Based on his work on primate distribution, Márcio Ayres formulated a synthetic speciation theory, the river-refuge hypothesis. The river-refuge model successfully resolved some of the historical and technical challenges of the earlier hypotheses. His work in *várzea* conservation, informed by this conceptual breakthrough, recognized that the maintenance of processes is at least as important as species numbers in prioritizing action. The work of Márcio Ayres broadened the scope of conservation in Amazonia by moving beyond the model of people-as-threats, and this was as great a conceptual contribution to conservation as anyone could make.

Keywords Refugia • River-refuge • Speciation • Connectivity • Conservation of dynamics

M.A. Pinedo-Vasquez (✉)
Center for Environmental Research and Conservation, Columbia University,
1200 Amsterdam Ave. New York, NY 10027, USA
e-mail: map57@columbia.edu

L.M. Dávalos
Department of Ecology and Evolution, State University of New York at Stony Brook,
650 Life Sciences Building, Stony Brook, NY 11794-5245, USA

1 Introduction

Marked differences in species richness and composition between different regions of the world motivate all biogeographic theories (Croizat 1981; Darlington 1957; Morrone and Crisci 1995; Prance 1982). The humid forests of the Amazon, home to thousands of plant and vertebrate species, captured the attention of the first biogeographers precisely for this reason (Wallace 1876). The continuity of Amazonian forests, however, proved puzzling from the beginning. Unlike island archipelagoes, such as the Galapagos or Hawai'i, Amazonia seemed to lack the isolating barriers that would explain differentiation into species (Wallace 1881). Although gradients in precipitation could explain biotic turnover across regions in Amazonia, they still cannot explain the central question of Amazonian biogeography: speciation (Haffer 1997).

Alfred Russell Wallace himself advanced a first explanation for speciation in Amazonia: the river hypothesis (Wallace 1853). The network of Amazonian rivers developed as recently as the Pliocene and Pleistocene (over the last five million years), leading Wallace and subsequent authors to propose that riverine barriers separated once continuous populations, leading to differentiation and, eventually, speciation (Bates 1863; Mayr 1942). The natural breaks that rivers and floodplains produce in the forest would amount to a species pump (Capparella 1988). The main criticism against early versions of the river hypothesis is that the forest, rivers, and floodplains developed together, so that the model of large continuous populations suddenly partitioned by incipient rivers was flawed (Fjeldså 1994; Patton et al. 1994). Current variants of the river hypothesis rely on recent changes in river courses, or dispersal across the river barrier to explain isolation on opposite banks. The distributions of species, subspecies, and morphs of butterflies, birds, and primates have all been thought to support the river hypothesis (Bates 1863; Capparella 1988; Hershkovitz 1977).

The most prolific of the Amazonian speciation hypotheses over the last 40 years is not concerned with the role of rivers, but rather with the formation of isolated forest enclaves or refugia (Haffer 1969; Vanzolini and Williams 1970). The refugia hypothesis posits that dry climate associated with glaciations made Amazonian forests recede into relatively small refugia. During interglacial periods, when humidity rose again and the forests grew back, isolated distinct species then expanded from the refuges where they had evolved (Haffer 1969; Vanzolini and Williams 1970). Criticism of this hypothesis mounted as it became clear that most species differentiation predates the Pleistocene glaciations (Ribas et al. 2005; Whinnett et al. 2005). Proponents of refugia argue that the relationship between climate, forest cover, and Amazonian speciation extends back to the Tertiary, so that the hypothesis can explain diversification at different temporal scales (Haffer 1993). Identifying the refugia has also proved difficult for biogeographers; refuges did not match across taxa (Oren 1982). Additionally, proposed plant refuges were found to be artifacts of data collection (Nelson et al. 1990), and vertebrate refugia roughly correspond to areas of endemism also isolated by rivers or corresponding to rainfall gradients (Endler 1982; Hayes and Sewlal 2004).

Both climate change and river dynamics have had effects on the distribution of Amazonian forests and their biota. Márcio Ayres and colleagues formulated a synthesis of the river and refugia hypotheses: the river-refuge model (Ayres and Clutton-Brock 1992). This hypothesis argues that during glaciations, Amazonian forests contracted but did not fragment. The contractions reduced forest cover at the headwaters of the Amazonian rivers, effectively isolating populations downstream. By identifying current areas of endemism as the major refugia and recognizing the intertwined history of forests and rivers, this hypothesis builds on criticisms of previous models. The distribution of primates and birds has been used as evidence for the river-refuge model (Ayres and Clutton-Brock 1992; Capparella 1991; Martins et al. 1988; Wallace et al. 1996).

The debate on Amazonian speciation spans the careers of some of the best biogeographers of the last century, but its interest extends beyond the discipline and has practical consequences. From the beginning, the discussion on the conservation of Amazonian forests was colored by speciation models – particularly the refugia hypothesis – and predictions of the model sometimes determined the designation of protected areas (Lovejoy 1982, 1983). In this light, speciation hypotheses are not just models of how history has shaped Amazonian biota; they are also blueprints for a future of conservation under human stewardship (Lovejoy 1982). At the same time, speciation hypotheses are not the only consideration in protecting Amazonian forests, nor have they been the most important variable in any such decision (Lovejoy 1983). In this paper we examine how hypotheses of speciation helped shape the Amazonian conservation agenda, with a particular focus on the work of Márcio Ayres and colleagues. Ayres was extraordinary in his profound interest in theoretical issues and appreciation of their importance in defining conservation goals, while he also engaged in applied conservation work in Amazonia. His theoretical and practical preference was to be inclusive, to appraise the possibilities of multiple causation, and use every opportunity for effective conservation. By assessing his approach to conservation of the *várzea*, perhaps the most dynamic and complex environment of Amazonia, we ask how his theories influenced current discussions on conservation.

2 Implications for Conservation

2.1 *A One-Way Street between Speciation Theories and Amazonian Conservation*

In 1981, when one of the most influential studies on Amazonian conservation was completed (Wetterberg et al. 1981), the refugia model was the dominant hypothesis in speciation studies. With its focus on narrowly endemic species (as opposed to broadly distributed species), its insistence on a general biogeographic framework across many taxa (as opposed to the status of one or a few populations), and its

appeal to an independent value system (history or, in the case of conservation, the protection of species), the refugia hypothesis itself was a precursor of subsequent assessments. The endemic, multitaxa, value-maximizing approach to Amazonian conservation was an innovation at a time when most conservation efforts were focused on flagship species and struggling to defend nature for nature's sake (Wetterberg et al. 1981).

Refugia offered theoretical support to conservation decisions that had to be made with whatever data were available (Oren 1982). Conservationists quickly realized that data on even intensively studied Amazonian birds and butterflies were scarce compared to, say, the North American or British breeding surveys. If history had shaped Amazonian biotic communities in such a way that the ghosts of speciation past determined its areas of highest diversity, conservation of refugia is justified, as the general speciation model would also have affected other groups of plants or animals (Lovejoy 1982). But the connection between refugia and Amazonian conservation only went so far: conservationists realized early on that the process of generating diversity, although critical in shaping a general conservation approach, was not as important as the fact of diversity (Lovejoy 1983). Protected areas could be, and were, justified on the basis of the species found in them, independently from how those species got there (Wetterberg et al. 1981).

Amazonian conservation benefited from the conceptual innovations of refugia without committing to the speciation model itself. To this day, conservation prioritization proceeds by using the tools first applied by refugia theorists: the distributions of many endemic or threatened species and the criterion of maximizing the number covered by areas at different scales (Williams et al. 2002). When watersheds were introduced in Amazonian priorities as management units, they were justified by defensibility rather than by the emerging river-refuge hypothesis (Peres and Terborgh 1995). This confirms the independence of conservation from speciation mechanisms, while stressing the difficulties in translating a hypothesis into a conservation plan: defensibility characterizes a forest only insofar as people enter the picture.

The variable missing from speciation hypotheses and yet crucial to any biogeographic analysis – whether conservation-related or not – is the people of Amazonia. Plant refugia were correlated to accessibility, the establishment of research centers, and sampling (Nelson et al. 1990). Bird refugia also reflect these biases (Nores 1999), which in turn correspond to how people have colonized the region. For biogeographers, the collecting localities and samples provided accurate measures of diversity, at least until the biases were quantified. But conservationists knew from the outset that these areas were properties, part of development plans, colonization frontiers, or indigenous territories (Peres 2001). These were human landscapes, even if the stated goal of some conservation plans was to transform a landscape into a reserve for the “absolute” protection of the biota (Peres and Terborgh 1995). The awareness of people in conservation is pervasive; it has to be, since one of its premises is the anthropogenic threat. Threats are always on the brink of transforming an ecosystem and reducing its biodiversity unless something is done to stop them (Burgess et al. 2006; Pitman and Jorgensen 2002). Threats are the catalyst that inspires conservation plans and justifies their urgency. It is at this point that the

relationship between speciation theories and conservation matters the most, and the next section will explain why.

2.2 *Parks, Reserves, and Networks*

It was relatively common at the time of the first broad Amazonian conservation plans, and for the next 20 years, to designate maximally protected areas as “parks” (Peres and Terborgh 1995). Despite being almost current, the term was inherited from 19th-century colonial usage (Neumann 1996, 1997). Aside from the possible social or political implications this etymology has, it carries a particular view of ecosystems and ecological communities. If, as many before the refugia hypothesis thought, Amazonian forests owe their high diversity to the stability of conditions over long periods of time (Darlington 1957), then maintaining whatever those conditions are will achieve the goal of conserving species. If changes in climate, geology, or hydrology have driven speciation in the region, then it is the process of change and not the stability of conditions that is needed to conserve species.

Over the last two decades conservation plans in Amazonia have embraced networks and corridors, in recognition that it is a dynamic environment that needs conserving if we are to maintain both species and ecosystem function (or even the potential for evolution). At the same time, Amazonian conservation has departed even further from speciation hypotheses. This is in part because discussion on Amazonian speciation continues unabated (Nores 2004), and conservation can hardly be justified on the basis of controversial science. Instead, conservation plans continue to unfold based on practical approaches such as better sampling, extensive mapping, large conferences of experts on different Amazonian taxa, and, of course, an up-to-date measure of anthropogenic threats (Laurance et al. 2002; Laurance et al. 2000; Laurance et al. 2004). The looming threat of climate change has inserted itself into the mainstream (Laurance et al. 2004), but this has not renewed interest in speciation models, even though conservation really is about maintaining processes. And yet, even as an urgent measure to preserve the “last of the wild,” plans for megareserves presuppose an understanding of both speciation and climate projections (Peres 2005). What would be the point of protecting an endemic-rich zoo that was expected to lose most of its species to increasingly arid conditions? If the future is what we care about, then the speciation process matters very much in our conservation choices.

3 Márcio Ayres on the *Várzea* and Conservation Science

Ayres acknowledged the conceptual and practical implications of the flood pulse concept in Amazonian ecosystems. The flood pulse concept links the maintenance of species diversity and ecosystem function to the seasonal cycles in the *várzea*

(Junk et al. 1989). In his own studies, Ayres had argued that the *várzea*'s landscape diversity results from the erosion, transport, and deposition of sediment that leads to the formation and erosion of islands, river channels, and lakes (Ayres 1986b). In turn, he observed that the biota of the *várzea* is adapted to its dynamic landscape and cannot survive without the river dynamics (Ayres 1986a; Ayres and Johns 1987). This intimate relationship with a biota that depends on change helped shape his hypothesis on Amazonian evolution and his conservation efforts.

The work of Márcio Ayres on *várzea* conservation highlights the complexity in defining, selecting, and establishing conservation areas. The river-refugia hypothesis broadened the scientific basis for conservation by incorporating simultaneous historical events into a single framework (Ayres 1986b; Ayres and Clutton-Brock 1992). The results of his work proved that fragmentation and recolonization are continuous processes that shape species diversity and relative abundance in the *várzea*. Data on the flora and fauna (in particular primates) showed that rivers function as ancient and present physical barriers, and as pathways enabling the dispersal of species enriching Amazonian landscapes. Based on this work, Ayres designed new methods to analyze how Amazonian biotas assemble over time. Ayres directly applied his theoretical findings by establishing the Mamirauá Sustainable Development Reserve as a corridor including all of the elements relevant to the *várzea*'s current dynamics, including people. The river-refuge hypothesis became, then, a practical conservation tool, rather than an abstract framework to explain diversity.

The insistence of Márcio Ayres on the need for conserving biological corridors or networks was at first challenging to the conservation community. How to accommodate local people that are affected directly or indirectly by the establishment of biological corridors or networks? His experience at Mamirauá showed that local people could be facilitators of, rather than an impediment to, conservation. Such an outcome, however, was not automatic and depended on trust built over the course of many years of research and conservation work on the ground. Just as the river-refuge hypothesis combined elements from competing biogeographic scenarios, his approach to conservation was synthetic and combined elements of radical preservationism with more practical conservation approaches. This approach reduced the scientific uncertainty surrounding conservation decisions, while maintaining the ecosystem function and species richness of a vast region. The work of Márcio Ayres broadened the scope of conservation in Amazonia by moving beyond the model of people-as-threats, and this was as great a conceptual contribution to conservation as anyone could make.

References

- Ayres, J. M. (1986a). The conservation status of the white uakari. *Primate Conservation*, 7, 22–26.
- Ayres, J. M. (1986b). *Uakaris and Amazonian flooded forest*. Cambridge: University of Cambridge.
- Ayres, J. M., & Clutton-Brock, T. H. (1992). River boundaries and species range size in Amazonian primates. *The American Naturalist*, 140, 531–537.

- Ayres, J. M., & Johns, A. D. (1987). Conservation of white uacaries in Amazonian várzea. *Oryx*, 6, 74–80.
- Bates, H. W. (1863). *The naturalist on the river Amazon*. London: Murray.
- Burgess, N. D., Hales, J. D. A., Ricketts, T. H., & Dinerstein, E. (2006). Factoring species, non-species values and threats into biodiversity prioritisation across the ecoregions of Africa and its islands. *Biological Conservation*, 127, 383–401.
- Capparella, A. P. (1988). Genetic variation in neotropical birds: Implication for the speciation process. In H. Ouellet (Ed.), *Acta XIX Congressus Internationalis Ornithologici*. Ottawa: University of Ottawa Press.
- Capparella, A. P. (1991). Neotropical avian diversity and riverine barriers. In B. D. Bell (Ed.), *Proceedings 20th international ornithological congress*. Wellington, New Zealand: Congressional Trust Board.
- Croizat, L. (1981). Biogeography: Past, present, and future. In G. Nelson & D. E. Rosen (Eds.), *Vicariance biogeography: A critique*. New York: Columbia University Press.
- Darlington, P. J., Jr. (1957). *Zoogeography: The geographical distribution of animals*. New York: John Wiley.
- Endler, J. A. (1982). Problems in distinguishing historical from ecological factors in biogeography. *American Zoologist*, 22, 441–452.
- Fjeldså, J. (1994). Geographical patterns for relict and young species of birds in Africa and South America and implications for conservation priorities. *Biodiversity and Conservation*, 3, 207–226.
- Haffer, J. (1969). Speciation in Amazonian forest birds. *Science*, 165, 131–137.
- Haffer, J. (1993). Time's cycle and time's arrow in the history of Amazonia. *Biogeographica*, 69, 15–45.
- Haffer, J. (1997). Alternative models of speciation in Amazonia: an overview. *Biodiversity and Conservation*, 6, 451–476.
- Hayes, F. E., & Sewlal, J. A. N. (2004). The Amazon river as a dispersal barrier to passerine birds: Effects of river width, habitat and taxonomy. *Journal of Biogeography*, 31, 1809–1818.
- Hershkovitz, P. (1977). *Living new world Monkeys (Platyrrhini)*. Chicago: University of Chicago Press.
- Junk, W. J., Bayley, P. B., & Sparks, R. E. (1989). The flood pulse concept in river-floodplain systems. *Canadian Special Publication of Fisheries and Aquatic Sciences*, 106, 110–127.
- Laurance, W. F., Lovejoy, T. E., Vasconcelos, H. L., Bruna, E. M., Didham, R. K., Stouffer, P. C., et al. (2002). Ecosystem decay of Amazonian forest fragments: A 22-year investigation. *Conservation Biology*, 16, 605–618.
- Laurance, W. F., Vasconcelos, H. L., & Lovejoy, T. E. (2000). Forest loss and fragmentation in the Amazon: Implications for wildlife conservation. *Oryx*, 34, 39–45.
- Laurance, W. F., Oliveira, A. A., Laurance, S. G., Condit, R., Nascimento, H. E. M., Sanchez-Thorin, A. C., et al. (2004). Pervasive alteration of tree communities in undisturbed Amazonian forests. *Nature*, 428, 171–175.
- Lovejoy, T. E. (1982). Designing refugia for tomorrow. In G. T. Prance (Ed.), *Biological diversification in the tropics*. New York: Columbia University Press.
- Lovejoy, T. E. (1983). The science of Amazon conservation. *The Environmentalist*, 3, 57–61.
- Martins, E. S., Ayres, J. M., & Ribeiro de Valle, M. B. (1988). On the status of *Ateles belzebuth marginatus* with notes on other primates of the Iriri river basin. *Primate Conservation*, 9, 87–91.
- Morrone, J. J., & Crisci, J. V. (1995). Historical biogeography: Introduction to methods. *Annual Review of Ecology and Systematics*, 26, 373–401.
- Nelson, B. W., Ferreira, C. A. C., da Silva, M. F., & Kawasaki, M. L. (1990). Endemism centres, refugia and botanical collection density in Brazilian Amazonia. *Nature*, 345, 714–716.
- Neumann, R. P. (1996). Dukes, earls, and ersatz Edens: Aristocratic nature preservationists in colonial Africa. *Environment and Planning D: Society & Space*, 14, 79–98.
- Neumann, R. P. (1997). Primitive ideas: Protected area buffer zones and the politics of land in Africa. *Development and Change*, 28, 559–582.
- Nores, M. (1999). An alternative hypothesis for the origin of Amazonian bird diversity. *Journal of Biogeography*, 26, 475–485.

- Nores, M. (2004). The implications of tertiary and quaternary sea level rise events for avian distribution patterns in the lowlands of northern South America. *Global Ecology and Biogeography*, 13, 149–161.
- Oren, D. C. (1982). Testing the refuge model for South America: A hypothesis to evaluate discrepancies in refuges number across taxa. In G. T. Prance (Ed.), *Biological diversification in the tropics*. New York: Columbia University Press.
- Patton, J. L., Da Silva, M. N. F., & Malcolm, J. R. (1994). Gene genealogy and differentiation among arboreal spiny rats (Rodentia: Echimyidae) of the Amazon basin: A test of the riverine barrier hypothesis. *Evolution*, 48, 1314–1323.
- Peres, C. A. (2001). Paving the way to the future of Amazonia. *Trends in Ecology & Evolution*, 16, 217–219.
- Peres, C. A. (2005). Why we need megareserves in Amazonia. *Conservation Biology*, 19, 728–733.
- Peres, C. A., & Terborgh, J. W. (1995). Amazonian nature reserves: An analysis of the defensibility status of existing conservation units and design criteria for the future. *Conservation Biology*, 9, 34–46.
- Pitman, N. C. A., & Jorgensen, P. M. (2002). Estimating the size of the world's threatened flora. *Science*, 298, 989.
- Prance, G. T. (1982). Biological diversification in the tropics. In G. T. Prance (Ed.), *Biological diversification in the tropics*. New York: Columbia University Press.
- Ribas, C. C., Gaban-Lima, R., Miyaki, C. Y., & Cracraft, J. (2005). Historical biogeography and diversification within the neotropical parrot genus *Pionopsitta* (Aves: Psittacidae). *Journal of Biogeography*, 32, 1409–1427.
- Vanzolini, P. E., & Williams, E. E. (1970). South American anoles: The geographic differentiation and evolution of the *Anolis chrysolepis* species group (Sauria, Iguanidae). *Arquivo Zoologico do Sao Paulo*, 19, 1–298.
- Wallace, A. R. (1853). *A narrative of travels on the Amazon and Rio Negro, with an account of the native tribes, and observations on the climate, geology, and natural history of the Amazon valley*. London: Reeve & Co.
- Wallace, A. R. (1876). *The geographical distribution of animals; with a study of the relations of living and extinct faunas as elucidating the past changes of the earth's surface*. New York: Harper & Brothers.
- Wallace, A. R. (1881). *Island life; or, the phenomena and causes of insular faunas and floras, including a revision and attempted solution of the problem of geological climates*. New York: Harper & Brothers.
- Wallace, R. B., Painter, R. L. E., Taber, A. B., & Ayres, J. M. (1996). Notes on a distributional river boundary and southern range extension for two species of Amazonian primates. *Neotropical Primates*, 4, 149–151.
- Wetterberg, G. B., Prance, G. T., & Lovejoy, T. E. (1981). Conservation progress in Amazonia: A structural review. *Parks*, 6, 5–10.
- Whinnett, A., Zimmermann, M., Willmott, K. R., Herrera, N., Mallarino, R., Simpson, F., et al. (2005). Strikingly variable divergence times inferred across an Amazonian butterfly 'suture zone'. *Proceedings of the Royal Society B: Biological Sciences*, 272, 2525–2533.
- Williams, P. H., Margules, C. R., & Hilbert, D. W. (2002). Data requirements and data sources for biodiversity priority area selection. *Journal of Biosciences*, 27, 327–338.