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Recent progress toward understanding the global diversity gradient

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Four years ago I published a guest editorial opining that we are making rapid progress toward understanding global patterns of diversity (Hawkins 2004). I also claimed that we still did not have a complete answer, because although the evidence that climate strongly influences the distributions of currently existing species is solid, there was little consensus about the mechanisms driving patterns over evolutionary time. Even so, the increasing availability of the right sort of data coupled with modern phylogenetic methods has us well on the way to finding the solution to the oldest problem in ecology and biogeography, and several important papers have appeared in the past four years. Although none of these provide incontrovertible evidence as to the final answer, in guest editorials the rules of evidence are more relaxed and one can make an argument without the formality that is required in a peer-reviewed article. Based on these rules, and hoping that taking a strong position in an informal setting might stimulate debate, I suggest that we now have sufficient evidence to conclude that niche conservatism and time for speciation are the primary drivers of the contemporary diversity gradient. And while it remains true that additional data on geographic variation in speciation/extinction rates and the strength of biotic interactions are needed, these appear to be secondary effects that do not need to be invoked to explain the general patterns we see; that is to say, they are details, and any differences we may find in these processes will not change the overall explanation for why the tropics have more species. Clearly, this is a strong opinion, so on what basis can I claim that we know the answer? Although a large number of papers have been published on this topic, three recent ones stand out as critical pieces of the puzzle: Wiens & Donoghue (2004), Currie et al. (2004) and Mittelbach et al. (2007).

Although the idea of niche conservatism did not originate with Wiens & Donoghue (2004), this short paper reminded many ecologists of its existence and succinctly described a potentially powerful explanation for higher tropical diversity, based on three sets of obser-

observations: (1) most very rich tropical groups originated there (giving them more time to speciate), (2) the world's climates were mostly 'tropical' until the Oligocene (providing a very large area for new clades to arise and subsequent radiations to occur), and (3) it has been difficult for species adapted to tropical climates to break into the younger, cool temperate zones (tropical niches are conserved over long time periods in many clades). Once these three tenets are accepted, higher tropical diversity is not only expected, it is virtually guaranteed. Numerous papers testing this idea have appeared in recent years (see Mittelbach et al. 2007), and the power of niche conservatism to explain diversity patterns at a range of spatial scales is rapidly becoming evident. It is notable that most of the papers in the recent special feature of *The American Naturalist* on evolutionary approaches to understanding diversity patterns discuss or test this (Harrison & Cornell 2007, Harrison & Grace 2007, Hawkins et al. 2007a, Roy & Goldberg 2007, Wiens 2007). One powerful aspect of niche conservatism is that it predicts diversity patterns based on the climatic conditions where (and perhaps when) groups arose and began radiating, and when niche conservatism is coupled with time for speciation it is



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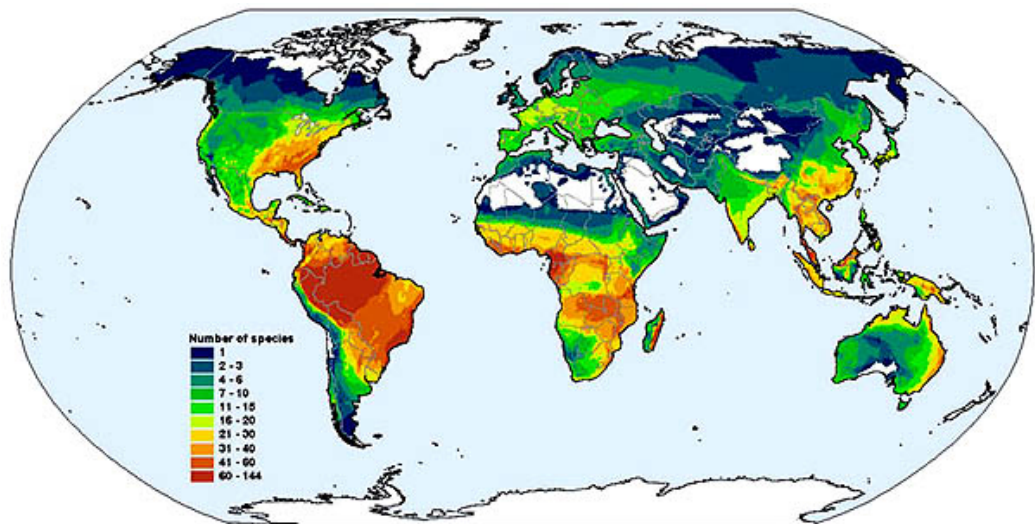
also able to explain why some groups are more diverse in cool climates than in warm ones (i.e., it explains exceptions to the general 'latitudinal gradient' as well as when it will exist). All in all, this is a potent hypothesis and is the one to beat, although one would have to be very brave indeed to claim that a single hypothesis can explain everything on both land and sea.

The second piece of the puzzle comes from Currie et al. (2004), although it mostly reports negative results rather than positive ones. The primary alternatives to historical hypotheses have been based on the often strong correlations between current climatic conditions and diversity, and there is no need to dwell on the debates in the literature over the past 20 years as to whether understanding richness gradients requires knowledge of the past or not. What Currie et al. (2004) showed was that predictions arising from hypotheses based on current climates (the 'more individuals' hypothesis and a dispersal based version of the 'physiological tolerance' hypothesis) are not well supported by the evidence. Another recent theory proposing that current temperature patterns explain diversity gradients, the metabolic theory of ecology (see Allen et al. 2002), is also not supported by empirical evidence (Hawkins et al. 2007b). So, if the evi-

dence is to be believed, one has to concede that history does matter after all, which allows us to stop arguing about 'if' and start focusing on 'how'. Although many previous papers dating back over 100 years have argued for the importance of history, many workers feel that rejecting hypotheses using empirical tests carries more weight than logical argument, so Currie et al.'s explicit tests represent real progress in my opinion. This paper also conducted a test, in so far as was possible, of one of the major evolutionary alternatives to niche conservatism and time for speciation, which they called the 'speciation rate' hypothesis, which proposes that tropical diversity is high due to accelerated speciation rates driven by climate. They found that tests were few, and the results were mixed. But this also set the stage for the third key paper, Mittelbach et al. (2007).

Although a review paper rather than a research paper, Mittelbach and an illustrious set of co-authors provide a thorough evaluation of the state of the field and lay out the issues involved very well. Indeed, this paper is required reading for anyone seriously interested in understanding the global diversity gradient. However, in the spirit of generating debate, one does not have to agree with all of their conclusions about the relative importance of

Global amphibian species richness gradient (map extracted from the Global Amphibian Assessment; IUCN, Conservation International, and NatureServe, 2006; original data available at <http://www.globalamphibians.org/>)



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particular evolutionary mechanisms. Not surprisingly, they see two general processes as possibly being important: time for speciation (which I would argue is a stronger explanation when coupled with niche conservatism), or higher diversification rates in the tropics, acting through either greater speciation or lower extinction. With respect to time for speciation, given the three tenets presented in Wiens & Donoghue (2004), greater tropical diversity is inevitable unless one is willing to accept some very unlikely scenarios. That is, the global diversity gradient would exist irrespective of spatial variation in speciation rates unless the latter were impossibly high in the temperate zones. If this is true, then arguments about relative diversification rates are really arguments about the magnitude of slopes of richness vs. environment regressions and not about the sign of the slopes.

Another telling point about the studies included in Mittelbach et al.'s review is that even if we ignore the serious difficulty in partitioning diversification rates into its components (which greatly reduces our ability to interpret such analyses), the results obtained so far have been mixed, as also reported by Currie et al. (2004). In some cases workers are finding faster net diversification, speciation or extinction rates in the tropics, sometimes they find the opposite, and sometimes there is no spatial pattern at all. But if increased tropical speciation rates are indeed the explanation for higher tropical diversity, the signal should be clear and consistent among groups. The fact that it is not suggests that it is not a strong or universal process and so must be secondary to some other dominating driving effect. Therefore, although Mittelbach et al.'s evaluation of the evidence is measured and gives all sides of the argument equal weight, a case could be made that time for speciation will ultimately prove to explain much more spatial variation in richness than variable speciation rates. Of course this does not mean that we

should ignore the latter issue, as there are many reasons to understand how the speciation process varies in time and space. As an aside, speciation rates in the tropics may actually be greatest in mountains (see e.g. Kozak & Wiens 2007), which raises some interesting questions about if they are more strongly influenced by the strength of local climatic gradients than by warm climates per se.

It is also probably the case that geographic variation in extinction rates is relatively more important than variable speciation rates, but extinction can largely be interpreted as a effect of niche conservatism in the face of climate change (see e.g. Hawkins et al. 2007a). And climate change also provides a pressing reason for studying extinction rates, since they appear to be on the rise. Irrespective, as far as understanding why Brazil supports more species than Alaska, niche conservatism in the face of global climate change since the Tertiary probably explains the bulk of the difference (and even further back for very old taxonomic groups). But we should not forget that climate patterns over ecological time spans matter as well; the Sahara is not depauperate because of history alone, but because all life requires access to water one way or another and this is as true today as it was in the past. The biotic responses to rapid climate change we are documenting now are evidence enough that contemporary events influence diversity. Although not everyone may agree about what aspect of the past ultimately drives diversity, no one denies that species have limited abilities to adapt to or track changing climatic conditions. These limitations extended over entire clades evolving over long time periods can also provide a parsimonious explanation for global patterns of diversity. Although the debate continues, at the current rate of progress we should be able to reach a consensus soon.

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