

Species richness in a tropical biodiversity hotspot



That biological diversity is higher in tropical regions is one of the longest standing patterns in macroecology, yet a consensus explanation of this diversity remains elusive (reviewed by Jablonski *et al.*, 2006). Evolutionary processes that influence species richness are, in simple terms, speciation, extinction and dispersal. There are numerous mechanistic hypotheses and empirical investigations of the factors that may influence the relative rates of speciation and extinction, and hence, biodiversity (e.g. Mittelbach *et al.*, 2007).

Climate has long been recognized as an important abiotic factor that influences species distribution patterns in both temperate and tropical regions (e.g. Wiens & Graham, 2005). Many hypotheses have proposed that ecological conditions in the tropics are associated with high speciation rates (see Wiens, 2011). For example, the ecological stability of the tropics may have provided the opportunity for niche specialization and allopatric speciation at fine scales (Mittelbach *et al.*, 2007). Other hypotheses suggest that climatic and ecological stability lead to reduced extinction and thus a high accumulation of species over evolutionary time scales. For instance, long-term climatic stability has been found to account for species persistence in tropical bolitoglossine salamanders (Kozak & Wiens, 2010), while the interaction between climate and orography was found to account for patterns of avian species richness in South America (Rahbek & Graves, 2001).

In their paper in *Journal of Biogeography*, Tolley *et al.* (2011) test mechanisms of diversification in chameleons occurring in the Eastern Arc Mountains (EAM) in southern Kenya and eastern Tanzania. Biodiversity hotspots such as the EAM are areas of high endemism and threat (Myers *et al.*, 2000). These regions are an obvious place to study drivers of diversification – not only because they have rich flora and fauna to test the plausibility of generalized mechanisms across a diversity of taxa, but also due to their conservation importance and priority.

The EAM are a chain of mountains isolated by hot and dry intervening lowland areas and are ranked among the highest for global conservation priority due to the extraordinarily high number of endemic plants and animals (Burgess *et al.*, 2007). Major hypotheses to explain high species richness and endemism include isolation through mountain uplift dating to the Miocene, high rates of speciation *in situ*, and low rates of extinction (Burgess *et al.*, 2007). The EAM have a complicated geological history with uplift occurring over the last 100 million years. Major climatic shifts resulted in fragmented lowland areas during the Pleistocene, but the mountain blocks have experienced relative climatic stability over the last several million years (Tolley *et al.*, 2011). Several phylogeographic studies have identified climate to be an important variable in the distribution of diversity in this region (see Lawson, 2010, and citations therein). However, discordant patterns of diversification among co-distributed frog taxa in the EAM indicated that the response to major climatic events depends on species-specific traits, varying even among closely related species (Lawson, 2010).

The high species diversity of regions such as the Eastern Arc Mountains begs an evolutionary explanation. Tolley *et al.* (2011) combine approaches from evolutionary and conservation biology to test the hypothesis that climatic stability underlies speciation in chameleons of the genus *Kinyongia* occurring in fragmented forests. Within *Kinyongia*, they calculated several indices commonly used in conservation and reserve design, including evolutionary distinctiveness (ED), reflecting the ‘uniqueness’ of each species, and phylogenetic diversity (PD), reflecting the diversity of the community relative to the broader species pool. Combined, their analyses reject a Pliocene–Pleistocene divergence and place differentiation within *Kinyongia* in the Miocene or Oligocene and indicate that these communities represent relictual palaeoendemics and not recent radiations within mountain blocks.

Tolley *et al.* (2011) add an important dataset to the study of speciation of the Eastern Arc Mountains and, more broadly, to studies of diversification. While there is not just a single mechanism at play, generalities, if they exist, may emerge by looking comparatively at multiple taxonomic groups with distinct demographic and natural histories (Vences *et al.*, 2009). For example, while it may not be surprising that *Kinyongia* chameleons with high habitat specificity and presumably low dispersal capacity are largely monophyletic within regions, it is interesting that this group is characterized by older diversification events. Other forest-restricted chameleons have experienced more recent radiations, indicating that a single mode of speciation does not characterize this group of lizards (Tolley *et al.*, 2006).

Tolley *et al.*'s (2011) study provides an excellent empirical example that incorporates climate, biogeography, and phylogenetic analyses towards understanding species richness patterns. Combining historical data on climatic and geological processes with evolutionary phylogenetic data provides important insights for understanding species richness patterns from biodiverse areas (e.g. Fine & Ree, 2006; Mittelbach *et al.*, 2007). As genetic datasets for multiple taxa from diverse regions become available, the application of non-traditional uses of molecular data (e.g. PD and ED) may prove fruitful for assessing community diversity structure and understanding global patterns of species richness. Finally, compiling data for many taxa with varied life history and dispersal capabilities is necessary to fully assess mechanisms and drivers of diversification.

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REFERENCES

- Burgess, N.D., Butynski, T.M., Cordeiro, N.J., Daggart, N.H., Fjeldså, J., Howell, K.M., Kilahama, F.B., Loader, S.P., Lovett, J.C., Mbilinyi, B., Menegon, M., Moyer, D.C., Nashanda, E., Perkin, A., Rovero, F., Stanley, W.T. & Stuart, S.N. (2007) The biological importance of the Eastern Arc Mountains of Tanzania and Kenya. *Biological Conservation*, **134**, 209–231.
- Fine, P.V.A. & Ree, R.H. (2006) Evidence for a time-integrated species–area effect on the latitudinal gradient in tree diversity. *The American Naturalist*, **168**, 796–804.
- Jablonski, D., Roy, K. & Valentine, J.W. (2006) Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science*, **314**, 102–106.
- Kozak, K.H. & Wiens, J.J. (2010) Accelerated rates of climatic-niche evolution underlie rapid species diversification. *Ecology Letters*, **13**, 1378–1389.
- Lawson, L.P. (2010) The discordance of diversification: evolution in the tropical-montane frogs of the Eastern Arc Mountains of Tanzania. *Molecular Ecology*, **19**, 4046–4060.
- Mittelbach, G.G., Schemske, D.W., Cornell, H.V. *et al.* (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters*, **10**, 315–331.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.
- Rahbek, C. & Graves, G.R. (2001) Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Sciences USA*, **98**, 4534–4539.
- Tolley, K.A., Burger, M., Turner, A.A. & Matthee, C.A. (2006) Biogeographic patterns and phylogeography of dwarf chameleons (*Bradypodion*) in an African biodiversity hotspot. *Molecular Ecology*, **15**, 781–793.
- Tolley, K.A., Tilbury, C.R., Measey, G.J., Menegon, M., Branch, M.R. & Matthee, C.A. (2011) Ancient forest fragmentation or recent radiation? Testing refugial speciation models in chameleons within an African biodiversity hotspot. *Journal of Biogeography*, **38**, 1748–1760.
- Vences, M., Wollenberg, K.C., Vieites, D.R. & Lees, D.C. (2009) Madagascar as a model region of species diversification. *Trends in Ecology and Evolution*, **24**, 456–465.
- Wiens, J.J. (2011) The causes of species richness patterns across space, time, and clades and the role of ‘ecological limits’. *The Quarterly Review of Biology*, **86**, 1–20.
- Wiens, J.J. & Graham, C.H. (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics*, **36**, 519–539.

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