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Interview with Robert E. Ricklefs, recipient of the 2011 Alfred Russel Wallace award

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Rosemary Gillespie: You started working on islands as a new graduate student. Why islands?

Robert E. Ricklefs: When I arrived at the University of Pennsylvania to begin graduate studies with Robert MacArthur, he and Ed Wilson had just published their seminal paper in *Evolution* on the "*theory of insular zoogeography.*" It was only natural that I turned my attention to islands—and birds because I had for years been an avid birdwatcher, as was MacArthur; the West Indies because James Bond at the Academy of Natural Sciences of Philadelphia had published a distributional checklist. I quickly developed a scheme postulating changes in bird distributions in the islands similar to Wilson's "taxon cycle," but MacArthur felt that historical hypotheses were untestable and discouraged further work. I slipped in some observations of bird distributions on the island of Jamaica one summer, which resulted in a 1970 publication, but did not return to the topic until I had become an Assistant Professor at Penn., and began a collaboration with George Cox, a superb ecologist and naturalist at San Diego State University. My doctoral thesis at Penn. addressed issues in bird life histories—nothing on community ecology or biogeography.

RG: You began your career in the 1960s, following in the footsteps of Hutchinson and MacArthur, and at a time when the ideas of Lotka and Volterra were highlighted, competitive exclusion was a new and important topic, along with related themes of niche specialization, ecological sorting, limiting similarity, and community saturation. How important were these in shaping your ideas and the field of biogeography in general?

RER: One had to be impressed by the power of competition, and other types of interactions, revealed in experimental studies. Most ecologists brought up in the Hutchinsonian tradition believed in niches and in resource limitation. These properties of systems were the basis for character displacement, density compensation, and other ecological and evolutionary phenomena. So, all these elements fit together well. Community saturation was perhaps the weakest aspect of the developing theory, as this was difficult to demonstrate experimentally in natural systems, and similar environments in different regions sometimes supported very different numbers of species. The degree to which species interactions constrained species ranges and probabilities of establishment following dispersal were harder to judge, although some ideas about biogeography, such as Jared Diamond's checkerboard distribution patterns, had an essentially ecological foundation.

RG: The 1960s were also the early days of plate tectonics, and the start of panbiogeography, cladistics and vicariance/dispersal debates. How much interaction did you see between these fields? How did they inform one another? How did discussions with the different players affect your thinking?

RER: As an ecologist, these developments had relatively little influence on me. Ecologists were relatively indifferent to phylogenetics (as opposed to evolution) at the time, and to any kind of historical explanation, although we were very much interested in adaptive radiation, convergent evolution, character displacement, and evolutionary ecology. From my perspective, the debates concerning panbiogeography, cladistics, and vicariance/dispersal were peripheral issues, and the kind of biogeography involved in these debates seemed to have little connection to ecology. These were historical/geographical issues, and were not discussed widely among ecologists.

Similarly, 'island biogeography' was considered as distinct from 'community ecology'. The

perception was that islands just didn't have enough species for ecological limitations on diversity to play a major role. The ecological space on islands wasn't saturated with species. Rather it was colonization limitation and area-dependent extinction that prevented the buildup of a lot of species. Islands were regarded as quite different from mainland continental areas. Moreover, Macarthur wanted ecology to have a quantitatively rational basis; he was very oriented towards understanding predictable processes. Considering these fields separately allowed them to develop in their own logical frameworks.

RG: Was there an active shift that really started the integration between island biogeography and evolutionary biology?

RER: One really has to go back to David Lack and the Galapagos finches. His book (*Darwin's Finches*) is very explicit about character displacement, mechanisms of diversification on islands, and how species partitioned resources. People tend to forget about his major contributions. Lack's themes were picked up by Peter and Rosemary Grant in their seminal work on *Geospiza*, and on it went from there. Likewise, the *Anolis* studies grew out of the Ernst Williams' group at Harvard. Williams had a lot of foresight, with much emphasis on morphology and taxonomy, even if not in a phylogenetic framework. So that was around, especially in the general context of adaptive radiation.

RG: What about phylogenetics being applied to vicariance, and the ordering of the break-up of the continents?

RER: That happened later —mid 1980s or 1990s, in particular, when it became possible to date events. The integration of these different fields can really be thought of as a large, braided river, with channels separating and reconnecting the way that areas of research branch apart and come together again in new combinations of ideas and approaches.

RG: You made several trips to the Caribbean early in your career. How important were these field trips in shaping your ideas. What advice would you give to beginning graduate students in terms of the importance and role of field work in developing projects and ideas?

RER: For ecologists, there is no substitute for working in the field —not just for gathering data, but also for developing 'insight' into natural systems, and making observations that challenge the views one has of nature. Perhaps biogeographers are more able to work solely from maps, but without the ecological dimension of space one can miss out on the transforming effect of environment on species and their distributions. I share the concern of many of the older generation of biogeographers that the increasing use of large-scale datasets and focus on computer-intensive data analysis is drawing students and young investigators away from the more time-consuming fieldwork. I also wonder whether the focus of macroecological studies on place —often latitude –longitude grid cells— is diverting attention from species distributions and ultimately might detract from the integration of ecology and biogeography.

RG: It seems that the early field excursion to Jamaica was very important in the development of your ideas. Would you recommend such an intensive field experience for beginning graduate students today?

RER: It's very difficult for students now, because the kinds of pressures they experience are much different than in earlier times. Having to produce 4-5 high-profile papers out of one's doctoral and postdoctoral years is a pretty high bar. So students feel a lot of pressure to publish results quickly, which is not entirely compatible with de-

tailed field observation and the development of expertise with a given taxon. Having too little time to master a group of organisms or the ecology and geography of a region can deprive a student of valuable insight.

RG: So maybe one of the important things for students to do is develop mastery of one taxon.

RER: Yes, it's helpful, but often not easy to achieve. Some institutions have maintained their emphasis in organismal biology, with courses tied to collections and taught by people that curate those collections. But many have let go of this side of the organism-oriented curriculum in favour of equally important training in genetics, population biology, and other more experimental and analytical sides of biology.

RG: Over the years, you have collaborated with many people working in diverse areas, starting in the early days with Henry Hespenheide, Reed Hainsworth, George Cox, and others. What advice would you give to others, and especially students, as to the importance of building collaborations?

RER: Beyond being, for me, one of the most pleasurable aspects of science, collaborations are very important in developing broader perspectives and fostering integration and synthesis. Of course, there are the practical considerations that a single person cannot do everything and so collaboration brings complementary expertise together. The most successful and satisfying collaborations occur when researchers challenge each other to integrate their approaches—to find the commonalities in their different concepts of biological systems.

RG: You have a long-held interest in how communities develop in the context of regional processes. How have your ideas changed over the years?

RER: Starting out as an ecologist with a strong interest in island biogeography, particularly in the context of MacArthur and Wilson's equilibrium theory, I have always had a strong sense of the impact of regional processes on localized ecological systems. Many other ecologists at the same time had similar perspectives, but from the 1960s through the 1980s, historical explanations were out of favour as being untestable and perhaps even unscientific for that reason. I was able to return to island biogeography 20 years after my initial work with George Cox, with the development of phylogeographic and phylogenetic analyses, and this allowed me and my collaborator Eldredge Bermingham to place distributional events on a time scale and test such time-dependent ideas as the taxon cycle hypothesis.

RG: You wrote the first version of the *Ecology* text early on. Where did you see the need at the time?

RER: The book was a major undertaking. In 1972 and 1973, 6 or 7 new ecology texts were published, largely as a reaction to the absence of population and evolutionary perspectives in the ecology texts available at the time. In ecosystem ecology, there was Eugene Odum's text —the text I used as an undergrad. But even that was primarily descriptive and not particularly quantitative, with little emphasis on formulating testable hypotheses in ecology. So people were reacting to this —ecology was becoming much more quantitative, much more scientific, much more process oriented, with a strong emphasis on adaptation, that is, evolutionary ecology.

RG: You have seen many significant developments in the field of biogeography over the years. What do you see as the major "game-changers" in the context of conceptual breakthroughs? Clearly the *Equilibrium Theory* was important. What other ideas stand out?

RER: Certainly the development of modern phylogenetic analysis has to have been the major game changer during the past decades. Placing a time scale and directionality on evolutionary divergences allowed one to infer areas of origin, directions and timing of major dispersal events, and to distinguish, in many cases, between vicariance and long-distance dispersal. Growing availability of palaeoclimate reconstructions and long

fossil series have also greatly strengthened our empirical foundations for interpreting the history and geography of life. Increasing data on distributions and improved analytic capacities are shaping many aspects of biogeography at the present time, although one might also lament the balancing decline of support for basic taxonomic and systematic research required to ensure data quality and to provide a context for determining the biogeographic implications of these data.

RG: There has been a lot of recent attention on community phylogenetics —ecological sorting, filtering, and niche modelling. Where do you see this going?

RER: This line of research has been productive, but often tells us little that we didn't already know in a less formalized context. Niche modelling has been used to look at changes in distribution under climate change scenarios and whether or not introduced species can spread. The problem is that one doesn't know ahead of time whether an introduced species can spread through conditions that are outside its range back home. So what is the appropriate distribution model for that species? How much is the distribution of that species back home controlled by factors that are unrelated to climate, but rather reflect interactions with other species? We really don't have a good handle on that. Moreover, in addition to climate, other factors such as soil and habitat structure, are important components. So progress will need to wait until we get a better handle on what the niche of a species is.

RG: What do you see are going to be the major exciting developments in the context of ecological/ evolutionary theory in biogeography?

RER: I would go back all the way to Ed Wilson and some of his contemporaries. What they considered important was the biogeography of species. At the moment we are hung up on the ecology and biogeography of places. We decompose regions into lat/long, grid cells, cataloguing what occurs in a particular place, rather than focusing on where a particular species occurs. So while environmental niche modelling and related approaches address species distributions, ecologists and many macroecologists focus on the local fitting of species into assemblages, rather than how populations of species are distributed and fit together in regional landscapes. So the integration of what species are doing individually, and what whole communities of species are doing in large regions, is ripe for development. I think that a focus on species populations as the fundamental units of ecology, evolutionary biology, and biogeography provides a natural direction for biogeography in the future.

RG: So how do we get there?

RER: Part of it may be giving up the place-oriented perspective that we have for research on certain types of questions. Islands are one thing — discrete, self contained. Quite different from setting down grid squares in South America, where it is better to look at distributions of species within these large regions and start to develop hypotheses as to why different species are distributed in different ways. Work has started, but in the context of trying to integrate all the species in a large area —their distributions, evolutionary history, interactions— we have a long way to go.

RG: How important do you think are the recent ideas that have come out of comparative phylogenetic and phylogeographic analyses of diversification?

RER: These models deal with evolution within phylogenies rather than evolution within communities or regions. Adding the additional layers of complexity is a challenge. Even defining the problems remains to be done in a useful way. The reality is that the diversity of species, and their geographic and ecological distributions within regions, unfold over evolutionary time. Do we have to tackle it at this level of complexity to really understand it? I suspect we do to achieve a fundamental understanding of what's going on. So how do we package this in such a way as to get all of that complexity and history and geography and evolutionary adaptation into a study system that is simple enough to get a handle on? Islands give

us advantages as they are discrete and not terribly diverse; and archipelagoes are very instructive because of their propensity to support species diversification. Whether we can scale up from these simpler systems is not clear, but it is a place to start.

RG: The argument has been made that the genomic era and the ability to sequence everything cheaply will allow us to answer many of these questions.

RER: I think that high throughput sequencing might make life even more confusing and challenging! Finally we will begin to understand the total diversity of ecological systems. And what is all this doing, and how is it maintained? We can generate hundreds or thousands of cytochrome b sequences or cytochrome oxidase I sequences from soil in a small patch of habitat, each representing a unique type of organism, with its own ecological role and history and distribution. It's obviously an important step towards characterizing diversity and distributions, but how will we generate new insights from such data.

RG: What would you recommend for students starting out in the field if they want to do something new and different?

RER: I would emphasize the importance of making connections across different traditions and areas of biology. Achieving integration and breadth is hard for students. We don't foster it enough in our academic structure, as departments are often divided and academic traditions confined. And it's often hard to master more than one area. But I feel that I have benefited from having a curiosity about many things —not unlike a stamp collector's curiosity! I find interest in almost anything. So I have pursued a lot of different issues in ecology and biogeography, which has enabled me to draw connections. I undoubtedly have sacrificed depth in some of my work, but it has allowed me to be more integrative and to pull disparate things together.

RG: Why do you think the public should care about (and fund) research in biogeography?

RER: I would certainly emphasize the commonly repeated social benefits of science in general: satisfying a deeply felt need to understand the world around us; providing information to help predict the consequences of global climate change, to help manage populations of economic importance and conservation concern, and to predict the emergence and spread of pathogens. Beyond these considerations, science is a defining aspect of our culture and civilization, and its practice in the context of a wide variety of phenomena, including the evolution and distribution of life on Earth, helps to maintain a certain level of analytical competence in society as a whole. Our success depends in large part on coming to rational conclusions and making informed decisions based on data. Of course, all scientists do this in the practice of their profession, but biogeographers uniquely work with evolutionary and ecological processes on global scales of time and space, maintaining valuable traditions within our culture.

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BIOSKETCH: Robert E. Ricklefs

Picture courtesy of Robert E. Ricklefs

I grew up close to nature in coastal central California and was fortunate to have teachers and other mentors who encouraged my interest in wildlife. Margaret Moody introduced me to bird watching as a child; Merton Hinshaw and Vern Yadon, Curators of the Pacific Grove Natural History Museum, were always patient answering my questions about natural history; several grad students and postdocs at the Hopkins Marine Station, who also taught in my school, opened my eyes to the marine world. I had an idyllic childhood! As a Biology major at Stanford University in the early 1960s, I was further exposed to wonderful mentoring, especially from Richard Holm and grad student John Lawrence, and a number of exceptional teachers, including several who inspired former Wallace Awardee John Briggs when he was a grad student in that department 10 years earlier.

As I was looking around for graduate schools in 1963, Paul Ehrlich, a young assistant professor at the time, advised me to head east to the University of Pennsylvania and Robert H. MacArthur. First-hand exposure to the exciting developments in population biology, evolutionary ecology and island biogeography in the mid-1960s set the course for the rest of my career. MacArthur left for Princeton in 1965, and I finished my doctorate at Penn. in 1967 under the supportive mentorship of W. John Smith. A post-doctoral year at the Smithsonian Tropical Research Institute in Panama, with Neal Smith, Stan Rand and Mike Robinson, prepared me well enough to return to Penn. as an assistant professor (MacArthur's replacement!).

My 27 years on the faculty at Penn. involved building a small but distinguished ecology program, writing two text-books (*Ecology*, 1973; *The Economy of Nature*, 1976), and developing research programs in island biogeography and the evolutionary and physiological ecology of avian life histories. Through this period, enjoyable and productive collaborations developed with George Cox, Matthias Starck, Joe Williams, Biff Bermingham and Dolph Schluter, among others, and with many outstanding graduate students. In 1995, so that my wife, Susanne Renner, and I could enjoy positions in the same institution, I moved to the University of Missouri-St. Louis, which has an outstanding program in tropical ecology. The past 16 years at UMSL have produced a further maturation of my research program, which has both returned to earlier research interests in island biogeography and turned in new directions towards fundamental issues in community ecology, including the influence of pathogens on the distribution and abundance of populations, the topic of my Wallace Award essay.

Looking back, one can always regret certain decisions and missed opportunities, but I have no complaints whatsoever. The profession, my students and colleagues, and my family have consistently provided inspiration and support, enough to keep me excited by, and engaged in, scientific inquiry into the natural world.

