



A call for a new paradigm of island biogeography

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ABSTRACT

MacArthur and Wilson's equilibrium theory of island biogeography quickly became the paradigm of the field in the 1960s and has strongly influenced this and other disciplines of ecology and conservation biology for the past three decades. Recently, however, a growing number of ecologists have begun to question whether the theory remains a useful paradigm for modern ecology. We now have a much better appreciation for the complexity of nature and we study patterns that span a very broad range in spatial, temporal and ecological scales. At such scales, assumptions that communities are in equilibrium, that species,

islands and intervening landscapes or seascapes are equivalent or homogeneous with respect to factors influencing immigration and extinction, and that *in situ* speciation can be overlooked become very tenuous. With this in mind, this and other papers of this special feature discuss the principal, conceptual shortcomings of the equilibrium theory and offer some modifications or alternatives to the theory that we hope will eventually lead to a more comprehensive understanding of the forces structuring insular communities.

Key words Biogeography, equilibrium theory, evolution, extinction, immigration, islands, MacArthur & Wilson.

INTRODUCTION

Biogeography has often been defined as the study of geographical distributions of organisms (Brown & Gibson, 1983), but it has become much more than this. In a broader sense, biogeography is the study of variation in any biological feature (genetic, morphological, behavioural, physiological, demographic or ecological) across geographical dimensions such as distance among sites or along gradients of area, elevation or depth (Brown & Lomolino, 1998). Ultimately, however, the great diversity of patterns studied by biogeographers all derive from two very general features of nature. First, as we move along any geographical dimension, environmental conditions tend to vary in a predictable manner. More distant sites tend to be more dissimilar, higher elevations tend to be cooler and wetter, and larger areas capture more solar energy and also tend to include a greater diversity of environmental conditions. Second, individuals, popu-

lations and species differ in their abilities to respond to geographical variation in their environment. These differences among life forms, while including a great diversity of responses (e.g. physiological, behavioural, developmental and evolutionary), ultimately influence the three fundamental biogeographic processes: immigration, extinction and evolution. All the biogeographic patterns we study derive from nonrandom variation in these processes across geographical gradients and across organisms.

The most important insights on the interplay of process and pattern in biogeography have come from insular studies. Edward Wilson's (1961) Taxon Cycle represents perhaps the most ambitious attempt to model the ecological and evolutionary dynamics of insular biotas. Yet despite its great heuristic appeal, the Taxon Cycle was quickly eclipsed by a much simpler model, one that Wilson coauthored with Robert MacArthur (MacArthur & Wilson, 1963, 1967). Their Equilibrium Theory quickly became the paradigm of island biogeography,

and has strongly influenced other fields of ecology and conservation biology as well (e.g. see Shafer, 1990).

After 35 years, however, a growing consensus of ecologists now questions whether the Equilibrium Theory remains a useful paradigm for modern biogeography. We now have a much better appreciation of the complexity of nature and we study patterns that span a very broad range of spatial, temporal and ecological scales. The very reason for its heuristic appeal now appears to be the most constraining feature of the Equilibrium model, i.e. its simplicity. The Equilibrium Theory was developed to explain variation in species richness at the scale of an archipelago during ecological time. MacArthur and Wilson could therefore make the simplifying assumption that evolution was unimportant for explaining variation in species richness at this scale (evolution, of course, was important in determining the pool of species that could inhabit the islands). Furthermore, their model assumed that immigration and extinction varied only with physical features of the island (area and isolation). That is, they assumed that species were equivalent with respect to their abilities to colonize and maintain populations on islands.

Despite what many now view as simplistic and tenuous assumptions, the Equilibrium Theory represented a great conceptual advance over the theories that dominated island biogeography in the mid-20th century. At that time, insular community structure was considered static, resulting from unique immigration and extinction (i.e. it was generally assumed that species composition did not change over time; see Dexter, 1978). If the island was within the dispersal range of the species, then colonization would eventually occur (with near certainty) and, providing the niche requirements of the species were satisfied, the colonists would survive in perpetuity. MacArthur & Wilson's revolutionary model challenged this assumption, asserting that immigration and extinction are recurrent, that these opposing processes eventually balance each other, and that the resulting equilibrium should be dynamic because species composition should continue to exhibit turnover as new species replace those that go extinct. The Equilibrium Theory thus represented a conceptually novel, unifying theory and one that stimulated many hundreds of studies on patterns in

species richness of a great variety of ecosystems and biotas.

As alluded to above, however, the Equilibrium Theory has some fundamental limitations that seem to make it inadequate as a modern theory of island biogeography. Three of the most important limitations are discussed below:

1 As we broaden the spatial and temporal scales of our studies, it becomes increasingly more clear that many systems are not only dynamic in species composition, but that they may seldom attain an equilibrium number of species. That is, many systems may still bear the imprint of speciation, major geological and climatic events, or anthropogenic disturbances that either modify the species pool or alter immigration and extinction rates before an equilibrium can be achieved.

2 The theory assumes that insular habitats and immigration filters (intervening landscapes or seascapes) are homogeneous within and among archipelagoes. On the contrary, much of the observed variation in insular species composition and richness within archipelagoes may result from predictable variation in habitat and other environmental conditions among islands (e.g. larger islands tend to include a greater diversity of habitats). Similarly, differences in patterns of community structure among archipelagoes may be attributed to: differences in immigration filters (e.g. bodies of water with and without strong currents [see Lomolino, 1994]; intervening landscapes dominated by different habitats [see Aberg *et al.*, 1995]; or to other factors that vary at geographical scales, e.g. clines in temperature and productivity along latitudinal gradients).

3 The theory is species neutral, i.e. it assumes that all species are independent and equivalent. Yet, as with many other complex systems, the structure and dynamics of insular communities are also influenced by feedback, i.e. interactions among species and other system components. Because the Equilibrium Theory assumed that species are equivalent, it ignored the potential role of inter-specific interactions. Moreover, this species-neutral model could not address patterns in species composition. Many of the most interesting patterns in biogeography concern not just how many, but which species inhabit islands.

This latter limitation is especially problematic for those attempting to conserve biological diversity on islands or isolated fragments of native

ecosystems. There is no compelling reason to believe that rare and geographically restricted species are identical to the more common and wide-ranging ones. On the contrary, endangered species are the oddballs, the species that are barely hanging on because of their relatively high resource requirements, limited dispersal abilities and high sensitivity to human disturbance.

DISCUSSION

Toward a new paradigm in biogeography

The task of developing a new, more comprehensive theory of island biogeography will be no less challenging for us now than it was when Eugene Gordon Munroe, then a graduate student at Cornell University, first proposed an equilibrium theory of island biogeography in 1948 (see Munroe, 1948, 1953; Brown & Lomolino, 1989). His model, although identical to MacArthur and Wilson's model in its salient features, was never embraced by his colleagues. Instead, it took another 15 years and the energies and insights of two revered ecologists to replace the static theory with a dynamic equilibrium model. It is now time to replace the Equilibrium Theory, a model that has reigned as paradigm for nearly 35 years. Rather than just dwell on its shortcomings, I will try to take a more positive approach by outlining some of the desirable features of a future paradigm for the field.

The model should be fundamentally simple and should be based on the conceptual tripartite of biogeographic processes: immigration, extinction and evolution (Fig. 1).

The model should be hierarchical and include the system features (e.g. isolation, nature of immigration filters, area, geology, and climate) that influence immigration, extinction and evolution at the spatial and temporal scales in question (Lomolino, 1999).

It should include potential feedback among system components (e.g. inter-specific interactions) and interactions among processes (e.g. the rescue effect [*sensu* Brown & Kodric-Brown, 1977]), which refers to the tendency for relatively high immigration rates to reduce extinction rates on near islands).

Finally, the model should be species-based. Species vary in many ways that affect immigration,

extinction and speciation, and many biogeographic patterns derive from, not despite, differences among species. For example, the form of the species-isolation and species-area relationships may reflect very general patterns of variation in immigration abilities and resource requirements among species.

CONCLUSION

The primary goal of this special feature is to advance island biogeography theory by offering some modifications or alternatives to MacArthur and Wilson's equilibrium theory. Each contribution focuses on one or more of the four features listed above and, using a combination of conceptual approaches and empirical patterns, attempts to identify some promising directions for future research into the forces structuring insular communities.

Seamus Ward and Ian Thornton (2000) consider the roles of stochastic and deterministic events in the ecological development of isolated communities. They show that, wherever processes of colonization and competition are important, such as in the development of forests of Krakatau, early development of insular communities should be relatively deterministic. In contrast, later development of these communities may be more strongly influenced by stochastic effects, including highly variable sequences, and intervals between, colonizations. Priority effects may be significant in these later stages, and their effects on insular community structure may differ among otherwise similar communities.

In their contribution, Barry and Marilyn Fox (2000) observe that the majority of studies of island biogeography, whether applied or theoretical, consider the traditional factors of area and isolation, but typically ignore other factors that also may influence the structure of insular communities. They then ask whether it 'is sufficient to obtain answers in agreement with observations or is it more important to also understand fully the mechanisms involved?' Based on their extensive studies of mammals inhabiting fragmented and otherwise isolated ecosystems of Australia, they conclude that the equilibrium theory of island biogeography, while still valuable, should be expanded to include the influences of habitat diversity, disturbance, and inter-specific interactions.

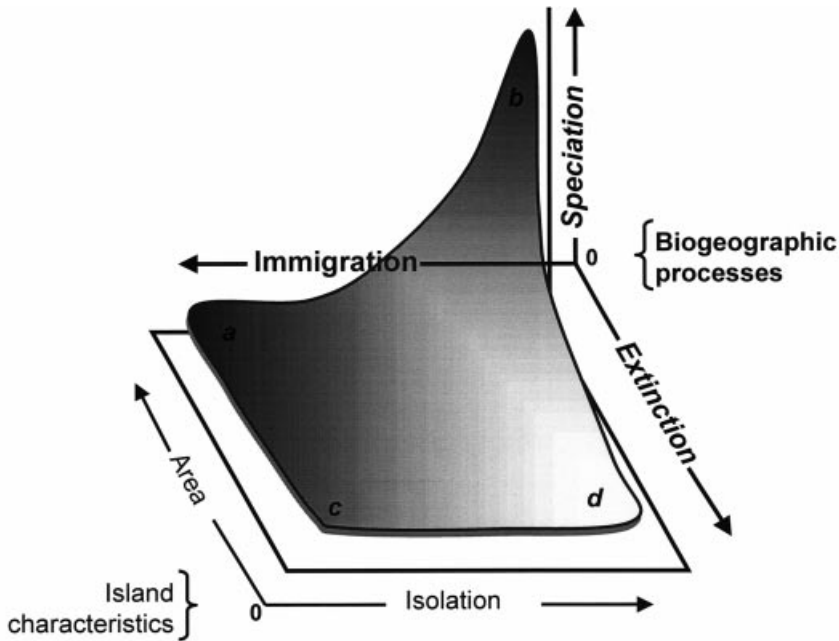


Fig. 1 A tripartite model of island biogeography illustrating the variation in the three fundamental biogeographic processes (immigration, extinction and evolution) as a function of characteristics of the islands in question. Immigration rates should increase with proximity to a source region and, equivalently, with immigration ability (ability to travel or be carried across a particular immigration filter) of the focal species. Extinction rates should decrease as island area increases, or increase with increasing resource requirements of the focal species. Speciation (phylogenesis *sensu* Heaney, 2000) should be most important where extinction and immigration are lowest and therefore increase with island area and isolation, but decrease with increasing resource requirements and vagility of the focal species. Shading indicates the relative levels of species richness, and the relative resistance to and resilience of insular biotas following disturbance. Community characteristics of islands within the four labelled regions of the shaded surface should be as follows: a) moderate to relatively high richness, low endemism and low turnover; b) moderate to relatively high richness, high endemism and low turnover; c) moderate to low richness, low endemism and high turnover; and d) depauperate islands.

In his contribution, Mark Lomolino (2000) presents a hierarchical, deterministic model of island biogeography that is based on the premise that most patterns of insular community structure derive from nonrandom differences among the component species. In addition to explaining patterns in distribution of particular, focal species, the model can be expanded to explore patterns in species richness and species composition (e.g. checkerboards and nestedness) of insular biotas. This model, however, does not explicitly include the influence of speciation and therefore is limited to two dimensions of the tripartite model (immigration and extinction, Fig. 1).

Larry Heaney (2000) takes up the challenge of developing a truly tripartite model in his contribution. In his long-term and large-scale perspective of mammalian communities of the Sunda Shelf, he argues cogently that a comprehensive understanding of these insular communities can only be gained by studies that explicitly consider the combined influences of colonization, extinction and phylogenetic diversification (phylogenesis). The relative importance of these processes varies in a nonlinear and perhaps complex fashion with island characteristics and therefore phylogenesis can not simply be viewed as another form of colonization.

Robert Whittaker (2000) places the equilibrium theory within a broad conceptual framework, one based on Haila's (1990) spatial-temporal continuum and bounded by four extremes of island conditions: i) dynamic equilibrium; ii) dynamic nonequilibrium; iii) 'static' equilibrium; and iv) 'static' nonequilibrium. Thus, the processes represented within the equilibrium theory may be prominent within only a limited portion of this continuum, while elsewhere they are subsumed by other processes including disturbance, ecological succession and speciation. Whittaker argues that, while island models should include a greater degree of complexity, key advances are often brought about by simple, but bold models that challenge existing paradigms.

In the capstone to this special feature, James H. Brown and Mark Lomolino (2000) provide an historical perspective and a critical, but we think accurate, assessment of the shortcomings of the equilibrium theory as a modern paradigm of island biogeography. In short, the equilibrium theory has not kept pace with advances in ecological theory. It was not developed, and in our opinion, can not be modified sufficiently, to account for the diversity of patterns we now study, many of which are just as intriguing and perhaps as general as species-area and species-isolation relationships.

While the course we have charted here will be a challenging one, the contributors to this special feature remain highly optimistic that biogeographers will be up to the task. Judging from the surging interest in biogeography over the past decade or so, our field may be primed for a second, modern revolution. Whatever their final form, the new models will likely build on the prescient insights of MacArthur, Wilson and other charter members of the previous revolution. Accordingly, while we recommend a relaxation of the equilibrium assumption, we continue to agree with MacArthur and Wilson's more fundamental assumption that insular community structure is dynamic, resulting from recurrent extinctions and immigrations (plus, speciation).

Finally, if our comments here seem irreverent, that is terribly unfortunate because few scientists admire MacArthur and Wilson's contributions more than we do. In fact, we believe that, were he still alive, Robert MacArthur himself would be very disappointed to see that his model,

largely unchanged, remained the paradigm of island biogeography for nearly 35 years. We feel strongly that the best way to honour MacArthur and Wilson's seminal contribution is to re-evaluate the equilibrium theory and replace it with one that offers a more versatile and comprehensive view of the fundamental processes influencing the structure of insular communities.

'Paraphrasing Picasso, MacArthur once observed "a theory is a lie which makes you see the truth". If the equilibrium theory forced us to pose new questions and to seek new evidence in order to better understand [insular] communities, its purpose has been fulfilled.' (after MacArthur's first graduate student, K.L. Crowell, 1986)

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