

Island Biogeography: Theory and Applications

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Island biogeography is the study of pattern in the distribution of species on islands as influenced by ecological and evolutionary processes related to island characteristics such as isolation and area. The MacArthur-Wilson theory of island biogeography asserts that two processes, immigration and extinction, determine the species diversity of an island's biota. As the number of species on the island increases, the immigration rate decreases and the extinction rate increases. The immigration rate decreases with isolation (distance effect), whereas the extinction rate decreases with island area (area effect). When the immigration and extinction rates are equal, an equilibrium of species diversity is reached. The extinction of species on an island and their replacement by the immigration of new species results in species turnover. The equilibrium theory of island biogeography has been one of the more influential concepts in modern biogeography, ecology, and evolutionary biology. It also has had a major influence on conservation biology, particularly with attempts to develop a theoretical basis for the design of

nature reserves. However, several aspects of the theory remain unsubstantiated, and therefore uncritical application of the equilibrium theory of island biogeography to nature conservation is unwarranted.

I. Introduction

Islands as ecological systems have such salient features as simple biotas and variability in isolation, shape, and size. These characteristics and their large numbers facilitate both intensive and extensive studies with the repeatability necessary for statistical validity. Since Darwin, islands have provided particularly important and fruitful natural experimental laboratories for developing and testing hypotheses on evolution, biogeography and ecology. The theory of island biogeography has been one of the more important products of island studies.

Eugene G. Munroe (1948, 1953) first developed the concept of an island having an equilibrium species number when he examined species-area relationships in his study of the

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distribution of butterflies in the West Indies (Brown and Lomolino 1989). Unfortunately, Munroe's ideas were unrecognized by biogeographers and ecologists until the 1980's, partially because they appeared only as a small portion of his dissertation at Cornell University and as an abstract in the proceedings of a regional conference. Later, Frank W. Preston (1962) made a significant contribution to the early development of island biogeography theory. However, it was Robert H. MacArthur and Edward O. Wilson (1963, 1967), working independently of Munroe and Preston, who provided a coherent, comprehensive theory with elegant mathematical models in their seminal, landmark monograph "The Theory of Island Biogeography." MacArthur and Wilson's work triggered explosive growth in the scientific literature on insular habitat studies and essentially transformed research on island biogeography from largely descriptive works to a more quantitative and predictive new stage. Modified and extended by many others, the MacArthur-Wilson theory continues to occupy a central position in basic and applied biogeography and ecology.

Many studies, inspired by the theory, have been conducted not only on oceanic and continental islands but also on a variety of other insular habitats, involving numerous different taxonomic groups of plants, animals, and microbes. The theory has also had a profound impact on conservation biology in both theory and practice. Although its inspirational role has been tremendous, the validity and applicability of the theory have been hotly disputed.

II. The Equilibrium Theory of Island Biogeography

Species-Area Relationship

A monotonic increase in the number of species with increasing island area (or sampling area of terrestrial communities) has long been recognized. Among various mathematical expressions for the species-area relationship, a power function of the following form has been shown to best fit observations in many cases:

$$S = cA^z \quad (1)$$

$$\text{or } \log S = z \log A + \log c \quad (2)$$

where S is species diversity (the number of species, i.e., species richness), A is area, and c and z are positive constants. c usually reflects the effect of geographical variation on species diversity, and z has a theoretical value of 0.263 and usually varies between 0.18 and 0.35. Linear regression typically has been used to estimate values for these constants.

Although the above equation has been widely used, it provides little explanatory or predictive power. Thus, three hypotheses have been proposed to account for the species-area relationship: (1) the habitat diversity hypothesis by Williams (1964), (2) the passive sampling hypothesis by Connor and McCoy (1979), and (3) the dynamic equilibrium hypothesis independently by Munroe (1948, 1953), Preston (1962), and MacArthur and Wilson (1963, 1967).

According to the habitat diversity hypothesis, the species-area relationship results from a positive correlation existing between area and habitat diversity and between habitat diversity and species diversity. In the passive sampling hypothesis, insular taxonomic groups are simply viewed as subsets or samples from larger communities. Therefore, species diversity is a function of both sampling size and intensity; Coleman et al. (1982) proposed a similar explanation that is referred to as the random placement hypothesis. The dynamic equilibrium hypothesis, the topic of this article, has been by far the most influential in island biogeography and ecology.

Basic Tenets and Mathematical Models of the Equilibrium Theory

MacArthur and Wilson theorized that species diversity on an island is primarily determined by two processes: immigration and extinction. If there are a limited number of empty niches or habitats available on an island, the more species already there, the less likely a successful immigration of a new species and the more likely an extinction of a species already present. For a given area and degree of isolation (usually represented by distance to the island's colonization source), immigration and extinction rates are expected to monotonically decrease and increase, respectively, as the number of established species increases. For a given

number of species, the immigration rate decreases with distance from the source of colonizing species because species have different dispersal abilities -- this is called the “distance effect.” On the other hand, the extinction rate will decrease with island area because the larger the area, the larger the species’ populations and thus the smaller the probability of extinction -- this is referred to as the “area effect.”

When the rates of immigration and extinction are equal, the island’s biota is at a state of dynamic equilibrium, i.e., species diversity remains relatively constant while a compositional change of species continues. These changes in species composition result from concurrent extinction of existing species and replacement by immigration of new species and are termed “species turnover.” The rate of change in species composition is termed turnover rate. In theory, the turnover rate at equilibrium is equal to the immigration or extinction rate (Figs. 1 and 2). If different groups of organisms are treated in parallel instead of collectively, it has been asserted that the turnover rate generally increases from higher to lower organisms (Schoener 1988).

The mathematical description of the MacArthur-Wilson theory takes the following general form:

$$\frac{dS(t)}{dt} = I - E \tag{3}$$

where I is the immigration rate and E is the extinction rate. Assuming homogeneity, temporal consistency, and additivity of immigration and extinction rates among species, a linear relationship between the rates and species diversity would be expected (Fig. 1). In other words, if all the colonizing species have similar per-species rates of immigration and extinction, if these rates are constant with changing species diversity, and if species interactions are insignificant, it holds that

$$I(s) = I_0(S_p - S(t)) \tag{4}$$

$$\text{and } E(s) = E_0 S(t) \tag{5}$$

where I_0 is the per-species immigration rate or immigration coefficient, E_0 is the per-species extinction rate or extinction coefficient, and S_p is the total number of potential immigrants in the colonization pool. Substituting equations (4) and (5) into (3) yields

$$\frac{dS(t)}{dt} = I_0 S_p - (I_0 + E_0) S(t) \tag{6}$$

This equation gives rise to the rate of change of species diversity with respect to time. The number of species on an island at any time t can be calculated by integrating the differential equation. That is,

$$S(t) = \frac{I_0}{I_0 + E_0} S_p - \frac{I_0}{I_0 + E_0} S_p - S(0) \exp(-(I_0 + E_0)t) \tag{7}$$

where S(0) is the initial number of species on an island.

The equilibrium value of species diversity, S_e , can readily be obtained from equation (6) by setting the rates of immigration and extinction equal (i.e., I = E):

$$S_e = \frac{I_0}{I_0 + E_0} S_p \tag{8}$$

Equation (8) states that the equilibrium species diversity is only determined by per-species immigration and extinction rates and the size of species pool. The rate of change in species number can also be related to the equilibrium value as:

$$\frac{dS(t)}{dt} = (I_0 + E_0)(S_e - S(t)) \tag{9}$$

That is, the change rate of species diversity is proportional to the difference between the equilibrium and non-equilibrium values of species diversity. Furthermore, the change rate becomes negative for $S(t) > S_e$, and positive for $S(t) < S_e$. Substitution of equation (8) into (7) yields

$$S(t) = S_e - (S_e - S(0)) \exp(-(I_0 + E_0)t) \tag{10}$$

which indicates the relationship among the values of species diversity at initial, non-equilibrium, and equilibrium states. From the above equation, one can predict the time required for an island in disequilibrium to approach or return to the equilibrium state. This can be done by solving equation (10) for t, resulting in:

$$t = -\frac{\ln R}{I_0 + E_0} \tag{11}$$

where

$$R = \frac{S(t) - S_e}{S(0) - S_e} \tag{12}$$

R is the ratio of the departure of $S(t)$ from equilibrium at time t to its initial deviation at $t = 0$. The (exponential) relaxation time, T_r , is usually defined as the time required for a departure of species diversity from equilibrium to decrease to $1/e$ (or 36.8%) of the initial departure. That is,

$$T_r = \frac{\ln(1/e)}{I_0 + E_0} = \frac{1}{I_0 + E_0} \quad (13)$$

From the above equation, 90% and 95% complete relaxations take 2.303 and 3 relaxation times, respectively.

It is important to notice again that the above quantitative description is necessarily based on the assumption that I_0 and E_0 are the same for all species, are constant in time, and are unaffected by species interactions. However, in nature immigration and extinction capabilities are species specific, temporal variability exists, and interactions occur among species. MacArthur and Wilson (1967) pointed out that non-linear concave curves may represent the rate-species diversity relationship more realistically than do the straight lines. They argued that species with the best colonizing abilities were most likely to establish first and that the weakest competitors would be expected to go extinct first. A gradient in species colonizing abilities would cause rapid initial drop in the overall immigration rate and the combined effects of diminishing population size and increasing species interference could yield a extinction curve that was approximately exponential (Fig. 2).

There also is empirical evidence that the per-species rates of immigration and extinction tend to decrease and increase, respectively, with increasing species diversity. In particular, some studies on birds have suggested that both curves are very concave, especially the immigration curve (Gilpin and Diamond 1976). Some studies also show that the rates of immigration and extinction have a roughly log-normal distribution among species, with differences ranging over many orders of magnitude (Gilpin and Diamond 1981). It has also been suggested that rate curves incorporating stochastic variations would be more appropriate than deterministic lines (Strong and Rey 1982). MacArthur and Wilson (1967) commented that the modifications in shape of

the two curves would not be critical, as long as the curves are monotonic.

Predictions of the MacArthur-Wilson Equilibrium Theory

Many controversies have developed in the literature over what the original equilibrium theory of island biogeography does and does not predict. It is, however, generally accepted that the core of the MacArthur-Wilson theory consists of the concept of species equilibrium and the postulation that the immigration and extinction curves are monotonic. Major predictions based on the equilibrium theory include the following: (1) there is an equilibrium for a given island biota that is achieved when the extinction and immigration rates are equal; (2) the immigration rate is primarily affected by the distance between the island and its continental colonizing source, and the extinction rate varies primarily with island area; (3) for a given island, the immigration rate decreases and the extinction rate increases with increasing number of species already on the island; (4) the number of species at equilibrium increases with island area and this increase should be faster on more remote islands; (5) the number of species at equilibrium decreases with island-continent distance and this decrease should be faster on smaller islands; and (6) the species turnover rate at equilibrium is greater on less distant and smaller islands (Fig. 2).

III. Modifications and Extensions of the Original Equilibrium Theory

The curves of immigration and extinction rates are central to the equilibrium theory of island biogeography. Studies have suggested: (1) the immigration rate, at least for plants, may initially increase with increasing species diversity as the original unfavorable environmental conditions of the island are ameliorated by the first colonists, and (2) slight rate heterogeneity and weak species interactions may alter both concave and convex curvatures, whereas great rate heterogeneity, temporal variability, and strong species interactions can produce significant changes in the rate curves such as discontinuities, non-monotonic features, etc. Wu and Vankat (1991) examined the effects of

several different sets of immigration/extinction rate-species diversity curves on the predictions of the MacArthur-Wilson theory through computer simulations. They found that different monotonic rate-species diversity curves do not affect the basic predictions of the theory of island biogeography; however, the level of equilibrium species diversity can be substantially affected. On the other hand, non-monotonic rate-diversity curves may result in potential multiple equilibria of species diversity.

Questions about the assumption of independence between immigration and extinction rates also have produced modifications in the original MacArthur-Wilson model. For example, researchers have claimed that the extinction rate of insular populations may be reduced when immigration of conspecific individuals provides demographic reinforcement and augments genetic variability of existing populations (e.g., Brown and Kodric-Brown 1977; Wright 1985). This phenomenon has been referred to as the “rescue effect.” It suggests that distance directly affects not only the immigration rate but the extinction rate as well. More specifically, with greater distance the extinction rate may increase as immigration of conspecifics decreases. This may initially increase the turnover rate before its expected decrease. The rescue effect is most likely when the immigration rate is very high or at least approaches local recruitment rate; therefore, it may not occur with truly isolated islands. Another example of the lack of independence between immigration and extinction rates is that island area may affect both, at least to the degree that larger islands are more likely to receive immigrants than smaller ones. The phenomenon of increasing probability of immigration with island area has been called the “target effect” (Gilpin and Diamond 1976).

Questions also have been raised about the assumption of the original MacArthur-Wilson theory that evolution rates are always much slower than colonization rates and therefore can be safely ignored. This assumption leads to the conclusion that the emergence of new species on an island results only from immigrations. Some studies on the isolated Hawaiian Archipelago have shown that the autochthonous speciation rate has exceeded the immigration rate and, with

adaptive radiation, has produced a species-area equilibrium involving a high degree of endemism (Juvik and Austring 1979). Other studies also have shown that island forms can evolve rather rapidly and differentiation to the subspecific level may occur in a single generation (Berry 1983). By restricting gene flow between islands and their species pools, isolation could facilitate inter-island evolutionary divergence and increase endemism. A long-term equilibrium of species diversity involving speciation, immigration, and extinction has been termed the “taxon cycle;” it describes the process of ecological and evolutionary diversification of species populations on islands (see Simberloff 1974).

The original simplistic equilibrium concept has been expanded to include four phases of an insular species equilibrium: the noninteractive equilibrium, the interactive equilibrium, the assortative equilibrium, and the evolutionary equilibrium (Simberloff 1974; Pielou 1979; Dickerson and Robinson 1985; Wu 1989). The first, the noninteractive equilibrium, is a temporary or short-term phase that involves a balance between immigrations and extinctions occurring when species populations are thought to be too small for interspecific interactions to be significant. The second phase, the interactive equilibrium, is reached as population sizes grow and some of the less fit original colonizers are lost due to competitive exclusion. Following this, the third phase of assortative equilibrium involves a long time period of colonizations by better-adapted species and extinctions of lesser-adapted species. This continual sorting of species composition, with or without change in species diversity, results in a non-random, coadapted set of species. The fourth phase, the evolutionary equilibrium, reflects the impact of natural selection on species diversity, as it represents the balance between the addition of species via increased species coadaptation and adaptation to physical environment and the deletion of species through extinction as niches evolve to be narrower. Over geological time, evolution tends to gradually increase the equilibrium number of species -- a number which is steady over ecological time.

Another development was Wu and Vankat's (1991) quantitative synthesis of the theory of island biogeography. They produced a

comprehensive system dynamics simulation model incorporating a variety of modifications and extensions, including area, distance, competition, habitat diversity, target, and rescue effects. A main purpose of their work was to provide a user-friendly simulation tool to enhance understanding of the internal structure and predictions of the theory when the modifications are taken into account.

IV. Applications of the Theory of Island Biogeography

MacArthur and Wilson conjectured that the theory of island biogeography should be applicable to insular continental habitats and habitat patches at various spatial scales. Since then, the theory has been applied to a variety of "habitat islands" such as individual plants, caves, lakes or ponds, mountain tops, microcosms, and patches of terrestrial ecosystems. In fact, it was the theory of island biogeography that most noticeably brought scientists' attention to spatial patchiness and the effects of habitat size and isolation on ecological and evolutionary processes.

The theory of island biogeography, therefore, has served as a conceptual framework for studies of impacts of habitat fragmentation on biological diversity and for research in conservation biology in general. It also has inspired theoretical investigations of population dynamics in heterogeneous environments and, more recently, provided an impetus to the development of the field of landscape ecology, particularly in North America. For example, consideration of the effects of patch area and inter-patch distance has been central to both empirical and theoretical studies of the dynamics of populations and flows across landscape mosaics. The equilibrium theory also has been adapted to help explain mass extinctions in geological time, as diversity at different taxonomic levels (species, genera, or family) is treated as the product of a dynamic equilibrium between origination and extinction. For example, the MacArthur-Wilson model was employed to explain changes in diversity of North American land mammal genera during the past 12 million years. However, such paleobiological models have received much criticism (Benton 1987).

Almost from its inception, the theory of island biogeography has had enormous impacts on both the theory and the practice of nature conservation. Indeed, among its numerous applications, the theory finds its widest, most conspicuous, and yet most controversial usage in the design of nature reserves to maximize species diversity -- with nature reserves being perceived as islands in a sea of human-transformed habitats. Such applications gained tremendous momentum during the early 1970's when general design principles based on the species-area relationship and the equilibrium theory were proposed. These principles became widely publicized in prestigious journals and books, including the "World Conservation Strategy" published by the International Union for the Conservation of Nature and Natural Resources in 1980. The so-called general design principles included: (1) a large reserve is superior to a small one; (2) a single large reserve is better than several small reserves with the same total area; (3) when two or more reserves are inevitable for some specific habitat or species, inter-reserve distance should be as short as possible; (4) corridors between reserves are recommended to increase inter-reserve immigration; and (5) a circular shape is optimal because it minimizes dispersal distances within the reserve.

The relevance of these design principles/recommendations has been heavily criticized. For example, several authors have pointed out that there is little evidence of a dynamic equilibrium in continental habitat islands, yet the assumption of equilibrium is essential to the theory of island biogeography. Also, the theory itself does not directly address questions of shape, including what is optimum (if there is an optimal shape). Several researchers have reached the conclusion that the matter of shape is trivial in the design of nature reserves, if the mechanisms controlling species diversity dynamics for reserves and for islands are comparable. Another criticism is that while corridors between reserves certainly may increase immigration, facilitate gene flow, and reduce local extinctions through the rescue effect, the effectiveness and significance of corridors may greatly depend on their content and dimensions, inter-reserve distance, and specific species involved. Moreover, corridors may increase the

spread of disease, disturbance, and exotic species. Hence, decisions about corridors ought to be case-specific rather than blindly follow general principles.

A particularly controversial aspect of applying the MacArthur-Wilson theory to nature conservation has been whether a single large or several small reserves (SLOSS), with the same total area, would better protect species diversity. The answer to the SLOSS question depends on the slope of the species-area curve, the proportion of common species in the small reserves, and the gradient of colonizing abilities among species in the available pool (Soulé and Simberloff 1986; Zimmerman and Bierregaard 1986; Burgman et al. 1988). Indeed, both theoretical analysis and empirical evidence have suggested that in some circumstances several small reserves may have more species than a single large one. Several small reserves may have compensating advantages such as greater overall habitat heterogeneity, lower intra- and interspecific competition, reduced spread of some diseases, disturbances, and exotic species, and more habitat for edge species. Moreover, the debate over SLOSS has overlooked the complexity of species diversity dynamics. Such factors as minimum viable population (MVP), minimum area to sustain MVP, and minimum dynamic area to maintain the ecosystem integrity must be considered in questions concerning nature conservation (Soulé and Simberloff 1986; Burgman et al. 1988; Wu 1989; Shafer 1990). In conclusion, it is generally accepted that the species-area relationship and the theory of island biogeography are equivocal with respect to the SLOSS issue.

V. Critiques of the Theory of Island Biogeography

The equilibrium theory of island biogeography, like many other ecological models, is difficult to test. For the purpose of validation, the following necessary but not necessarily sufficient conditions have been suggested: (1) a strong species-area relationship; (2) an equilibrium state of species diversity; (3) an appreciable species turnover rate; and (4) detectable distance and area effects. Therefore, a strong species-area relationship alone neither

suffices to validate the equilibrium theory itself nor to warrant its application to a particular set of insular habitats. MacArthur and Wilson clearly pointed out in their original work that a species-area curve does not prove the existence of an equilibrium.

Many attempts have been made to verify or falsify the MacArthur-Wilson model; however, direct experimental examinations, which would be most convincing, have been uncommon. Simberloff and Wilson (1969, 1970) designed an experimental test involving removing the fauna from a group of six small red mangrove islands in the Florida Bay while leaving two similar ones as controls. They concluded that their results supported the theory although the turnover rates were substantially overestimated. Another experimental test (Rey 1981) demonstrated the dynamic equilibrium and the area effect but did not clearly detect the distance effect. Other work purporting to validate the equilibrium theory has been controversial. Studies often have been insufficient or erroneous because of misunderstanding the theory or misinterpreting the data collected. Recent work shows that the testing processes may also be confounded by artifactual ratio correlation when relative rates of immigration, extinction, and turnover are used (Schoener 1988).

Since the late 1970's, the validity of the equilibrium theory has been increasingly questioned and criticized on several grounds. In spite of an extraordinary number of studies regarding this theory, it has been frequently criticized for lack of convincing evidence to support the existence of a species equilibrium, species turnover, and area and distance effects. The theory also has been criticized for over-aggregating many affecting factors into essentially two variables, area and distance, and leaving out species-specific population demographic and genetic information which may provide the mechanism for species diversity dynamics. Several recent reviews concluded that the equilibrium theory of island biogeography remains insufficiently validated and its application to nature conservation is premature (e.g., Boecklen and Gotelli 1984; Simberloff 1986; Soulé and Simberloff 1986; Zimmerman and Bierregaard 1986; Burgman et al. 1988; Wu 1989). These criticisms have led to efforts to

develop non-equilibrium theories of island biogeography which emphasize the importance of such characteristics of island biotas as habitat heterogeneity and transient (non-equilibrium) dynamics.

VI. Concluding Remarks

The MacArthur and Wilson's dynamic equilibrium theory has had revolutionary impact on island biogeography in particular and on biogeography in general by providing a conceptual framework and insight into the dynamics of geographical patterns of species diversity. It has been one of the more influential concepts in biogeography, ecology, and evolutionary biology. However, several aspects of the equilibrium theory remain unsubstantiated, and, while it appears to hold in some specific cases, it does not in many others. Uncritical application of the theory to nature conservation is unwarranted and may lead to misleading conclusions.

In general, as with other equilibrium paradigms in ecology, the equilibrium theory of island biogeography is being treated with increasing skepticism. Nevertheless, the criticism does not completely negate the value of the theory of island biogeography. Qualitative use of the theory can result in valuable contributions to studies even when its quantitative application may be invalid. More specifically, the theory was and still is important in guiding scientists in constructing conceptual frameworks for addressing relevant questions in which patchiness and isolation otherwise may not have been sufficiently emphasized or even identified. In fact, as indicated in the preface of their book, even MacArthur and Wilson did not believe that the equilibrium model would exactly fit all field observations; instead, they hoped that the theory would provide stimulus and impetus for advancing "new forms of theoretical and empirical studies." In this regard, the equilibrium theory of island biogeography is one of the most successful theoretical developments in the history of biogeography and ecological science.

Glossary

Area effect The phenomenon that species extinction rate is reduced with increasing island area.

Distance effect The phenomenon that species immigration rate is reduced with increasing distance between an island and its continental source of colonizing species.

Extinction curve The curve relating species extinction rate to the number of species already present on an island.

Immigration curve The curve relating species immigration rate to the number of species already present on an island.

Island biogeography The study of pattern in the distribution of species on islands as influenced by ecological and evolutionary processes related to island characteristics such as isolation and area.

Rescue effect The phenomenon that species extinction rate is reduced when immigration of conspecific individuals provides demographic reinforcement and augments genetic variability of existing populations.

Species-area curve The curve relating number of species to island area.

Species diversity Either the absolute number of species (species richness), or a measure that incorporates both the number of species and their relative abundance.

Species turnover Changes in species composition resulting from concurrent extinction of existing species and replacement by immigration of new species.

Target effect The phenomenon that species immigration rate increases with increasing area of islands, when distance is constant.

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immigration and extinction (I and E, respectively) and the number of species present (S) on an island. These relationships assume homogeneity, temporal consistency, and additivity of immigration and extinction rates among all species in the species pool. An equilibrium value of the number of species (S_e) is reached when the rate of species immigration from a colonizing pool of size S_p is equal to the rate of species extinction on the island. Species turnover rate at equilibrium (\hat{T}) is equal to the immigration or extinction rate.

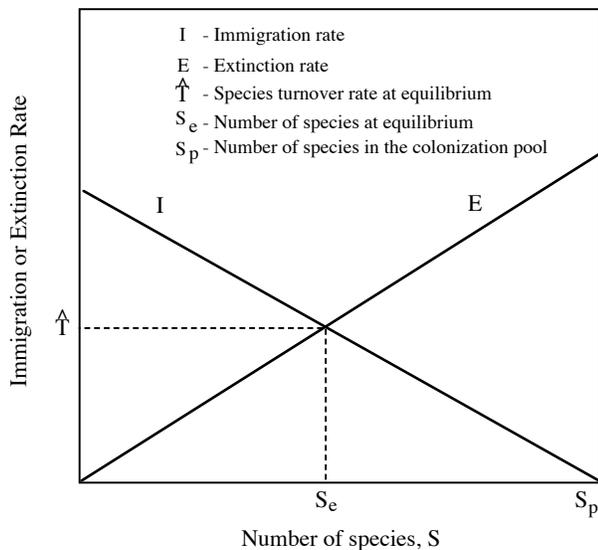


Figure 1. The simplest version of the equilibrium model of island biogeography with linear relationships between the rates of

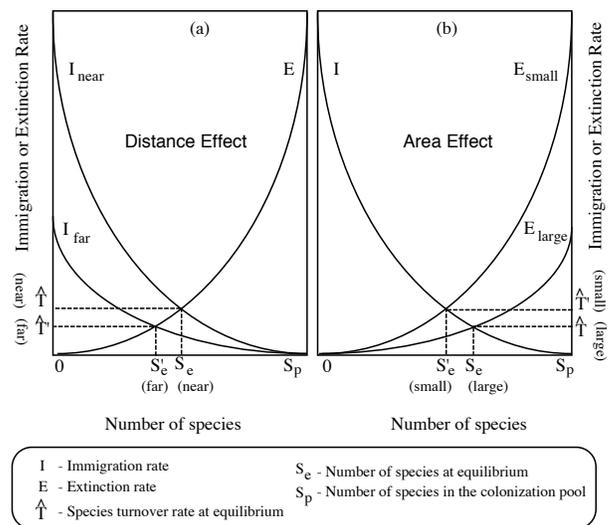


Fig. 2. The main tenets of the MacArthur-Wilson theory of island biogeography. The number of species on an island is determined by two processes: immigration and extinction. With an increase in the number of species on an island, the immigration rate (I) decreases monotonically and the extinction rate (E) increases monotonically. For a given number of species, the immigration rate is smaller for more distant islands (distance effect, part a), whereas the extinction rate is larger for smaller islands (area effect, part b). As a result, the number of species at equilibrium (S_e) is greater on larger and less distant islands than on smaller and more remote ones. Species turnover rate at equilibrium (\hat{T}) is greater on less distant and smaller islands. (Adapted from Daniel S. Simberloff 1974).