

# Island Biogeography Theory: Emerging Patterns and Human Effects

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## Island Biogeography

Islands are conventionally (and narrowly) referred to as isolated lands in surrounding waters. However, in broad senses and when loosely defined, 'islands' also include insular areas or entities such as mountain tops, lakes (e.g., potholes in northern Great Plains in North America), oasis (in deserts), and springs (especially in deserts) that support unique species assemblages relative to surrounding habitats (e.g., [Brown, 1978](#); [Lomolino et al., 2006](#)). Mostly because of the insular nature, habitats on oceanic islands are often different from those on the nearest mainland even when latitudes (climates) and the sizes (areas) are the same. For example, islands often support unique species assemblages with proportionally more rare and endemic species with small population sizes (e.g., reduced body size or the so-called insular dwarfism and dispersal). Partly because of their unique features (e.g., isolation) and conservation values, islands are extremely attractive for intensive efforts in exploration, research, and conservation (e.g., [Kalmar and Currie, 2006](#)).

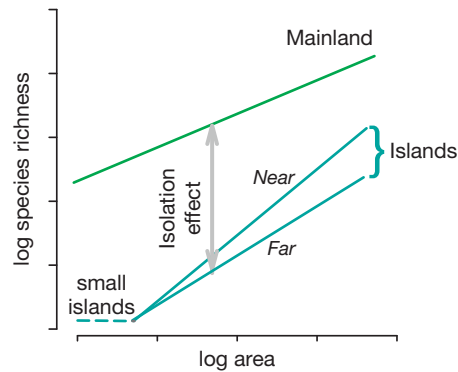
Island biogeography studies the biogeography of the isolated units mentioned in the preceding text, especially in the context of species diversity and related patterns and ecological processes. As a major advance and guide in related research arena on islands, [MacArthur and Wilson \(1967\)](#) developed the theory of island biogeography (next section) based on observations of many earlier naturalists made during their explorations around the world. To date, this relatively simple heuristic model has paved the ground and continues to inspire many individuals for further exploration and in some cases has resulted in with much greater effort and investment in such research.

## The (Equilibrium) Island Biogeography Theory

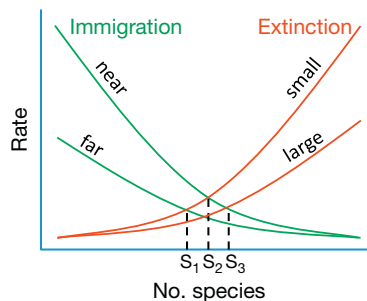
The species–area relationship was discovered much earlier than [MacArthur and Wilson's \(1967; 'MW' hereafter\)](#) island biogeography theory (e.g., [Preston, 1962](#); [Williams, 1964](#)). A unique development made in the island biogeography theory by MW is the species–isolation relationship that was solely developed at least initially for islands. Thus, as a major advance of the island biogeography theory, MW jointly considers two key 'island' features: area and isolation ([Figure 1](#)). MW predicts that species richness (the number of species) increases with island area but decreases with isolation (distance from the mainland or other islands); this prediction laid the foundation of island biogeography theory. Additionally, the equilibrium island biogeography theory considers both the immigration ( $I$ ) and extinction rates ( $E$ ) that at some point are balanced ( $I=E$ ): the former decreases with isolation, while the latter increases.

Thus, it may be reasonable to consider the general island biogeography theory as two related components: (1) the combined effects of area and isolation and (2) the companion dynamic 'equilibrium' between  $I$  and  $E$ . Based on the premises of the general patterns in island biogeography related to area, isolation, and species turnover, the 'equilibrium' of the island biogeography theory assumes that at a given time, species richness on island is saturated (static); for a new species to colonize as an immigrant, an existing (resident) species has to become locally extinct ([Figure 2](#);  $I=E$ ) due to competition with other species for niches and resources. In the original MW and in most following descriptions,  $I$  and  $E$  have often been drawn as symmetrical across the equilibrium for the same island (as in species equivalency as described in the neutral theory; [Hubbell, 2001](#)). The first component is generally well appreciated but the latter is not. In fact, understandably for convenience, most of the earlier tests of the MW model were based on area and/or isolation only (the first component) because immigration and extinction rates need much more time and greater effort to measure. It is likely that the 'equilibrium' points (i.e.,  $S_1$ ,  $S_2$ , and  $S_3$  in [Figure 2](#)), if they ever emerged, would be highly transitional at best. Yet, it is the core aspect of the MW theory related to 'equilibrium' that is still under debate, especially related to conservation applications.

With hundreds and possibly thousands of studies either related to or directly testing the island biogeography theory, a key question still remains: After all the human impacts (e.g., land use/travel) and associated species invasions on most world islands, does the island biogeography theory still apply, and if so, to what degree and to which species groups (the natives (MW's original



**Figure 1** A representation of the island biogeography theory that takes both area (habitat size) and isolation (distance to species sources) into account. (The short, dashed line that is not in the original MW model indicates ‘small island effect’ due to lack of suitable habitats; see references in Lomolino et al., 2006). The islands show steeper species–area slopes than the mainland. The results based on this theory that do not include the equilibrium point (i.e., immigration = extinction or  $I = E$ ) as a requirement have been widely observed in field research.



**Figure 2** The equilibrium island biogeography theory (revised from MacArthur, R. H. and Wilson, E. O. (1967). *The theory of island biogeography*. Princeton: Princeton University Press).  $S_1$ ,  $S_2$ , and  $S_3$  represent equilibrium points of islands with different sizes and distances to the mainland. In reality,  $I$  and  $E$  are most likely asymmetrical in opposite directions, and their positions and shapes could vary drastically among islands and different taxonomic groups; the curves also affect each other (e.g., ‘rescue effects’; see Brown and Kodric-Brown, 1977).

intent), exotics (i.e., human-introduced species that unquestionably affect natives in many ways), or all species combined (the true species diversity on an island))?

## History of Research and Applications

Like any other major theory in ecology, the MW theory was developed based on numerous observations by earlier naturalists such as Charles Darwin, Alfred Wallace, Joseph Hooker, and many others, especially portion of the theory that addresses species–area relationships (see MacArthur and Wilson, 1967). In the past, many attempts including field experiments have been made (1) to examine the species–area–isolation relationships and (2) to test whether an equilibrium ( $I = E$ ) truly exists and, if so, under what conditions; for example, can new species colonize or emerge only after a corresponding number of resident species either go extinct or emigrate?

The MW theory is useful, not only for basic research regarding the diversity on islands but also because it provides the basis for the metapopulation dynamics models and species-based models, which are developed mainly for population- and species-level conservation. For conservation purposes such as reserve design, the MW theory seems to suggest that larger areas of ‘reserves’ are needed in more isolated locations to maintain the minimum population size of species of concern.

One of the two important processes that the equilibrium theory stresses can be either a cause or a result of the other. For example, colonization or immigration ( $I$ ) could be due to an extinction event that vacates a niche, leading to species replacement or turnover. Conversely, local extinction of a species could occur due to a new invader. Specifically, when local species for some reason go extinct, this opens up niches for invaders that otherwise may not establish even when they reach the island. When competitive invaders are introduced by humans, their fast expansion would cause extinctions of local species. It is well acknowledged that most new colonizers – through either natural dispersal or human introduction – have not established after initial colonization. The theory therefore offers insights into invasion biology and has profound implications on invasive species management (Losos and Ricklefs, 2010).

Time is a critical factor in controlling the existence and/or positions of the ‘equilibrium’ point. Take succession (e.g., after volcanic eruptions) as an example. After an island ecosystem has been destroyed by volcanic eruption, it is likely that only

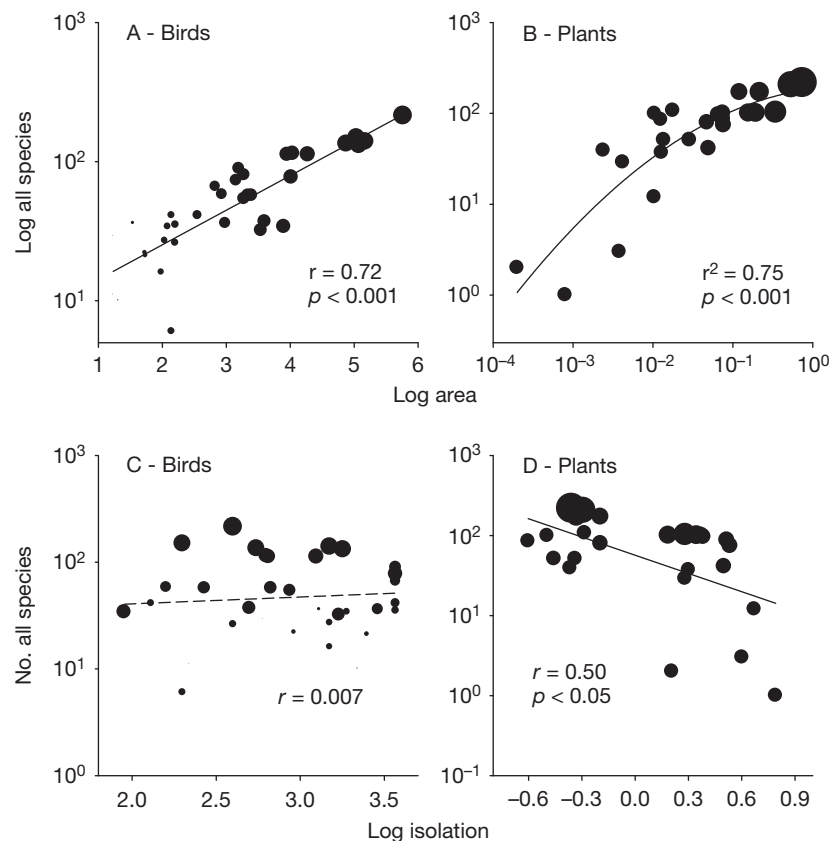
immigration (not extinction) occurs. Extinction only takes place when succession reaches a late stage when the community becomes relatively stable and 'crowded' (interspecific competition becomes intense). Therefore, the equilibrium may not emerge or will be highly transitional in most of the earlier stages of succession. For this reason, horizontally comparing islands in different successional stages would be less ideal. The same is true when considering taxon cycles discussed in the MW theory.

As mentioned in the preceding text, earlier debates about the MW theory and its applications have primarily been related to conservation issues such as reserve design (e.g., Wu and Vankat, 1995). These efforts are sometimes made in conjunction with the applications of metapopulation dynamics models and other related community ecology theories.

## Present Research and Conservation

Because of isolation, oceanic islands are often used as ideal natural laboratories for studying and testing related theories such as species assembly rules (Whittaker and Fernández-Palacios, 2007). In the past, most studies have compared different sets of islands (i.e., of a particular region or type), rather than most if not all islands across the globe (but see Kalmar and Currie, 2006) mainly because of data availability, leading to inconsistent results and conclusions. If still possible, comparisons between natural- and human-altered island systems with similar geographic settings could offer insights regarding the application of the MW theory under human impacts. An alternative approach would be to use historical records to compare the performance of the MW theory before and after the islands have been heavily invaded by exotic species.

Another approach would be to compare the performance of native species with that of exotics and with that of all resident species (i.e., natives plus exotics) on the same islands. For example, in a recent synthesis with ten sets of islands invasions by different taxonomic groups around the world, it seems that the island biogeography theory still better explains patterns such as the species–area and species–isolation relationships (Guo, 2014) for the native diversity or even for the overall diversity (natives plus exotics). In contrast, the species–area–isolation patterns for exotic species are highly variable, depending on the relative roles of



**Figure 3** An example showing the consequence of species invasions on islands. Species–area relationships for both birds (a) and plants (b) are much stronger for all species present (natives and exotics are combined) than for either native or exotics (data from Blackburn et al. (2008) and Long et al. (2009)). However, birds (c) and plants (d) show very different species–isolation relationships. Symbol size represents relative isolation. Adapted from Guo, Q. (2014). Species invasions on islands: searching for general patterns and principles. *Landscape Ecology* 29(7), 1123–1131, Figure 2, with permission from Springer Science+Business Media.

human versus natural dispersal and on geographic contexts (e.g., the number and location of islands; [Figure 3](#)). The context- and taxa-dependent patterns of species invasion on islands highlight the challenges of searching for general patterns and of using island biogeography theories in island invasion and conservation.

Controversy continues to persist over one large reserve versus several small reserves for effective conservation: Single large reserves are better for minimizing extinction, but several small reserves are more effective for sustaining more rare and endangered species and thus maximizing overall species diversity ([Simberloff and Abele, 1976](#)). The final decision of whether to focus on a single large reserve or several small one would likely depend on which particular species are the targets for conservation; if there is no such target species, preserving the overall island ecosystem would be a more efficient approach.

With biotic invasions induced by humans, initially  $I$  is greater than  $E$ , leading to higher overall diversity on the island ([Sax et al., 2002](#)). Under this condition, the equilibrium points shift to the right in [Figure 2](#). But as invasive species rapidly grow and expand, they may cause species extinction (mostly of rare or endangered species) and decline in overall species diversity (the equilibrium point then shifts to the left). This process thus involves 'extinction debt' at a certain point ([Sax et al., 2002](#)).

Recent efforts that apply island biogeography theory have been increasingly linked to the application of metapopulation dynamics models mainly designed for individual species (chapters in [Losos and Ricklefs \(2010\)](#)). Studies that test the applicability of the established MW theory in the context of land use and exotic species invasions associated with travel/trade change constitute another highly attractive field in present-day research. The latter is because most islands around the world have been invaded by varying degrees ([Guo, 2014](#)), but at much higher levels than when the MW theory was published.

## Challenges and Opportunities

Many subjects and ideas developed in the island biogeography theory, such as the role of dispersal from the species sources and species evolution and speciation on the islands themselves, are still poorly studied (see chapters and references in [Losos and Ricklefs \(2010\)](#)). For example, the speciation rate might be higher on more remote islands where gene flow from other islands is lower. Speciation would thus increase species richness on such islands, but the degree of this contribution is still largely unknown.

The parts of the island biogeography theory that only involve area and isolation appear simple and straightforward; however, testing and application of the theory are often complicated and challenged by other key variables that are intertwined: latitude, elevation, type (continental vs. oceanic vs. volcanic), isolation (absolute and relative: to mainland only vs. to other islands), context (e.g., geographic locations, oceanic vs. inland islands such as those in large lakes, and 'all' vs. a subset of islands; see [Guo, 2014](#)), time (succession and taxon cycle), exotic invasion (which affects native richness), and habitat destruction by human activities ([Lomolino et al., 2006](#)).

At present, many, if not most, islands are suffering the consequences of global change: (1) Climate warming and sea-level rise both may push resident species upward in elevation on islands and may further exacerbate the 'small island effect,' and (2) increasing species invasions due to intentional and unintentional introductions could put future generations of native species under great pressure. Thus, the applicability of the MW equilibrium theory may undergo even closer scrutiny. First, as opposed to natural colonization of species generally from nearby sources, human-induced biotic invasions bring highly competitive invasive species either intentionally or unintentionally from remote regions for various purposes (not 'normal' native species), reducing the 'isolation effect.' Second, human activities often cause direct disturbances on and destruction of native habitats on islands, and such effects are not even among islands, making the 'area effects' less predictable. These human interventions on islands make future attempts to rigorously test the MW theory especially difficult. How much have humans altered the world's island systems through the two dominant processes described in the preceding text? With much alteration and species introduction, do the island biogeography theories still apply? It is a fact, for example, that human intentional and unintentional introductions of exotic species have caused homogenization among island floras and faunas ([Blackburn et al., 2008](#)).

Finally, a few other key issues need to be resolved more fully in future exploration. First, to understand the present and to predict the future, we need more information about the geologic past. To date, such information about the geologic history of island floras and faunas (e.g., fossil records) is still critically lacking for most islands around the world. Second, as previously stated, the MW theory needs to be tested or examined at multiple organizational levels (e.g., individual, metapopulation, species, and community) while considering multiple related hypotheses and theories such as the central-marginal models in population genetics/dynamics (gene flows affect genetic diversity of populations), neutral theory, and network theories (species interactions such as pollination and predation on each island and species exchanges among nearby islands).

In sum, despite some uncertainties and controversies, the value and contribution of the (equilibrium) theory of island biogeography to modern ecology and biogeography are undeniable. The theory continues to play a key role both in basic research and in designing nature reserves for conservation, especially when the theory is applied to broadly defined 'islands.' Future studies should be long-term and focus on the stability or shifts of the emerged equilibrium points ([Figure 3](#)) and on how the shapes of the  $I$  and  $E$  curves may vary across islands and species groups. At present, the unprecedented human-caused species invasions could be the most important event that could either verify or challenge the MW theory. With so many highly invasive species immigrants on islands, does the MW theory still apply? And if it does, to what degree and to what species group (natives, exotics, or both groups combined; [Guo, 2014](#))?

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