Equilibrium Theory of Island Biogeography: A Review

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Abstract—The topography, climatic pattern, location, and origin of islands generate unique patterns of species distribution. The equilibrium theory of island biogeography creates a general framework in which the study of taxon distribution and broad island trends may be conducted. Critical components of the equilibrium theory include the species-area relationship, island-mainland relationship, dispersal mechanisms, and species turnover. Because of the theoretical similarities between islands and fragmented mainland landscapes, reserve conservation efforts have attempted to apply the theory of island biogeography to improve continental reserve designs, and to provide insight into metapopulation dynamics and the SLOSS debate. However, due to extensive negative anthropogenic activities, overexploitation of resources, habitat destruction, as well as introduction of exotic species and associated foreign diseases (biological invasions), island conservation has recently become a pressing issue itself. The objective of this article is to analyze previously published data, and to review theories from numerous research studies that attempt to explain species patterns on islands. In effect, this analysis brings insight into current issues of continental reserve design and island conservation efforts.

Introduction

The equilibrium theory of island biogeography (ETIB), proposed by MacArthur and Wilson, is a relatively recent development that has sparked a tremendous amount of scientific controversy. Initially introduced to the public in 1963 as "An Equilibrium Theory of Insular Zoogeography," the idea was expanded in 1967 into a book publication. The ETIB implies that island fauna and flora (biota) eventually reach an equilibrium point between extinction and immigration. Although species rarely reach equilibrium due to the extremely dynamic island system, MacArthur and Wilson note that the ETIB permits general predictions of future island biodiversity patterns. In this article, the theory of island biogeography is examined in reference to island environments, including topographic origins and characteristics, as well as climatic patterns. A comprehensive analysis of the theory is discussed, such as species-area relationship, dispersal mechanisms and their response to isolation, and species turnover. Additionally, conservation of oceanic and continental (habitat) islands is examined in relation to minimum viable populations and areas, metapopulation dynamics, and continental reserve design. Finally, adverse anthropogenic impacts on island ecosystems are investigated, including overexploitation of resources, habitat destruction, and introduction of exotic species and diseases (biological invasions). Throughout this article, theories of many researchers are re-introduced and utilized in an analytical manner. The objective of this article is to review previously published data, and to reveal if any classical and emergent theories may be brought into the study of island biogeography and its relevance to mainland ecosystem patterns.

Island Environments

Island Formation and Topography

Island topography is primarily determined by the geophysical origins of the island. Marine islands may be subdivided into two geophysically distinct categories: continental shelf islands (land-bridge islands) and oceanic islands. Continental shelf islands are likely to be physically connected to the mainland during low sea level periods. Due to their connection, these islands have similar geological structure to the nearby mainland (Williamson 1981). This similar topography, coupled with the island's close proximity to the continent, results in the proliferation of similar flora and fauna (biota).

Oceanic islands are typically more isolated, and may have never been physically connected to a continental landmass. There are three main types of oceanic islands: oceanic ridge islands, hot-spot islands, and the individual islands of island arcs. Oceanic ridge islands and hot-spot islands are volcanic islands because they are formed from ocean-floor volcanoes. Islands that are part of island arcs also have a volcanic origin, involving the collision of continental and oceanic plates, resulting in islands that consist of both basalt and granite rock (Williamson 1981).

All of the geological processes occurring volcanic islands can produce islands with high elevations, with peaks of at least 2,000 m (fig. 1) (Williamson 1981). Volcanic islands are typically steeper and become increasingly dissected with age. This phenomenon has important implications for island biota because a wide range of elevational gradients and associated ecological attributes allows for the persistence of diverse habitats. The elevation of islands also has important influences on the climatic regime.

In: McArthur, E. Durant; Fairbanks, Daniel J., comps. 2001. Shrubland ecosystem genetics and biodiversity: proceedings; 2000 June 13–15; Provo, UT. Proc. RMRS-P-21. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

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Figure 1—A map indicating all islands with a peak of 2000 m or higher. Larger islands are shaded, smaller islands are denoted by Δ (Williamson 1981).

Island Climate

Island climate is determined by both external influences, such as ocean circulation and atmospheric circulation, and internal influences, such as island size, shape, and topography. Ocean circulation and atmospheric circulation consist of water currents and air currents, respectively, that have similar movements of upwelling and sinking. If an island is in the path of a moving current or is located where two currents intersect, this can alter the climate significantly. In addition to circulation influences, the proximity of an island to a continental landmass also affects the island's climate. Islands located close to a mainland, such as land-bridge islands, are likely to be influenced by the continental climate. Remote oceanic islands, on the contrary, are influenced by the maritime climate.

Internal influences, such as island size and elevation, can have a substantial impact on the precipitation regime on the island. Whittaker (1998) states that low islands typically have relatively dry climates and high islands are wetter through orographic rainfall, resulting in the creation of extensive arid regions due to the rain shadow effect. These higher islands often contain diverse habitats within a relatively small area. Due to the impact of elevation on island climate, research studies have indicated that elevation is a critical variable in analyzing species diversity on islands. Telescoping, a compression of elevational zones, is fairly common on small tropical islands. Leuschner (1996) proposes that forest lines on islands are generally 1,000 to 2,000 m lower than forest lines on continents. Hence, telescoping creates smaller patches from a variety of habitats favorable to many species, and permits high- and low-elevation inhabiting species to coexist in a relatively small area (Whittaker 1998).

Island Patterns

The Equilibrium Theory of Island Biogeography (ETIB) revolutionizes the way in which biogeographers and ecologists viewed island ecosystems. Prior to the ETIB was the static theory of islands (Dexter 1978), which hypothesizes that island community structures remain relatively constant over geological time. The only mechanism for biological change was the gradual evolutionary process of speciation. Few successful colonization events would occur due to a limited number of ecological niches on the island (Lack 1976). Once these niches are completely filled, no space and resources are available for new immigrants, and they may not become successfully established on the island. The ETIB refutes the static theory, indicating that island communities exhibit a dynamic equilibrium between species colonization and extinction, or species turnover. The immigration curve is descending and is shaped concavely because the most successful dispersing species would colonize initially, followed by a significant decrease in the overall rate of immigration (fig. 2). The extinction curve, on the contrary, is an ascending curve because as more species inhabit the island through time, more species would become extinct exponentially (fig. 2). Such a trend is amplified due to a combination of population size and negative biotic interactions among

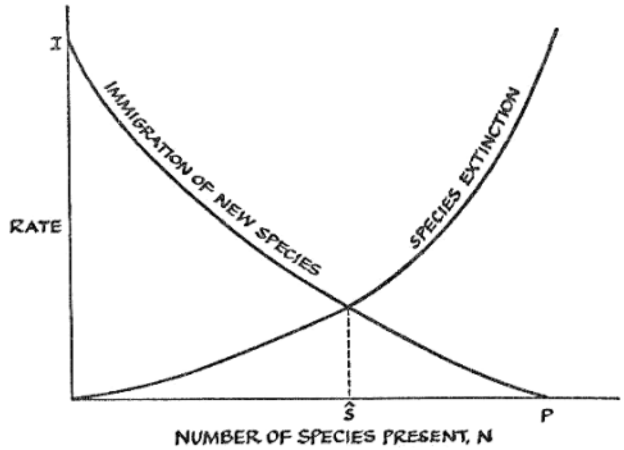

Figure 2—The equilibrium model of species present on a single island. The equilibrium number of species is reached at the point of intersection between the rate of immigration and the rate of extinction (MacArthur and Wilson 1967).

different species. This model graphically and mathematically represents an equilibrium point, S, in which the immigration and extinction curves intersect (fig. 2). This point represents the actual number of species present on an island at equilibrium. Moreover, figure 3 accounts for trends in island size and degree of island isolation (distance from mainland). Patterns regarding the species-area relationship and the species-isolation relationship have been acknowledged by biogeographers since the beginning of the 19th century. Therefore, the contribution made to island ecosystem study by MacArthur and Wilson was a compilation of these well-known ideas into one, integrated paradigm (Brown and Lomolino 1998).

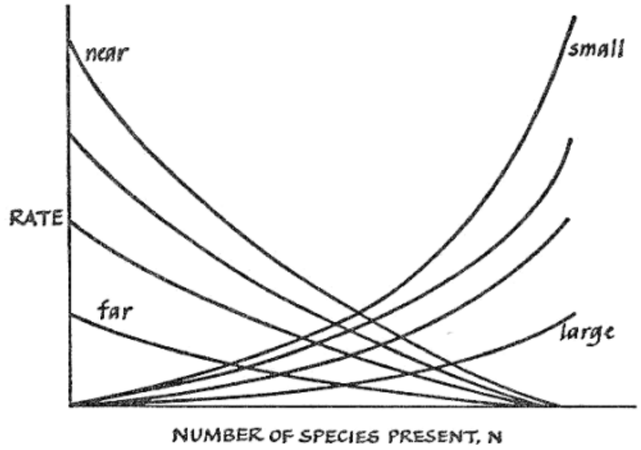

Figure 3—The equilibrium models of species of several different islands with a various degrees of isolation and size. An increase in isolation (near to far) decreases the immigration curve, while an increase in area (small to large) decreases the extinction curve (MacArthur and Wilson 1967).

Species-Area Relationship

A positive relationship exists between island size and island species richness (fig. 4). These two variables, nevertheless, do not always exhibit a linear correlation. Arrhenius represented this non-linear trend in mathematical form in 1920 with the following equation:

$$S = cA^Z$$

In this equation, S = the species richness on an island, c = a constant depending on biotic and biogeographic region, A = the area of the island, and z = a constant representing the slope of S and A on a logarithmic scale (z changes very little among different taxa or same taxon from different regions.).

There are two potential explanations for the positive correlation between island size and species diversity. First, large islands generally contain more diverse habitats and, thus, more biota compared to small islands. Although this is a logical explanation, ecologists and biogeographers have a difficulty to prove in the field because habitat diversity has no distinct parameters and is a challenge to measure. Many parameters are approximated to determine the number of species inhabiting various islands. Second, the island size, rather than the habitat diversity, is the main factor in determining the number of species on islands. This theory is also difficult to prove in the field because habitat diversity and island size are strongly correlated, and it is nearly impossible to distinguish the two.

Species-Isolation Relationship (Distance Effect)

Isolation is a critical component when examining evolutionary processes since it allows for allopatric speciation to occur. Islands offer prime examples of isolation effects on biota (Cox and Moore 1993). Specific adaptations, such as seed parachutes, are necessary for plants to disperse across large bodies of water. Such dispersal invokes survival of a sweepstakes route, an extensive barrier permitting only a

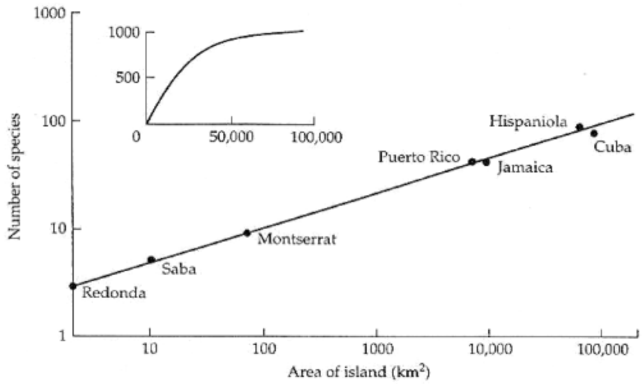

Figure 4—The correlation between species number, S, and island area, A, for reptiles and amphibians of the West Indies. Both axes are logarithmic and a best-fit line is used. The inset represents this relationship arithmetically (Brown and Lomolino 1998).

stochastic set of immigrants to successfully colonize the island (Brown and Lomolino 1998). The more remote the island is from a continental landmass, the more severe the sweepstakes route and the smaller the number of species that would successfully colonize and become established on the island. This is known as the species-isolation relationship on islands. The number of species would decrease exponentially as a function of isolation because the species-isolation correlation should account for a pool of species (fig. 5) (Brown and Lomolino 1998). Successful colonization over large bodies of water is potentially easier for plants than for animals. Many species of plants possess dispersal mechanisms, such as "parachutes and "wings," to allow new generations of plants to be carried far from the parent plant by wind currents. Without having a mate to reproduce, plants only require one fertile seed or spore to colonize a remote island. Other mechanisms, such as sticky seeds, permit seeds to be transplanted by animals. Through animal assistance, the chance for successful plant immigration is greatly enhanced. In addition, some plants are able to withstand long periods of seawater immersion, and successfully colonize remote islands. Such adaptive characteristics are essential in creating plant communities on both nearby and remote islands.

Species Turnover

Species turnover on islands is also critical to the ETIB model. The cycle of extinction of certain established species and the immigration of new species permit the equilibrium point to maintain its value over geological time. Such species turnover, however, can be extremely difficult to quantify in the field. Whittaker (1998) detects two main problems with quantifying extinction and immigration rates on islands. Firstly, species turnover is a situation in which surveys on islands are at irregular intervals. This phenomenon allows for some species to become extinct and possibly re-migrate during periods between the surveys, resulting in a depression of turnover rates (Simberloff 1976). Secondly, there is potential for pseudoturnover on islands, implying that information with regard to breeding conditions is fragmentary or incomplete. Under such circumstances, species appear to have turned over when, in fact, they have simply been overlooked. With such potential inaccuracies, the ETIB requires an extensive attention to census detail, causing it to be a relatively difficult theory to prove under natural island conditions.

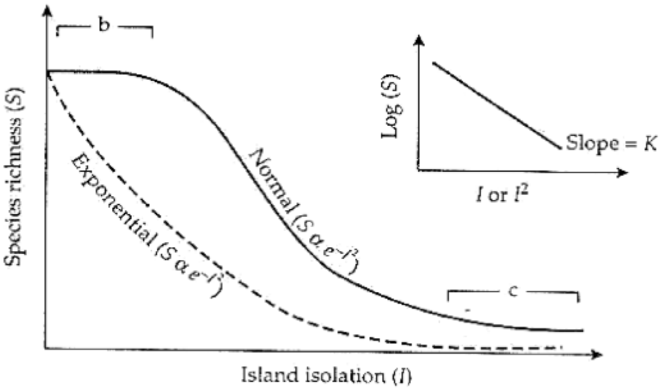

Figure 5—Display of a negative relationship between species richness (S) and island isolation (I). The inset represents the log-transformed equivalent of this relationship (Brown and Lomolino 1998).

ETIB Strength and Weaknesses

In addition to the limitations in detecting species turnover, Brown and Lomolino (1998) note a number of major weaknesses in the theory initially proposed by MacArthur and Wilson. First, many island species rarely achieve equilibrium. The number of species at the equilibrium point may change over geological time, especially when immigration and extinction coincide with periods of anomalous climatic and geological (disturbance) events. Second, not all species have identical immigration and extinction rates. For instance, birds generally have a higher immigration rate than large, heavy reptiles and mammals. Third, the ETIB model regards immigration and extinction as being independent variables when, in many cases, they are closely related. For example, when there is a depression or extinction of a population on an island, a rescue effect may occur, thus increasing species numbers once again. Fourth, the model does not consider specific characteristics of species, such as species fitness and dispersal ability. Fifth, species inhabiting a single island may be derived from several mainland and island sources. It may be challenging to determine the source pool for a species on an island without a comprehensive study on the historical and current distribution of the species. Sixth, the ETIB model does not incorporate speciation, which may exceed immigration rates as a potential mechanism affecting an island system. Species present by speciation do not add to the overall species diversity of the island. This model should include the effects of both speciation and immigration. Seventh, anthropogenic-induced habitat fragmentation or destruction may isolate once massive and continuous ecosystems on an island. Eighth, the ETIB model does not consider periodic rescue effect and target area effect. The rescue effect reduces species extinction, while the target area effect enhances immigration on large islands. Finally, the use of island size is extremely general and does not consider the impact of habitat heterogeneity (complexity of habitats and natural landscapes) on species diversity.

These main arguments against the ETIB are important to examine. However, modifications of the ETIB are a possibility to account for such problems. Despite such flaws, the ETIB is still acceptable by some modern scientists in at least three ways. Firstly, the theory may be graphically simplified, and makes logical sense to a wide array of audiences. Secondly, this theory forms a link between traditional notions of ecology and biogeography, thereby enriching the information of both types of study. And, thirdly, this theory provides a clear and testable strategy for population pattern predictions not only on islands, but also on localized continental systems.

Island Conservation

The initial objective for the ETIB was to gain a better understanding of island ecosystems and their dynamic processes. Nevertheless, as studies continued, many ecologists, biogeographers, and conservation biologists discovered a parallel between oceanic islands and fragmented habitats on continental landmasses. Most species have a range of habitat in which they prefer to live, yet it has become evident that human activities such as deforestation, habitat destruction, and urban and suburban development, have all contributed to a significant fragmentation of natural habitats. The continuation of such fragmentation has resulted in species extinction from local to global scales (Whitmore and Sayer 1992). The remaining patches of these relatively natural areas may be perceived as habitat islands (fig. 6). From the similarities between habitat islands and actual oceanic islands, biogeographers utilize the ETIB as a guideline to preserve biodiversity in these patches (Whittaker 1998). This notion, ironically, spawned a great controversy in the field of biogeography and conservation biology. Janzen (1983) argues that natural habitats such as parks and nature preserves vary significantly from true oceanic islands, and thus the ETIB would not be completely applied to continental reserves. Unlike continental parks, Janzen (1983) points out that islands are encompassed by water, an extremely different type of habitat. Habitat islands can be surrounded by a landscape containing a variety of species that are potentially capable of establishing populations within the habitat patch. This event often introduces negative biotic interactions, such as competition, predation, and parasitism, within the habitat island that is not experienced by true oceanic island ecosystems. Likewise, species within the habitat island are capable of escaping the patch and influencing populations of species within the degraded or fragmented landscape. These are important biotic interactions that do not occur on oceanic islands, and must be considered when attempting to apply theories of island biogeography to habitat islands on continents. The scale and degree of insularity are critical components when making such comparisons. For these reasons, in addition to theories concerning oceanic island biogeography, issues such as minimum viable population and area, along with metapopulation dynamics must be evaluated when determining the most effective continental reserve design.

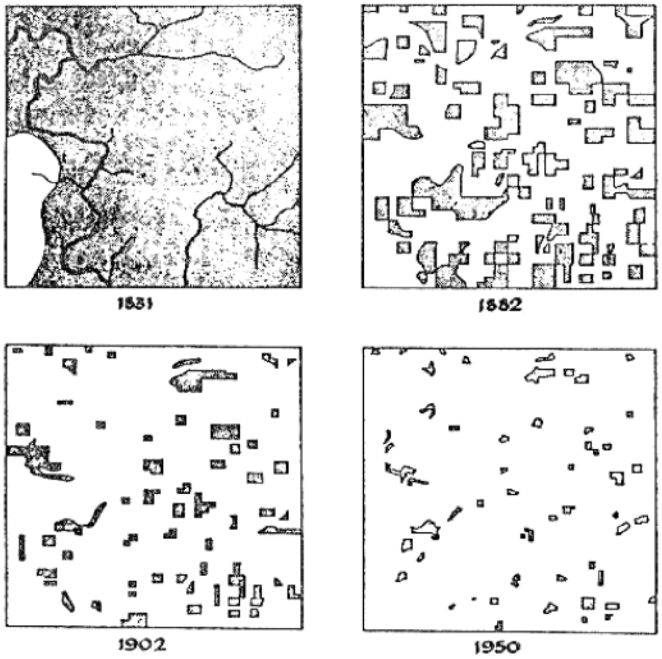

Figure 6—The fragmentation of forested land in Cadiz Township Green County, Wisconsin (94.93 km^2), into habitat "islands" during the era of European settlement (Shafer 1990).

Minimum Viable Population and Minimum Viable Area

The study of population dynamics of a species is critical when attempting to support the future success of the species' population. When evaluating populations of species inhabiting a reserve, survival pressures on these populations are compounded. Smaller areas tend to support smaller numbers of species as noted by the species-area concept. Consequently, the proposal of the minimum viable population (MVP) concept emerged. Shaffer (1981) tentatively defines the minimum viable population for a given species in a given habitat regardless of the impacts of demographic stochasticity, environmental stochasticity, genetic stochasticity, and natural catastrophes. Under this definition, the survival of the species must not only endure normal conditions, but also endure episodic catastrophes in order to persist through geological time.

Shaffer (1981) attempts to give a definitive measure in order to conserve species living within a restricted area because this would allow conservation biologists to have a framework in which to proceed. However, Thomas (1990) argues that the MVP theory is not realistic with regard to actual population dynamics within a limited geographical range. Additionally, Thomas (1990) states that in certain large-scale, remote areas, the MVP concept would be too difficult to quantify due to the paucity of available information.

The theory of minimum viable area (MVA) resembles the theory of minimum viable population. If a determined area of minimum size is conserved, the species inhabiting such area is conserved as well. The MVA often corresponds to the range size in which this particular species is found. Species located higher on the trophic level generally require more area or space to ensure maximum survival. Hence, for certain species, the MVA is considerably large in order for a MVP to persist within the designated area (Whittaker 1998).

The MVA approach may be effective to help preserve entire ecosystems since various species coexist and interact closely within the MVA. However, this concept assumes that each area is discrete, and has no biotic (genetic) exchange with other surrounding areas. The MVA must account for the immigration and colonization of species in and out of the area (Whittaker 1998). Consequently, the MVA is difficult to quantify due to its extremely dynamic nature.

Metapopulation Dynamics

Metapopulation models first emerged in 1969, and have since evolved into a dynamic concept involving wildlife conservation and population turnover. A metapopulation is a discontinuous distribution of a population of species. This population is geographically spread over disjunct fragments of suitable habitat separated by intermixed fragments of unsuitable habitat through which little migration occurs (McCullough 1996). As a result, there is a limited movement of population among suitable patches, and populations remain spatially separated. However, when a metapopulation becomes environmentally and physiologically stressed, the population crashes; the patch may be recolonized by a nearby metapopulation, and may eventually bring the population back up to threshold (fig. 7). Therefore, although populations of the same species are spatially separated, migration and gene flow still occur among suitable patches to ensure long-term survival of the species (Whittaker 1998).

Gotelli (1991) realizes two main dilemmas in studying metapopulation models. Firstly, the dynamics of metapopulations may be difficult to replicate, especially when considering the temporal-scale in which metapopulation changes may occur under natural settings. Secondly, the subdivision of populations may occur at many levels, and the degree of separation in metapopulations is often subjective.

Despite potential weaknesses as suggested by Haila (1990), the metapopulation concept forms a link between population ecology studies and island biogeography theory. Metapopulation models are comprised of dynamic, interdependent island systems in which population fluctuations are determined by the degree of isolation (Gotelli 1991; Whittaker 1998). These geographically distinct metapopulations may be viewed as habitat islands due to an extensive human colonization and development (McCullough 1996). Such metapopulation pattern is evident in both population ecology and island biogeography studies. Hence, the research used for island biogeography study may allow for the postulation of a unified concept concerning isolation, area, and species number on mainland metapopulation systems (McCullough 1996). However, the application of island biogeography theory to the patch dynamics of metapopulations has many flaws. Most importantly, habitat patches on a continental landscape rarely, if ever, resemble true oceanic islands. Ecotones and edge effects tend to be less dramatic gradients of habitat than distinct changes from terrestrial landscapes to seascapes. This dissimilarity introduces two additional differences between these seemingly analogous habitats. First, the surrounding area represents a gradient of habitat, rather than a distinct boundary. The surrounding habitat may simultaneously offer both advantages, such as additional food sources, and disadvantages, such as competitors, predators, and pathogens. Second, through properly designed corridors, the surrounding matrix permits periodic migrations among suitable patches; the degree of spatial isolation is considerably less on habitat islands than on true oceanic islands.

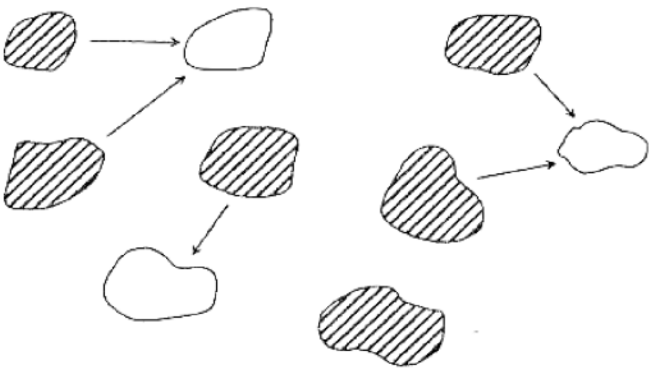

Figure 7—The classic metapopulation model in which occupied patches (shaded) will re-supply patches in which the population has decreased or vanished (unshaded). Movement is denoted by the arrows (Whittaker 1998).

Continental Reserve Design and the SLOSS Debate

Metapopulation dynamic theory is utilized to find the most effective and efficient strategies for continental reserve design, and has allowed for a better understanding of population ecology. Many opinions exist concerning the most effective and "natural" design theory, the size and shape of reserves, and the number of reserves necessary to maintain the optimum amount of biodiversity. The SLOSS debate (Single Large or Several Small) emerged in 1976, and proposed two schools of thoughts regarding reserve design. One extreme option was to create a single large reserve. The other option was to create several small reserves that, combined, would equal the same area as the large reserve. Diamond (1981) supports large reserves, using managerial considerations as a main determining factor. Nilsson (1978) is also in favor of large reserves, using field data on plant and bird observations as support. Conversely, Simberloff and Gotelli (1984) argue that several small reserves would maximize local biodiversity. Shafer (1990) and Simberloff and Gotelli (1984) utilize plant data to reveal that small reserves are as effective as a large reserve in maintaining biodiversity. Like true oceanic islands, a higher degree of isolation on continental reserves would result in decreased migration levels to and from the reserve. Furthermore, the destruction and degradation of habitat surrounding the reserve would increase extinction rates, as habitat becomes unsuitable to sustain high biodiversity. A new equilibrium number would be reached as suitable habitats become less available (fig. 8). While the reserve is being properly designed and developed, supersaturation may result primarily due to an excess of species as displaced populations flee into the still relatively pristine reserve system. The reserve may not have the capacity to sustain such high biodiversity, and relaxation of species numbers into a new point of equilibrium may eventually occur (fig. 8). The new equilibrium number may be estimated after information regarding area and degree of isolation is gathered. Diamond and May (1981) use the equilibrium point from ETIB to determine what type of reserve would maximize the species richness and abundance. Whittaker (1998) postulates that larger reserves are

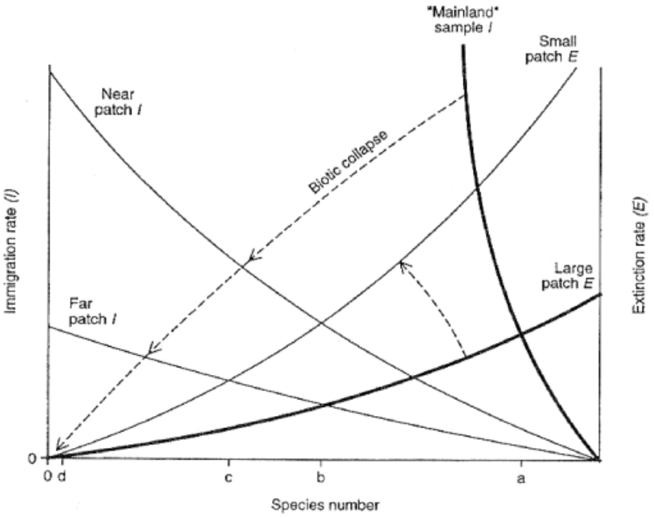

Figure 8—According to the assumptions made by the ETIB, as reduction in area will cause supersaturation as immigration rates decrease and extinction rates increase. This causes a "relaxation" into a lower species equilibrium point. Under extreme circumstances, "biotic collapse" may occur and the results may be an immigration rate so low that the equilibrium number is zero.

more effective than smaller reserves, shorter distances between reserves are better than longer distances, circular shaped reserves are better at maintaining reserve species than elongated shaped reserves due to a reduction of edge effects, and corridors connecting large reserves would be more favorable than without corridors (fig. 9).

The use of island biogeography theory has two main limitations when applying it to the continental reserve design. Firstly, the ETIB focuses on overall species richness of a habitat island by using species-area equations. The ETIB does not allow for the prediction of species with the highest probability of becoming extirpated from the remaining patch (Saunders and others 1991; Whitmore and Sayer 1992; Whittaker 1998; Worthen 1996). This approach then does not permit the investigation of specific species circumstances within the reserve, and may prove harmful if requiring in-depth analysis. Secondly, the ETIB model itself is flawed. Any application of this concept to the continental reserve design and conservation policy also contains such flaws (Whittaker 1998). If the use of this theory is not meticulously studied on a case-by-case basis, certain flaws are not only represented in reserve design, but also perhaps even amplified.

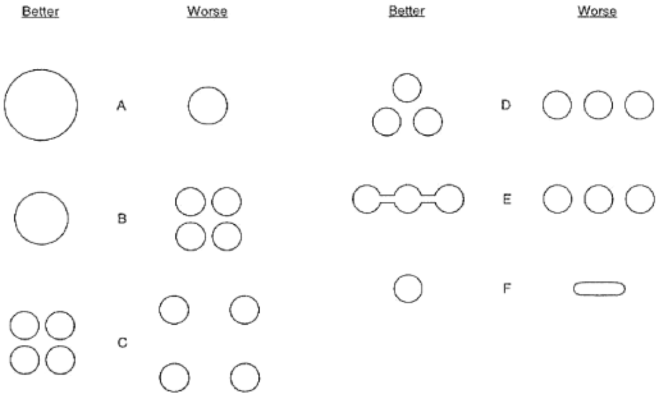

Figure 9—The simplified geometric principles for nature reserve designs derived from island biogeography research (Diamond 1975; Whittaker 1998).

Human Impact on Island Ecosystems

The utilization of island biogeography theory in determining the most effective reserve design has recently been an important issue in conservation. Yet, islands themselves have also been an issue in conservation biology, mainly due to detrimental human impacts in island environments. There are numerous heated debates as to what type of impact the earliest human colonizers had on island ecosystems. Some ecologists and biogeographers argue that most of the earliest island colonizers were respectful of the island ecosystem, and that negative impacts occurred only after secondary arrivals of colonizers conflicted with the interests of the initial inhabitants. Others argue that earliest inhabitants of some islands devastated the environment because of their ignorance and negligence concerning island ecosystems. One rather undisputed fact is that as human communities on islands reached the carrying capacity, humans often modified island landscapes to support the rapidly growing population. A classic example is the terracing of steep terrain on islands in order to maximize agricultural productivity (Nunn 1994). Through history and into the modern age, negative anthropogenic impacts have continued and increased. Humans can easily damage pristine island environments in four ways: overexploitation and predation by humans, habitat loss, fragmentation, and degradation, as well as introduction of exotic species and diseases (biological invasions).

Overexploitation and Predation by Humans

Many islands contain unique endemic species because the remote quality of islands allows for the speciation of flora and fauna to be considerably different from mainland taxa. A classic example of predation of island species by humans is that of the dodo bird (*Raphus cucullatus*), once populated on the island of Mauritius, located east of Madagascar in the Indian Ocean. Dodo birds were endemic and were highly adapted to island conditions. By the early 17th century, Dutch settlers began to colonize the island, hunting both dodo birds and tortoises as food sources. Dodo birds became extinct by the year 1690. Predation of species by humans not only occurred for food sources, but also for tribal (in other words, vibrantly colored bird feathers) and exportation reasons. Moreover, fruit bats are currently being exported from the Polynesian islands. Not only is the declining population of fruit bats an issue of conservation, but also these bats play an imperative role in pollination and seed dispersal of island flora. Therefore, the absence of fruit bat population can also harm the proliferation of many plant species (Whittaker 1998). A secondary extinction can occur under extreme cases.

Habitat Loss, Fragmentation, and Degradation on Island Systems

For centuries, island ecosystems have been the target for habitat loss, fragmentation, and degradation primarily for agricultural reasons. In addition, the wood from the forested trees was used for fuel and residential cooking (Heywood 1979). Such habitat destruction not only directly damages the island flora, but also reduces the faunal biodiversity. As forested areas are diminished, suitable habitats and food resources for fauna also diminish. As habitat fragmentation (deforestation) continues at an alarming rate, it creates major ecological dilemmas on islands such as Madagascar.

Another mechanism of habitat degradation or simplification is human-induced fires. Fires are often utilized for hunting purposes or to clear a plot for agricultural purposes. Frequent fires in areas with a low natural fire frequency can be tremendously destructive. Such prescribed burning can clearly destroy the present island ecosystem and permanently transform the island landscape.

Impact of Exotic Species and Associated Diseases on Island Ecosystems

As humans travel the globe, different species have been intentionally and inadvertently introduced into new ecosystems. Many island species, also known as the native biota, are particularly vulnerable to biological invasions due to their isolation through evolutionary time. The absence of herbivory, for instance, has resulted in the persistence of many island flora with no defensive mechanisms against grazing pressures. Isolation, in a sense, has protected such plant species that, otherwise, would have become extinct on the mainland (Melville 1979). Nevertheless, the presence of abundant herbivores, such as cattle, sheep, goats, and pigs, has led to extreme habitat degradation. Historically, humans intentionally introduced these grazing animals to ensure abundant food supply, without even considering the negative ecological consequences. However, many of these animals have become feral and extremely detrimental to the island landscape. Overgrazing has caused massive erosion on the hillsides, leading to large-scale landslides. Similarly, heavy grazing has encouraged the proliferation of exotic species. The introduction of exotic species into an island ecosystem is typically irreversible. Some exotic species, in fact, are more successful in these foreign environments than in their native landscape. Once those exotic species have established, their populations rapidly proliferate, making it nearly impossible to completely extirpate them from the island.

Foreign diseases on islands are closely associated with biological invasions onto islands. An exotic species is frequently infected with a disease, and can introduce additional harmful diseases onto the island. If island biota is immune to the ill effects of the disease, there is little or no negative impact on the native biota. Conversely, if native island biota is susceptible to foreign diseases, the results can be disastrous. The entire island biota is adversely affected, and many species can be extinguished from the island. If this species is endemic with a narrow geographic range, the entire population of this species is likely to become extinct.

Conclusions and Implications

This article re-examines the equilibrium theory of island biogeography initially proposed by MacArthur and Wilson in 1963. Island environments including topographic origins and characteristics, along with climatic patterns have been discussed. The ETIB is analyzed using essential components, such as species-area relationship, island isolation, dispersal mechanisms, and species turnover. The strengths and weaknesses of the ETIB model are evaluated. Additionally, continental conservation theories that apply the ETIB concept are assessed in terms of minimum viable populations and areas, metapopulation dynamics, continental reserve design, and the SLOSS debate. Lastly, adverse anthropogenic impacts on island ecosystems, such as overexploitation of resources, habitat destruction, and introduction of exotic species and diseases, are examined. This article has primarily re-investigated the research performed by ecologists, biogeographers, and conservation biologists at the forefront of island study. The ETIB has been an issue of heated debate since its emergence nearly four decades ago, and still today, the vitality of the concepts is evolving as researchers gain better understanding of island ecosystems and their pertinence to mainland habitats. This trend will undisputedly continue, but hopefully researchers will be able to unlock all of the knowledge to be gained by these delicate ecosystems before they become relics of the past.

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