The river-refuge hypothesis and other contributions of Marcio Ayres to conservation science

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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 Marcio 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 varzea conservation, informed by this conceptual brealthrough, recognized that the maintenance of processes is at least as important as species numbers in prioritizing action. The work of Marcio Ayres broadened the scope of conservation in Amazonia by moving beyond the model of people-as-threats, and this as great a conceptual contribution to conservation as anyone could make.

Introduction

Marked differences in species richness and composition between different regions of the world motivate all biogeographic theories (Croizat 1981; Darlington 1957; Morrone & 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 1876a, b). 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 to 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 5 million years), leading Wallace and subsequent authors to propose that riverine barriers separated once continuous populations leading to differentiation and, eventually, speciation (Bates 1863a, b; 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 1863a, b; 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 & 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 & 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 & Sewlal 2004).

Both climate change and river dynamics have had effects on the distribution of Amazonian forests and their biota. Marcio Ayres and colleagues formulated a synthesis of the river and refugia hypotheses: the river-refuge model (Ayres & 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 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 & 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 Marcio 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 varzea, perhaps the most dynamic and complex environment of Amazonia, we ask how his theories influenced current discussions on conservation.

Implications for conservation

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 in a general biogeographic framework across many taxa (as opposed to the status of one or a few populations), and the 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, multi-taxa, 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 or 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, and 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 & 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 & 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 & 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.

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 & 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 based on 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 the 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 mega-reserves 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.

Marcio Ayres on the varzea 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 varzea (Junk et al. 1989). In his own studies, Ayres had argued that the varzea'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 varzea is adapted to its dynamic landscape and cannot survive without the river dynamics (Ayres 1986a; Ayres & 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 Marcio Ayres on varzea 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 & 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 varzea. 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 Mamiraua Sustainable Development Reserve as a corridor including all of the elements relevant to the varzea'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 Marcio 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 Mamiraua showed that local people could be facilitators, 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 Marcio Ayres broadened the scope of conservation in Amazonia by moving beyond the model of people-as-threats, and this as great a conceptual contribution to conservation as anyone could make.

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