



COMMENTARY



## In search of general models in evolutionary time and space

The Alfred Russel Wallace award was established by the International Biogeography Society (IBS) in 2004 to recognize a lifetime of outstanding contributions by an eminent scholar in any sub-discipline of biogeography. Past award winners include Jack Briggs, Jared Diamond and John Avise. The latest recipient is Robert Ricklefs, who gave his Wallace award address at the IBS meeting in Crete in January 2011. The *Journal of Biogeography*, which sponsors the Wallace award, is pleased to feature the written version of the address in this issue (Ricklefs, 2011).

In his paper Ricklefs (2011) reflects on several long-standing themes that have motivated his interests in biogeography, including the evolutionary development of Caribbean birds, the role of pathogens, and the nature of the community. The importance of field experience, of gaining a detailed acquaintance with a functioning ecological system, and of examining data in map form are also evident through his account (and see *Frontiers of Biogeography*, 2011, issue 3, pp. 31–36). Indeed, he began his work on West Indian birds by mapping all the species, in the process generating a set of observations and ideas that have provided a rich seam to which he has returned throughout his career.

Ricklefs began graduate school under the mentorship of Robert MacArthur, a towering figure within 20th century ecology. His first year in graduate school coincided with the publication by MacArthur & Wilson (1963) of the short paper in *Evolution* in which they outlined their dynamic equilibrium theory of island biogeography. This theory represented a pioneering effort to drag biogeography into a new quantitative, mathematical tradition, vital to a stronger general theory. In an oft-quoted passage of their subsequent monograph (MacArthur & Wilson, 1967, p. 5) they described biogeography as largely *ad hoc* and historically oriented, commenting that 'partly because such questions are concerned with a limited number of higher taxa, and partly because of

the considerable intrinsic interest in these taxa in the first place, the historical solutions have tended to be satisfying in themselves and have not encouraged generalizations'. Interestingly, Ricklefs (2011) remarks that MacArthur discouraged him from pursuing the work he had started on the 'basically historical, non-equilibrium phenomenon' of the taxon cycle in West Indian birds, commenting that 'MacArthur explicitly ignored history because he was interested in general patterns...'. This distinction between historical or time-bound knowledge on the one hand and dynamic or timeless knowledge on the other reflects a dichotomy perceived in other areas of the natural sciences at the time. For example, in a passage attributed to the geomorphologist A.N. Strahler by Schumm (1991, p. 5), it is suggested that 'historical investigation be defined as referring to the analysis of complex states having very small probabilities of being repeated, that is to states of low recoverability. Dynamic investigation in the same context refers to the analysis of states having a high degree of probability of being repeated, such analysis leading to the formulation of laws of general validity.' By identifying questions such as 'What was the ultimate origin of the Antillean vertebrate fauna' as an example of *ad hoc* and historically oriented biogeography, MacArthur & Wilson (1967) effectively dismiss such work as being time-bound and unlikely to lead to general models and insights. Yet, while Ricklefs' subsequent corpus of work certainly contains much that strives to identify exceptions from general patterns, and to identify how the contingencies of history have uniquely shaped particular patterns of distribution and diversity (e.g. Qian & Ricklefs, 2000), might it be that, with a deeper temporal perspective, the taxon cycle in West Indian birds can be seen as more general and less time-bound than MacArthur initially suspected?

The taxon cycle label was first formerly applied in the context of Melanesian ant

distributions within a series of papers by E.O. Wilson (e.g. Wilson, 1961). Wilson's work, although seminal, attracted little direct critique or testing. In contrast, the independently derived and subtly different taxon cycle model developed by Ricklefs & Cox (1972, 1978) for Caribbean birds was subject to pointed critique. It was criticized for being something of a 'just-so' story, for settling prematurely on only one of several possible historical explanations, and for being based on an implausible mechanism: counter-adaptation. This was the idea that a newly arriving colonist species initially enjoys a competitive advantage because none of the interacting species 'have their number', so such species build large population sizes, but over time predators and pathogens enjoy increasing success in exploiting the abundant resource provided by the now well-established colonist. Hence, this species subsequently declines in abundance and distribution, while in time new species colonize and re-start the cycle.

Following the criticisms of the Ricklefs and Cox model, a few more papers appeared concerning other putative taxon cycles, but to a large degree there things rested. Time passed. Then, from 1989 onwards, Ricklefs began a new collaboration with Eldredge Bermingham and they set out to collect phylogenetic data for members of the Antillean avifauna. In a series of papers they provided a comprehensive analysis supporting the generality of the taxon cycle process, at least for this system (Ricklefs, 2011).

Increasingly, Ricklefs and his colleagues emphasized the possibility that pathogens were the key to understanding the process. The metaphor of the elephant in the living room is used to denote the unmentioned, avoided, but obvious factor in relation to a problem. Yet elephants in living rooms are easy business compared to the pathogen in the island avifauna, the less easily detected, less charismatic, often entirely cryptic and species-specific small things that eat away and debilitate the host. Unlike commonly selected explanatory factors in island

biogeography, such as energy availability, island area and isolation, pathogen loading in species or assemblages is hard to determine. Consequently, whether pathogen loading is the key mechanistic basis for the taxon cycle remains unresolved, notwithstanding anecdotal and corroborative evidence (Ricklefs, 2011).

Ricklefs (2011) provides far more than a mere resumé of the Caribbean bird taxon cycle work, extending his scope to broadly review community ecology and diversity theory, while expanding on ways taxon cycle ideas could be applied to mainland, as well as island, biotas. His comments on the largely neglected work of John C. Willis may help renew interest in Willis' interesting, if flawed, theory of *Age and Area* (Willis, 1922), now that molecular tools enable critical tests of the links between phylogenies and the histories of the land masses (cf. Emerson & Gillespie, 2008; Whittaker *et al.*, 2008; Cardoso *et al.*, 2010). These same techniques allow the exploration of the dynamics of island biotas over vastly extended time periods than possible in the 1960s and 1970s, and hold the promise of developing more complete and integrative general models of island biogeography (Whittaker *et al.*, 2008; Losos & Ricklefs, 2010).

Ricklefs (2011) ends his review with a series of ten speculations/predictions as directions for future research. Central to these statements is that pathogens have been neglected by biogeography and related disciplines, and that while we have bashed away, largely inconclusively, at the role of interactions in the larger organisms and trophic level(s) of our interest (mammals, birds, plants, snails etc.), we have neglected the possibility that species-specific loadings imposed by typically small and fast-breeding parasites and pathogens may matter more. The latter may serve to upset the finely tuned calculations inherent to several other branches of ecological biogeography, notably: (1) the application of ecological niche models (species distribution models), which

often seem still to confuse the realized range (or niche) for the fundamental range (or niche); (2) assumptions in competition theory about co-existence of species, which may be easily tilted one way or another by pathogens; and (3) assumptions about range heritability, which need to take account of the lability of this trait over the lifetime of a species.

The ten predictions serve to synthesize the arguments as to how species-specific idiosyncrasies, differences and contingencies may yet be consolidated together to constitute '... a general model for distribution and abundance in natural systems, emphasizing the population as the primary unit in community ecology and the region as the setting for community interactions' (Ricklefs, 2011). By this perspective, the outcomes of long-term biogeographical dynamics, as encapsulated in taxon cycle models, may be remarkably predictable at the community assemblage level and thus closer to constituting dynamic, timeless knowledge (*sensu* Schumm, 1991) than initially suspected. The lesson seems to be that in the search for general models in evolutionary time and space we just have to be prepared to take the longer view.

ROBERT J. WHITTAKER<sup>1,2\*</sup> AND  
JEREMY T. KERR<sup>1,3</sup>

<sup>1</sup>*School of Geography and the Environment, University of Oxford, South Parks Road, Oxford, OX1 3QY, UK,* <sup>2</sup>*Department of Biology, Center for Macroecology, Evolution and Climate, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark,*

<sup>3</sup>*Present address: Department of Biology, University of Ottawa, 30 Marie Curie, Ottawa, ON, K1N 6N5, Canada*

\*E-mail: Robert.Whittaker@ouce.ox.ac.uk

## REFERENCES

Cardoso, P., Arnedo, M.A., Triantis, K.A. & Borges, P.A.V. (2010) Drivers of diversity

in Macaronesian spiders and the role of species extinctions. *Journal of Biogeography*, **37**, 1034–1046.

Emerson, B.C. & Gillespie, R.G. (2008) Phylogenetic analysis of community assembly and structure over space and time. *Trends in Ecology and Evolution*, **23**, 619–630.

Losos, J.B. & Ricklefs, R.E. (eds) (2010) *The theory of island biogeography revisited*. Princeton University Press, Princeton, NJ.

MacArthur, R.H. & Wilson, E.O. (1963) An equilibrium theory of insular zoogeography. *Evolution*, **17**, 373–387.

MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ.

Qian, H. & Ricklefs, R.E. (2000) Large-scale processes and the Asian bias in species diversity of temperate plants. *Nature*, **407**, 180–182.

Ricklefs, R.E. (2011) A biogeographical perspective on ecological systems: some personal reflections. *Journal of Biogeography*, **38**, 2045–2056.

Ricklefs, R.E. & Cox, G.W. (1972) Taxon cycles in the West Indian avifauna. *The American Naturalist*, **106**, 195–219.

Ricklefs, R.E. & Cox, G.W. (1978) Stage of taxon cycle, habitat distribution, and population density in the avifauna of the West Indies. *The American Naturalist*, **112**, 875–895.

Schumm, S.A. (1991) *To interpret the Earth: ten ways to be wrong*. Cambridge University Press, Cambridge.

Whittaker, R.J., Triantis, K.A. & Ladle, R.J. (2008) A general dynamic theory of oceanic island biogeography. *Journal of Biogeography*, **33**, 977–994.

Willis, J.C. (1922) *Age and area: a study in geographical distribution and origin of species*. Cambridge University Press, Cambridge.

Wilson, E.O. (1961) The nature of the taxon cycle in the Melanesian ant fauna. *The American Naturalist*, **95**, 169–193.