



Concluding remarks: historical perspective and the future of island biogeography theory

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ABSTRACT

MacArthur and Wilson's equilibrium theory revolutionized the field of island biogeography and, to a large degree, ecology as well. The theory, which quickly became the ruling paradigm of island biogeography, has changed little over the past three decades. It has not kept pace with relevant theory and our growing appreciation for the complexity of nature, especially with empirical findings that species diversity on many islands: 1) is not in equilibrium; 2) is influenced by differences in speciation, colonization, and extinction among taxa; and 3) is influenced by

differences among islands in characteristics other than area and isolation. The discipline of biogeography, itself, is in a state of disequilibrium. We may again be about to witness another paradigm shift, which will see the replacement of MacArthur and Wilson's theory. Wherever this shift may take us, we are confident that the next generation of biogeographers will still look to islands for insights into the forces that shape biological diversity.

Key words Biogeography, equilibrium theory, extinction, immigration, islands, MacArthur & Wilson, nonequilibrium, paradigm shift.

HISTORICAL PERSPECTIVE

The perspective of this overview comes from our several decades of experience in biogeography. Indeed, the senior author was a graduate student at the University of Michigan in the mid-1960s when Larry Slobodkin received a book manuscript from Robert MacArthur and Ed Wilson. The first page was messy. There were three titles: first, *The Theory of Biogeography*, crossed out; second, *The Theory of Biogeography: I. Islands*, also crossed out; and finally *The Theory of Island Biogeography*. This says volumes about the bold thinking of MacArthur and Wilson, and their deliberate attempt to transform biogeography from a discipline tied to descriptive taxonomy to one based on modern ecological and evolutionary theory. MacArthur and Wilson's book, published in 1967 under the last of the above titles, was viewed as revolutionary. Eugene Munroe's earlier

publication of virtually the same theory (Munroe, 1948, 1953; see Brown & Lomolino, 1989) had been ignored by a scientific community not yet ready for such radical thoughts. MacArthur and Wilson's ideas had an immediate and controversial impact. They were viewed with scepticism by many systematists, who constituted the biogeographic establishment of the day. But they were eagerly embraced by many young evolutionary ecologists, ourselves included. At least in the shorter term, the latter group prevailed. MacArthur and Wilson's elegantly simple conceptual framework was the dominant influence on theoretical and empirical biogeography for the next three decades. Only in the last few years has this influence begun to wane.

Most great ideas in science do not endure forever as laws or principles. Instead, they serve as stepping stones to newer theories and better understanding of the workings of nature. This is

likely to be the role of MacArthur and Wilson's theory. Its many shortcomings have finally become apparent. Some of these, such as the nonequilibrium nature of land bridge islands and other historically interconnected insular systems, were pointed out decades ago (e.g. Brown, 1971; Diamond, 1972; Barbour & Brown, 1974; Heaney, 1986), but interpreted by the majority of biogeographers as 'exceptions which prove the rule' rather than fundamental challenges to the theory. But the number of cases which could not adequately be explained continued to mount. Now, there are too many complications, exceptions, and violated assumptions to ignore. This is the common theme of the papers in this special feature.

Enormous advances in phylogenetic reconstruction have breathed new life into historical biogeography, and forged new ties between biogeography and systematics. Initially, the emerging 'phylogeography' appeared to supply a missing historical dimension for patterns of endemism at the scale of continents, rather than to challenge the equilibrium theory at the smaller scale of islands and other insular habitats. When phylogeographers turned their attention to islands, however, they found strong and widespread influences of past geological and evolutionary events. Phylogenetic analyses revealed that some lineages had long histories in an archipelago, and that the origin of species on an island was often due to some combination of colonization from other islands and speciation within the archipelago — and even within an island. Examples are provided by the excellent recent work on Hawaii (e.g. Wagner & Funk, 1995) and the Philippines (e.g. Heaney, 1986, 2000; see also contributions in Berry, 1983; Grant, 1998).

The concept of a biota in a contemporary equilibrium between colonization and extinction was also challenged by new finds of fossils. Soon after publishing their 1967 monograph, MacArthur and Wilson, as well as Hamilton *et al.* (1964), Hamilton & Armstrong (1965), Diamond (1969, 1972), and many others, reported that the model accurately predicted contemporary patterns of bird species richness and turnover as a function of island area and isolation. The explanatory power of these two variables and, by implication, the equilibrium paradigm, was dealt a serious blow by the discovery of fossils showing that oceanic islands had harboured many

more species only a few centuries ago (e.g. Olson & James, 1982a, b, 1984; Steadman, 1989, 1995), before aboriginal colonists initiated a wave of extinction that has continued right up to the present. Fossils of other groups paint a similar picture of insular faunas far from equilibrium, with recent immigration either inadequate to compensate for past episodes of anthropogenic extinction or supplying exotic invaders which are greatly increasing species richness.

These and other studies have cast doubt on the fundamental assumptions of MacArthur and Wilson's theory:

- species are essentially identical, and islands are identical except for the critical variables of area and spatial isolation;
- immigration and extinction are independent, opposing forces, with extinction affected only by island area and immigration only by isolation;
- and, perhaps most critically, rates of immigration and extinction are sufficiently high that contemporary patterns of species richness and composition result from a dynamic equilibrium between these opposing rates.

A large body of work (e.g. see Brown & Lomolino, 1998, pp. 411–423; Lomolino, 1984, 1986, 1993, 2000a; Fox & Fox, 2000) shows clearly that the differences among both species and islands (in characteristics other than area and isolation) really matter. Species differ in their ecological interactions with other organisms and their abiotic environment. These differences affect the assembly of insular biotas by influencing the capacity to disperse across different kinds of barriers, and to establish and persist on islands with different abiotic conditions and species composition. In addition to area and isolation, characteristics of islands that affect species diversity and composition include the influence of currents, ice formation, human transport, and other factors which affect the permeability of barriers, and habitat heterogeneity, disturbance regimes and the presence of humans and other interacting organisms, which affect both the establishment of colonists and the persistence of natives. The rescue effect, a major influence on island biogeography and underlying metapopulation dynamics (e.g. Brown & Kodric-Brown, 1977; Lomolino, 1986; Gilpin & Hanski, 1991) shows that immigration and extinction cannot be regarded as independent processes.

The most fundamental idea in MacArthur and Wilson's theory, that species diversity on an island represents a dynamic equilibrium between contemporary rates of immigration and extinction, is clearly contradicted by phylogenetic and fossil evidence of a long, pervasive legacy of history on the diversity and composition of most insular lineages (see above). Even the relatively recent development of the fauna and flora of Krakatau following its eruption in 1883, once interpreted as exemplifying the rapid re-establishment of equilibrium (e.g. MacArthur & Wilson, 1967; Brown, 1971; Brown & Gibson, 1983), has since been shown to have a complex history due to nonequilibrium processes (e.g. episodic extinctions associated with severe storms and tectonic activity; see Whittaker *et al.*, 1989; Thornton *et al.*, 1990; Bush & Whittaker, 1991; Whittaker, 1995, 1998, 2000; Thornton, 1996; Ward & Thornton, 2000).

Just as important, the equilibrium theory, now over three decades old, has not kept pace with the continuing advances in ecological theory and our greater appreciation for the complexity of nature. Modern biogeographers now look beyond relatively simple, equilibrium explanations for species-area and species-isolation relationships to address a diversity of patterns in community assembly and evolution — patterns that likely derive from the complex interactions of processes operating across a broad range of temporal and spatial scales. In retrospect, it seems ironic that MacArthur and Wilson's revolutionary theory was conceptually more limited than Wilson's earlier theory on taxon cycles (Wilson, 1961) and that it would never address one of MacArthur's most fundamental subjects — alternative assemblages of species (MacArthur, 1972; Diamond, 1975). We can add to this a long list of other patterns in community assembly and evolution that have remained well beyond the conceptual envelope of the equilibrium theory (patterns well-known to MacArthur and Wilson when they developed their theory): exclusive distributions of species such as 'checkerboards' (Wilson, 1961; Diamond, 1975), nestedness of insular communities (Darlington, 1957; Wilson, 1961; Patterson & Atmar, 1986), density compensation (Crowell, 1962), evolutionary trends in body size of insular vertebrates (Foster, 1963, 1964; Lomolino, 1985; Brown & Lomolino, 1998), shifts in reproductive biology and growth form

of insular plants (Darwin, 1859; Carlquist, 1965, 1974; Barrett, 1998), flightlessness of insular birds and insects (Darwin, 1859; Darlington, 1943; Roff, 1990; McNab, 1994a, b), biogeographic correlates of endemism (Wilson, 1961; Diamond, 1980; Heaney, 2000) and the ecological, geographical and evolutionary shifts hypothesized to be associated with the taxon cycle (Wilson, 1961; Ricklefs & Cox, 1972; Roughgarden *et al.*, 1989).

FUTURE PROSPECTS

The above arguments, along with those presented in the papers of this special feature all illustrate deep conceptual and empirical problems with MacArthur and Wilson's equilibrium theory. These problems are fundamental. They go beyond a small number of exceptions that can readily be explained as 'proving the rule' or incorporated into the general framework by making small changes. In our opinion, the problems point to critical flaws in MacArthur and Wilson's basic concept of insular biotas in equilibrium between contemporary rates of immigration and extinction. A new theoretical framework is required. One of us has begun to develop such an alternative: a species-based theory of island biogeography (Lomolino, 1986; 2000b). This formulation focuses on the importance of differences among species (and also implicitly, on differences among islands) in determining the assembly of insular biotas, and the resulting patterns of species richness and composition. This model is much less revolutionary than MacArthur and Wilson's original theory. Yet, it seeks to preserve some of their most valuable insights, especially the observation that insular biotas reflect the interplay between recurrent immigration and extinction events, but not necessarily an equilibrium between these processes. Elsewhere in this special feature, both Whittaker (2000) and Lomolino (2000a) present broad, conceptual frameworks for island biogeography. By aiming to be more realistic and more general than MacArthur and Wilson's theory, such efforts might aspire to be stepping stones toward better understanding and new paradigms. Whether they will eventually be seen as having played such a role, will be for history to determine.

What does seem clear is that the discipline of biogeography is again, as in the 1960s and 1970s, in transition and ferment. The simple old paradigms are not holding up. This is true not only of MacArthur and Wilson's equilibrium theory, but also of the vicariance approach that sought to use phylogenetic reconstructions of lineages to interpret the histories of regions and their biotas (e.g. Rosen *et al.*, 1979; Nelson & Platnick, 1981; Humphries & Parenti, 1986; Brown & Lomolino, 1998). For example, the phylogenies of several lineages inhabiting the Hawaiian Islands show not just one highly concordant pattern as predicted by vicariance theory, but a diversity of relationships reflecting differences in colonization sequences and ecological requirements among the clades, and differences in barriers to dispersal and modes of speciation within and among islands (Wagner & Funk, 1995; Brown & Lomolino, 1998). The papers in this special feature are symptomatic of the discipline as a whole.

What is not so clear is where the current trends are heading. Does the future hold the promise of developing and testing theories that may apply across a broad range of taxonomic groups, types of ecosystems, and geographical regions? Or does it hold the less exciting prospect of entering another stage of descriptive science, in which each situation is treated as a special case? Lacking a crystal ball, we can only note that currently the discipline of biogeography itself is far from equilibrium. Its present unsteady state reflects not only the inadequacy of the traditional approaches and theories, but also, so far, the absence of accepted alternative frameworks to supply theoretical and empirical direction. In the past, as MacArthur and Wilson's changing titles imply, biogeographers often looked to islands for inspiration. While islands may not be such simple systems as MacArthur and Wilson's theory envisaged, they still represent some of nature's most invaluable experiments. They are replicated systems, which typically have limited biological diversities, relatively well-understood histories, and only moderate environmental complexities. Islands will continue to offer invaluable insights into how earth history, phylogenetic history, and contemporary and past environments have interacted to shape biodiversity.

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