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EQUILIBRIUM THEORY OF ISLAND BIOGEOGRAPHY AND ECOLOGY

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THE BIOLOGICAL IMPORTANCE OF ISLANDS

Oceanic islands and archipelagoes are intrinsically important to biologists; 5% of the land surface of the earth is insular, and if South America, which has been an island throughout most of its existence, is included the figure rises to 19%. Significant portions of the evolutionary histories of many economically and biologically important species occurred on oceanic islands, and if the earth were not liberally sprinkled with isolated bits of land in addition to the "world continent," its biota would be much poorer.

But the intrinsic importance of islands, scientific or economic, has not inspired the intense research in island biogeography which justifies this review of recent advances. Rather it is the realization that oceanic islands are paradigms for geographic entities ranging in size from tiny habitat patches (52, 53) to continents (86, 92, 112) or even the entire earth (74). It is almost a platitude that Darwin's observations in the Galapagos Archipelago and Wallace's in the Malay Archipelago crystallized the then nascent concept of organic evolution by natural selection (13, 110), and many other classical evolutionary advances rest originally on insular observations. Because islands are so clearly isolated from other land masses, island population data contributed heavily to the realization that most speciation is allopatric (54). Wallace's Malaysian observations allowed strong inferences about changing sea levels, past land connections, and the position of a line separating two great biogeographic provinces (110). Insular isolation is important ecologically because it allows us to be virtually certain that an organism encountered on an island is a true nesote. Consequently, problems in community structure and function, such as the distribution of individuals into species or the trophic relationships among populations, are more readily attacked in an island setting; any organism found there is assuredly a member of the biotic community.

This first salient island characteristic, isolation, leads to the second, biotic depauperization. The relative simplicity of insular biotas allows interactions among populations to be deduced which would be obscured in a more complex mainland context. For example, that addition of a predator trophic level can impart stability to an otherwise unstable herbivore-plant association (63) is indicated in the simplified Isle Royale ecosystem, in which a moose population feeding on vegetation was stabilized by the addition of wolves. Such clarity would be difficult to achieve on the mainland, where alternate food sources and other agents of mortality abound. Similarly, regional pest control schemes are frequently tested on islands because efficacy and the presence of unexpected side effects are more easily assessed on simplified insular communities. That release of sterile male screw-worms could eradicate this dipteran livestock pest over wide areas was first confirmed on tiny Sanibel Island and then on Curacao (3). Potential ecosystem disruption through use of a molluscicide to control the snail vector of the cattle liver-fluke was tested on the small island of Shapinsay, in the Orkneys (39).

From an evolutionary standpoint the importance of insular depauperization has been to allow the continued existence of forms which would have been selectively eliminated through various sorts of interactions in a richer biota. The depauperization is generally not random, but rather, poorly dispersing species are differentially absent, causing island biotas to be "disharmonious" in their composition, i.e. overly rich in certain groups and disproportionately poor in others, vis-à-vis the mainland (6). Large predators, for example, are relatively rare on islands and a major mainland selective pressure is consequently absent or severely reduced. One result of such slackened selection has been the frequent evolution of bizarre plants and animals on islands (6), while another is the notorious fragility of island communities, their rapid destruction with the arrival of Western man, and the great number of extinctions of island endemics upon interaction with introduced species (6, 22). But to a theoretician looking for nomothetic importance in his observations, the key feature of evolution in a depauperate community is that co-evolutionary selective pressures are easier to deduce and the reasons for a species' particular morphology, behavior, and general niche characteristics more easily determined. The very introductions that endanger island communities may yield information on such phenomena as ecological release, species replacement, and niche shift (60) much more quickly and clearly than on the mainland.

Any patch of habitat isolated from similar habitat by different, relatively inhospitable terrain traversed only with difficulty by organisms of the habitat patch may be considered an island; in this sense much of the biotic world is insular, for habitats are often not homogeneous but rather are arranged as patches in a crazy quilt. Consequently, any model of island biology should be relevant to small scale, local systems, as well as to larger ones. General theories of the essential insularity of mainland community dynamics (40, 52, 53) remain untested except for a group of caves as islands colonized by arthropods (10) and a single application to ants on truly oceanic islands (55); however, aspects of an hypothesis originally proposed for oceanic islands (59, 60) have been tested with some success in the field on several

"habitat islands": fresh water colonized by assemblages of both plants and animals (41, 62, 87), artificial and natural substrates colonized by aquatic (5, 70) and marine (68, 79) organisms, caves for both aquatic and terrestrial animals (9, 11, 109), and montane areas for birds (108) and mammals (4). Such clearly insular microhabitats as cow pats, sand dunes, and bromeliad containers can also be viewed as islands.

THE ECOLOGY OF ISLAND COMMUNITIES

The Equilibrium Theory of Island Biogeography

A decade ago, Preston (72) and MacArthur & Wilson (59, 60) revolutionized biogeography with the suggestion that the biota of any island is a dynamic equilibrium between immigration of new species onto the island and extinction of species already present. Species number would then be constant over ecological time, while evolution would act gradually over geological time to increase the equilibrium number of species (119). Although a few voices (50, 78) still call for an idiographic approach to biogeography, with each island examined as a unique locus of species assembled for idiosyncratic reasons that can tell us little about other islands, the equilibrium hypothesis has been experimentally confirmed for oceanic islands, proved useful in interpreting many other insular situations, and spawned a mass of research which has given biogeography general laws of both didactic and predictive power. It has been both a partial cause and a major result of two continuing trends: an increasing emphasis on extinction as a common, local, ecologically important event, rather than a rare, global, evolutionary one, and a shift of focus from the individual and the species to the local population as the fundamental unit in both ecology and evolution (91, 93).

The oceanic island data originally available to test directly the basic assertions of the equilibrium theory, i.e. that "turnover" of species constantly occurs but number of species remains unchanged, were consistent with the hypothesis but did not confirm it. The colonization of Krakatau occurred without a preeruption census and involved few and differentially exhaustive monitorings, while the data on plants of the Dry Tortugas proved only that natural extinction occurs frequently in that archipelago. Much stronger evidence has recently been published.

A direct test was performed by Simberloff & Wilson (88, 94, 95, 120), who "defaunated" a group of six small red mangrove islands in Florida Bay by methyl bromide tent-fumigation, while leaving two similar islands as untreated controls. These islands were different distances from the main Florida Keys, and, because they had no supratidal ground, their animal communities consisted of only 20–50 arboreal arthropods (of hundreds in the Keys species pool), primarily insects. Exhaustive censuses were made before the defaunation and periodically afterwards. The number of species remained unchanged on the control islands, though composition changed continually. That the dynamic equilibrium model is generally accurate was indicated explicitly by the following facts:

1. On all islands but the most distant, species number rose slightly above the predefaunation number, then fell and oscillated about that number. The characteris-

tic overshoot was interpreted as caused by the small population sizes in the early stages of colonization, allowing more species to coexist than would be possible on a more crowded, untreated island. On the most distant island, the relatively fewer species that were able to invade early built up abnormally large population sizes in the absence of competitors and predators, eliminating the overshoot and retarding attainment of the equilibrium.

2. The equilibria were dynamic; turnover rate at equilibrium on an island 200 m from potential source areas was 0.5–1.0 species ($\sim 2\%$ of the biota) per day. Most turnover was produced by propagules obliged to be transients on these simple islands for want of suitable food or habitat, but extinctions of bona fide mangrove colonists were frequently observed.

If the mathematics of the simple equilibrium model are manipulated appropriately, further qualitative predictions are generated for testing against the results of the mangrove island experiment. Both Simberloff (88) and MacArthur (56) have shown that the same qualitative predictions hold if the original model, based on equivalence of all species in the species pool in abilities to disperse to and maintain populations on islands, is made more sophisticated by assuming different invasion and colonization capabilities for different species.

First, it is clear from even the simplest equilibrium model that distant islands ought to have fewer species than near islands, and that small islands ought to have fewer species than large ones (Figure 1). The experimental mangrove islands conform to this pattern, but since any natural historian was well aware fifty years before

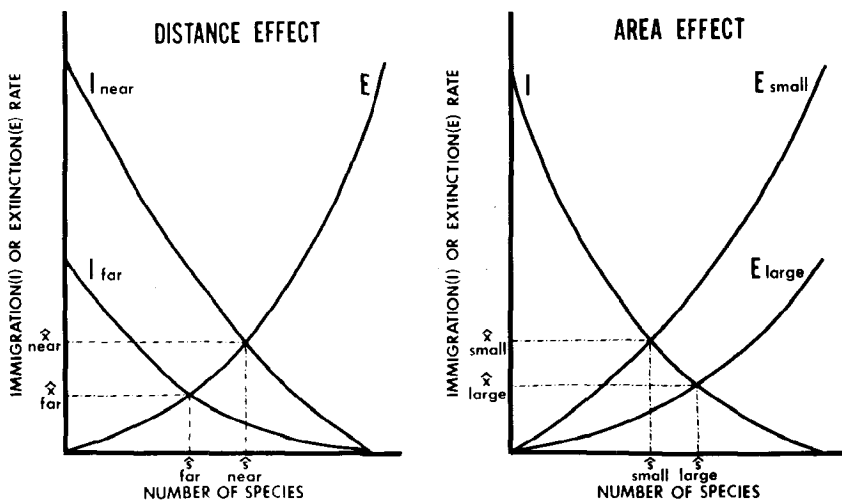


Figure 1 An island biota is an equilibrium in ecological time between immigration of new species and extinction of those already present. (Left) Distance effect; a near island has larger equilibrium number of species (\hat{S}) and turnover rate (\hat{X}). (Right) Area effect; a large island has larger \hat{S} and smaller \hat{X} .

the equilibrium theory that distant islands were depauperate and that large areas tended to have more species than small ones, this observation should not be construed as yielding strong support to the details of the equilibrium model. Other interpretations may be given to both the distance and area effects.

However, the dynamic nature of the model allows further, less intuitively obvious predictions about rates and time scales. For example, the equilibrium model equations can be rearranged to show that distant islands not only ought to have fewer species but also should take longer to reach any fraction of the equilibrium number from a sterile or defaunated condition. MacArthur & Wilson suggested 90% as a standard fraction, and $t_{0.90}$, the time required to reach 90% of equilibrium, as the standard time period for comparison of colonization episodes. Diamond (19) has recently generalized the concept of return to equilibrium from a perturbed state to include perturbations, such as area reduction or mass invasion by a group of immigrant species, resulting in an island's being oversaturated with species, in addition to those (like defaunation) that leave it undersaturated. The generalized interval he proposed for the asymptotic return to equilibrium is the "relaxation time," (t_r), which he suggests should be the time required for the displacement from equilibrium to fall to $1/e$ (36.8%) of the value caused by the perturbation. This time interval is a natural one only if immigration and extinction rates are constant, and seems not to constitute a conceptual advance over $t_{0.90}$. In any event, on the defaunated mangrove islands $t_{0.90}$ was consistently greater on the more distant islands, in accord with equilibrium theory.

The theory yields a prediction for the shape of the colonization curve of number of species vs time, $S_t = \hat{S}(1 - e^{-Gt})$, where S_t is the number of species at time t , \hat{S} is the equilibrium number of species, and G is a constant. [A modification of the theory to allow for differences in invasion and survival proficiencies among species predicts a sum of terms, each of which has an equation formally similar to the above one (88). The summed curve is shaped like the MacArthur-Wilson curve, asymptotically approaching an equilibrium.] The colonization curves of the experimental islands were all consistent with this mathematical shape except for the small overshoot, but could not be construed as validating the theory because of the large standard deviation of the predicted curve (88).

Finally, an equation can be deduced relating $t_{0.90}$, \hat{S} , and equilibrium turnover rate \bar{X} for any island, $t_{0.90} = 1.15 \cdot \hat{S}/\bar{X}$. When observed values of \bar{X} and \hat{S} for the defaunated islands were inserted into this equation, the resultant $t_{0.90}$ was within the range of the observed $t_{0.90}$ allowed by the errors of approximation for all variables.

Hubbell (42) recently constructed a Laplace-transformed linear systems version of the equilibrium model that allows inferences concerning when an island's species number should be oscillatory even with constant propagule invasion rates. In particular he demonstrated mathematically that for any distance from a source area there is a range of island sizes that will have oscillatory species numbers, and that the greater the distance from the source area, the narrower the area range for oscillations. This is compatible with the Simberloff-Wilson experimental data, in which the most distant island showed no overshoot. However, this is not surprising since Hubbell's model assumes competition to increase as population sizes increase, and

Simberloff & Wilson (88, 94) explain the overshoots or lack thereof as consequences of observed population increases. Hubbell's model goes further, however, and treats the results of an oscillatory invasion rate as well as the fluctuations in species number to be expected in archipelagoes. Although the defaunated islands provided no data to test this aspect of the model, Simberloff has recently created a series of archipelagoes by dividing large mangrove islands into groups of small ones, and as data from this experiment are gathered they may be compared to Hubbell's predictions.

Heatwole & Levins (37) have reexamined the colonization data for the defaunated islands and have shown that, if the arthropod colonists are divided into broad niche types (detritus-feeders, herbivores, wood-borers, etc), the defaunated islands not only gradually achieved their original number of species, but also their original broad trophic structure, or distribution of species into the different niche types. This observation is exciting, for it implies that the groups on these islands are true interacting communities, and not just haphazard assemblages which arrived and were extinguished fortuitously. Although the arboreal red mangrove system does not appear to be one in which species interactions are particularly pronounced, it is possible that evolution has gradually molded the source fauna so that the mangrove resource is utilized in some canonical, nearly optimal way, with the result that random subsets of this source biota are likely to be rather close to the canonical structure.

MacArthur (56) demonstrated that a group of competitors would be expected to evolve so as to minimize the squared deviation of resource usage from availability, while May (63) has shown that the trophic relationships among any collection of species are constrained within severe limits if the collection is to be stable. If considerations such as these force even the initial colonists to fall within a circumscribed set of distributions into niche types, continued immigration and extinction would be expected to produce ever more highly coadapted sets of species. For whenever turnover results in a more stable group of species, that group is expected to persist longer than its predecessor. Wilson & Simberloff (95, 119) termed the initial relatively stable number of species the "noninteractive equilibrium," and viewed the sequence of increasingly coadapted groups as "interactive equilibria" leading to an "assortative equilibrium" with a lower turnover rate. They also proposed that the interactive equilibria will be successively larger on the grounds that the component species in a more highly coadapted complex might be expected to have smaller niches. MacArthur (56) and May (63) showed that minimization of squared unused resources is indeed facilitated by more species, but that a limit to species packing is set by increased probability of extinction as niches are narrowed.

Data gathered on birds and plants of the Channel Islands off Southern California provide yet another test, both direct and indirect, of the equilibrium theory of island biogeography. The clearest evidence for its essential truth is that presented by Diamond (14), who showed that number of species of land and freshwater birds (for each island but a fraction of the California pool) changed only slightly between 1917 and 1968, while composition changed markedly; turnover was between 0.3 and 1.2% per year, and these are extreme minima since immigration and extinction

probably occurred between the two censuses without having been recorded. In work with just a single taxon (birds, in this study), one must always consider whether the observations are not an artifact of the taxon, or whether, for example, the entire fauna of these islands might not be in equilibrium. Other than major changes recently wrought by man (49), there is no reason to disbelieve the implication that the islands are in equilibrium, and birds probably constitute such a large, distinct, and unified ecological group that observations on birds alone are a valid test of the equilibrium model. Johnson (49) believes that avian turnover in the Channel Islands is not nearly so high as Diamond states, presumably because one or both censuses were deficient. But since Diamond's figures are probably underestimates for reasons already given, his claim of considerable turnover in ecological time is almost certainly correct.

Figure 1 shows that, all other things being equal, one would expect higher relative turnover rates the smaller the island and the nearer the island to the mainland. Diamond's data for Channel Island birds show no correlation between avian turnover and island size or isolation. If the turnover rate data are in error, as Johnson claims, this finding need not contradict the equilibrium theory. Diamond offers two other explanations. The first is that the mainland-island distances in this system are so small (61 miles maximum) relative to the flight capabilities of the birds that all islands are equally attainable; Johnson points out that some members of the California species pool would be limited by distances in this range, but concurs with Diamond's contention so long as it is limited to those species that are likely to attempt island colonization at all.

Diamond's second suggestion is that the effects of distance and area on turnover rates and equilibrium numbers may be masked if islands differ in other important parameters. Since 1835, over a century before the publication of the equilibrium theory, it has been observed that number of species tends to increase with area, whether one examines mainland quadrats or an archipelago of islands (21), but it has only been recently that area per se has been accorded a role in the determination of species number (91). Rather, area has been thought to act primarily or exclusively through habitat diversity; as area increases, so usually does the number of habitats, each with its complement of species. Johnson et al performed multiple regression analyses of plant species number on the Channel Islands plus adjacent mainland areas (46). Although area was the single best predictor of species number, they viewed this as a result of its high correlation with ecological diversity, and elevation range and latitude (indicators of ecological diversity and ecological richness, respectively) contributed significantly to the prediction of species number. So did isolation of the islands, more distant islands having fewer plant species, all other things being equal. This last observation is consistent with equilibrium theory predictions, but since no data on turnover were presented the study cannot be considered a direct test of the theory.

Power (71) constructed a path diagram to model the regulation of numbers of plant and bird species on the Channel Islands, again using multiple regression as a test for significant effect of various environmental variables. His results for plant species agreed with those of Johnson et al, except that island isolation had little effect

in his analysis. Plant species number was the best predictor of bird species number, although insular isolation also accounted for significant variation in number of bird species. So Diamond's hypothesis—that turnover rates do not correlate with area and distance as predicted by the equilibrium model because an even more important factor, ecological diversity, varies somewhat independently of them—is consistent with available data.

Before leaving the Channel Islands I should point out a shortcoming of multiple regression analysis as a test of the equilibrium model. At best, such an analysis can render the model plausible, if species number correlates appropriately with island isolation and area. But regression cannot demonstrate causality; we have already seen that a correlation between area and species number can be (and has been) construed as demonstrating the effect of habitat diversity, without reference to any dynamic equilibrium, while fewer species on more distant islands can be interpreted as the result of the distant islands' not yet being full. Furthermore, a path diagram such as Power's, even if based on a stepwise multiple regression analysis, is subjective. Without our own biological insights we could as well have viewed bird species number as a determinant of plant species number, than vice versa. Paine (69) and Janzen (44) have done something very similar in ascribing number of species in a trophic level to amount of predation on that level. A regression analysis might also omit subtle environmental variables important to the organisms under investigation. Diamond's work, on the other hand, constitutes an objective test of part of the model; turnover was demonstrated.

A slight deductive step from the equilibrium theory provides a means by which area may affect species number completely independently of habitat diversity. If extinction is, in fact, a common event, its frequency should increase as population sizes decrease. That is, on a small island with lower carrying capacities, any extant population will likely be extinguished more quickly from either interactive or noninteractive causes than would a conspecific population on a larger island with larger carrying capacities; this is the basis for the raised extinction curve in Figure 1. MacArthur & Wilson (60) claim that for every combination of per capita birth (λ) and death (μ) rates there is some carrying capacity (K) such that a propagule landing on an island with carrying capacity greater than K is much less likely to be extinguished than if the carrying capacity were lower. Put another way, for every species there is a critical carrying capacity (and presumably, associated critical island area) such that extinction is much more likely on islands of less than critical size than on those of greater than critical size. The key quantity in calculating critical size is λ/μ , rather than the intrinsic rate of increase $r = \lambda - \mu$. A reexamination of this hypothesis (75) confirms its general conclusion of a critical size, above which successful colonization is much more likely, and shows that if $1 \leq \lambda/\mu \leq 1.5$, the expected time to extinction even for an established population is not extremely long; that is, extinction may well be a common event even on large islands.

Crowell (8), in extensive experiments on three rodent species on small islands in Penobscot Bay, provided evidence not only that turnover occurs, but that the hypothesis of a critical population size determined by per capita birth and death

rates is valid. The fates of introduced populations of various sizes were monitored, as were those of extant populations and of islands from which the resident populations were removed by trapping and poison. Per capita birth and death rates were estimated, and the pattern of turnover on these islands accorded well with the equilibrium model. A further conclusion was that competition is much less likely to prevent colonization in this ecosystem than is poor dispersal aptitude.

Critical population sizes would produce a clear, dynamic effect of area on species number, but so long as extinction probability decreases monotonically with population size and population size increases monotonically with area, area per se would be expected to influence island species number independently of an effect through habitat diversity (30, 60). Simberloff has demonstrated this effect directly by censusing nine homogeneous mangrove islands, then removing various fractions on all but one control island, and recensusing after a period for reequilibration had passed. The size of the control fauna was unchanged, while species number fell by $\sim 5\text{--}10\%$ on all the reduced islands. Since no microhabitats were removed and the microhabitat proportions were virtually unchanged, area clearly had an independent effect on species number. For very small islands one can probably separate the effects of increased area and added habitats because it may be obvious, as in the mangrove island colonization experiment, which species are precluded by absence of appropriate habitat. Such a distinction has been drawn for plants of tiny atoll islands (113) and animals of sand cays (54). Each habitat may be viewed as possessing an equilibrium number of species, though for species which span two or more habitats this is an oversimplification.

In addition to these three direct demonstrations (in the Florida Keys, the Channel Islands, and Penobscot Bay) of equilibrium maintained on oceanic islands by frequent extinction and immigration, observations of turnover and apparent equilibrium have been reported for birds on Karkar Island in New Guinea (17) and Mona Island in the Caribbean (105), and for invertebrates and plants on small islands near Puerto Rico (38, 54, 55). (The Puerto Rican studies also present data relating life history parameters to expected length of colonization, and demonstrating an approximate trophic structure equilibrium as well as a species number equilibrium.) But clearly nonequilibrium situations can also yield relevant data, both lending support to the dynamic equilibrium hypothesis and allowing interpretation of apparently anomalous distributions in light of the hypothesis.

The Florida Keys defaunation experiment is an example of how the dynamics of a nonequilibrium situation, the presence of a series of "empty" islands capable of supporting animals, can verify the equilibrium hypothesis. But natural occurrences such as the production of a new island (the volcanic island of Surtsey off Iceland, various "fill" islands such as the Dutch polders, or islands risen from intertidal sand banks such as Memmert in the North Sea) or sterilization of preexisting islands (the volcanic defaunation of Krakatau in the East Indies and Long Island near New Guinea) also leave undersaturation.

By comparison to a regression equation for New Guinea satellite islands, with area, distance from New Guinea, and maximum elevation (a partial measure of insular habitat diversity) the independent variables, Diamond (18) calculated an

equilibrium number of bird species for islands suspected of being out of equilibrium. Using these numbers, he estimated that $t_{0.90}$ for Long Island is less than 300 years and for Krakatau less than 80 years (presumably because reforestation occurred more quickly on Krakatau; the relationship between plant and bird species numbers has already been discussed). He pointed out that these are probably underestimates since they rest on the assumption that immigration rate is a constant fraction of the species that have not yet colonized. Actually it is biologically evident (56, 59, 60) that dispersal differences among species of potential colonists cause this fraction to decrease, as the good dispersers are differentially removed from the pool of species that have not yet colonized.

Diamond also examined the islands of the D'Entrecasteaux Shelf, which was a single island of about 7430 square miles in the Pleistocene, but has been fractionated into several small islands by rising seas. One might expect these islands to be oversaturated for their areas, with increased extinction, fostered by the decreased area, gradually reducing species number. In fact, large islands of this shelf all fall above Diamond's regression, supporting the contention that they are oversaturated. Calculated relaxation times for these islands were in the range of 15,000 years. That the approach to equilibrium after oversaturation should be so much slower than after defaunation (or undersaturation generally) is probably partly due to different time scales for the underlying biological process (extinction and colonization, respectively) and partly to differences in the extinction probabilities among species in the pool (18, 59, 60). The least suited island colonists are extinguished first, lowering island extinction rates both because they can no longer be extinguished (they no longer exist on the island!) and because their absence lessens competition. Small islands on this shelf have much lower relaxation times, presumably because extinction probabilities increase with decreasing area, as discussed above.

Islands which have once been connected by land bridges to New Guinea are also oversaturated, as evidenced by their positions above the regression equation. Again the larger islands have relaxation times estimated in the range of 7000 years, while the small island estimates are much lower. Similar results were produced by analyzing islands that had been connected by land bridges not to New Guinea proper, but to satellite islands. Terborgh (103) has used a related kinetic analysis to explain the gradual reduction in bird species number on Barro Colorado Island, formed some sixty years ago during the construction of the Panama Canal.

Simberloff (92) has demonstrated that the mass extinction of more than half the marine invertebrate families during the Permo-Triassic may be interpreted as relaxation to a new and lower equilibrium; the extinctions coincided with a two-thirds decrease in area of the shallow marine seas, possibly fostered by sea-floor spreading (86). The model is fundamentally different from Diamond's in two regards. First, origination must replace local immigration as the force tending to increase family number, and so the number of families present increases rather than decreases the number of opportunities for further families to exist, since each family must arise from a preexisting family. Second, extinction and origination rates varied with the square of the deviation of number of families from an equilibrium estimated from area.

Terborgh (102), analyzing the evolution of plant species number, suggested that local patches of some habitat will support a local equilibrium number of species determined by immigration from other patches of the same habitat and competitive extinction proportional to the square of the number of species present. [Similar hypotheses of local patch diversity maintained in equilibrium through interpatch migration have been proposed (40, 52, 53).] The number of species in the habitat as a whole, however, is viewed as a function of area, the speed of evolutionary response to changed conditions, and the patchiness of the habitat, and is thought to evolve through a series of nonequilibrium states. Extinction, independent of species number, is believed to be caused by major climatic or topographic changes. Webb (112) has shown that the number of genera of North American land mammals through the late Cenozoic was determined by balanced extinction and origination, with occasional nonequilibrium episodes caused by habitat fractionation, lowered sea levels, and other environmental changes.

Many analyses have been performed that regress numbers of species of different taxa on oceanic islands of an archipelago on area, isolation, and a variety of parameters related to habitat diversity, such as elevation range, number of plant species (for birds), number of soil types, and latitude (2, 31–36, 46–48, 111). Similar regressions have been done on caves, rivers, and mountaintops as habitat islands (4, 87, 108, 109). The primary pattern that emerges is that area is usually the best single predictor of species number, though the degree to which it accounts for variation in species number decreases markedly as better indicators of habitat diversity are used. I have already discussed the limitations of multiple regression and the independent evidence that area is important, but these studies are nevertheless consistent with the equilibrium model. Early indications that area did not contribute significantly to the determination of bird (33, 34) and plant (35) species number in the Galapagos have proven incorrect when a more complete flora was used (36, 47); the inference may now be made that bird and plant species numbers are determined by the same factors as in the Channel Islands. Brown's evidence that mammals on mountaintop islands are not in equilibrium (4) may equally well be interpreted as showing only that relaxation times are very long.

Interactions Among Island Populations

In the equilibrium model, species number is assumed a sufficient parameter for describing and predicting the course of island colonization; all species are considered equivalent members of a species pool. An analogy may be made to a chemical equilibrium of the form $A + B \rightleftharpoons AB$. Under constant conditions, the amounts of the molecules A, B, and AB are approximately constant. If we actually counted the number of each kind of molecule we would see minor fluctuations, but these would be so small compared to the total numbers of molecules that it would be virtually impossible to observe them; the statistical means of the amounts are sufficient for most purposes. That different individual molecules of A and B are randomly bound in AB at different times is unimportant; all comparative areas of biology emphasize differences among species, and it is intuitively clear that the equilibrium constellation of species found on an island is not a random subset of those available in the

pool. The observation (37) that the faunas of the fumigated mangrove islands converged to a canonical distribution into trophic classes is perhaps the clearest experimental demonstration of this fact.

The data adduced as evidence for the nonequivalence of species' colonizing potential are often inappropriate, however. Although better dispersers might be expected to reach islands more than other species, and better competitors ought to persist on them longer once established, numerical analyses, as opposed to detailed observation and experiment on the species of interest, may be misleading. MacArthur et al (57), examining the 59 land bird species of the Pearl Islands, listed 19 of the 47 Panamanian families as absent, including 6 with 11–22 mainland species. (Actually, their data show 18 families absent; the Sylviidae are represented by *Polioptila plumbea* on Rey.) They state, "While the absence of families with one or two mainland representatives might be merely a result of random sampling of species, the absences of families with 11–22 mainland species is very unlikely to be accidental." In fact, in 20 random computer draws of 59 species from the 642 in Panama, only three times was no family with 20 or more species omitted, while three times families of 30 or more species were missed, and one draw did not include families with 23, 22, 17, 17, 16, and 13 species, respectively! The expected number of families in a random draw of 59 species from the Panamanian pool is 26.16 with standard deviation 2.31 (106); the Pearl Islands actually contain 29 families. If anything, then, there are more families present than there ought to be in an avifauna this size. In sum, evidence of nonrandom colonization is not to be found in the Pearl Islands' presence or absence data alone. Rather, the important observation is that many of the same families that are absent from the Pearl Archipelago are also missing from other islands (57).

A similarly inaccurate inference, that the relative paucity of congeneric species on islands is caused by increased difficulty of coexistence in typically resource-poor island ecosystems (23), was shown by identical methods to be artifactual (89). Actually, island biotas tend to have slightly more congeneric pairs than would a randomly drawn, equal-sized subset of the mainland pool. In both instances, the tendency of confamilial and congeneric species toward increased competition and rather similar dispersal powers is probably insufficiently strong to allow major insights. In this area of biogeography, in contrast to the equilibrium theory, laborious autecological studies are more likely than statistics to be illuminating. In any event, as both Simberloff (89) and Terborgh (101) have pointed out, degree of congeneric sympatry must itself be an equilibrium between the increased probability that near relatives will be able to disperse to the same places and their increased difficulty in coexisting. Terborgh's method is to construct species-area curves for different families of birds in the West Indies, then to intercept all these curves by vertical lines drawn through given areas and to read off the number of species in each family. From such an analysis he observed that changing degrees of sympatry [or "disharmony," to use Carlquist's (6) term] are expected with changes in island size. As it is a trival computer exercise to draw randomly any number of species from a species pool and then to calculate expected degree of sympatry, species-area curves for individual families are a tortuous way of demonstrating disharmony, and

since the data on which the curves are based come from the islands about which the predictions are to be made, this method does not actually explain disharmony.

But an autecological examination of the families, combined with historical data about the islands, allowed Terborgh to rationalize the apparent rough equilibrium levels of sympatry and the existence of a few aberrant islands. The extent of determinism in West Indian bird faunas turns out to be quite high; Terborgh calculated similarity coefficients between the avifaunas of different islands, extrapolated to find what the coefficients would be if the islands were in the same location, and concluded that perhaps 88% of the fauna, species for species, of a small or medium-sized island can be predicted from area and location alone.

Several detailed autecological studies have attempted to explain observed levels of sympatry on islands as a consequence of competition for limited resources. Such work tacitly assumes that immigration is a negligible force in that islands are saturated with all the species they can contain, given the available resources; a higher immigration rate would only be balanced by a higher extinction rate, with the species equilibrium remaining unchanged. Competition and resource limitation are also assumed, and direct evidence is only rarely available. Wider variability in trophic structures for island species has been adduced as evidence for wider niches upon release from competition, but relationships among morphological variability, niche width, and number of coexisting species remain unproven (25, 98, 107, 116). One would hope that either the level of some limited resource could be changed, with concomitant changes in population sizes of putative competitors, or that removal or addition of a putative competitor should affect the population size of some species. But the techniques required for such experiments are difficult, and researchers are usually forced to infer competition from differences in a species' niche among different sets of other species or from morphological differences among coexisting species.

Lack claims that hummingbirds disperse readily among the West Indies, and that the nearly universal existence of two species on low islands and three species on mountainous ones is due to competition for food (51). That the two species on low islands are always comprised of one large and one small form is strong circumstantial evidence for this hypothesis, as is the restriction of the third species on mountainous islands to the montane humid forest. Further indirect confirmation comes from observed habitat expansion for two species on islands where apparent competitors are absent, and the observed replacement in the Virgin Islands of one hummingbird by another, similar one.

Lizards of the genus *Anolis* in the West Indies have been exhaustively studied by Williams (115) and Schoener (80–85). Islands have up to 23 species, and the number on a given island is not directly limited by immigration rate; one can infer many failed invasions. Rather, these lizards partition resources by habitat and size differences and apparently exclude by competition potential immigrants. Although the niche has many subtle dimensions, perch size, height, insolation, and time of perch utilization appear to be most important; it is possible for any island to construct for *Anolis* as Lack did for hummingbirds a fundamental fauna with an approximate number of species of certain size, habitat, and feeding characteristics, and to view

deviations from the predicted, fundamental fauna as variations on a theme. Additional strong evidence that competition structures the insular subsets of anoles consists of different niche parameters for a given species coexisting with different groups of congeners; ecological release and various kinds of niche shift, some involving sexual dimorphism, have been documented. McNab (61) constructed similar fundamental bat faunas for tropical islands, with food size (inferred from body size) and food type as key parameters.

Niche shifts in birds of the Pearl Islands (57), West Indies (104, 105), and islands near New Guinea (15, 19), and in ants of the Puerto Rico region (55) and Dry Tortugas (60) have been reported, and MacArthur & Wilson (60) discussed some earlier examples of niche shift and ecological release on islands. But as MacArthur & Wilson pointed out, in many instances there is no evidence whatsoever of niche shift in depauperate faunas, and perhaps absence of striking changes in resource utilization is more the rule than the exception. Evolution of increased niche width during ecological release should be particularly slow in sexual species (77). Diamond (15) has shown for the southwest Pacific islands that changes in habitat are most frequent and immediate, changes in foraging behavior rarer and dependent on evolution of appropriate morphology, and changes in food rarer still, while half of all colonizing populations undergo no changes in niche. Part of the explanation for the apparent inability to utilize newly available food supplies lies in degree of initial preadaptation to the new resource and differences in genetic plasticity (15), but another possible explanation is that competition is not always important and populations need not be limited by resource shortages. The yellow-faced grassquit on Jamaica ought to be released from competition with many seed-eaters in Central America, yet is less abundant, occupies the same number of habitats, and has the same morphology (73). The only observed difference was less stereotypy in seed size among Jamaican birds.

Two meticulous studies on island colonization have indicated a nearly deterministic pattern completely predictable from a knowledge of the pairwise interactions among species. Morse (65, 66) observed that when one warbler was found on a small island off the coast of Maine it was always the Parula Warbler; when two species were present they were always the Parula and Myrtle. The Black-throated Green was only present with the other two on slightly larger islands. The number of species depended on forest size, and the order of colonization was due to the greater plasticity of foraging behavior of the Parula and Myrtle Warblers, allowing them to expand their habitat usage and thus to survive on small, resource-poor islands. The Black-throated Green, by contrast, has highly stereotyped behavior (a consequence of its high population densities and dominant position on the mainland), which prevents adjustment to small-island life. Apparently the subordinate positions of the Parula and Myrtle Warblers preadapt them to successful colonization. There was no evidence of interspecific competition on the islands among the three species; rather, their short-term success or failure on small islands depends on intrinsic behavioral traits evolved over long time periods on the mainland, possibly in response to long-term competitive pressure there. The stylized behavioral resource partitioning also allows these three species to coexist on larger islands while the

American Redstart and Yellow Warbler, lacking such a well-defined interspecific social hierarchy, exclude one another.

Myomorph rodents exist on islands in a variety of combinations. Crowell's study in the Gulf of Maine (8) demonstrated that the joint distribution of *Microtus*, *Peromyscus*, and *Clethrionomys* could be satisfactorily explained by intrinsic dispersal and survival capabilities, and that competition appeared to be unimportant. Grant examined species of the same genera plus *Apodemus* and decided that competitive exclusions are more important than dispersal and establishment abilities, a conclusion which he has buttressed by cage studies of pairwise interactions (26, 27). Crowell suggested that different immigration rates for different archipelagoes are the basis for his and Grant's conflicting results. It should be added that Grant's island data do not evidence competition directly (through population size changes) and that his competition experiments showing population size changes were in a mainland setting very different from Crowell's tiny islands.

Differences in avian population density between islands and mainland have also been related to competition. Niche expansions upon release from competition have been inferred as the reason that island densities are higher than or equal to mainland densities in the PEARL Islands (57, 58), Tres Marias (24), Mona Island (105), Lesser Antilles (104), and Bermuda (7), despite reductions in species number. On New Guinea satellite islands, however, total densities are severely reduced (16). Diamond has suggested (16) that one must examine the species involved; where insular densities exceed those of the mainland, the nesioties are largely found in their mainland habitat or one quite similar, while on New Guinea satellites habitat expansion has been greater, resulting in occupancy of major parts of the islands by relatively maladapted birds. The claim that insular resource paucity causes population sizes of potentially competing congeneric species to be more disparate than those on the mainland (24) has been questioned (90), and population density statistics are generally not likely to illuminate island ecology without detailed niche data on the component species. Recent work on island vs mainland insect abundance suggests that disproportionate insular depauperization of predators can profoundly and complexly affect densities of lower trophic levels (1, 45).

ISLAND SPECIES AND EVOLUTION

The Taxon Cycle

We have seen that insular disharmony is a consequence of more than just the inevitable statistical changes in species-genus-family distribution when species number is reduced. Certain species are preadapted to insular colonization because they are adept at either overwater dispersal or survival on islands. Wilson proposed that the distribution of ants in Melanesia is due to a taxon cycle (117, 118) in which widespread Asian species adapt evolutionarily to marginal habitats, especially shore conditions that facilitate dispersal to islands. Some propagules reach similar littoral habitats on New Guinea and surrounding islands, where they either die or invade (in evolutionary time) the inner rain forests and mountains. If they are not extin-

guished in the rain forests, their evolutionary divergence ultimately results in new species. Most are restricted, but there may be habitat expansion including readaptation to littoral habitats from which the cycle may once again be started. Larger islands are more likely to produce expanding species which may initiate the cycle, presumably because the competition from greater numbers of species leads to fitter species and produces more pressure to occupy marginal habitats.

The taxon cycle is itself a dynamic long-term equilibrium process dictating which species contribute to the immigration and extinction rates that establish the short-term island equilibrium number of species. It is also ultimately responsible for the degree of sympatry or disharmony which I have already described as an equilibrium, within the island equilibrium, between increased probability of related species' jointly colonizing an island and increased likelihood of exclusionary competition once they do. In a sense, we have three equilibria depending on the scale with which we view islands: the taxon cycle is a long-term equilibrium flux of species involving speciation, immigration, and extinction, and generates pressures the short-term local expressions of which are dynamic equilibria of number of species and degree of sympatry. The taxon cycle has been shown, with minor local modifications, to be consistent with distributional and ecological data on birds, lizards, and insects of several island groups (12, 15–17, 20, 28–30, 76, 115).

Overlaying this strictly biotic-based dynamic scheme for determination of how many and which species will be present on any island are geological and sea level changes that create and destroy land bridges, join several shelf islands to one another and/or the mainland, and fractionate a single land mass. During periods of connection entirely new short-term equilibria prevail and dispersal is facilitated. Expanding species inhabiting marginal regions are still more likely to reach areas that were or are destined to be parts of different islands, so that the equilibrium level of sympatry may not be disturbed. But if an entire taxon with poor over-water dispersive powers is precluded from some islands that are never united to the mainland and allowed on others that have periods of connection, very different faunas may result, both in species number and type of disharmony. These effects have been demonstrated from paleontological evidence for Pleistocene mammals of the Aegean Sea (96, 97). MacArthur and Diamond (18, 56, 57) have emphasized how important the geological history of an island group is in explaining the distribution of so mobile an order as the birds. They distinguish between land-bridge and oceanic islands, and from island distributions and autecological data deduce the species in the Pearl Islands and the New Guinea satellites that are likely to require a connection in order to immigrate. The main conclusion has already been stated in the context of Diamond's island relaxation time work: higher extinction rates on small islands decrease the time until a new short-term equilibrium number of species is achieved after a geological event changes immigration rates. In other words, very small land bridges and oceanic islands may have very similar biotas.

A final factor affecting the short-term immigration–extinction balance is a gradual rise in the equilibrium as species evolve so as to be more highly coadapted to one another and to the local environment (95, 119). This “finer tuning” of an island community should decrease niche widths and extinction rates, thus permitting the coexistence of more species. Yet another equilibrium is ultimately reached, however,

Table 1 Nested, interdependent equilibria which simultaneously determine the status of an island biota. Geological events and introductions act particularly on asterisked equilibria to produce temporary nonequilibrium states.

	Equilibrium	Time Scale	Balanced Forces
Biogeographic Region	Evolutionary*	Evolutionary	+ Speciation - Extinction
Island	Taxon cycle	Evolutionary	+ Immigration of expanding mainland species - Extinction of contracting species on island
	Evolutionary	Evolutionary	+ Increased adaptation to local physical conditions and coadaptation among species - Increased extinction as niches evolve to be narrower
	Assortative and Interactive	Ecological (long)	+ Increased coadaptation of successive colonizing subsets - Increased extinction because of present narrow niches
	Noninteractive*	Ecological (short)	+ Immigration - Extinction
	Sympatry of close relatives*	Ecological	+ Similarity of dispersal powers - Tendency to increased competition

as there is a limit to how narrow niches may be before extinction rates rise dramatically (56, 63). The exact capacity for evolutionary increase in the short-term equilibrium must depend on the taxon, biogeographic region, and island size. A comparison between small Pacific islands with recently colonizing, widely ranging "tramp" ant species and those with old, presumably coadapted native ant faunas suggested that a doubling of species number is possible (121). The various equilibrium processes that determine the instantaneous status of an island biota are listed in Table 1.

Distance and Time in Host Plant Islands

Janzen (43) has suggested that the equilibrium theory of island biogeography should be applicable in evolutionary time to plant species as host plant islands for phytophagous insects, with phylogenetic distance between plant species an additional parameter that must be considered in assessing whether a particular plant has its equilibrium number of insects. An examination of the tree species of Great Britain and several other regions led Southwood (99) to conclude that the number of insect pest species for each tree species increases with the range of the tree, but that if an equilibrium exists, it is achieved only in evolutionary time; introduced plant species thus have relatively few insects. Whittaker (114) even claimed that phytophagous insect communities may never reach equilibrium, but rather species number in-

creases indefinitely, unlike vertebrate assemblages. Strong (100) disputed both aspects of this hypothesis, presenting evidence that initial phytophagous insect community equilibration occurs in ecological time, and the equilibrium reached [an "assortative" equilibrium in Wilson's (119) terms] depends largely on the present range of the plant. Opler (67) demonstrated that eighteen species of oaks were indeed islands in evolutionary time, with number of species of leaf-miners an equilibrium between speciation and extinction. Plant range was the chief determinant of this number, and the data fit an equation of the form $S = kA^z$ just as they do for various taxa on oceanic islands. The appropriate distance parameter is unclear; geographic distance from other "islands" is important, as the apparent source for most colonizations is a sympatric tree species. Taxonomic distance between tree species is not monotonically related to ease of inter-island colonization by insects of the trees as islands, but Opler dealt with a single closely related group of plants. Relaxation time for an oak "island" isolated from larger islands and left with many more insect species than the equilibrium predicted by its area is at least half a million years, but Opler presented no evidence on tree species islands that are suddenly "undersaturated," such as by an introduction, so that his hypothesis need not conflict with Strong's claim that introduced host plants equilibrate rapidly. One must recall the difference in relaxation times for birds on over- and undersaturated islands off New Guinea.

CONCLUSIONS

Island biogeography has changed in a decade from an idiographic discipline with few organizing principles to a nomothetic science with predictive general laws. The dynamic equilibrium theory which effected this transformation has been shown to describe one level of a multi-level process occurring in both ecological and evolutionary time; the major insight leading to the theory is that local extinction and immigration are relatively frequent events. Both species number and species composition result from the interactions of several concurrent equilibria, though departures from one or more of the equilibria frequently arise from singular events such as introductions or geological changes. The equilibria are ultimately quasiequilibria (119) then, since they are subject to long-term change. "Equilibrium" in this sense is synonymous with "compromise," and the realization that island communities are compromises parallels the view that individual species are compromises and the application of optimization theory in an attempt to understand the particular compromises achieved by natural selection.

Even more important than an increased understanding of oceanic island biotas is the realization that many habitats are somewhat insular and their biotas are in equilibrium just as are those of oceanic islands. We can therefore use island biogeographic theory to further our understanding of a variety of evolutionary and ecological phenomena and even to aid in the preservation of the earth's biotic diversity in the face of man's ecological despoliation (103).

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CONTENTS

THE EVOLUTION OF WEEDS, <i>Herbert G. Baker</i>	1
THE ECOLOGY OF SECONDARY SUCCESSION, <i>Henry S. Horn</i>	25
THE ECOLOGY OF MANGROVES, <i>Ariel E. Lugo and Samuel C. Snedaker</i>	39
THE ECOLOGY OF MACROSCOPIC MARINE ALGAE, <i>A. R. O. Chapman</i>	65
THE USES OF CLADISTICS, <i>Peter D. Ashlock</i>	81
METHODS OF COMPARING CLASSIFICATIONS, <i>F. James Rohlf</i>	101
FREQUENCY-DEPENDENT SELECTION, <i>Francisco J. Ayala and Cathryn A. Campbell</i>	115
CLOSED ECOLOGICAL SYSTEMS, <i>Frieda B. Taub</i>	139
EQUILIBRIUM THEORY OF ISLAND BIOGEOGRAPHY AND ECOLOGY, <i>Daniel S. Simberloff</i>	161
WARFARE IN ECOLOGICAL PERSPECTIVE, <i>Andrew P. Vayda</i>	183
DESERT ECOSYSTEMS: HIGHER TROPHIC LEVELS, <i>Immanuel Noy-Meir</i>	195
CONTINENTAL DRIFT AND VERTEBRATE DISTRIBUTION, <i>Joel Cracraft</i>	215
BIOGEOGRAPHICAL CONSIDERATIONS OF THE MARSUPIAL-PLACENTAL DICHOTOMY, <i>Jason A. Lillegraven</i>	263
THE MEASUREMENT OF SPECIES DIVERSITY, <i>Robert K. Peet</i>	285
STREAM DRIFT AS A CHRONOBIOLOGICAL PHENOMENON IN RUNNING WATER ECOSYSTEMS, <i>Karl Müller</i>	309
THE EVOLUTION OF SOCIAL BEHAVIOR, <i>Richard D. Alexander</i>	325
EFFECTS AND FUNCTIONS IN THE EVOLUTION OF SIGNALING SYSTEMS, <i>Daniel Otte</i>	385
THE DEMOGRAPHY OF PLANTS, <i>J. L. Harper and J. White</i>	419
INDEXES	
AUTHOR INDEX	465
SUBJECT INDEX	476
CUMULATIVE INDEX OF CONTRIBUTING AUTHORS, VOLUMES 1-5	486
CUMULATIVE INDEX OF CHAPTER TITLES, VOLUMES 1-5	487