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Dissertation: Diversity dynamics across scales

Comments of R. E. Ricklefs

In this dissertation, Macháč addresses the interesting and important point that whether we perceive the species richness of a clade of organisms as continually expanding, or as static, might depend on the geographic (and temporal) scale of analysis. Clearly, owing to the relatively unvarying diversity of life on earth during the most recent period of its history, the dynamics of species production and extinction must be approximately balanced on the regional scale, while turnover of major groups of organisms during this same period suggest that some lineages have experienced rapid diversification while others have declined, in some cases to extinction. It is the nature of turnover under a constant global diversity constraint that some lineages fare better than others, and this is the issue that Macháč explores, and for which he develops significant insights. The three papers that constitute this dissertation, published in a top journal in the field—*Global Ecology and Biogeography*—were coauthored with several established scientists. However, and as confirmed by Professor Graham, Mr. Macháč's contributions to these publications was substantial and critical to their development.

In the following paragraphs, I offer some observations on the subject matter of Mr. Macháč's thesis chapters and suggest some topics for further discussion.

Thesis summary:

Macháč (and many others) have made the point that understanding biodiversity dynamics is essential to designing conservation and management strategies. Yet, little is said concerning this relationship in this thesis other than placing special value on phylogenetically isolated (hence, evolutionarily unique) taxa. Although it is not the central concern of this thesis, the implications of biodiversity dynamics for management policy would be an interesting point for further discussion.

Whether contemporary geographic regions and ecological communities are saturated by species is intensely debated. Species introduced by humans often can find a place in local communities suggesting that communities are not filled with species at any given time, but what does "filled" mean when communities are considered as dynamic systems balancing local introduction and extirpation of species?

I was particularly pleased to see some of the older literature on the topic of diversity included in the thesis, particularly the paper by Willis (1922) on "age and area." This paper was not received enthusiastically at the time and is virtually unknown to modern readers, yet it contains many interesting insights. It would be interesting to know the extent to which Willis, and other early writers, anticipated issues that are elaborated the present dissertation.

The introduction to the thesis places our understanding of variation in diversity into a framework that closely parallels the equilibrium theory of island biogeography, developed by R. H. MacArthur and E. O. Wilson, which views diversity as reflecting a balance between immigration (i.e., speciation) and extinction. Further discussion of the parallels between these perspectives might be worthwhile, particularly with respect to Hubbell's neutral ecological dynamics for species diversity based, in part, on insights from MacArthur and Wilson.

One might argue that the dichotomy between expansionary and equilibrium dynamics is artificial, unless species diversification might lack an equilibrium point under some circumstances. The key might be understanding the conditions under which clades exist with fewer species than the potential "carrying capacity" of the region for these species at any given time, and then determining the circumstances—whether primarily ecological or evolutionary—that create this condition in a seemingly repeatable fashion. Clearly, when a new taxon arises (i.e., is recognized as such) its diversity is minimal (i.e., a single lineage), and so our estimate of average diversification

rate over time will depend on where we place the beginning. It is interesting that in the analysis of mammal faunas in Oliveira, Macháč, et al. (2016), evolutionary time influenced functional diversity, but not species richness, which was more closely associated with environmental variables.

The possibility raised in the thesis overview, and developed in the papers by Graham et al. (2018) and Macháč et al. (2018), that three phases of diversity dynamics (expansion, slowdown, saturation) are governed by different mechanisms related to different aspects of the environment, is potentially very exciting, and contrasts with a view that similar processes act throughout, but that their relative rates determine the diversity trajectory at any given time. An interesting question is the degree to which these diversification phases are determined by the environment as opposed to reflecting intrinsic attributes of diversifying clades.

One frequently hears that clades tend to be in equilibrium at large (phylogenetic) scales and perhaps are expanding at small scales. If this were the case, some clades at small scales must be contracting, as well, to result in equilibrium at large scales. Can we simply not see this in phylogenetic data? What are the implications of this (almost necessary) duality of circumstances?

Macháč, A., C. H. Graham, and D. Storch. 2018. Ecological controls of mammalian diversification vary with phylogenetic scale. *Global Ecology and Biogeography* 27:32-46.

The distinction between old and large clades having reached equilibrium with their environments, whereas young and small clades have not, seems at odds with the fact that old, large clades are made up of young, small clades. There must be something ecological about a clade's propensity to diversify in addition to its age and size, or else clade age and size are related to ecology, in some way.

"Declining clades, whose speciation rates exceed extinction rates, cannot be inferred within a likelihood framework" How are these clades identified? If diversity has remained more or less constant over long periods, would declining clades not be more or less as numerous as expanding clades? How is saturation captured by the natural logarithm of clade richness? Or is this transformation applied to estimate a level assuming saturation? In which case, how is saturation identified based on a phylogeny?

Analysis based on clade area is problematic. Residuals from the area-richness relationship might identify additional, cryptic, factors because large residuals with respect to area pertain, by definition, to clades with relatively low diversity.

Does the large proportion of "slowing" clades suggest that clades become ecologically saturated at low numbers of species, and that replacement of clades by ecologically similar lineages is infrequent? Do clades that invade new ecological space behave differently from those that diversify in areas of high diversity? Figure 3 indicates that clade richness is generally negatively correlated with ecological productivity (i.e., Carnivora, Chiroptera with respect to temperature and precipitation). It is also interesting that clade richness at saturation decreases with increasing environmental temperature (i.e., tropics to arctic). This seems counter to the general increase in species richness of most groups towards the tropics. Are mammals different in this respect?

The use of all clades (nodes) in a phylogeny results in considerable nesting of young clades within older clades and potential data redundancy and sample inflation. I assume that these issues are somehow taken care of through phylogenetic correction, but additional discussion of this issue would be informative.

The relationships of diversification rates to clade age estimated by Medusa and BAMM have distinctly different shapes. Is there a simple explanation for this in terms of the way each of these programs handles the data?

The result that diversification tends to slow when the spatial overlaps between species in a clade increases, suggesting the filling of 'niche' space, is intriguing and ecologically satisfying. Could one also argue, however, that increased overlap reflects reduced physical heterogeneity in the environment and less opportunity for allopatric species formation?

In the paragraph before the discussion, it is mentioned that “declining” clades exhibited, roughly a third of each, (a) constant diversification, (b) slowdowns, and (c) saturation. Perhaps ‘declining’ should have been ‘remaining’ considering that classes (a) and (c) represent clades whose diversity is either unchanging or increasing.

It has been suggested that clades go through a progression of diversification, from youth to maturity to old age and decline; what do the present analyses have to say about the probabilities of lineage splitting/extinction as a function of clade age? Do clades have a life history, as opposed to Van Valen’s formulation? What is the status of a clade as an individual entity? More generally, concerning the nestedness of nodes in a phylogeny, can one distinguish clades in any useful way, perhaps as taxonomists have found convenient?

Oliveira B. F., Macháč A., Costa G. C., Brooks T. M., Davidson A. D., Rondinini C., Graham C. H. (2016) Species and functional diversity accumulate differently in mammals. *Global Ecology and Biogeography*. 25: 1119-1130.

The decoupling of species diversity and functional diversity, at least at high levels of species richness, raises serious problems with classical ecological interpretations of niche filling, community assembly, and the regulation of species richness. These results are extremely interesting in this context. In Figure 3, functional diversity plateaus at high species richness. Is this the consequence of limited ecological possibilities for mammals, or increasing turnover of similar species between locations within regions? It is interesting that old and young mammal faunas seem to require similar times to reach equilibrium functional diversity. Might this be because the ecologies of regions are constantly changing over time, so that old regions demand continuing evolutionary adjustment?

Graham C. H., Storch D., Macháč A. (2018) Phylogenetic scale in ecology and evolution. *Global Ecology and Biogeography*. 27: 175-187.

This is an important discussion of the methods of analysis of ecological and phenotypic data in the context of evolutionary relationships. General concepts and methods of analysis, as well as potential pitfalls and limitations, are outlined in detail. This paper should be the starting point for anyone interested in conducting phylogenetically informed analyses, or in reading the literature based on these analyses.