Although the present location of systems such as Izu-Bonin-Mariana and Tonga-Kermadec appear to be remote (hence the term *intraoceanic*) from the nearest continents, it is important to bear in mind the evolution of these systems. For example, a series of continental fragments of eastern Australia (Lord Howe Rise, Norfolk Ridge) have been rifted off during the late Cretaceous through Tertiary periods, accompanied by a series of arc-back-arc developments along their eastern and northern margins. Similarly, the Kyushu-Palau Ridge is developed across a series of Cretaceous arc-back-arc systems that may have been proximal to Asia. The important point is that nominally intraoceanic arcs may have been initiated much closer to continental masses. We have few examples of subduction initiation in truly remote intraoceanic settings: the New Britain-New Ireland-Bougainville-Solomons-New Hebrides may be one such. Other island arcs are clearly developed on continental fragments such as Japan; during the Miocene epoch (20 million years ago), fragments of modern Japan migrated away from eastern Asia with the development of a back-arc basin (Sea of Japan). Some of this archipelago's most frequent earthquakes are on the Sea of Japan side of Honshu, marking the inception of a new subduction zone and closure of the Sea. Japan is destined to collide with its formerly rifted parent land mass.

More generally, despite the inherent gravitational instability of oceanic lithosphere, it is plausible that subduction initiation is propagated from elsewhere as a type of "tectonic infection," emphasizing the importance of the third dimension in our cross-sectional depiction of arc systems. We know that initial development of the Izu-Bonin-Mariana system was submarine in an extensional setting involving extensive pillow lava-dike (including boninite) emplacement. Ocean drilling has shown that subaerial, explosively eruptive conditions were temporarily reached a few million years after inception. Submarine growth stages are likely characteristic of many island arcs, as a growing body of survey data in the western Pacific has revealed. But we have sparse current examples of subduction inception: The Hjort Trench-Macquarie Ridge complex south of New Zealand is a possibility, but detailed swath mapping has failed to reveal volcanic activity, with the exception of a single active subaerial volcano (Solander).

The demise of arc systems includes the cessation of eruptive activity on remnant arcs and their general submergence. Changes in general plate tectonic frameworks can also lead to subduction and arc demise, as in the case of the Greater Antilles (Cuba–Hispaniola–Puerto Rico), where relatively large emergent islands remain. Another example is the South Shetlands off the northern coast of the Antarctic Peninsula, where sparse volcanic activity continues (e.g., Deception Island). Collision with a neighboring continent also leads to arc demise: Examples include multiple collisions of arc systems with western North America and the southern margin of central Asia during the Mesozoic. An ongoing example is the collision of the West Bismarck Arc with mainland Papua New Guinea. Volcanic activity is terminating progressively in this collision zone from northwest to southeast.

In conclusion, island arc systems are dynamic constructs with geologically ephemeral subaerial island development at varying distances from large land masses. Peripheral addition to continents and reworking of the constituent lithologies through metamorphism and igneous processes are important in continued continental evolution. The mobility of arc systems from initiation through migration and potential collision with continents is clearly significant from biogeographic perspectives, and there is much to learn from the combination of such studies with geological understanding.

SEE ALSO THE FOLLOWING ARTICLES

Antilles, Geology / Hydrothermal Vents / Island Formation / Japan's Islands, Geology / Kurile Islands / Oceanic Islands / Plate Tectonics

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ISLAND BIOGEOGRAPHY, THEORY OF

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The theory of island biogeography, developed by Robert H. MacArthur and Edward O. Wilson successively in 1963 and 1967, argues for the existence of a dynamic balance in species richness on islands, as a function of the addition

of species through the immigration of propagules to the island, plus any speciation within it (dictated by the degree of isolation from the mainland), and of species extinction from the island (dictated by island area). The result of these opposing forces, given enough time, is a dynamic equilibrium in which the species number remains approximately constant through time but species composition is continually changing. As a result of its quantitative approach and predictive power, the theory has transformed island biogeography into a mature scientific discipline. It rapidly achieved paradigmatic status, with numerous studies setting out either to confirm or reject its predictions, focused both on a large variety of taxonomic groups (plants, vertebrates, invertebrates, protozoa) and island types (real and habitat islands). It has thus inspired a substantial advance in our knowledge of insular biotas and processes. Finally, it has provided the foundation of a substantial (if controversial) body of theoretical work on the design/implications of protected area networks.

FUNDAMENTAL PRINCIPLES OF THE THEORY

The theory of island biogeography was developed in large measure to account for apparently systematic variation in species–area relationships. Basically, the theory considers that there are two major processes shaping the species richness that a given island can carry. How they vary is described in a straightforward graphical model (Fig. I), considered by some a key ingredient in the adoption of the theory. The first process is the immigration (arrival)



FIGURE 1 A version of MacArthur and Wilson's (1963, 1967) equilibrium model of island biogeography, showing how immigration rates are postulated to vary as a function of distance, and extinction rates as a function of island area. The model predicts different values for *S* (species number), which can be read off the ordinate and for turnover rate (*T*) (i.e., *I* or *E*, as they are identical at equilibrium). Each combination of island area and isolation should produce a unique combination of *S* and *T*. To prevent clutter, only two values for *T* are shown. Source: Whittaker and Fernández-Palacios (2007).

of a propagule of a species that is new to the island, and its rate depends on the island's isolation (the distance from the mainland source). Nearer islands are easier to reach by mainland species than farther ones, therefore the immigration rate curve (I) tends both to flatten with increasing islands isolation, and to decline exponentially through time as initially empty islands fill up with species. Hypothetically, the immigration rate would decline to zero if the islands were near enough to the mainland to enable the whole mainland species pool (P) to disperse to them. However, because islands are smaller than mainland sources this point is never reached because of the counterbalancing second process, extinction. The theory of island biogeography posits that the extinction, or total disappearance, of a species from an island is dependent on the island area. So, larger islands can support larger populations than smaller ones, and as extinction risk is inversely related to population size, the extinction rate curve (E) tends both to flatten with increasing island area and to increase exponentially as initially empty islands (where E = 0) fill up with species. The increase of E with species richness is explained by the fact that the higher the number of species on a given island, the smaller the population sizes that can be maintained for a given species, hence the higher the extinction risks.

When the trajectories of the immigration and extinction rates (as the ordinates) for a given island with a specific area and isolation are plotted on a graph against species richness on the abscissa (Fig. 1), the projection to the abscissa from the point at which the two curves intersect defines the species richness that this island can carry, whereas the projection from this point to the ordinate defines the turnover rate (T), or number of species extinguished and replaced per unit time. Thus, species richness, as well as immigration, extinction, and turnover rates, are island-specific parameters that vary with the island's area and isolation in a dynamic equilibrium, where species richness tends to remain constant through time although species composition continues to turn over. Each combination of island area and isolation should produce a specific combination of species richness and turnover rate. Thus, the theory predicts that large, near islands tend to have higher species richness and lower species turnover than small, far islands, whereas small, near islands as well as far, large islands should have intermediate values (Fig. 1).

Finally, colonization, defined as the relatively lengthy persistence (e.g., through at least one life cycle) of an immigrant species on an island, can be plotted through time to obtain the colonization curve, or temporal change of numbers of species found together on an island (Fig. 2). The colonization curve starts from zero, when the island



FIGURE 2 Integration of immigration and extinction curves (left) should theoretically produce the colonization curve as shown (right). Source: Whittaker and Fernández-Palacios (2007).

has not yet been colonized by any species, then rises rapidly as the island accumulates new species (notwithstanding the gradual rise in extinction events) until the curve flattens approaching asymptotically the island's species carrying capacity, as determined by its area and isolation.

OBJECTIONS AND EMBELLISHMENTS TO THE THEORY OF ISLAND BIOGEOGRAPHY

The theory of island biogeography assumes that all species are equal in their probabilities of immigrating onto the island or of going extinct once there. With the development of Hubbell's *Unified Neutral Theory of Biodiversity and Biogeography*, there has been a resurgence of theory regarding the importance of such neutral processes in dictating species composition in a given community. It appears that species do differ in their chances of colonizing and persisting on an island.

Although MacArthur and Wilson's monograph (1967) includes a chapter called "Evolutionary Changes Following Colonization," the mechanism through which speciation can substitute for immigration is not well developed, and there is general agreement that the theory is more readily applied to islands driven by "ecological" processes, where the frequency of immigration events precludes speciation, than for very remote islands, where species diversity is dictated mainly by "evolutionary" processes and in situ speciation is more frequent than immigration as the source of new species. Several approaches have been developed to include more information about speciation, the third main biogeographical process, together with immigration and extinction, within the framework of the theory of island biogeography (M. V. Lomolino, L. R. Heaney, etc.), in order to increase the generality of the theory.

Another limitation in the model is that isolation is considered to dictate rates of immigration only. However, island isolation has been shown also to play an important role in influencing extinction rates through a phenomenon known as the rescue effect (Fig. 3): the supplementary immigration from the mainland of propagules of species present on the island in small population sizes and that would otherwise go extinct (such supplementation does not count as immigration if the focal species is rescued prior to actually going extinct). This possibility was noted by MacArthur and Wilson but was not included in the model, yet the effect can be important on small islands near to the mainland, thus modifying the extinction rate, and equilibrium point. In addition, area is considered to dictate only extinction in the model, although MacArthur and Wilson noted the potential importance of island area in influencing the immigration rate as well. Through the latter phenomenon, known as the target effect (Fig. 4), larger islands provide easier targets for passively dispersing propagules, such as windborne and waterborne plants, thus increasing their immigration rates. These two effects undermine the predictive power of the simplified model in Fig. 1.

MacArthur and Wilson also recognized that biologists can rarely, if ever, be certain of recording all immigration and extinction events in real-world systems, especially if large islands are considered, and thus species turnover calculations for large islands can contain important



FIGURE 3 The rescue effect is the reduction in the extinction rate of near islands versus distant ones. Whereas the MacArthur and Wilson model predicts higher turnover on near islands (A), the rescue effect may increase turnover on more distant islands (B). T_n is the turnover rate on the near island; T_r is the turnover rate of the far island. Source: Gotelli (2001).



FIGURE 4 The target effect is the increase in the immigration rate on large islands versus small ones. Whereas the Mac-Arthur and Wilson model predicts higher turnover on small islands (A), the target effect may increase the turnover on large islands (B). T_s is the turnover rate on the small island; T_l is the turnover rate on the large island. Source: Gotelli (2001).

biases. Two main problems arise when trying to calculate species turnover rates: cryptoturnover and pseudoturnover. Cryptoturnover is the real turnover of species not detected because of too great a gap between census intervals, as for instance, when a species undergoes extinction and later re-colonization, or vice versa, in the time interval occurring between two consecutive inventories. The effect leads to underestimation of the real turnover rate. Pseudoturnover, conversely, is the apparent disappearance and reimmigration of species in consecutive surveys when they were actually present throughout, or alternatively, were only ever present as vagrant individuals. Such incomplete surveying leads to overestimation of the real turnover rates. Attempts have been made to quantify both of these sources of error, but they are inherently hard to estimate precisely, especially for larger islands.

It has been argued that habitat diversity and not area per se is the true determinant of island species richness, because more habitats will offer more opportunities for the colonization of species differing in their ecological requirements. Although this is undoubtedly true, it is also the case that habitat diversity is generally correlated with island area. Indeed, it was partly for the lack of adequate data on habitat diversity (still a limitation today) that MacArthur and Wilson focused only on area in their monograph. Their specific mention of this point makes clear that they used area in the theory as a measure of the combined effects of area per se and habitat diversity.

Finally, it has been argued that some insular systems do not achieve equilibrium, even after extended periods of time. Three alternative states have been recognized. First, "static" nonequilibrium systems include those where species losses (such as those due to postglacial isolation of mountaintop systems preventing further immigration across arid lowlands) are occurring, but so slowly as to be effectively unmeasurable on ecological time scales. Second, "dynamic" nonequilibrium systems are those that are frequently impacted by extreme events, such as volcanic eruptions or hurricanes, which resets the community development iteratively, preventing the attainment of equilibrium. Third, "static" equilibrium systems are those archipelagoes that, over ecological time scales, have a clear species—area relationship (consistent with the theory of island biogeography) but with no turnover (not consistent with the theory), as for instance appears to apply to some oceanic island avifaunas.

These different scenarios have allowed fine-tuning of the theory of island biogeography, with an expanded framework.

THE THEORY OF ISLAND BIOGEOGRAPHY AND CONSERVATION

One of the main applications of the theory of island biogeography outside its academic context has been within the field of conservation biology. The increasing worldwide anthropogenic fragmentation experienced by continental ecosystems has transformed once continuous habitats into complex landscapes containing many patches of relict habitats, differing in size, shape, isolation, or degree of disturbance, surrounded by a more or less penetrable matrix of arable land, pasture, urbanized areas, and/or built infrastructure (e.g., roads). As the new geographical framework for the species of the relictual habitats increasingly resembles an archipelago more than a continent, many authors have attempted to apply the principles of the theory to generate guidelines for these new anthropogenic landscapes. Although there have been many theoretical developments (e.g., metapopulation scenarios, source-sink relationships, edge effects), at the core of this work is the use of the theory of island biogeography to predict the eventual species losses following fragmentation, as immigration rates decline as a result of increased isolation, and extinction rates rise as a result of reduction in contiguous area of habitat. The process of species losses is termed relaxation. At the point of habitat disruption, residual fragments may become supersaturated (i.e., have

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temporarily high species numbers), and may take time to reach their new equilibrium. The terms "lag effect" (duration of delay) and "extinction debt" (magnitude of the losses) are each used to describe the delay in species losses following fragmentation of habitat. Rather more controversially, the theory of island biogeography has also been invoked in the design of protected areas networks. It has been proposed that, in general, the theory favors deploying resources to protect fewer large reserves rather than many smaller ones (the "SLOSS Debate"), short rather than long inter-reserve distances, circular rather than elongated reserves (to minimize edge effects), and the use of corridors, when ever possible, to connect reserves and facilitate dispersal between them.

SEE ALSO THE FOLLOWING ARTICLES

Extinction / Fragmentation / Relaxation / Species-Area Relationship

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ISLAND FORMATION

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To understand how islands form, continental islands must be distinguished from oceanic islands, the former being pieces of continents with the connection submerged, the latter being younger islands that originated exclusively within the ocean basins. However they appear today low or high, limestone or volcanic—all oceanic islands began life as ocean-floor volcanoes. Those that have not

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yet reached the ocean surface (and many never do so) are referred to as seamounts, whereas those that were once emergent but have since been submerged are often distinctively flat-topped and are called guyots.

OCEAN-FLOOR VOLCANOES: ORIGINS AND GROWTH

It comes as no surprise to learn that we are not very knowledgeable about ocean-floor volcanism because of the difficulties in actually observing it. Most ocean-floor volcanism occurs in the dark beneath 4 km of ocean water. It is not that the technological difficulties are insurmountable, just that it is difficult to be sure that researchers are getting an accurate picture of what is going on. In this regard, places where the ocean floor actually rises above the ocean surface are extremely valuable as observation sites. Second best are places where seamounts have been thrust up above sea level and have their insides exposed for scientists to see how they were built up.

The finest example of the first situation—where the ocean floor actually rises above the ocean surface—is the island of Iceland in the northern Atlantic Ocean. Iceland is part of the Mid-Atlantic Ridge (a divergent plate boundary) that lies at a plate triple junction and where eruptive activity has been unusually voluminous over the past few million years. The mid-ocean ridge—a common site of ocean-floor volcanism—actually passes through the center of Iceland. From studies of this, we learn that the earliest type of ocean-floor volcanism is commonly along fissures. As fissure eruptions continue, some parts of the fissure become blocked, and eruptions begin to occur at points. Point volcanism results in the build-up of the earliest types of seamounts.

Studies of emerged seamounts—which rise from ocean floor that has been thrust upward by tectonic forces have also given us a lot of information about the undersea development of oceanic islands. In particular, it is clear that intrusion of igneous rocks is at least as important as extrusion is in building seamounts in many parts of the ocean basins.

Another important issue is the depth of overlying ocean water in places where seamount eruption occurs. In most places below about 600 m the weight of overlying water is so great that, however powerful the volcanic eruption, it will not be explosive, and the material produced will generally be pillow lava. At depths shallower than 600 m (the hydroexplosive zone), on the other hand, the weight of overlying water is not always sufficient to subdue explosive eruptions, and there is a reaction between the cold ocean water and the hot magma (liquid rock)