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Speciation in the world's greatest forest

Mammals of the Rio Juruá and the Evolutionary and Ecological Diversification of Amazonia

by J.L. Patton, M.N.F. Da Silva and J.R. Malcolm. American Museum of Natural History, 2000. $30.00 pbk (306 pages)
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During his extensive fieldwork throughout Amazonia, A.R. Wallace observed that '…the Amazon, the Rio Negro, and the Madiera formed the limits beyond which certain species never passed'. He noted in the same paper that 'In these observations I have only referred to the monkeys, but the same phaenomena occur both with birds and insects, as I have observed in many instances'[1].

These observations represent the earliest hypothesis of a biogeographical mechanism for species diversification in Amazonia, the 'Riverine Barrier Hypothesis' (RBH). The main premise of the RBH is that major rivers divide Amazonia into large blocks, and delimit discrete geographical areas within which, there is a similar community of species but, between which, species compositions are different. The RBH implies that evolution has proceeded along independent trajectories in these different blocks and that rivers have served as causal mechanisms for this divergence[2]. A corollary of the RBH is that the strength of any river barrier should be a function of its width and flow; so that isolation should be greatest at the river mouth and should decrease towards the headwaters, where species might cross the relatively narrow channel[2]. This was supported by a recent study of Amazonian primate community composition[3], which showed that species similarity on opposite sides of rivers decreased as an increasing function of river size[3].

The Patton *et al.* monograph stands out not only because the work was carried out along a river bisecting the heart of the largest and most sparsely populated of the world's three major tropical wilderness areas (the others being the Congo River Basin and the islands of New Guinea and Melanesia)[4], but also because every aspect of the monograph exemplifies the 'real work of systematics'[5]. The work is based on an inventory of small mammals (predominantly marsupials, and echimyid and murid rodents), collected during a year-long survey of the 1000 km-long Rio Juruá in western Brazil, and the objectives were twofold. First, the authors summarize patterns of ecological and geographical distribution, genetic differentiation and phylogeography of multiple co-distributed species of terrestrial mammals in this basin. Second, they integrate patterns of distribution and differentiation of these species into the broader region of Amazonia.

The sampling design was based on 16 trapping stations distributed along the river, with sampling of both river banks carried out so as to survey canopy and terrestrial faunas, in both seasonally flooded *várzea* and unflooded upland *terra firme* forests. These forest types are expected to respond very differently to seasonal flooding and long-term meandering of Amazonian rivers. Low vagility species confined to *terra firme* forests are expected to show differentiation, as specified by the RBH because they are isolated by the river and its wider flood plain, whereas those confined to the *várzea* forests are expected to experience passive gene flow via occasional lateral channel shifts along these rivers[6]. The design provided a critical test of the RBH as a primary cause of speciation in these taxa. Both the number of species tested and the phylogeographical analyses employed meant that the authors successfully moved such studies far beyond previous work, which was hampered by either inadequate sampling and/or collection of allele-frequency data in such a way that precluded the separation of historical versus ongoing demographic influences.

To place the phylogeographical studies into a taxonomic context, the authors thoroughly review all the species covered, including revisions and descriptions of new species. For many species, accounts include not only the expected distribution maps and summary tables of the voucher specimens examined, but also photographs of karyotypes, skulls and dental patterns, haplotype cladograms, summaries of external and cranial measurements, bivariate plots of discriminant function analyses, bivariate plots of genetic or morphological divergence and geographical distance, descriptions of habitat preferences, reproductive cycles and fecundity and estimated growth rates. General patterns of community structure show that the number of species at any given pair of cross-river sites is approximately equal along the total length of the river, but that there is turnover in species composition among sites, a shift more pronounced in the *terra firme* than in the *várzea* forests. On the scale of greater Amazonia, patterns of species diversity in these three groups show strong geographical structure, with community similarities clearly divisible into eastern and western groups, along an approximate N–S axis formed by the Rio Madiera and Rio Negro.

The authors summarize patterns of genetic differentiation (in mtDNA cytochrome-*b* sequences) for 41 species of mammals, most of which falsify RHB expectations, but phylogeographical patterns for many species show up- and downriver groups of reciprocally monophyletic mtDNA clades. Levels of divergence suggest pre-Pleistocene separation events for most clades, and concordance in the geographical placement of clade boundaries across multiple taxa and, in association with an underlying geological feature (the Iquitos Arch), imply a shared history strongly structured by previously underappreciated tectonic events. The authors emphasize the difficulty of identifying speciation mechanisms in such an environment because many of the previously proposed multiple models[7] were not testable unambiguously . These limitations compound logistical problems, and the inadequacy of available specimens for even

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well-known groups, such as birds[8]. Nevertheless, recent studies on the role of ecotones in generating rainforest biodiversity provide other clearly testable hypotheses[9,10], and Patton *et al.* have provided a remarkably synthetic study that should serve as a benchmark and a model for all future efforts to disentangle speciation mechanisms in Amazonia.

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Wetland ecology for plant ecologists

Wetland Ecology: Principles and Conservation
by Paul A. Keddy. Cambridge University Press, 2000. £50.00 (xiv + 614 pages).
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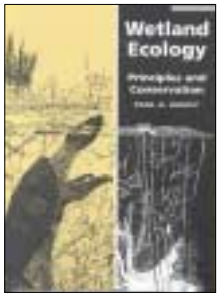

In the late 1970s, the number of researchers in the USA actively working on freshwater wetlands could fit easily in a moderately sized conference room. Today, the Society of Wetland Scientists boasts over 4500 members and there are two journals devoted exclusively to wetland ecology. Where did all these people come from? Most wetland ecologists were trained as terrestrial ecologists, limnologists or wildlife biologists and the origins of most wetland ecologists are still strongly reflected in their writings. The wetland ecologist, Paul Keddy, was trained as a terrestrial plant ecologist and his new book, *Wetland Ecology: Principles and Conservation*, is an excellent plant community ecology textbook with wetland examples.

The stated goal of *Wetland Ecology* is to provide 'some unity and coherence in the study of wetland ecology'. Or, in more operational terms, the aim is to illustrate what Amazonian floodplains, prairie potholes, boreal peatlands and tidal marshes have in common. Keddy's hope however, is that this book will not just contribute to a better understanding of wetland ecology. It is also intended to illustrate ways to 'dissect' ecological communities that can be applied to other vegetation types. The intended audiences are senior undergraduates, wetland managers and any scientists intending to begin working on wetlands.

The strong bias of this book towards plant community ecology is both its biggest strength and its major weakness. Keddy is fully aware of the limited coverage of his book and says that it is deliberate. In fact, he recommends Mitsch and Gosselink's *Wetlands*[1] and other wetland books for information on mineral cycling and other major topics not covered in his own. Because of its limited scope, the coverage of many important topics in *Wetland Ecology* is poor to nonexistent. For example, wetland soils and how they form is covered in less than three pages with no mention of wetland soil classification systems. Wetlands as sinks for nutrients, a major topic of most wetland ecology courses, is ignored, although the effects of increased nutrient levels on wetland plant communities is covered. In short, *Wetlands* is a much better source of information on almost any process or functional aspect of wetland ecology. There are, however, some exceptions. For example, *Wetland Ecology* includes a discussion of the effects of burial by sediment on wetlands, an important but neglected topic in wetland ecology, which is barely mentioned in *Wetlands*.

The orientation of this book will surprise no one familiar with the numerous publications of Keddy and his co-workers. He does an excellent job of synthesizing and interpreting the literature on wetland community ecology, especially on zonation/succession, species diversity, competition, production, herbivory and disturbance. Not only is the wetland literature on these topics well covered, but also the relevant terrestrial ecology literature. His interpretation of the literature is sometimes biased, but to his credit, he always acknowledges this. This book is Keddy's summary statement about the nature of plant communities and how plant ecologists should approach their study. He has been one of the most important thinkers on these topics for the last 20 years and *Wetland Ecology* provides a wonderful introduction to his always interesting and sometimes provocative views.

This book reads like the transcript of a series of well prepared and delivered lectures, complete with asides to the audience. Unlike most texts, it is enjoyable reading. Keddy's stated aim to stress principles, however, is sometimes undermined by the fact that some chapters, for example, the diversity chapter, are little more than engaging case histories strung together with few if any discernible principles tying them together. Because of its narrow scope, *Wetlands Ecology* is not an ideal text for most undergraduate wetland ecology courses; however, it is suitable for graduate courses and seminars in community or wetland ecology, and it should be on the shelf of anyone working with wetland plant communities. Because of its broader coverage of the field, *Wetlands* remains the better introductory text. Unfortunately, the new third edition of *Wetlands* lacks the emphasis on principles and generalities that characterizes *Wetland Ecology*. What those of us who teach wetland ecology need urgently is an updated and expanded version of John Etherington's now out-of-print textbook, *Wetland Ecology*[2]. In less than 70 pages, Etherington captured the essence of wetland ecology better than either Keddy or Mitsch and Gosselink.

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