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Evolutionary macroecology

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During the last 600 million years, life has developed an astounding diversity of forms to fill Earth's geographical and ecological space. This spectacular variety of living things has risen and fallen over time, with diversity sometimes shrinking to as little as one-twentieth of its original level (Sepkoski *et al.*, 1981; Raup, 1991; Jablonski, 2001; Benton and Twitchett, 2003; Alroy, 2008). Yet, even after the most severe mass extinctions, the rebounds in diversity have been extraordinary (Jablonski, 2001). Although forms that vanished never came back to life, the ones that replaced them have shown remarkably similar patterns of diversity and phenotype distributions in space (Foote, 1997; Erwin, 2001; Wagner, 2010). Thus, the trends studied by macroecologists – general patterns in species distribution in space (Brown, 1995; Rosenzweig, 1995; Blackburn and Gaston, 2003) – are, in principle, amenable to palaeobiological testing (Lieberman *et al.*, 2007). In fact, trends such as Bergmann's rule, the diversity/latitude relationship, the island rule, and patterns of species range distributions have been shown to apply to fossil clades (Klein, 1986; Miller, 1997; Crame, 2001; Jernvall and Fortelius, 2004; Hawkins *et al.*, 2006; Raia and Meiri, 2006; Foote *et al.*, 2007, 2008; Carotenuto *et al.*, 2010, 2015; Lyons *et al.*, 2010; Polly *et al.*, 2011; Fritz *et al.*, 2013; Jablonski *et al.*, 2013).

Some 'rules', however, are specific to fossils, whose bearing on the geography and ecology of life today is arguably extremely important yet remains to be elucidated (Mittelbach *et al.*, 2007; Araújo *et al.*, 2008). For instance, taxonomic diversity more often than not achieves a peak around the middle of the existence of a clade (Foote, 2009). But the relationship between clade age and diversity is uncertain (Ricklefs, 2007; Rabosky *et al.*, 2012). Thus, testing for differences in diversity among living clades and trying to distinguish between Raup's (1981) widely accepted reasons for a clade to survive – good genes (the phenotype) and bad luck (accidents of history) – makes little sense except in a temporally resolved context (McPeek and Brown, 2007).

That is also the kind of context in which the effects of mass extinctions can be explored properly. For example, some would suggest that the rules of evolution change in the aftermath of a crisis. If that is the case, new groups will emerge after a crisis at a faster pace than

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they otherwise would. Or perhaps diversification events are insensitive to whether or not ecospace has been cleared catastrophically (Jablonski, 2005; Roopnarine, 2006; Brusatte *et al.*, 2008; Sahney and Benton, 2008; Wagner, 2010; Ruta *et al.*, 2011). Such questions also touch upon the nature of adaptive radiations and their influence on the current distribution and species richness of clades (Rosenzweig and McCord, 1991; Rabosky, 2009; Losos, 2010; Yoder *et al.*, 2010).

Advances in community phylogenetics have provided an array of tools to deepen our understanding of how modes, trait evolution, and climate history impact the current distribution of species (Cavender-Bares *et al.*, 2009; Kembel, 2009; Ives and Helmus, 2010; Pavoine *et al.*, 2011; Pearse *et al.*, 2014). Community phylogenetics draws directly on comparative phylogenetics, which provides a vast and rapidly growing number of methods that rely on phylogenetic trees to determine the history of clades and traits (Felsenstein, 1985; Harvey and Pagel, 1991; Blomberg and Garland, 2002; Losos and Glor, 2003; O'Meara, 2012).

Yet, none of these methods explicitly takes the history of fossil diversity into account, nor do they address how diversity interacts with the taxic evolution of clades (Villalobos *et al.*, 2016). Only very recently have studies sought to use the fossil record directly to model the evolution of clade diversification, competition among clades, and the influence of traits on diversification (Hunt, 2007; Hunt *et al.*, 2015; Silvestro *et al.*, 2015). The importance of the fossil record to the current distribution and diversity of species is now becoming more widely understood, even in a field as distinct from palaeontology as conservation biology (Diniz-Filho *et al.*, 2013).

Spatially explicit palaeontological information and methods are thus necessary to help understand why diversity looks the way it does, or why and how species numbers vary over space and time. Two issues of *Evolutionary Ecology Research* are dedicated to the integration of fossil and neontological information in an attempt to better understand both species and phenotype diversity in space and time.

In this, the January issue, we look at the path taken by diversity through time. Sahney and Benton (2017) provide evidence that the rise in generic diversity towards the recent is not an artefact of improved sampling towards the present (the so-called Pull of the Recent effect). Castiglione and colleagues (2017) analyse the path taken by diversity in Palaeozoic and Mesozoic fossil marine clades and find that, in more than 90% of them, the models producing the observed diversity patterns include a rapid early diversification phase followed by steadily rising rates of extinction. Silvestro and associates (2017) provide a novel approach to the study of the age-old macroevolutionary question of whether clades compete with each other in time. Polly and colleagues (2017) look at the evolution of cursoriality in American Carnivora. They find that clade-level trait-based sorting has a strong impact on community-level trait distributions but population-level selection is either too weak or ineffective to produce hind limb trait gradients within carnivore species. Finally, Lima-Ribeiro and Diniz-Filho (2017) find that, contrary to conventional wisdom human over-exploitation (the overkill hypothesis) is unlikely to explain the end-Pleistocene extinction of the ground sloth (*Megatherium*).

The March issue focuses on phenotypic evolution. Maiorino and colleagues (2017) present an extensive study of cranial shape evolution in ceratopsian dinosaurs. They discover that cranial shape and angiosperm occurrences are closely related. They also discover a trend for decreasing shape differentiation in psittacosaurids. Villalobos and colleagues (2017) look at body size evolution in pterosaurs. They find that these winged ornithodirans did not follow Bergmann's rule; during the Cretaceous, pterosaurs even followed the reverse pattern. Schnitzler and associates (2017) address shape evolution in fossil Musteloidea (the clade that includes weasels, martens, and badgers). Their study provides evidence for a trend of increasing digitigrady in this group – crucially, however, this trend is evident only when fossil information is included. Finally, Feranec and Pagnac (2017) study the evolution of molar isotopic composition in Miocene horses. Surprisingly, they find that C_4 grasses occurred in the mid-Miocene in southern California, up to 8 million years before the global spread of C_4 ecosystems.

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REFERENCES

Alroy, J. 2008. Dynamics of origination and extinction in the marine fossil record. *Proc. Natl. Acad. Sci. USA*, **105** (suppl. 1): 11536–11542.

Araújo, M.B., Nogués-Bravo, D., Diniz-Filho, J.A.F., Haywood, A.M., Valdes, P.J. and Rahbek, C. 2008. Quaternary climate changes explain diversity among reptiles and amphibians. *Ecography*, **31**: 8–15.

Benton, M.J. and Twitchett, R.J. 2003. How to kill (almost) all life: the end-Permian extinction event. *Trends Ecol. Evol*., **18**: 358–365.

Blackburn, T.M. and Gaston, K.J. 2003. *Macroecology: Concepts and Consequences*. Cambridge: Cambridge University Press.

Blomberg, S.P. and Garland, T. 2002. Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. *J. Evol. Biol.*, **15**: 899–910.

Brown, J.H. 1995. *Macroecology*. Chicago, IL: University of Chicago Press.

Brusatte, S.L., Benton, M.J., Ruta, M. and Lloyd, G.T. 2008. Superiority, competition, and opportunism in the evolutionary radiation of dinosaurs. *Science*, **321**: 1485–1488.

Carotenuto, F., Barbera, C. and Raia, P. 2010. Occupancy, range size, and phylogeny in Eurasian Pliocene to Recent large mammals. *Paleobiology*, **36**: 399–414.

Carotenuto, F., Diniz-Filho, J.A.F. and Raia, P. 2015. Space and time: the two dimensions of Artiodactyla body mass evolution. *Palaeogeogr., Palaeoclimatol. Palaeoecol*., **437**: 18–25.

Castiglione, S., Mondanaro, A., Carotenuto, F., Passaro, F., Fortelius, M. and Raia, P. 2017. The many shapes of diversity: ecological and evolutionary determinants of biodiversity through time. *Evol. Ecol. Res*., **18**: 25–39.

Cavender-Bares, J., Kozak, K.H., Fine, P.V.A. and Kembel, S.W. 2009. The merging of community ecology and phylogenetic biology. *Ecol. Lett*., **12**: 693–715.

Crame, J.A. 2001. Taxonomic diversity gradients through geological time. *Divers. Distrib*., **7**: 175–189.

Diniz-Filho, J.A.F., Loyola, R.D., Raia, P., Mooers, A.O. and Bini, L.M. 2013. Darwinian shortfalls in biodiversity conservation. *Trends Ecol. Evol.*, **28**: 689–695.

Erwin, D.H. 2001. Lessons from the past: biotic recoveries from mass extinctions. *Proc. Natl. Acad. Sci. USA*, **98**: 5399–5403.

Felsenstein, J. 1985. Phylogenies and the comparative method. *Am. Nat*., **125**: 1–15.

Feranec, R.S. and Pagnac, D.C. 2017. Hypsodonty, horses, and the spread of C_4 grasses during the middle Miocene in southern California. *Evol. Ecol. Res*., **18**: 201–223.

Foote, M. 1997. The evolution of morphological diversity. *Annu. Rev. Ecol. Syst*., **28**: 129–152.

Foote, M. 2009. Symmetric waxing and waning of marine invertebrate genera. *Paleobiology*, **33**: 517–529.

Foote, M., Crampton, J.S., Beu, A.G., Marshall, B.A., Cooper, R.A., Maxwell, P.A., *et al.* 2007. Rise and fall of species occupancy in Cenozoic fossil mollusks. *Science*, **318**: 1131–1134.

Foote, M., Crampton, J.S., Beu, A.G. and Cooper, R.A. 2008. On the bidirectional relationship between geographic range and taxonomic duration. *Paleobiology*, **34**: 421–433.

Fritz, S.A., Schnitzler, J., Eronen, J.T., Hof, C., Böhning-Gaese, K. and Graham, C.H. 2013. Diversity in time and space: wanted dead and alive. *Trends Ecol. Evol.*, **28**: 509–516.

Harvey, P.H. and Pagel, M.D. 1991. *The Comparative Method in Evolutionary Biology*. Oxford: Oxford University Press.

Hawkins, B.A., Diniz-Filho, J.A.F., Jaramillo, C.A. and Soeller, S.A. 2006. Post-Eocene climate change, niche conservatism, and the latitudinal diversity gradient of New World birds. *J. Biogeogr.*, **33**: 770–780.

Hunt, G. 2007. The relative importance of directional change, random walks, and stasis in the evolution of fossil lineages. *Proc. Natl. Acad. Sci. USA*, **104**: 18404–18408.

Hunt, G., Hopkins, M.J. and Lidgard, S. 2015. Simple versus complex models of trait evolution and stasis as a response to environmental change. *Proc. Natl. Acad. Sci. USA*, **112**: 4885–4890.

Ives, A.R. and Helmus, M.R. 2010. Phylogenetic metrics of community similarity. *Am. Nat.*, **176**: E128–E142.

Jablonski, D. 2001. Lessons from the past: Evolutionary impacts of mass extinctions. *Proc. Natl. Acad. Sci. USA*, **98**: 5393–5398.

Jablonski, D. 2005. Evolutionary innovations in the fossil record: the intersection of ecology, development, and macroevolution. *J. Exp. Zool.*, **304B**: 504–519.

Jablonski, D., Belanger, C.L., Berke, S.K., Huang, S., Krug, A.Z., Roy, K. *et al.* 2013. Out of the tropics, but how? Fossils, bridge species, and thermal ranges in the dynamics of the marine latitudinal diversity gradient. *Proc. Natl. Acad. Sci. USA*, **110**: 10487–10494.

Jernvall, J. and Fortelius, M. 2004. Maintenance of trophic structure in fossil mammal communities: site occupancy and taxon resilience. *Am. Nat.*, **164**: 614–624.

Kembel, S.W. 2009. Disentangling niche and neutral influences on community assembly: assessing the performance of community phylogenetic structure tests. *Ecol. Lett.*, **12**: 949–960.

Klein, R.G. 1986. Carnivore size and quaternary climatic change in southern Africa. *Quaternary Res.*, **26**: 153–170.

Lieberman, B.S., Miller, W., III and Eldredge, N. 2007. Paleontological patterns, macroecological dynamics and the evolutionary process. *Evol. Biol.*, **34**: 28–48.

Lima-Ribeiro, M.S. and Diniz-Filho, J.A.F. 2017. Climate change, human overkill, and the extinction of megafauna: a macroecological approach based on pattern-oriented modelling. *Evol. Ecol. Res.*, **18**: 97–121.

Losos, J.B. 2010. Adaptive radiation, ecological opportunity, and evolutionary determinism. *Am. Nat.*, **175**: 623–639.

Losos, J.B. and Glor, R.E. 2003. Phylogenetic comparative methods and the geography of speciation. *Trends Ecol. Evol.*, **18**: 220–227.

Lyons, S.K., Wagner, P.J. and Dzikiewicz, K. 2010. Ecological correlates of range shifts of Late Pleistocene mammals. *Phil. Trans. R. Soc. Lond. B: Biol. Sci.*, **365**: 3681–3693.

McPeek, M.A. and Brown, J.M. 2007. Clade age and not diversification rate explains species richness among animal taxa. *Am. Nat.*, **169**: E97–E106.

Maiorino, L., Farke, A.A., Kotsakis, T. and Piras, P. 2017. Macroevolutionary patterns in cranial and lower jaw shape of ceratopsian dinosaurs (Dinosauria, Ornithischia): phylogeny, morphological integration, and evolutionary rates. *Evol. Ecol. Res.*, **18**: 123–167.

Miller, A.I. 1997. A new look at age and area: the geographic and environmental expansion of genera during the Ordovician Radiation. *Paleobiology*, **23**: 410–419.

Mittelbach, G.G., Schemske, D.W., Cornell, H.V., Allen, A.P., Brown, J.M., Bush, M.B. *et al.* 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecol. Lett.*, **10**: 315–331.

O'Meara, B.C. 2012. Evolutionary inferences from phylogenies: a review of methods. *Annu. Rev. Ecol. Evol. Syst.*, **43**: 267–285.

Pavoine, S., Vela, E., Gachet, S., De Bélair, G. and Bonsall, M.B. 2011. Linking patterns in phylogeny, traits, abiotic variables and space: a novel approach to linking environmental filtering and plant community assembly. *J. Ecol.*, **99**: 165–175.

Pearse, W.D., Purvis, A., Cavender-Bares, J. and Helmus, M.R. 2014. Metrics and models of community phylogenetics. In *Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology* (L.Z. Garamszegi, ed.), pp. 451–464. Berlin: Springer.

Polly, P.D., Eronen, J.T., Fred, M., Dietl, G.P., Mosbrugger, V., Scheidegger, C. *et al.* 2011. History matters: ecometrics and integrative climate change biology. *Proc. R. Soc. Lond. B: Biol. Sci.*, **278**: 1131–1140.

Polly, P.D., Fuentes-Gonzalez, J., Lawing, A.M., Bormet, A.K. and Dundas, R.G. 2017. Clade sorting has a greater effect than local adaptation on ecometric patterns in Carnivora. *Evol. Ecol. Res.*, **18**: 61–95.

Rabosky, D.L. 2009. Ecological limits on clade diversification in higher taxa. *Am. Nat.*, **173**: 662–674.

Rabosky, D.L., Slater, G.J. and Alfaro, M.E. 2012. Clade age and species richness are decoupled across the eukaryotic tree of life. *PLoS Biol.*, **10**: e1001381.

Raia, P. and Meiri, S. 2006. The island rule in large mammals: paleontology meets ecology. *Evolution*, **60**: 1731–1742.

Raup, D.M. 1981. Extinction: bad genes or bad luck? *Acta Geol. Hisp.*, **16**: 25–33.

Raup, D.M. 1991. A kill curve for Phanerozoic marine species. *Paleobiology*, **17**: 37–48.

Ricklefs, R.E. 2007. History and diversity: explorations at the intersection of ecology and evolution. *Am. Nat.*, **170**: S56–S70.

Roopnarine, P.D. 2006. Extinction cascades and catastrophe in ancient food webs. *Paleobiology*, **32**: 1–19.

Rosenzweig, M.L. 1995. *Species Diversity in Space and Time*. Cambridge: Cambridge University Press.

Rosenzweig, M.L. and McCord, R.D. 1991. Incumbent replacement: evidence for long-term evolutionary progress. *Paleobiology*, **17**: 202–213.

Ruta, M., Cisneros, J.C., Liebrecht, T., Tsuji, L.A. and Müller, J. 2011. Amniotes through major biological crises: faunal turnover among parareptiles and the end-Permian mass extinction. *Palaeontology*, **54**: 1117–1137.

Sahney, S. and Benton, M.J. 2008. Recovery from the most profound mass extinction of all time. *Proc. R. Soc. Lond. B: Biol. Sci.*, **275**: 759–765.

Sahney, S. and Benton, M. J. 2017. The impact of the Pull of the Recent on the fossil record of tetrapods. *Evol. Ecol. Res.*, **18**: 7–23.

Schnitzler, J., Theis, C., Polly, P.D. and Eronen, J.T. 2017. Fossils matter – understanding modes and rates of trait evolution in Musteloidea (Carnivora). *Evol. Ecol. Res.*, **18**: 187–200.

Sepkoski, J.J., Bambach, R.K., Raup, D.M. and Valentine, J.W. 1981. Phanerozoic marine diversity and the fossil record. *Nature*, **293**: 435–437.

Silvestro, D., Antonelli, A., Salamin, N. and Quental, T.B. 2015. The role of clade competition in the diversification of North American canids. *Proc. Natl. Acad. Sci. USA*, **112**: 8684–8689.

Silvestro, D., Pires, M.M., Quental, T.B. and Salamin, N. 2017. Bayesian estimation of multiple clade competition from fossil data. *Evol. Ecol. Res.*, **18**: 41–59.

Villalobos, F., Carotenuto, F., Raia, P. and Diniz-Filho, J.A.F. 2016. Phylogenetic fields through time: temporal dynamics of geographical co-occurrence and phylogenetic structure within species ranges. *Phil. Trans. R. Soc. Lond. B: Biol. Sci.*, **371**: 20150220.

Villalobos, F., Olalla-Tárraga, M.Á., Marques Vieira, C., Diniz Mazzei, N. and Bini, L.M. 2017. Spatial dimension of body size evolution in Pterosauria: Bergmann's rule does not drive Cope's rule. *Evol. Ecol. Res.*, **18**: 169–186.

Wagner, P.J. 2010. Paleontological perspectives on morphological evolution. In *Evolution since Darwin: The First 150 Years* (M.A. Bell, D.J. Futuyma, W.F. Eanes and J.S. Levinton, eds.), pp. 451–478. Sunderland, MA: Sinauer Associates.

Yoder, J.B., Clancey, E., des Roches, S., Eastman, J.M., Gentry, L., Godsoe, W. *et al.* 2010. Ecological opportunity and the origin of adaptive radiations. *J. Evol. Biol.*, **23**: 1581–1596.