

## The 2015 Ramon Margalef Prize to Robert E. Ricklefs: A passion for evolutionary ecology

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**Summary.** Two passions were the starting points of Robert Ricklefs' career: the reproduction of birds and the biodiversity of the tropics. It is important to underlie his key contribution to the unification of the biological sciences that he achieved to demonstrate by the unifying nature of his work and by suggesting the scale of the scientific background on which it rests. Among his multiple contributions to the science of ecology is the notion of evolutionary trade-off that included functional, metabolic, demographic and population considerations. He has made a crucial contribution to the consolidation of the theory of life histories. We might even say that the impact of his critiques of the theories of biological diversity of communities has a relevant part in the research agenda in the coming years. In contrast to the prevailing dualism to explain biodiversity (niche theory and neutral theory), Professor Ricklefs provides solid empirical data and realistic arguments calling for an urgent update of the current paradigm. [Contrib Sci 12(1):23-25 (2016)]

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When talking about a naturalist, as Robert Ricklefs defines himself, it is a good idea to refer albeit briefly to his childhood because it was on the privileged peninsula of Monterey in California, where he grew up and which triggered his early curiosity about nature. Attracted right from the very beginning by botany and ornithology, the young Ricklefs went to Stanford University at the age of 16 and when he was 24 earned his doctorate at Pennsylvania University, where he would become a professor one year later in 1968. Coming forward in time, from 1995 to the present he has

been based at Missouri University State at St. Louis. It is now 50 years since at the age of 22 he published his first article in the journal *Condor*. Throughout his career, which remains fully active and creative today, he has carried out vast quantities of research in various fields of ecology on over 300 scientific articles, some written entirely by himself, not to mention the many chapters he has contributed to specialist publications. Plus at the age of 30 he published his book *Ecology*, and three years later *The Economy of Nature*, general treatises which have been updated in successive editions, the last

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in 2014. We can say without hesitation that Ricklefs is in the first rank in the scientific community where he is also one of the best known and most appreciated people in teaching and popularizing ecology around the world.

Ricklefs' work has been recognized by numerous academic awards. By way of example there is the Sewall Wright Award in 2005, which is presented for scientific careers that have made a key contribution to the unification of the biological sciences. It demonstrates the unifying nature of his work and suggests the scale of the scientific background on which it rests, something which I am keen to corroborate in that tribute.

Ricklefs acknowledges the direct academic and personal influence of his mentors, including Paul Ehrlich at Stanford, who was also awarded the Ramon Margalef Prize in 2009, and Robert MacArthur at Pennsylvania during his doctoral studies. The intellectual ferment of those years, with the birth of evolutionary ecology focused on life histories on the one hand and the resurgence of community ecology focusing on biodiversity on the other, stimulated Ricklefs and made it fertile ground for the cultivation of his two passions, the reproduction of birds and the biodiversity of the tropics. Regarding the first point, Ricklefs successfully produced one of the first quantitative predictive models about a vital feature, the optimization of the growth rate, published in the journal *Ecology* in 1984. He developed the notion of "evolutionary trade-off" and included functional, metabolic, demographic and population considerations in his objectives. His ability in analytic resolution is coupled with his capacity for synthesis, which leads him to explore the interaction of vital traits, revealing the "unity in diversity" of patterns in the life histories of the various taxa. This skill enables him, for example, to extrapolate and predict the ageing style of specific and now extinct groups from fossil records, such as the *Tyrannosaurus*.

If Ricklefs has made a crucial contribution to the consolidation of the theory of life histories, his impact on the critique and deconstruction of the theories that explain the biological diversity of communities is equally significant. Indeed, we might even say it is more relevant due to the drastic change in direction entailed by his theories which are set to revitalize the research agenda in the coming years.

In contrast to the prevailing dualism to explain biodiversity (niche theory and neutral theory), Ricklefs provides solid empirical data and realistic arguments calling for an urgent update of the current paradigm. As he says "neither niche theory nor neutral theory provide a satisfying narrative for understanding biodiversity." Here Ricklefs is a combative and activist advocate of a deterministic assembly of communities

## About the author

**Joan L. Pretus** (1961) is staff professor at the University of Barcelona, where he has developed research projects to characterize community and ecosystem level processes in Mediterranean-type aquatic food webs. His current interests focusses on life-history trait evolutionary responses to shifts in selection pressures for selected species both aquatic and terrestrial, and its relevance in conservation biology. He is lecturer in evolutionary ecology, emphasizing the relevance of an eco-evolutionary synthesis as a basic fundamental instruction addressing forthcoming issues in field, theoretical and experimental biology.



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and minimizes the role of stochastic processes because in his view "regional deterministic processes responsible for diversity patterns dominate the weak influence of chance," so that "nature may appear neutral, but that is primarily because nature is complex."

However, within this determinism Ricklefs redirects formulating hypotheses towards other still poorly explored mechanisms that he envisions, once he has argued with em-

pirical clarity the inability of conventional niche theory to explain changes in local biodiversity patterns in different and ecologically equivalent biogeographic areas. He proposes re-connecting ecology and biogeography, the regional and local scale. It is in any case the alleged niches that would adapt to the richness of the species under robust and predictable regional influences, rather than the niches determining this richness.

Ricklefs has challenged the very concept of community. See, for example, the article he published in 2008 in the journal *American Naturalist*, where the title “Disintegration of the Ecological Community” speaks for itself. Yet, he also does not subscribe to current conventional trends to explain biodiversity which, inspired by the concept of metacommunity, make dispersion and connectivity into the key players. In them, Ricklefs still sees the influence of the powerful carrying capacity prejudice—the Verhulst equation—but now in a contrived way, what is called limiting similarity or packaging of species and consequent saturation of the local richness of the community. In its place he advocates an open, unrestricted community depending on the regional biogeographical context. Yet, he goes further and proposes an intrinsically biological mechanism for diversity, little connected to limitation by resources or the forcing imposed by environmental gradients. This is a mechanism of coevolutionary interaction of species with their specific pathogens and parasites. This is where Ricklefs unifies and reconnects seemingly unconnected phenomena such as the diversity of the rainforest and the—until now misunderstood—taxonomic cycle of Edward O. Wilson, and bases it on the dynamics of coevolutionary interaction that is little recognized in ecology.

Ricklefs produces flowing arguments and, as in the case of Ramon Margalef, bases them on an enormous capacity to combine observational data. “Observation—Ricklefs says—has inspired my career much more than theory.” He reorganizes, crops if necessary, renews or replaces theories for use based on his observations and generates new predictions. His procedure is both surgical in criticism and inclusive in the presentation of the solution, and provides a research agenda. That is because Ricklefs’ way of doing science is unusual today: it is inductive science, capable of generating hypotheses from the accumulation and detailed consideration of numerous observations, of which Darwin, Edward O. Wilson and Ramon Margalef are also masters. At any event, it is a way of building knowledge that is the reverse of the hypothetical-deductive model which excessively tightens and strangles ecology as heir to natural history. In a nutshell, Ricklefs turns ecology into an observational science, or as he puts

it: “the process of inductive reasoning involves arriving at a conclusion from observed facts placed in a framework of generally accepted principles, or premises.” Ricklefs is thus a naturalist due to his rich and contrasting argumentative connections who also has a powerful methodological arsenal as an ecologist.

Finally, which is Professor Ricklefs’ basic message? I would say it is to relearn how to observe. Ricklefs wrote in 2012: “There is a growing tendency for observation to serve theory rather than provide new insight or to test the predictions of theory.” This tendency, he says, “is reinforced by the general decline of teaching focused on organisms and habitats in favor of an emphasis on ecological concepts.” Based on this, it might be useful to critically ask ourselves how far ecology is a victim of Goethe’s premonition when he wrote that “every science of observation must take care not to get lost among its own artifacts.” Thank you, Robert, because while enjoying your encouraging example, we also realize how useful it is to learn to break away from compartmentalization, the partly inevitable sub-product of science. And how the ecologists take control for this purpose when they think like naturalists. I would like to finish with some of your own words: “the pressure to publish leaves little room for observation and reflection, much to the detriment of our science and of the pure joy of being a scientist.” ■

**Competing interests.** None declared.