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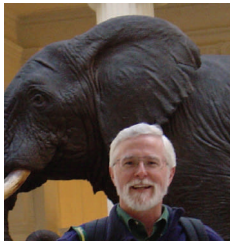
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Models of oceanic island biogeography: changing perspectives on biodiversity dynamics in archipelagoes



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Abstract. Models of biogeographic processes can both enhance and inhibit our ability to ask questions that guide our understanding of patterns and processes. The two ‘traditional’ models of island biogeography, the Equilibrium Model and the Vicariance Model, raise important and insightful questions about relevant processes, but both fail to raise many crucial questions. An example involving the non-volant mammals of the Philippine archipelago shows that both models highlight some, but not all, relevant patterns and processes. The more recently proposed General Dynamic Model successfully combines many of the positive aspects of the two traditional models, but leaves some important questions unasked. We pose a number of questions here that may help guide further development of models of island biogeography.

Keywords. Colonization, Equilibrium Model, extinction, General Dynamic Model, geomorphology, hot spots, Philippines, speciation, subduction zones, timescale, Vicariance Model

Introduction

The progress of science is guided by the models that we use. Much useful science can be conducted that is ‘model-free’, but by definition it is purely descriptive. When we choose to ask questions and to make comparisons, and especially in deciding how to interpret our results, we rely on models, explicitly or implicitly. New models often emerge when the existing ones have increasing difficulty with allowing us to ask or answer relevant questions, or when patterns become evident that are not addressed by the existing models. Models and paradigms (the larger conceptual framework for a model) are useful to the extent that they help us ask good questions; they are obstructive to the extent they prevent us from asking good questions.

A change in models may represent a simple shift from one model to another while remaining in the same paradigm, but sometimes a change in models is associated with a fundamentally different way of thinking—a paradigm shift. We have become convinced that such a paradigm shift is taking place in island biogeography, with some rather profound effects on how we can and do

conceptualize the dynamics of the origin and maintenance of biological diversity on islands (Heaney 2007, 2011a). This paradigm shift is associated with what we view as a movement away from the two ‘classical’ models of island biogeography, both of which came to prominence nearly simultaneously in the 1970s: the Equilibrium Model of MacArthur and Wilson (1963, 1967), and the Vicariance Model developed by Brundin, Croizat, Nelson, Platnick, Rosen, and others (e.g., Rosen 1978, Nelson and Platnick 1981).

This shift in paradigms is not taking place because either of these two models is ‘wrong’ in the sense that they focus on processes that either do not exist or do not describe important phenomena; rather, it is apparent that the processes are quite real, and that the issues are quite important. Instead, it has become apparent that each model is limited in scope and fails to ask essential questions about processes of great importance, and each may lead to some profound misunderstandings about the nature of island life. Most strikingly, though intending to provide an understanding of biodiversity dynamics of the same organisms on the same islands, the two models are

nearly mutually exclusive, with virtually no overlap in the processes and perspectives that they consider (Whittaker and Fernández-Palacios 2007). Although they existed side-by-side for decades without attempts at integration, new perspectives and syntheses have emerged recently, pointing the way to a deeper understanding of island biogeography.

This brief paper is offered not as a comprehensive review of the subject; instead, it is greatly streamlined, and deliberately somewhat provocative. It is intended primarily as an invitation to island biogeographers to further consider these issues, and to engage in a discussion about the challenges that are implied. Island biogeography has been one of the most influential fields of biodiversity science since the study of biological diversity began; it has great potential to remain one of the most dynamic and forward-looking.

Our descriptions of the two foundational models that follow here are brief to the point of being caricatures. We do this to highlight the contrasts between the two as they have usually been treated in the published literature. More nuanced versions of both exist, and many exceptions to each model have been noted. However, in their essential features, they each have core perspectives that are simple and unambiguous – and are mutually incompatible in crucial respects. Our description of the most prominent of the new models is equally brief, and also intended to highlight what we view as limitations and areas for further development.

Two classical models: a study in contrasts

The Equilibrium Model

First proposed in 1963 in a brief paper, and developed in a monograph in 1967, MacArthur and Wilson's theory of island biogeography was exceptionally wide-ranging, dealing with such topics as patterns of colonization and extinction, niche width, invasion abilities of species and invasibility of communities, and life history tactics and selection on aspects of reproductive fitness. Although a brief nod is given to speciation, adaptive radiation, and the role of long-term biological processes, MacArthur and Wilson's emphasis was

placed on phenomena that take place over 'ecological time', not 'evolutionary time'. Subsequent to publication of the monograph, use of their theory has contracted progressively to focus heavily on the iconic Equilibrium Model and its component processes of colonization and extinction (Lomolino et al. 2010a). As often stated, the impact of this model on ecology has been enormous, providing context for thousands of studies of islands and island-like habitats, as well as providing the framework for much of the research conducted for several decades on conservation strategy and planning (see Lomolino et al. 2010b, Losos and Ricklefs 2010, Sax and Gaines 2011).

The fundamental tenet of the Equilibrium Model is that species distributions in island ecosystems are highly dynamic. Colonization is viewed as being frequent, measured in decades or centuries, or at most in millennia, in the examples MacArthur and Wilson cited and in most of the studies that followed. Extinction is seen as being roughly equally frequent as colonization, leading to a situation in which the number of species on an island is nearly constant, but the composition changes frequently due to on-going turnover; as colonization and extinction take place, an equilibrium in the number of species is established. Some of the extinctions are driven by competition with invading species; those species that have come most recently from continents are generally assumed to be competitively superior to island endemics. Communities on islands are therefore regarded as loose assemblages of species that are good dispersers that have arrived on a given island at different times, and not to have co-evolved to a significant degree.

Discussion of island biogeography that takes place in this framework typically disregards speciation and diversification as significant generative forces in influencing species richness on islands. Questions about the phylogenetic relationships and 'deep history' of species are typically not raised. Although species distributions are treated as dynamic, the islands on which they live are most often regarded as fixed entities, without dynamic histories of their own. When island history is considered, usually it is in the context of rising

sea level at the end of the last glacial episode, or of forest vegetation retreating into mountains from what has become lowland desert or grassland. The Equilibrium Model, in its most common usage, has become a profoundly ecological model, one that disregards any aspect of evolutionary or geological 'deep history'; only those processes that operate on a very short time-scale require investigation.

The Vicariance Model

The Vicariance Model was developed during the late 1960s and early 1970s in a series of publications, principally by Brundin, Croizat, Nelson, Platnick, and Rosen (see Humphries and Parenti 1986). It was developed in the context of the emerging paradigm shift in geology regarding the tectonic history of the earth. The evidence that the entire surface of the earth has a dynamic history of movement carried profound implications for interpretation of biogeographic patterns, and the essence of vicariance biogeography is that the earth is dynamic. This model examines processes that take place over long time-spans, i.e., over 'geological' or 'evolutionary timescales', and deals with the phylogeny and diversification of organisms. It has provided the framework for interpreting countless phylogenies, having in many respects become an adjunct to the development of the phylogenetic/cladistic perspective of biodiversity that has taken place since the early 1970s (e.g., Wiley 1981, Parenti and Ebach 2009).

The primary tenet of the Vicariance Model is that geological processes are active, causing splitting of land-masses and populations of the organisms that live on them, with hostile habitat—often sea-water—isolating formerly contiguous populations. In the absence of gene flow, divergence is followed by speciation, with the phylogenetic relationships of the organisms mirroring the geological history of fragmentation by the land on which they live. Lineages are presumed to persist for long periods of time (many millions of years) and the lineages on a given island are therefore likely to show evidence of a shared biogeographic history.

Analysis following the procedures of vicari-

ance biogeography assumes that most land-living organisms disperse (= colonize) poorly, and that if a given pattern of phylogeny with geography exists, the pattern must be assumed to be due to vicariance. Colonization is assumed to be rare among most organisms, and to take place in a geographically and temporally random fashion, and therefore to produce no repeated ('strong') patterns. Persistence of species and lineages is generally assumed, and extinction is considered only for the difficulty it may pose in interpreting patterns of vicariance in a lineage of extant species. Questions about levels of species richness on a given island, and the issue of the existence or absence of equilibrium in species richness on the island, are not considered. Although a necessary outcome of these circumstances is that communities are composed of species that have evolved in association with the same set of members over long periods of time, i.e., over their phylogenetic history, questions about the long-term co-evolution of species within island communities are not raised. The Vicariance Model is, thus, overwhelmingly historical in its perspective, concerned with phylogenetic diversification operating on an evolutionary timescale, and giving little heed to the impact of ecological processes at any time-scale.

Challenges to island models from an oceanic island biota

Our perspectives on these issues have been informed and molded in part by the past and ongoing research we have conducted with our colleagues on the mammals of the Philippine Islands (e.g., Heaney 1986, 2000, 2001, 2011b, Heaney and Rickart 1990, Rickart et al. 1991, 2011a, 2011b, Rickart 1993, Steppan et al. 2003, Jansa et al. 2006, Heaney et al. 2009, Heaney and Roberts 2009, Balete et al. 2011, 2012, Esselstyn et al. 2011), and we will briefly refer to the biogeographic patterns of these animals as an example. Many other study systems would serve this purpose equally well (e.g., Gruner et al. 2008, Borges and Hortal 2009, Losos 2009, Gillespie and Baldwin 2010, Steinbauer et al. 2012).

The Philippine archipelago, with over 7000 islands, provides an ideal system for developing this integrated approach to biogeographic dynamics. The archipelago is primarily an island-arc system that developed adjacent to a series of subduction zones that have formed south and east of the Asian continent over the course of the last ca. 40–50 million years (Hall 1998, 2002, Wolfe 1988, Yumul et al. 2009). During this time, the archipelago has tended (with fluctuations) to become larger (in terms of number of islands and land area) and less isolated both internally and with respect to the Asian continent. Although some mountain ranges have persisted for ca. 20 million years, much of the current geomorphological diversity is the result of eruptions, uplift, erosion, etc., within the last 5–8 million years. The archipelago is currently about as large and as little isolated as at any time in its history. The Philippine Islands have one of the globally highest levels of terrestrial endemism, and many species are members of large endemic clades (Catibog-Sinha and Heaney 2006, Brown and Diesmos 2009). For example, >90% of the more than 130 species of non-volant native mammals are endemic, and most of these are members of just two endemic clades of rodents. Diversification within these two clades has commonly involved both colonization between isolated islands, and vicariance and colonization among highland areas within islands. Colonization within the archipelago has often proceeded from large, old, species-rich islands to nearby smaller and/or younger, species-poor islands, forming consistent patterns of phylogeography.

Many Philippine non-volant mammal species are endemic to a single island, and most of those endemic to a single large island actually occur only in one isolated part of the island; usually this is a highland region of montane or mossy forest habitat. Based on temporally calibrated DNA sequence data, most species diverged from their closest relative within the last 5 million years – a time scale similar to that of the geological development of the current archipelago. The longevity of these lineages strongly implies persistence, in spite of the high frequency of major typhoons (up to 30 per year) and massive volcanic eruptions

(once every few centuries). The diversification of clades appears to track the geological history of the ‘birth’ and ‘death’ of the island and/or of endemic-rich mountainous areas on large islands; for example, in a clade of endemic rodents, there is a correlation between the estimated age of endemic species and the age of the volcanic island on which they live (Steppan et al. 2003). Such patterns lead us to conclude that the process of speciation, and patterns of species richness, have been substantially driven by the geological history of the archipelago. Long-distance colonization (from continental areas to the Philippines) appears to be crucial but rare on a geological time-scale. Short-distance colonization between islands and between mountain ranges within islands by non-volant species appears to be common on a geological time scale and rare on an ecological time scale.

Many of the species of the diverse non-volant small-mammal communities that occur syntopically over much of the archipelago are members of two large, ecologically and morphologically diverse groups of murid rodents that have a clade age of ca. 10–15 million years. For example, at many localities on Luzon, in syntopic communities of small mammals with 10–14 species, we have found that 25–35% of the species are members of the ‘cloud rat’ clade, 35–45% are members of the ‘earthworm mouse’ clade, and only 20–25% are members of other clades that have arrived in the Philippines in the last 2–4 million years. In other words, up to 80% of the species at a given locality and/or on a given mountain may be members of clades that have co-occurred for 10–15 million years on a single island, and only a few species are members of recently arrived clades. These are, thus, speciation-derived communities, not ‘randomly derived assemblages’ in any sense; community members have had the time to become tightly coevolved, and often have highly specialized ecologies. Exotic species (such as members of the *Rattus rattus* group) have very poor success at invading natural habitat where they appear to be actively excluded by the native rodents, except where the native fauna is depauperate. Although exotic species may thrive in

highly disturbed situations, habitat regeneration results in their displacement by native species.

Integrating evolutionary and ecological processes: the General Dynamic Model

We believe that our observations on the mammals that live in the Philippine archipelago, a largely oceanic, geologically complex set of plate-margin islands, is broadly representative of patterns of biodiversity dynamics being documented in many other oceanic archipelagoes globally. These observations point to the need for models that explicitly incorporate colonization, extinction, and speciation as primary factors, and that explicitly deal with the influences of geological phenomena that operate over all time-scales. This need has begun to be met by some recent general conceptual models, especially by the “general dynamic model of oceanic island biogeography” developed by Whittaker and colleagues (e.g., Whittaker et al., 2007, 2008, 2010), which has been developed in the context of more limited prior efforts (e.g., Heaney 1986, 2000, 2007, Heaney and Rickart 1990, Lomolino 2000), and recent conceptual and empirical studies (e.g., Sax et al. 2005, Stuessey 2007, Gillespie and Baldwin 2010, Santos et al. 2010, Bunnefeld and Phillimore 2011, Hortal 2012, Steinbauer et al. 2012, Triantis et al. 2012), some of which have been influenced by the neutral theory of biodiversity developed by Hubbell (2001, 2010; e.g., Rosindell and Phillimore 2011).

In Whittaker et al.’s model, a single island is described as having an explicit ‘life history’ of volcanic origin, growth, and expansion, following by volcanic quiescence (as the hot spot magma plume erupts elsewhere), erosion that initially increases topographic diversity, followed ultimately by erosion down to sea level (i.e., disappearance). Species richness is modeled as slowly increasing initially due to rare colonization, but with indigenous phylogenetic diversification quickly (measured over geological time) outpacing direct colonization. As island area and topographic complexity increase, species richness rises; but as erosion continues in the absence of further volcanic activity, both area and topographic complex-

ity decline and species richness plunges. Colonizing species predominate very early in the history of the island, endemic clades of closely related species predominate in the middle phase, and endemic clades of a few distantly related species predominate in the later phase as species richness progressively declines to zero as the island disappears. The entire biological and geological processes are seen as usually taking roughly 4 to 8 million years (though sometimes longer, based on local geological conditions), based on empirical observations of actual islands and biotas.

Within this context, many questions can be addressed that were outside the realm of both ‘traditional’ equilibrium and vicariance biogeography. The ‘life history’ of individual islands, and the impact of these geological processes on both ecological and evolutionary biodiversity patterns, are highlighted as topics for study, and the relative importance of, for example, resource availability and competition during the phases of island birth, development, and death through erosion, can be evaluated. Application of this perspective leads the investigator to examine the roles and processes of colonization and speciation equally in evaluating the dynamics of biodiversity within any given system.

Further questions

This view of the dynamics of biodiversity in oceanic island archipelagoes is far more complex than what is considered under either the Equilibrium or Vicariance Model. We view the General Dynamic Model as representing a substantial step forward in developing a comprehensive model that will lead to an integrated, realistic understanding of these very complex geological and biological interactions. However, we also believe that many questions have not been adequately defined or investigated, and still others have barely been considered. The following is a brief, undoubtedly incomplete list of issues that we consider to be of broad importance in moving forward in developing a comprehensive model.

Islands rarely exist as single, isolated entities; rather, they most often occur in groups, due to the geological processes that produce them,

and organisms (and the dynamic processes that influence them) thus exist within these complex geomorphological groupings. Oceanic archipelagoes (island groups that have had no dry-land connections to more species-rich continental areas) are of two broad types: hot-spot archipelagoes, which form over a single plume of magma (Hawaii is a premiere example), and plate-margin archipelagoes, which form beside subduction zones (the Philippine archipelago is such a group). The former typically occur in a nearly linear string of islands that form quickly then erode away; the latter form through a series of eruptions over the period of existence of the subduction zone, and often undergo progressive (though irregular) increase in area over time, persist much longer than hot-spot islands, and often undergo mergers between formerly isolated islands as volcanic materials progressively fill intervening basins. These differing 'life histories' for the two types of archipelagoes lead to the question, do hot-spot vs. plate-margin archipelagoes differ consistently in their species-richness dynamics? For example, does indigenous phylogenetic diversification result in more species richness in the latter than in the former, given their typically greater persistence and greater area? When islands merge in plate-margin archipelagoes, to what extent do species spread out and increase total species richness, and to what extent do these 'invasions' precipitate a wave of extinctions? What geological processes promote speciation within old, geologically complex islands individually and collectively as archipelagoes, as dictated by the processes of volcanic dynamics and geomorphological development? Within an archipelago, how much biodiversity results from inter-island vs. intra-island speciation, for organisms of varying vagility?

The General Dynamic Model explicitly models a general interaction between colonization and phylogenetic diversification as they together fill 'ecological space', raising some additional questions. To what extent do 'adaptive radiations' fill 'niche space' (and to what extent may a radiation generate new 'niches'), and do they do so to the extent that later colonizers are inhibited or prevented from invading successfully? Does each suc-

cessful colonization by a given taxon (e.g., by a previously absent family of beetles, flowering plants, or rodents) into an archipelago result in an increase in standing diversity, or does the new colonizer cause the extinction of an 'old endemic'? Conversely, does the presence of 'old endemic' species cause the failure of colonization by the newly arrived species? In general, are species/lineages prone to extinction or to persistence? To what extent do ecological and geological processes influence taxa and the communities in which they live, and how do these two types of processes interact?

On a still broader level, we might ask, how much do rates of diversification differ based on dispersal ability, 'newness' of habitat, body size, trophic level, etc., of the arriving taxa? Do island biotas exist in a state of equilibrium, or disequilibrium? Indeed, is there such a thing as an equilibrium value of species richness, and if so, is it ever actually achieved in a geomorphologically active archipelago? To what extent are the processes that produce species richness patterns deterministic, probabilistic, or random? Finally, how do these processes influence the response of island communities to habitat disturbance or invasion by introduced exotics?

We believe that these questions, and undoubtedly many more not posed here, must be asked, and empirical data developed so that they can be answered, if we are to develop an accurate and fully-formed understanding of the dynamics of species diversity in oceanic island archipelagoes. We believe that few of these questions could have been posed as long as 'ecological' and 'evolutionary' island biogeography were treated as distinct topics. The General Dynamic Model prompts us to integrate ecological and evolutionary perspectives in more complex and therefore more realistic ways than prior models, but remains limited by focusing on one island at a time, and by application to islands with only the 'hot-spot island life history'. By broadening our models to incorporate the dynamics of archipelagoes and more complex island life histories, we will allow even broader and more integrative conceptualizations of island biogeography dynamics to be developed.

We find it noteworthy that in *Island Life*, A. R. Wallace's (1880) grand synthesis that established island biogeography as a distinct field of scientific study, Wallace strongly emphasized both the reality of long-term geological change and its impact on organismal distribution and diversity, and the reality of both long-timescale and short-timescale ecological factors (such as climate change) and dispersal (Heaney 2013). His explicit call for integrative approaches that recognize multiple processes, patterns, and timescales within any given archipelago serves us well as a framework in our current reconsideration of the dynamics of biodiversity on islands.

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