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The equilibrium theory of island biogeography: fact or fiction?

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ABSTRACT. The development of the equilibrium theory of island biogeography and its basic concepts are outlined. Studies purporting to validate the theory are critically examined, and it is concluded that there is little support for its tenets. The application of the theory to nature conservation and ecology is therefore premature.

Introduction

The class of phenomena to which Science is relevant is only a part of the limitless range of events past, present and future, which impinge upon us all. In scientific investigations it is essential that experiments be carried out carefully and rigorously in order that they be logically acceptable to the corpus of scientific reasoning and cannot be challenged on purely technical grounds. It is a sad fact that many, even the majority, of problems are examined in an uncritical and imprecise manner; it is my contention that this has occurred in the enquiry into and the exploration of the consequences of the equilibrium theory of island biogeography.

In order that results be 'scientific', certain criteria must be met, the major ones being the principles of falsifiability and repeatability. These remove the problems of *ad hoc* hypotheses and ostensive definitions (see Popper, 1968). Similarly the correct procedure is the adoption of the null hypothesis and its attempted refutation; there has been a lack of such rigour in many of the studies that I shall consider.

I shall first outline the theory of island biogeography as proposed by MacArthur & Wilson (1963, 1967) and how it has been modified and extended by later contributions, and then go on to look at the various experimental and observational attempts at proving it. I consider significant the fact that one of

the champions of the equilibrium theory, D. S. Simberloff, has in the last few years completely revised his opinions, and is now seen to be urging caution in the interpretation of the results (compare his 1974 review with the critique in 1976b). This *volte face* has not gone unpenalized; one need only look at the set of replies (Diamond, 1976a; Terborgh, 1976; Whitcomb *et al.*, 1976) to one of Simberloff's papers (Simberloff & Abele, 1976a) in *Science* to realize that now he has been cast as one of the 'bêtes noires' of conservation for his views. The critique referred to (Simberloff, 1976b) has, rather interestingly, gone uncited in nearly all subsequent papers that I have examined. The major conclusion of my review is that Simberloff's critique should not be ignored, and that the equilibrium theory remains insufficiently validated to permit its widespread application to many problems of biogeography, ecology, and nature conservation.

The equilibrium theory

The equilibrium theory of island biogeography was developed from an attempt to understand the observations summarized by Preston (1962) and Williams (1964): communities were shown to have various statistical properties, in that statistical distributions could be fitted to data on the relative abundances of species, and one characteristic

feature of these data is that there are very many more comparatively rare than common species. An attempt to analyse this by Fisher, Corbet & Williams (1943) led to the conclusion that a logarithmic series could be fitted, and Preston (1962) showed that, by converting the abundances to canonical form (i.e. a geometric scale), one could obtain a normal distribution. The relationship between the number of species and their canonical abundances is therefore log-normal. A major difficulty of this scientific 'fact' is that it exists purely as a singular statement, part of no explanatory theory, and as such it generates no testable hypotheses; it is merely a convenient description of the state of Nature. Another difficulty is that it assumes that the relative abundances do not change with the passage of time. This is patently untrue: the classical example of fluctuating sizes of populations in the arctic has been superseded by other demonstrations of cycling numbers from both temperate and tropical environments.

When faced with a highly complicated phenomenon where the observed effects result from an interaction of many factors, themselves complex and poorly understood, one must deliberately choose a situation where many, if not most, of these factors are simplified. Thus, in the judgement of the experimenter, these factors can to all intents and purposes be regarded either as constant, or too insignificant to be worth including in the study. But here there is a grave risk of the 'circle of affinity' (Tansley, 1935) being incomplete, and any result may thus be excluded from the corpus of scientific knowledge because it may not satisfy the criteria to which I have referred.

The 'very special case of island species' (Krebs, 1972) results from their being a trap that collects successfully dispersing and colonizing species. In the words of Slud (1976), reviewing the literature dealing with avifaunas of islands throughout the world: '... islands come closest to constituting discrete independent ecosystems or natural laboratories; this makes islands desirable for the study of geographical variation'.

Preston (1962) pointed out that a relationship could be derived from his canonical abundances of species if one assumed that the

number of individuals in a taxon on an island could be represented by the product of the density of those individuals and the area. This relationship is:

$$S = cA^z$$

where S is the number of species inhabiting an island of area A , and c and z are constants. Latitudinal gradients in the diversity of species were construed to be 'due' to variation in the value of c , taken to represent the 'biotic richness' of a particular region. Theoretically, z takes a value of 0.263.

When, using 'nested' areas on a continent, such a regression line is plotted, values for oceanic islands are seen to lie below the line, consistent with the observation that islands are impoverished relative to the mainland in terms of the number of species that they support. This is 'a reflection of unfilled niches owing to the difficulties of over-water colonisation' (Slud, 1976; supported by Abbott, 1978), or, if the habitats are ecologically 'full', then it may be due to an impoverished habitat caused by an absence of suitable niches (Lack, 1973). The great problem was the biological significance of the canonical distribution, which was inexplicable then, as now.

Other deductions from the corpus of factual data on the diversity of species include modern niche theory, which owes a good deal to the work of MacArthur. He developed the idea of 'diffuse competition' (see MacArthur, 1972), whereby a set of very different species compete indirectly with one another and with potential invaders, preventing colonization.

The considerations outlined above led MacArthur & Wilson (1963, 1967) to propose their equilibrium theory, combining these factors with the basic phenomena of immigration and extinction, to suggest that the number of species on an island, S , tended towards an *equilibrium* number, \hat{S} . This equilibrium is the result of a balance between the rate of immigration and the rate of extinction, and the equilibrium number is determined by the island's *area and position only* influencing these rates. The equilibrium is therefore dynamic, and this should be in evidence as a *turnover* of species constant for any one island from year to year once equilibrium has been reached.

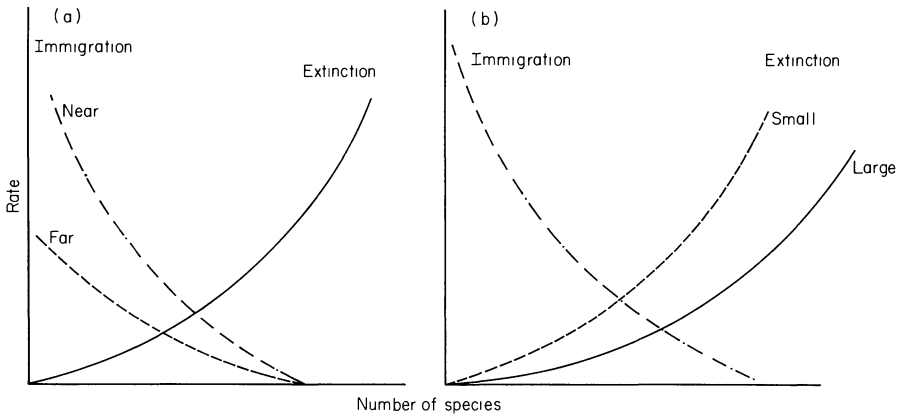


FIG. 1. (a) MacArthur & Wilson's diagram showing the effect of distance; rates of immigration are plotted for islands 'near' and 'far' from the source of the colonists, together with the extinction rate. The model predicts different numbers of species at equilibrium (where the rates of immigration and extinction are equal) for differing distances from the source. (b) MacArthur & Wilson's diagram showing the effect of area, which is postulated to act on the sizes of populations and hence on the rates of extinction. Once again the model predicts different numbers of species at equilibrium for 'large' and 'small' islands.

This is not the only explanation for the relationship between the area and the number of species; others are, for example, that large islands have more habitats than small ones, or that the biota of a larger island constitutes a larger sample of the total number of species available for colonization (Simberloff, 1978b).

MacArthur & Wilson presented their ideas graphically (see Fig. 1) and their treatment resulted in an asymptotic curve of colonization of the form

$$S_t = \hat{S} (1 - e^{-Gt})$$

where G is a constant, \hat{S} is the equilibrium number, S_t is the number of species at time t .

The theory went on to consider briefly the qualitative differences between species, and then demonstrated the importance of 'stepping stones', i.e. chains of islands. The mean lifetime of a population from colonization to extinction was derived mathematically, and the insular species were noted to have larger population sizes and niches – the so-called phenomenon of 'ecological release' or 'niche expansion' – than their conspecifics inhabiting the mainland. Evolution was seen as strictly allopatric, and the authors considered that there would be a gradual rise in the equilibrium number over long time spans. As

required, the theory generated several falsifiable predictions:

(i) that the observed turnover in the composition of species is considerable;

(ii) that $\log \hat{S}$: (a) increases more rapidly with $\log A$ on distant islands than on islands near a source of potential immigrants, and (b) increases more rapidly with the reciprocal of distance on smaller islands than large:

(iii) that, at equilibrium, for a set of similar islands,

$$\frac{\text{variance } (\hat{S})}{\text{mean } (\hat{S})} \leq \frac{1}{2}$$

and for islands initially devoid of species, the ratio of the variance to the mean number of species begins at a value of 1, and falls to 0.5 as they approach equilibrium; and

(iv) that the rate of turnover, T , can be estimated from the time taken for an initially uninhabited island to reach 90% of its equilibrium number (\hat{i}_{90}), using the equation:

$$T = 1.16\hat{S}/\hat{i}_{90}$$

MacArthur (1972) reiterated the basic tenets and provided some supporting evidence from studies done between 1963 and the time of writing; these will be considered in detail below.

We must recognize that the basis of the theory rests on the assumption that the number and composition of species on islands is solely the result of population phenomena, and ignores totally any competitive effects. In this, the equilibrium theory is set apart from the holistic traditions of ecology (Simberloff, 1978b), and it is also set apart from the mainstream of community ecology by its explicitly stochastic nature. This aspect seems to have been forgotten by all except Simberloff (1978a; Connor & Simberloff, 1978); even Diamond (1975b), one of the leading exponents of the equilibrium theory, has provided sets of rules for the composition of avian communities on islands which have a decidedly deterministic flavour (see also Smith, 1979).

Having tested experimentally some of the theory's predictions (Simberloff & Wilson, 1969, 1970), Simberloff (1969) extended the theory of colonization by considering these findings in conjunction with some published results. He improved on earlier deterministic equations by deriving an expression for the variance and the mean of the equilibrium number:

$$\text{Mean} = \sum_{\alpha=1}^P \frac{I_{\alpha}}{I_{\alpha} + E_{\alpha}}$$

$$\text{Variance} = \sum_{\alpha=1}^P \frac{I_{\alpha} E_{\alpha}}{(I_{\alpha} + E_{\alpha})^2}$$

where I_{α} and E_{α} are the rates of immigration and extinction of each species in turn, and P is the number of potential colonists. His equations are dependent on I_{α} and E_{α} not being affected by the species already present, i.e. the assumption of no competition, and upon I and E being constant. As we shall see, Simberloff postulated a 'non-interactive' colonization to 'supersaturation' (i.e. $S > \hat{S}$), followed by either an interactive 'relaxation' to equilibrium, or a damped oscillation about the equilibrium number which dies away to this number (Hubbell, 1973). Gilroy (1975) thought that the pool of potential colonists should be characterized not only by the number of species, but also by an 'activity' parameter: this appears to have been necessary because he was trying to apply a 'molecular model'.

Concerning the process of 'relaxation' from supersaturation to equilibrium, Terborgh (1974) proposed that the kinetics followed a pattern described by the equation:

$$dS/dt = kS^2 \quad k = \text{constant}$$

and applied it to the data of Willis (1974) (see below).

The concept of regarding patches of particular habitats on continents as 'islands' had been circulating for many years (e.g. Kilburn, 1966), and the specific connection with the equilibrium model to this was made almost immediately (Vuilleumier, 1970) and apparently indiscriminately (Terborgh, 1973a). Janzen (1968, 1973) extended the concept and the relevance of the equilibrium model to different aspects of the natural world, and he proposed the ingenious idea of host-plant *species* being islands in 'evolutionary time' to their associated insect fauna, as well as *individual* plants being islands in 'contemporary time' for individual insects. Webb (1969) also used the theory in an evolutionary context, with the rate of immigration being represented by the rate of origination of taxa.

Diamond & May (1976) attempted to combine Lack's (1973) views of the existence of a permanent core of resident species, with the MacArthur–Wilson model, and produced a modified graph (Fig. 2).

Predictions about the rate of turnover were modified by Brown & Kodric-Brown (1977),

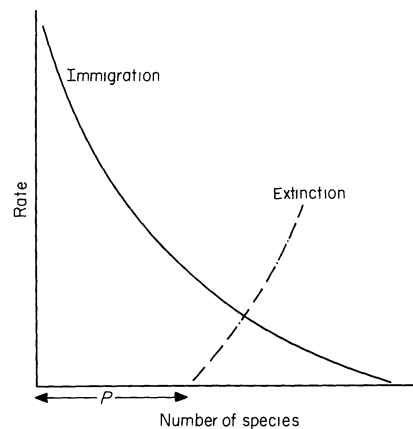


FIG. 2. The attempt of Diamond & May (1976) to incorporate a permanent core of resident species (P) into the equilibrium theory. This was to some extent to reconcile the views of Lack with the tenets of the MacArthur–Wilson model.

Diamond & May (1977) and Williamson (1978). The first, partly in order to account for the anomalous results of Diamond (1969), suggested that instead of being directly proportional to the inverse of the degree of isolation, the rate of turnover could actually increase with increasing distance, as Diamond found. This occurs when the rate of immigration is very high, since the immigration of certain individuals prevents the extinction of populations of some species by contributing demographic and genetic elements to those populations (Fig. 3).

Williamson (1978) considered that such a result of Diamond's (1969) happens because one cannot expect that the absolute rate of turnover will change consistently with the number of species, unless the studied islands are characterized by variation in area, or distance from the mainland, but not both. He claimed that the relative rate of turnover would change with distance in an opposite sense to the absolute rate of turnover. The error involved in estimating the rate of turnover with an increasing time interval between censuses was considered by Diamond & May (1977). This error arises because, if the interval between censuses is too large, the study will underestimate the rate due to intervening cycles of colonization and extinction. Diamond & May obtained an expression for T as a function of the time interval, t :

$$T(t) = \frac{1}{t\hat{S}} \sum_i \frac{\mu_i \lambda_i}{(\mu_i + \lambda_i)^2} [1 - (1 - \mu_i - \lambda_i)^t]$$



FIG. 3. The modification to the equilibrium theory introduced by Brown & Kodric-Brown (1977) to account for their own results from patches of thistles, and the results of Diamond (1969).

where λ_i and μ_i are the probabilities of immigration and extinction.

Diamond, Gilpin and Mayr collaborated in a series of papers (Diamond, Gilpin & Mayr, 1976; Gilpin & Diamond, 1976; Diamond & Mayr, 1976; Mayr & Diamond, 1976) in which they claimed to have discovered the biological significance of the parameters of their species-area relationship. They produced their 'equations of best fit' to the data base:

$$S = a + b \log A. \exp [-D^x/y A^z]$$

$$I = (1 - [S/P_0])^m \exp [-D^p/D_0 A^v]$$

$$E = E_0 S^n / I_0 A$$

where D = dispersal distances, p = pool of colonists, and lower case letters denote fitted constants. Their claim will be examined later. Finally, Taylor & Regal (1978) consider a 'peninsular' effect in the light of equilibrium biogeography.

The theory of an equilibrium number of species on 'islands', however defined, rests on the work of the above authors. The mathematical statements of the basic concepts have a beguiling simplicity seeming to correspond very well with the so-called 'principle of parsimony'; but there is an epistemological problem associated with this concept of simplicity that is philosophically insoluble (Popper, 1968). Practically it is possible of course to pick out simpler theories from the more complex ones; however, the danger lies in equating a simpler explanation with one that is more aesthetically pleasing. Although one may believe in the 'austerely beautiful simplicity of the world' as revealed by 'natural' laws, these laws are created by the human intellect and are artificial. Post-Baconian science tries to determine the actual structure of the universe. Although one can always obtain a better approximation of the natural state merely by incorporating a greater number of variables and parameters, this is analogous to Heisenberg's Principle of Uncertainty in that the heuristic value of the model is reduced. The task in hand is to produce a simplification that is not itself necessarily simple, and which involves the smallest practicable number of elements. The MacArthur-Wilson model is certainly parsimonious, and that capricious Nature should

conform to such a law would seem surprising; in fact, not even the species–area relationship is as straightforward as it would seem at first. Some of the expositions propounded after 1967 contain some highly abstruse and sometimes specious arguments ‘judged not on empirical tests but on the difficulty of the mathematics, or the obscurity of the theoretical development’ (Stearns, 1976; for an example see Gilpin & Diamond, 1976). This is an unfortunate tendency in modern ecology and biogeography that has no excuse.

In order to demonstrate unequivocally that the MacArthur–Wilson model applies in any particular situation, I consider it necessary to show that: (i) a close relationship exists between insular areas and the number species they contain; (ii) the number of species remains constant; (iii) an appreciable fraction of the complement of species changes in identity over periods of time related to the scale of the system. As an example of a study claiming to investigate an ‘equilibrial’ situation, and in fact fulfilling none of these three criteria, we may cite Platt’s (1975) paper about plants growing on prairie ground disturbed by badgers.

The species–area relationship

(i) *Oceanic islands*

The strictly delimited boundaries of oceanic islands, and the comparative ease of making counts of the total numbers of species, have made the method of demonstrating a species–area relationship the most popular means of providing evidence for the theory, and the number of such studies is great. It is instructive to consider how far such a demonstration goes towards proving the MacArthur–Wilson model, and whether indeed it supports it at all. Simberloff (1974) pointed out the well-known but often forgotten shortcomings of the multiple regression techniques used in these studies: ‘At best, such an analysis can render the model plausible, if species number correlates approximately with island isolation and area. But regression cannot demonstrated causality’.

It is clear that a mere demonstration of such a correlation contains no information whatsoever about a ‘turnover’ of species at

any ‘equilibrium’. It may be argued that since immigration and extinction undoubtedly occur, a constant number of species indicated by the correlation must imply a dynamic equilibrium. That this is false logic can be seen in the fact that the correlation deals with logarithms, which damp down variations (see below), and from the example of the island of Cocos. Mayr (1965) stated that ‘the smaller the island, the lower the percentage of endemics’ because the rate of turnover is so high that no colonist survives to speciate. Ever since the taxonomic recognition of this island by ornithologists, the composition of its endemic species has remained constant. Furthermore it has the highest percentage of endemic avian species in the world apart from Madagascar.

In fitting data of any sort in a regression, there is inevitably some scatter of points around the regression line; papers dealing with this particular relationship are noticeable for stating the confidence limits neither of the constants (c and z) nor of the line itself. In fact these confidence limits are usually wide to very wide (Haas, 1975), and should be discussed before trying to interpret any variations in the value of the constants, which are very sensitive to the inclusion or exclusion of extreme points. Haas (1975) has pointed out that poor fits ‘rock’ the regression line about the mean, causing the confidence limits to ‘flare’ at the ends. This means that if one wants to use the line to *predict* the number of species on a nearby island (see Diamond, 1972; Terborgh, 1974), then the investigator ‘must be ready to accept almost any number as fitting his prediction’ (Haas, 1975).

Those studies whose authors evidently believe that a demonstration of the species–area relationship proves the equilibrium theory to be true are Brown & Kodric-Brown (1977), Culver, Holsinger & Baroody (1973), Diamond (1974), Diamond *et al.* (1976), Diamond & Marshall (1977), Dritschilo *et al.* (1975), Lassen (1975), Lawton & Schroder (1977), Pictou (1979), Power (1972), Schoener (1976), Seifert (1975), Sepkoski & Rex (1974), Simpson (1974), Smith (1974), Strong (1974a, b), Strong & Levin (1975), Strong, McCoy & Rey (1977), Tepedino & Stanton (1976), Vuilleumier (1970, 1973) and Whitehead & Jones (1969).

Clearly the validity of the interpretations of these studies is open to question. But what of the general validity of the species–area relationship itself? It has been shown many times that natural phenomena, although perhaps conforming in some general way to various predictive formulae, are not determinate. Indeed the whole principle of determinism is suspect when applied to such a complex and dynamic system as that described by ecology, where so many of the factors affecting the systems involved are stochastic to an extent that even statistical inferences must be regarded as tentative. Three hypotheses, not mutually exclusive, which can account for the species–area relationship have been outlined above (see Simberloff, 1978b), and MacArthur & Wilson admitted that use of area alone is misleading. They envisaged the possibility that the areal effect acts through an increase in the number of habitats with area, and thus area acts as a surrogate variable in their equations. But Simberloff (1976a) has provided evidence that area has an effect independent of the effect of habitat, and Abbott (1978) has demonstrated that, at least for the islands off the coast of Western Australia, there is no relationship between area and the diversity of habitats. Flessa (1975) found a relationship between the diversity of genera, families and orders, and the areas of whole continents. He found this puzzling, since it seems unlikely that the habitat diversity would increase above a certain area, much smaller than the size of continents. In addition, the equilibrium theory was based on an areal effect controlling the sizes of populations, and Preston (1962) has based his equation on a linear increase in population size with area. Both Jaenike (1978) and Case (1975) found non-linearity in this relationship.

MacArthur & Wilson (1967) cited the lizards of some West Indian islands as one of their examples of the species–area relationship, and their few plotted points on the graph of $\log \hat{S}$ against $\log A$ all lay almost exactly on the straight line. But they used only the four major islands of the Greater Antilles at one end, and three of the smallest and northern-most of the Lesser Antilles at the other. If a plot of the avifaunas of the same islands is drawn, a perfectly straight line is

again achieved; but the inclusion of the data of the other islands of the Antilles creates a picture much less clear (Slud, 1976), the correlation, however, remaining very high. Williams (1969) suggested, on the basis of his observations, that the distribution of herpetofaunas in the West Indies, rather than lending weight to the MacArthur–Wilson model, supports Lack’s theory, that the number of species is determined by ecological limitation. Another example of a plot of $\log \hat{S}$ against $\log A$ by MacArthur & Wilson (1976, p. 23) included some very extreme points, which contributed disproportionately to the steep slope. If these points are excluded (Slud, 1976), the gradient and therefore the value of z is much reduced, the middle range of areas tending to have more or less equal numbers of species. This feature is also apparent in Slud’s West Indian avifaunal plot (see below). Again, MacArthur & Wilson’s curve for Kapingamarangi atoll is inconsistent with the data since it was fitted by eye and not mathematically; if mathematical methods are used, no sharp inflexion results (Whitehead & Jones, 1969), and the curve then becomes more consistent with the ecology of the atolls.

Therefore MacArthur & Wilson seem to have carefully selected their examples of Preston’s hypothesis. A survey of most of the rest of this literature shows that in only one case was area suggested as the exclusive predictor of the number of species (Diamond & Mayr, 1976), and even in this study the authors claimed the correlation coefficient of 0.99 for the ‘lowland’ birds only. Their value for the gradient was 0.087, much lower than other estimates, and they ‘explained’ this by assuming that the immigration rate between the islands was very high.

More usually, as the theory requires, an ‘isolation’ index together with area is claimed to provide good estimates (e.g. Heatwole, 1975). Area is usually the major contributor to the variance in the number of species as determined by the multiple regression techniques so favoured in these studies. But even when good predictions can be made with linear combinations of variables, independent tests of the predictions are hardly ever made.

Hamilton, Barth & Rubinoff (1964) found that area was the major source of variation for tropical avifaunas; Hamilton & Armstrong

(1965) obtained a correlation coefficient of 0.99 using the variables area, elevation, and distance from the mainland, for insular avifaunas of the Gulf of Guinea; for the Orthoptera of the Californian Channel Islands, area and elevation are the only significant predictors (Weissman & Rentz, 1976). These results alone should make us wary of using only area and distance as the predicting variables, and there are many studies where area and distance play minor roles.

Williams (1969) found no areal relationship at all for West Indian *Anolis* lizards (cf. MacArthur & Wilson, 1967), and competitive exclusion by one species of all others occurred for areas smaller than a certain 'critical' size. Johnson & Simberloff (1974) used multiple regression of ten variables on the number of plant species on British islands, and found that the statistically best model (explaining 95% of the variance) used the number of soil types, the log of the latitudinal range, log *A*, and the log of the number of soil types, in that order of importance. The number of soil types was significantly correlated with the area of the islands. Power (1972) suggested that for the birds of the Californian Channel Islands the best predictors were, in order of decreasing usefulness, the number of plant species, elevation, area, latitude, and two isolation indices. Stepwise multiple regression produced only the number of plant species as a significant predictor.

The number of plant species on the Galapagos Islands has been studied by Johnson & Raven (1973), Simpson (1974) and Connor & Simberloff (1978). The first found that elevation was the best variable to use; Simpson claimed that only area was significant, and that even higher values of R^2 in her multiple regression could be obtained using areas and distances calculated for the end of the Pleistocene, ten thousand years ago. Connor & Simberloff have comprehensively debunked the latter's claims, and have shown that the number of collecting trips paid to each island shows very high correlations in both simple and log-transformed regressions (R^2 is 0.97 and 0.92, higher than any other variable examined) with the number of plant species recorded.

No areal relationship at all was found for the herpetofaunas of sandy cays in the New

Guinean archipelago (Heatwole, 1975), snails of the family Enidae (Heller, 1976), West Indian bats (Koopman, 1958), or ants of the Central Seychelles (Mühlenberg *et al.*, 1977). Lillegraven (1972) found no relationship between area and the diversity of orders and families of Cenozoic mammals, in contrast to the later findings of Flessa (1975).

The occurrence of contrasting conclusions from the examination of the same taxa of the same group of islands suggests that the area and distance effects are not absolute, as required by the equilibrium model, and the danger of using correlations as causal relationships is clearly emphasized by these studies.

Among those for whom the species-area relationship and the equilibrium theory are viewed as fact, one of the early topics of discussion was the significance of variations in the value of *z*, the slope of the regression line. It is said that this takes a value less than the theoretical 0.263 (Preston, 1962) for continental nested areas *because* of very high immigration rates, ignoring the implication of high rates of extinction that this would entail (see Smith, 1975). It is further claimed that *z* is greater than 0.263 for 'non-equilibrial' and isolated situations (for theory see Schoener, 1976); i.e. the aberrations are explained away (see Diamond & Mayr, 1976). These are glaring examples of untestable *ad hoc* hypotheses, for whatever value is found for the gradient can be conveniently 'explained' in this way by what amounts to pure speculation. Since the value of *z* has wide or very wide confidence limits in most of these studies, such speculation is futile.

The only direct proof of an independent effect exerted by area was reported by Simberloff (1976a), who removed portions of red mangrove islands off the coast of Florida and observed the fall in the number of species. But the results also showed that an islet split into two smaller islets could end up with more species, in opposition to the predictions of the theory. This is important in the context of conservation, and yet was dismissed as 'scarcely relevant' by Diamond (1976a). The reality of this effect was confirmed by Abele & Patton (1976) for coral 'heads', and treated analytically by Simberloff & Abele (1976a). The latter theorized that, in considering two islets of the same total area as one larger one,

ceteris paribus, the former would have fewer species than the latter only if the larger island managed to collect more than 96% of the pool of colonizing species.

Diamond and his co-workers take to the limit extrapolations from a simple species–area regression. Diamond & Marshall (1977) went so far as to calculate the numbers and proportions of montane and lowland species of birds for the New Hebrides using an equation derived from a different group of islands, the relevance of which was established on the basis of a single test of one island. Further detailed calculations were made and the authors concluded that ‘the species–area–distance relation for New Hebridean birds fits well with the interpretation than an island species number approaches an equilibrium between immigration and extinction, that extinction decreases with island area, and that immigration decreases with isolation’. Any gaps in the distributions, they claimed, must mean that extinction had occurred. Even more questionable is the study of the birds of the Solomon islands carried out by three co-workers (Diamond *et al.*, 1976; Mayr & Diamond, 1976; Diamond & Mayr, 1976; Gilpin & Diamond, 1976). Their studies produced a complex equation (see above) that, it is claimed, describes to an accuracy of 98% the number of species on any one of their ‘core islands’, but they fail to meet the criterion of repeatability since nowhere do the authors record the actual species present on each of the island, but merely state the numbers of ‘lowland’ and ‘montane’ species. The lowland species are then described by the equation:

$$S = 34.7 + 12.08 \log A \quad (r = 0.99)$$

which has a different form from any other in the literature, and which furthermore applies only to ‘non-isolated’ islands of the group. Their sources of information were censuses carried out in 1929–30 and 1968–74, and therefore their totals for the numbers of species assume that there is no turnover. Eventually they arrive, by an exceptionally tortuous statistical path, at the equations reproduced in the introduction above, the deductions from which seem in any case to be rather obvious: for example, that as a model

of dispersal, a straight line is better than a ‘random walk’.

The evidence for a species–area relationship for tropical birds was comprehensively reviewed by Slud (1976); he used all islands for which counts of species are known, and when ‘log \hat{S} ’ is plotted against log A a good straight line emerges. However, on a semilog plot it is clear that a good deal of information is obscured in the former graph: most areas less than 1000 sq. miles, and all less than 100 sq. miles, have fewer than fifty species. The proportion of islands with total numbers of species greater than fifty suddenly rises near an area of 1000 sq. miles; few islands of area less than 1000 sq. miles have more than 100 species, and none more than 150. More than 20% of islands with areas between 1000 and 50 000 sq. miles still have fewer than fifty species. Slud concludes: ‘Insular biotas... conform to no universal standard and their compositions are each the unique result of interplay among many factors that are differentially peculiar to islands: this makes islands synecologically nonintercomparable’ (sic!).

(ii) *Habitat ‘islands’*

Many attempts have been made to show that the same relationship holds for ‘insular’ continental habitats, and Simberloff (1974), before his change of heart, saw no reason that it should not: ‘... any model of island biology should be relevant to small scale, local systems, as well as to larger ones...’. It is a noticeable feature of such studies that discrepancies occur between their findings and the predictions of the MacArthur–Wilson model, and these are almost universally ignored or explained away, often in a very imprecise and dubious manner. The values of z obtained from these regressions are very often, but by no means always, lower than those from truly insular situations, but the ‘scatter’ of the points is nearly always even greater, rendering Haas’ (1975) objections even more apposite (for an example of the over-interpretation of variations in z , see Picton, 1979).

Culver *et al.* (1973) tried to show that the species–area relationship held for cave-limited arthropods, and produced an expression for the terrestrial species, $\log \hat{S} = \log (0.18) +$

0.72 log A . The manner in which they did this is far from convincing since it was necessary to define area in a slightly less than rigorous manner, and to exclude various sections of the fauna. The variation in 'area' was said to account for 89% of the variation in the number of species, but they showed a distressing lack of scientific method in not stating how this was calculated, nor even whether 'area' was significantly correlated with the number of species. In fact \hat{S} and A were *not* significantly correlated for the aquatic species, but the authors still produced an equation ($c = 2.14$, $z = 0.19$). The Tessin caves of southern Switzerland were studied by Vuilleumier (1973), who compiled from the scientific literature lists of species of arthropods for forty-eight caves. He then performed 'stepwise multiple regression' analyses with various indices of area, environmental rigour, and isolation, as the independent variables. He found significant correlations in the case of 'area' (the combined length of all the galleries), but none for any measures of isolation. 57% of the variance of the number of species was accounted for by five independent variables, and three consistently high contributors were 'area', a water scale, and the density of bats! Vuilleumier does provide all of his data, and it can be seen that they give scant support to the application of the equilibrium theory to caves.

Vuilleumier's documentation of his studies provided an opportunity to demonstrate the development of statistical methods, for he carried out a similar stepwise multiple regression analysis of the birds living in the paramos, 'islands' of montane vegetation in the Andes of Colombia, Venezuela, and Ecuador. Again, lists of species were compiled from literature published between 1917 and 1969 (an invalid procedure if the turnover rate is high), and a total of eighty-three species, fifteen 'islands', and seven independent variables were used. But Mauriello & Roskoski (1974) re-examined these data, using 'ridge-regression' methods in which the stability of the values are indicated when variables are eliminated one by one. They showed that the data were non-orthogonal, i.e. the variables were not independent, and that Vuilleumier's conclusions, namely that the best predictors of the number of species were area and the

distance to 'paramo I' (considered the 'source'), were unaltered, but the coefficients of distance now became negative as required by the equilibrium model.

Simpson (1974) examined the flora of the paramos habitat as well as that of the Galapagos considered above, and claimed a high correlation with area, and an even higher one with the Pleistocene areas. In the light of Connor & Simberloff's (1978) findings, her interpretation now seems questionable.

Johnson (1975) studied boreal birds, and Brown (1971) the mammals, of the isolated mountaintops in the Great Basin of the Sierra Nevada and the Rockies. The former, again using stepwise multiple regression, found that area was not a good predictor of the number of species, and that the only highly significantly correlated variables were an index of habitat diversity and the minimum inter-island distance. He interpreted these and other correlations as indicating that it is the quality of remote insular habitats, rather than the difficulty of access, that restricts the number of species. The effect of distance he viewed as due to the impoverishment of the habitat, following Lack (1973). Brown found an areal effect, but was obliged to exclude many species, e.g. the larger carnivores, because their distributions had been drastically altered by man before records were kept. Picton (1979) reported the occurrence of ten species of large mammals in twenty-four mountain ranges in Montana, and claimed that the value of z had changed from 0.15 'historically', to 0.23 when hunting pressure was intense, ending finally at 0.25 in the era of conservation. Large areas alone, he suggested, changed similarly from 0.39 to 0.29 when conservation measures were introduced. Apart from giving no indication of how he arrived at the historical or any other result, it is somewhat dubious to conclude that, because 0.25 is close to the theoretical value of 0.263, these 'restored' populations are 'probably near the biological equilibrium situation'.

With respect to continental situations, the best documented application of the MacArthur-Wilson model is perhaps that of the breeding birds of woods. I shall have cause to discuss several of the studies again in the context of turnover, but here one can see that not all of them have found consistent

relationships. Kilburn (1966) found that for plants the value of the constant c varied between 7.5 and 16, and z between 0.26 and 0.43; for woods larger than 100 m², however, the calculated number of species became vastly greater than the actual, and a sigmoid curve could be assumed (as in Slud, 1976). A variation in the value of c from 0.19 to 0.5 was noted by Hooper (1971) in accordance with the degree of isolation experienced during the history of the woods concerned; Galli, Leck & Forman (1976) used a method of standardized walking, and found that an equation of the form $S = 0.81 + 4.54 A^{1/2}$ could be applied. Here area had no effect on the 'foliage height diversity' (supporting Abbott, 1978). Galli *et al.* then concluded somewhat illogically that the variation in the number of species was solely due to variations in area, and not area acting through a relationship with their measure of diversity.

Moore & Hooper (1975) tested 433 woods in the British Isles and deduced a value of z of 0.27, in contrast to an earlier British Trust for Ornithology survey, which had obtained a value of 0.37.

The census returns from 1934 to 1975 for Trelease Wood, a 22 ha plot, were used by Whitcomb *et al.* (1976), who found that the average number of breeding bird species was 23.3 (SD = 4.9) from 1934 to 1953. By 1953, the 'elms were dying from Dutch elm disease', and the average number of species increase to 32.5 (SD = 2.8; $P < 0.01$ that this is due to chance). This is an unchanging set of conditions with identical area and distance, and their *ad hoc* hypothesis invoked to 'explain' the supposed increase is unfalsifiable. If it is disallowed, the variation in the number of species becomes unacceptably large for its acknowledgement as 'constant'.

Helliwell (1976), like Moore & Hooper, examined breeding data of birds from British woods, and disagreed with their findings. His analysis suggested that the size of woods had little effect on the number of species of birds; similarly, neither the density of woods in the neighbourhood nor the distance of other woodland areas had any detectable effect. For the number of plant species, fifteen variables could only account for 21–24% of its variation, and ordination and association analyses had no major axes or divisions related to the

size or isolation of the sample areas. He concluded that these factors were not major elements influencing woodland floras. However, Harner & Harper (1976) claimed that 98% of the number of species of a shrub-dominated community in Utah was predictable from the area and 'environmental heterogeneity'.

Barbour & Brown (1974) found no evidence of any species–area relationship for the fish of ponds and lakes, but Lassen (1975) claimed that his figures showed that z took a value of 0.37 for small eutrophic lakes, 0.09 for large eutrophic lakes, and 0.25 for oligotrophic lakes, in the case of Danish freshwater snails. The disjunction between the regression lines for eutrophic lakes seems a little hard to justify, and a quadratic function would obviate the necessity for its explanation, which included some psychological attributes of ducks!

Very sophisticated mathematical techniques were used by Sepkoski & Rex (1974) to claim that coastal rivers were biogeographic islands for unionid snails. However, like Gilpin & Diamond (1976), they thought that merely because they had shown that a species–area relationship existed, this meant that their complicated modelling of immigration and extinction would be valid. The study again highlights the innate difficulties of invoking causal explanations for correlative data.

Following the ideas of Janzen (1968, 1973), the theory has been applied to single plants. For instance, Brown & Kodric-Brown (1977) chose to look at patches of the thistle *Cirsium (sic) neomexicanum*, which are colonized and inhabited by arthropods (spiders and some insect orders were studied). They state that they discovered that 'the number of arthropod species increased with increasing size of the patch, and decreased with increasing distance between patches' but, because they give no detailed figures to substantiate them it is difficult to assess the validity of these claims. Seifert (1975) studied insect communities on *Heliconia* blossoms, and found that there was a highly significant relationship between the number of flowers per plant and the number of species, with differing values of z for the two species of *Heliconia* that he considered. Davis (1975)

introduced his paper with the tenets of the equilibrium theory, but then did not apply them to his data. Ward & Lakhani (1977) found that the numbers of species of phytophagous arthropods associated with juniper was related to the number of bushes in the sampled plot.

The evolutionary aspect of Janzen's ideas has been studied mainly by Strong and his associates. Again, most of the evidence for an equilibrium number of species rests upon the species–area relationship. Strong (1974a, b) found this relationship between the geographical area of distribution of species of trees and the number of associated insect species, but Van Valen (1975) pointed out that the slope of his regression line was not significantly different from zero, or from one. Even when two extra species were added (Strong, 1975), the probability of the slope being significantly different by chance from zero was still too great to reject the null hypothesis. Claridge & Wilson (1978) point to both floral and faunal inadequacies in Strong's data, doing the same analysis with improved floral records. They claimed that their measure of recent abundance (the number of fossil records for the past 2000 years) was better than Strong's, concluding that their data supported the existence of a relationship between the abundance of a host-plant and the number of its associated insect species. Birks (1980) emphasized the inadequacy of fossil records as measures of the recent abundance of trees, even over the last two millennia, and showed that another hypothesis, dismissed by Strong, was still capable of providing an explanation (see below). Strong & Levin (1975) produced a regression line for the number of parasitic fungi on different species of trees, but the whole slope and significance of the regression line is determined by just two points. Opler (1974) found a regression for Californian oaks and their leaf-miners. Similar regressions have been claimed for perennial herbs, woody shrubs, weeds, and monocotyledons of Britain (Lawton & Schroder, 1977), and cushion plants (*Astragalus* but not *Phlox*: Tepedino & Stanton, 1976). With all these studies, an equilibrium interpretation is not a logical consequence of the discovery of a species–area relationship.

Finally, the number of mites living or being carried on North American cricetid rodents is claimed to show such a relationship with the geographical range of their hosts (Dritschilo *et al.*, 1975): it was claimed that, because a well-studied genus showed a better correlation than a poorly studied one, any scatter of the points was due to unevenness in the data.

Although Diamond (1974) claimed that 'a linear logarithmic relationship between S and A ... describes the distributions of most plant and animal groups on most... archipelagoes', it seems to me to be difficult to base a theory of the numbers of species on islands upon such evidence as is presented above, let alone one with such wide ramifications. Lack disputed the validity of the equilibrium model, preferring to believe that stretches of water were not great barriers to colonization; the paradox of Lack's concept applied to the West Indian hummingbirds (Lack, 1973) was that these birds showed a high incidence of endemism in the islands. This can be resolved by supposing a high rate of speciation: there is no conceptual difficulty in this postulate (see Johnson & Selander, 1964), but there is now evidence that insular impoverishment is at least partly due to the difficulties of over-water colonization (e.g. Abbott, 1978). These considerations aside, I think it is clear that the best way of providing support for the equilibrium theory of island biogeography is to document the processes of colonization and extinction and thereby demonstrate that a dynamic equilibrium exists. It is to these studies that we now turn our attention.

Colonization and extinction

The characterization of colonization is fraught with many difficulties, including sampling, which may disturb the process of immigration if carried out too early. Most studies have been done using microecosystems in order that it be practical to observe the whole process, but this brings its own problems, most important of which is the extent to which one may extrapolate from small- to large-scale systems.

The earliest attempt was made by Patrick (1967) using glass slides placed in a current, and observing their colonization by diatoms.

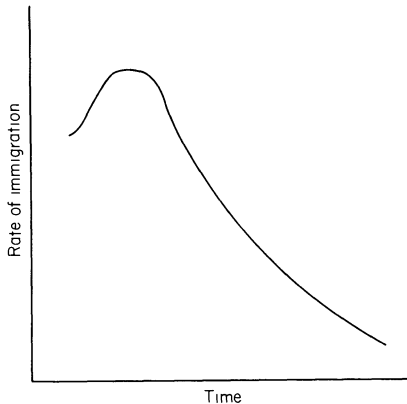


FIG. 4. The shape of the invasion curves found by Patrick (1967) for the colonization of glass slides by diatoms.

Although she found that an increase in the area of the slide resulted in an increase in the number of species, the shape of the invasion curve was not that predicted by the equilibrium model (Fig. 4). An increase in the number of species was accompanied by an increase in the rate of turnover of species, again opposite to the result expected by the theory.

Cairns *et al.* (1969) studied the colonization of submerged plastic sponges by Protozoa, squeezing out 10 cm³ samples and paying particular attention to the Ciliata. They found that the values for the rate of immigration could be expressed as an asymptotic curve 'significantly' different from a straight line ($P < 0.10$, a rather liberal probability). However, the rate of extinction could not be expressed in the same way, and was not different from a straight line. The authors then seem to ignore their own data, assuming that they supported the MacArthur–Wilson model, whereas this model requires that the rate of extinction is asymptotic also. Similar experiments were performed by Schoener and colleagues (Schoener, 1974; Schoener, Long & De Palma, 1978) in a marine context. The first experiment used 220 species and counted 26,000 individuals; the curve of colonization 'levels off' in her view, although this can only be said to happen statistically, and she concluded that 'this supports the equilibrium concept of the MacArthur–Wilson model' (Schoener, 1974). The rest of the paper was

constructed assuming that this model did apply, and even the values of the rates of turnover were calculated from MacArthur & Wilson's equation (see above), using some dubious assumptions to obtain the equilibrium number and \hat{i}_{90} . An identical shorter set of experiments showed no asymptote to the rate of invasion of species. Her data also show that the rate of turnover for her 'large' island was greater than that for the small. This study has often been cited as important evidence for the 'essential truth' of the equilibrium model. Schoener *et al.* (1978) went on to look at geographical variation in the curve of colonization. It is surprising to see works cited in this paper as supporting the equilibrium theory, when they suggest the opposite (e.g. Abbott & Grant, 1976). The data are both scant and extremely variable, hardly justifying the conclusions of the authors, and anomalies seem to be just explained away. A 'red tide' which killed many animals in Florida in 1971 was used by Dauer & Simon (1976) and Smith (1979) to study recolonization. Dauer & Simon analysed the data for the polychaetous annelids in Tampa Bay, and found that the curve of immigration was consistent with the equilibrium model. The curve for the rate of extinction, however, was not significantly different from zero, and the authors failed to demonstrate the occurrence of any turnover, an equilibrium number, or a species–area relationship. Smith (1979) studied the return of reef fish after the red tide had killed 77% of the shallow water species. He found that, while certain of the characteristics of the colonization were consistent with the MacArthur–Wilson model, others contradicted its predictions, finding in particular that there was no turnover of species. The composition of species after colonization was complete was almost identical to that before the mass mortality, arguing against the stochastic processes assumed by MacArthur & Wilson.

The colonization of an artificial substratum was observed by Goren (1979), and he documented a high rate of turnover of species. The species diversity varied widely, however, and the number of species rose gradually and linearly from month to month.

Davis (1975) studied the colonization of 'defaunated' patches of nettles, and concluded very little of interest in our context. Crowell

(1973) was forced to conclude that the rates of immigration of *Peromyscus* and *Clethrionomys* were zero to his islands, and that the immigration rate of *Microtus* was very low. Brown (1971) reported similar results for some of the boreal mammals living on the mountaintops in the Great Basin. Crowell's study constitutes a unique attempt to verify the prediction of MacArthur & Wilson's model regarding the success of colonization, and was cited by MacArthur (1972) as important evidence in favour of the theory. The study, however, suffers from some major limitations. Crowell introduced numbers of *Peromyscus maniculatus* and *Clethrionomys gapperi* onto some of the islands within 8 km of Deer Island, off the coast of Maine. Different-sized inoculants of mice and voles from Deer Island were used, and the parameters (r , λ , μ and K), needed to provide a 'predicted' success of colonization, were estimated from trapping data. The predicted probability of immigration (i.e. the probability of establishment once the island has been reached) is $(\mu/\lambda)^n$, where n is the size of the inoculant in pairs. The results were quoted as agreeing well with the predicted values, but whilst the values for *Peromyscus* could be described as agreeing, albeit poorly, those for *Clethrionomys* could not. In either case the results are only provisional due to the inadequate number of replicates (three, two, one in all except one case). As stated above, Crowell could not demonstrate any natural immigration or extinction of populations of either vole, and therefore his claim that their distributions are accounted for by the equilibrium theory is open to question. The equation predicting the time to extinction of a population of size K (t_K) is:

$$t_K = \left(\frac{\lambda}{\mu}\right) \left(t_1 - \frac{1}{r}\right) \left(1 + \frac{1}{2} + \frac{1}{3} + \dots + \frac{1}{K}\right)$$

where

$$t_1 = \frac{\lambda}{\mu} \cdot \frac{1}{\lambda} \left(1 + \frac{\lambda}{2\mu} + \dots + \left[\frac{\lambda}{\mu}\right]^{K-1} \cdot \frac{1}{K}\right)$$

The predicted times for his populations ranged from 27 to 10,000 years. However, later field work showed that several populations, including the one supposed to last for

100 centuries, has already disappeared. Crowell did not 'regard this as grounds for questioning the MacArthur–Wilson theory within the limitations of its assumptions' because he thought it reflected the inadequacies of the logistic model of population growth used by them (addendum sent with Crowell's paper, undated).

An ingenious simulation of the process of insular colonization was constructed by Wallace (1975) using a complicated system of islands: eighteen species of *Drosophila* colonized the system by dispersal involving an intricate set of rules. Wallace suggested that the rate of immigration varied widely between the species, and that the equilibrium number was best estimated from Simberloff's (1969) non-interactive model. It is difficult to see how this conclusion arises from the data since he quotes no values of significance. The probabilities of immigration and extinction of each species depended on the composition of the 'species pool', a fact difficult to reconcile with the functioning of the equilibrium theory.

A study by Taylor & Regal (1978) attempted to provide a model which would predict the decline in the number of species to heteromyid rodents down the peninsula of Baja California, using probabilities of immigration and extinction. The authors assumed a chain of discrete suitable sites, and found that only very severe constraints upon their assumptions and parameters could produce the observed pattern, concluding that the equilibrium model was inadequate in this situation.

Contributory evidence was provided by Jaenike (1978), who showed that a positive relationship existed between small areas and the density of *Drosophila* populations. However, the population density reached a ceiling at areas between 10 and 100 ha, and Jaenike found it impossible to reconcile his results with the equilibrium theory: 'The assumptions that population size is a linear function of island area and that populations tend to remain near a constant equilibrium level may lead to serious errors in a predictive theory of island biogeography'.

Schoener & Schoener (1978) found an *inverse* relationship between the survival of *Anolis* lizards and the size of an island, con-

trary to the assumption of the MacArthur–Wilson theory.

Janzen (1968, 1973) proposed that a host-plant was an ‘island’ in ‘evolutionary’ time to phytophagous insects, contradicting the previous hypotheses devised in order to try and explain the diversity of such insect species. One of these hypotheses is that the length of time that the plant has been available for colonization determines the diversity. Strong (1974a, b) rejected this latter hypothesis on the basis of his species–area relationship, which, he claimed, showed that introduced species of trees were distributed about the regression line no differently from native species. Van Valen (1975), Moore (1975), Claridge & Wilson (1978) and Birks (1980) have criticized this regression on various grounds, and in particular Birks has shown that the rejection of the time hypothesis by Strong was premature. Birks obtained a significant correlation between the earliest known radiocarbon dates for British trees and the numbers of their associated insect faunas ($r = 0.58$, $P < 0.001$). A similar study by Strong & Levin (1975) of the numbers of fungi associated with trees produced the same conclusions as Strong’s previous papers, and these are subject to the same reservations, and also some more general ones (e.g. Haas, 1975; see above). Focussing on one detail, their regression line seemed to be determined in slope and significance by just two points, those for *Juglans* and *Salix*.

The best evidence for Janzen’s extension of MacArthur & Wilson’s theory comes from a study of the pests of sugar cane (Strong *et al.*, 1977). The dates of introduction and areas of cultivation of this crop were recorded for fifty-one regions and correlated against the number of pest species. Of 1645 pest species, 959 occurred only in one region, 156 in two, and only eighteen in more than ten regions. This enabled the authors to reject the hypothesis that these pests are carried around the world with the crop; on the contrary, an adaptation of the local fauna seems to have taken place. Multiple regression analysis could identify no influence of time on the number of species, only area being significantly correlated. However, Strong (1979) himself now seems to be wary of interpreting his work in terms of the equilibrium theory.

It is gratifying to find an extremely detailed study of the process of insular colonization, provided by Simberloff & Wilson (1969, 1970; Wilson & Simberloff, 1969; Simberloff, 1969). They fumigated small mangrove islets in Florida Bay, and observed their subsequent recolonization for 2 years with good census techniques. The results bear witness to the careful planning and execution of this experiment for they constitute possibly the only irrefutable evidence in favour of the equilibrium theory. The unequivocal conclusion was that the number of species did rise to an asymptote, but the figure for the rate of turnover that was claimed initially (0.5 extinctions per day), has recently been reduced to a minimum of 1.5 extinctions per year (Simberloff, 1976b). Heatwole & Levins (1972), re-examining these data, tried to show the same trophic structure was re-established, i.e. there are some determinate elements in the colonization. Their conclusion has, however, been challenged on statistical grounds by Simberloff (1978b). Simberloff (1978a) and Connor & Simberloff (1978) used distributional data to test the null hypothesis that the observed patterns are only the result of chance dispersal and the characteristics of the individual populations. This hypothesis was an assumption of MacArthur & Wilson’s theory, and requires that there be no effect of competition on the probabilities of immigration and extinction of species. The authors considered two sorts of hypothesis: first, that all the probabilities of colonization of the different species are the same; and second, that they are different for different species. Their analyses showed that the null hypothesis had to be rejected for the data of Simberloff & Wilson (1969) and for the flora and avifauna of the Galapagos Islands. They claimed, however, that although this was the case, a substantial proportion of the numbers of species on the islands could be explained by accepting the null hypothesis, and that ‘the fit seems good enough to suggest that...[it]...accurately depicts a large fraction of the colonisation process in this system’. As Connor & Simberloff (1978) acknowledge, the method by which they calculated the weighting of colonizing probabilities would have included the effects of competitive interactions. Terborgh’s (1973b) claim that 93% of the

distribution of West Indian birds on small or intermediate islands, and 80% on larger islands, was explicable deterministically, was effectively dismissed by Simberloff (1978a). Terborgh's paper is extraordinarily mystifying, claiming that the equilibrium number is really an oscillation about the equilibrium level 'held within close bounds by the opposition of contrary tendencies', a phrase whose meaning is very difficult to extract from the preceding discussion.

Simberloff (1974) summed up the mangrove experiments by stating that communities were 'not just haphazard assemblages', but that there is a definite sequence of events. This changes from a 'non-interactive' rise to equilibrium produced by purely random immigration, through a series of increasingly co-adapted 'equilibria', towards a final 'assortative equilibrium with a low turnover rate' (my emphasis, supported by Simberloff, 1976b, and Abbott, 1978). The only reservation that can be voiced concerning these experiments is that they concern very small islands of a single type of habitat, and it might be logically invalid to extend the results to larger islands. This is particularly emphasized by other work (e.g. Slud, 1976; Whitehead & Jones, 1969) that suggests that very small islands may be bad examples of biogeographical laws due to the stochastic problems associated with small population sizes. Islands with many habitats may not be subject to the same rules.

The final category of evidence in this section is the studies of the process of 'relaxation', the loss of species caused by an excess of extinctions over immigration. This occurs, it is claimed, when the area of an island is contracted, for example by an increase in the level of the sea. The studies of Diamond (1971, 1972, 1974) and Terborgh (1974) are prominent here, and are based on largely unstated assumptions (see Simberloff & Abele, 1976b) which are open to many criticisms (e.g. Haas, 1975). They provide questionable support for the equilibrium theory because the 'relaxation times' (defined in Diamond, 1971) calculated by Diamond are so long that by the time that the number of species on a 'supersaturated island' has reached even half way along the path towards the equilibrium number, the latter is likely to

have been altered by climatic and geological changes. The actual number of species therefore continually 'hunts' after a changing equilibrium number (Abbott & Grant, 1976; Strong, 1974a). Islands that were formerly connected to the mainland are used in these studies, and Terborgh (1974), for example, seems to have ignored the problems and inherent assumptions involved; in particular, he ignores the influence of man upon large mammals and birds (see below).

Wilcox (1978) purported to find a relationship between the time of isolation of various 'land-bridge' islands in the region of Baja Californian and the diversity of species of lizard. The latter had to be 'corrected' for variations due to area and latitude. Apart from the statistical uncertainties of this method, his result is dependent upon the controversial estimates of the timing and magnitude of eustatic rises in sea level. However, it is an original method of trying to prove the equilibrium theory, and it remains to be seen whether it can be adapted to a more rigorous test. Lizards are, however, poor examples for such a study (Williams, 1969).

Simberloff (1976a) has produced the best experimental evidence for the process of relaxation by splitting or removing parts of mangrove islets. The results are consistent with the idea of a dynamic equilibrium, but demonstrate the stochastic nature of the process, which does not seem to have been envisaged by Diamond or Terborgh.

Studies of continental areas have noted, for example, that small woods contain no species characteristic of the forest interior (Whitcomb *et al.*, 1976), but other studies have contradicted this (e.g. Helliwell, 1976). Relaxation has been regarded as important in the field of conservation, but many workers have failed to show that it has any relevance to the equilibrium theory (e.g. Picton, 1979). One of the most frequently cited examples of the predictive powers of biogeographical theory is the analysis of Terborgh (1974), using Willis' (1974) data. Willis worked on Barro Colorado Island, created in 1910–14 by the rising waters of Gatun Lake, part of the Panama Canal. He studied the birds of the island for 10 years, concentrating on the species which followed army ants. In the 1920s the area had been studied by Chapman, who had

counted 208 breeding species; by 1970 this total had been reduced by forty-five species, made up mostly of those characteristic of open fields and early secondary growth. This was because the land had been farmed before being cut off by water, and was returning to jungle (Simberloff & Abele, 1976a). Thirteen of the extinctions were deep-forest species, and eight of these were ground-nesting; Willis points out that their disappearances can be attributed to the unusually high concentrations of monkeys, coatis, and opossums present because there are too few predators to keep their numbers down. Terborgh accepts that the majority of the extinctions have been associated with the regrowth of the forest, but ignores Willis' explanation of eight of the remaining disappearances, even increasing the number of 'forest' species to eighteen by including 'borderline' species not stated to be such by Willis. Terborgh states that: 'The disappearance of so many small ground-dwelling... species is more puzzling, especially in view of the fact that there have been no extinctions recorded from the large canopy community'. Thus only five of the extinctions cannot be directly attributable to any specific cause, and Willis proposes two explanations: the regrowth of the forest, or the contraction in area (no species recolonized from the mainland, only 500 yards away at the nearest part). If we accept Willis' view, the Terborgh's estimate of 16.6 extinctions for the island from his theoretical analysis diverges too much from the observed figure to be acceptable as a reasonable explanation. This is perhaps not surprising when we realize that Terborgh was relying on regression lines determined from as few as three points. His 'log-log' regression of the 'extinction coefficients' against area had only five points, four of which were clustered closely together on the graph and showed no relationship at all. The value for Trinidad was the only factor enabling a regression line to be drawn.

Finally, there is circumstantial evidence for a 'relaxation' occurring amongst the Permian-Triassic marine invertebrates, where a mass extinction of half the known families took place concurrently with a two-thirds decrease in the area of shallow waters (Simberloff, 1974). Flessa (1975), however, doubted whether such large areas could effect the

probabilities of extinction of individual genera of families.

A recent example of the way in which the ideas of 'relaxation' can be applied to nature conservation, with apparently no useful results, is seen in the paper by Soulé, Wilcox & Holtby (1979).

The rate of turnover at equilibrium

In this section we consider the most direct method of demonstrating the equilibrium proposition, whereby actual turnover among insular populations is documented whilst the *total number species remains constant*: this last seems to me the crux of the matter. Altogether I have managed to find twenty-five instances of investigations carried out in order to demonstrate the turnover of species at equilibrium. By far the most widely cited examples of such studies are those by Diamond (1969, 1971), Simberloff & Wilson (1969, 1970) and Terborgh & Faaborg (1973); I have already discussed the experiments of Simberloff & Wilson. With the emendations of Simberloff (1976b), I regard their conclusions as valid. This is not the case, however, with most of the other studies, and I hope to establish the proposition that these other reports suffer from grave defects which severely limit their use in testing the equilibrium theory.

Smith (1975) argues that: 'Fluctuations may bring a species to extinction in a system. I can accept a moderate amount of this but not very much. Obviously, extinction is more frequent in smaller systems. At a ridiculous extreme every death or movement creates extinction at that exact point. Robins become extinct in an apple tree many times each day whenever they fly elsewhere. To me, frequent extinction is a signal that the system under study is not large enough to include the processes being studied. Move the system boundaries out until extinction becomes rare. This ensures that the organising forces of the system lie within the system...'

It is true that the rapid rates of extinction reported in some of the studies considered were found on small islands, and we should bear these remarks in mind while assessing the results.

Because of the very large contribution of Diamond to the literature of the equilibrium theory, and because his paper of 1969 in particular has been cited in virtually every relevant paper written since that date, I will examine this paper in some detail. I will consider the sequence of reports that provide a series of experiment, critique, and reply, seen in Diamond (1969), Lynch & Johnson (1974) and Jones & Diamond (1976). This will provide a background with which to view other studies.

Diamond conducted surveys during 1967–68 in order to find out the differences in the composition of species between the breeding avifauna of the Californian Channel Islands then, and those of 60 years ago as published by Howell (1917) and others. He concluded that: (i) the total numbers of species on most islands had remained approximately constant, and therefore at equilibrium, during the 51 years between censuses; (ii) the composition of most of the island's species had changed markedly, with up to 62% of the breeding species as a maximum; (iii) rates of turnover were independent of the size of the island or the distance to the mainland, but were inversely proportional to the number of species.

The last point seems paradoxical if the species–area relationship is valid for the birds of these islands, and is contrary to the predictions of the theory. Lynch & Johnson pointed out that the data based used by Diamond to establish the numbers of species breeding on each island in 1917 (Howell, 1917), was in fact a summary of all known breeding records, some of which date from the decade 1860–70. If the rates of turnover are as high as Diamond claimed, then this data base is invalidated. This criticism was not answered by Jones & Diamond in their supposed refutation of Lynch & Johnson's allegations. The latter's doubts as to the adequacy of the coverage by Howell are refuted by Jones & Diamond solely on the basis of the near equality of the numbers of species!

One cannot assess Diamond's paper adequately since he did not tabulate the species involved in his calculations, and Lynch & Johnson had laboriously to reconstruct these from later publications. They could only identify a proportion of the birds to the

species and island where the change had taken place. This allegation of bad scientific method was also left unanswered. For some islands, even Diamond acknowledged that Howell's survey had been incomplete, and yet he calculated the rates of turnover and used them in his analysis. His claim that the islands were in 'approximate equilibrium' meant that less than 16% of their species had changed between 1917 and 1967–68, and only six of the nine islands conformed to this. The other three had changes of 79%, 40% and 36%, two of which Diamond attributed to the incomplete nature of Howell's survey. The other was Santa Barbara, whose vegetation had been destroyed by a fire in 1959. Even Simberloff (1974), discussing this paper, claimed that the numbers of species had 'changed only slightly' between 1917 and 1968, saying that there was 'no reason to disbelieve the implication that the islands are in equilibrium'.

Thus, Diamond concluded, 'the postulate that insular species diversity represents a dynamic equilibrium is valid for the birds of the Channel Islands'. He minimized the effects of man as 'greatly in the minority' because the changes were not systematic ones by habitat, and claimed a 'nearly perfect inverse correlation' between the rate of turnover and the number of species (calculation from his data shows $r = 0.80$, $t = 5.9$, $P < 0.001$ for 7 d.f.). Since there was no correlation between the rates of turnover and distances from the mainland, he concluded that these distances must be small compared with the capabilities for dispersal of the potential colonists: this view was disputed by Johnson (1972), Lynch & Johnson (1974) and even Diamond himself in another context (contra Lack, 1973, in Diamond *et al.*, 1976).

Simberloff (1974) regarded this paper as the 'clearest evidence of (the equilibrium theory's) essential truth', and considered Diamond's claim for appreciable turnover within short time intervals as 'almost certainly correct'.

Lynch & Johnson (1974) and Johnson (1972) disputed these conclusions in some detail. Jones & Diamond (1976) dismissed these critiques solely on the basis of their own work fulfilling Lynch & Johnson's prediction that 'if equilibrium turnover rates are indeed as high as has been claimed... then

changes in the species composition of *resident* insular avifaunas should be detectable within, say, 5–10 years'. Jones & Diamond therefore thought that 'it remains to point out factual errors' in the critiques, and proceeded to do so without answering any of the allegations made in Lynch & Johnson's paper.

It is clear that Diamond had not considered adequately the effects of the activities of man; for example, he included birds of prey in his calculations, and it is almost certain that these were eliminated on these islands, as elsewhere, by the effects of pesticides and hunting. Lynch & Johnson satisfactorily demonstrated that there was no reliability in supposing that the rates of turnover were significantly different from zero. A reappraisal of the evidence from one island where adequate records are available (San Nicholas), resulted in a minimum estimate of the rate of turnover of zero. The critics emphasized the need for 'publishing sufficiently detailed supplementary information to allow the reader to make an independent assessment'; indeed, the principle of falsifiability requires that this be the case.

Diamond went on to carry out a similar investigation on the island of Karkar near New Guinea (Diamond, 1971), which suffered from even greater defects because the earlier survey had made no field notes and Diamond was relying exclusively on a collection of specimens. His computations would therefore only be valid if the early collectors not only saw every species on the island, but also collected them all (Lynch & Johnson, 1974). Even his calculations have been called into question (Slud, 1976), making rather doubtful Diamond's comparison between the turnover rates in tropical and temperate conditions.

Terborgh & Faaborg (1973) completed a similar study on the island of Mona in the West Indies, where the number of species was very limited. They state that there has been 'little disturbance by man', yet the coastal plain carries 'planted mahogany groves', three game birds have been introduced, and the formerly resident parakeet has been exterminated by 'hunting pressure' and 'blasting for guano mining'. The early expeditions, which 'seem to have been exhaustive', had seen a particular species of dove only once, but because it is not known to migrate, Terborgh &

Faaborg concluded that it was then resident and has since disappeared. Some of their 'immigrations' have similarly been called into question (see Lynch & Johnson, 1874). Slud (1976) recalculated the rate of extinction, obtaining 0.35% per year as opposed to the 0.23% per year calculated by Terborgh & Faaborg. The latter claimed that the prediction that small, far (Mona) and large, near (Karkar) islands should have similar rates of extinction was 'gratifyingly upheld by these two tropical islands on opposite sides of the globe'; this would not be supported by their figures, if Slud's calculations are to be believed. The authors also assumed that the island was comparable with Guanica Reserve in south-west Puerto Rico, claiming that all the land birds resident on Mona constitute a subset of those of the reserve and that therefore the latter could be regarded as the immigrant pool. Their claim, however, is false (Slud, 1976).

Following Diamond, Hunt & Hunt (1974) looked at the apparent turnover on the island of Santa Barbara off the coast of California. Diamond (1969) claimed that the number of species breeding on this island had decreased from ten to six between 1917 and 1968 with 62% of the complement of species changing in identity. This island constitutes an inappropriate test of the equilibrium theory because it is very small (1 square mile) and lost most of its vegetation in a fire in 1959. Hunt & Hunt used the same authors as did Diamond to establish their 'accurate baseline' and their study is open to similar criticisms. The authors state there is 'no reason documented for [the] extinction' of the birds of prey, and therefore assumed that man's activities had played little part.

Heatwole & Levins (1973) observed the plants and invertebrates of Cay Ahogado, a shifting sand cay of average area 650 m² and maximum elevation above the highest tides of 1 m. The total number of species of plant varied between twenty-one and six, hardly an equilibrium, and yet the authors took the average (11.2) as their equilibrium number. Coastal birds of the Kunnit Islands in the Gulf of Bothnia were the subjects of a study by Väisänen & Järvinen (1977). They calculated rates of turnover only for the waders, since this was the only group with approximately

constant numbers, and this then made their calculations rather suspect because they were dealing with very low numbers. Some of their figures, for example the 'time to saturation', are based on a single event.

Yet another series of surveys of the avifaunas of the Californian Channel Islands was conducted by Jones & Diamond (1976) between 1973 and 1976, in order to try to document turnover from year to year. The values obtained averaged 0.5–1.0% per year for the four larger islands, and 1.2–3.6% per year for the smaller ones; values calculated from yearly censuses were even higher (0.9–1.9% per year, and 1.6–5.6% per year respectively). In spite of this apparent correlation with area, the rates of turnover were not related to the distances of the islands from the mainland. This was explained away, first, by repeating Diamond's (1969) claim about the relative dispersal distances of the resident Californian species; second, by assuming that the 'rescue effect' of Brown & Kodric-Brown (1977) operated in this case; and last, that any surplus deviation from the MacArthur–Wilson model was due to differences in habitat between the islands, affecting the species–area relationship. The other main criticism of this work is that the authors appear to regard a 25% change as the dividing line between 'equilibrial' numbers of species, and others for which various explanations are deemed necessary to convince the readers that these islands *would* have been at equilibrium but for some traumatic experience in their history. The validity of this assumption is questionable; a coefficient of variation would have been more appropriate. Diamond & May (1977) did use a coefficient of variation in their examination of the data for the breeding birds of the Farne Islands: the dividing line in this paper appeared to be a CV of 20%. These authors produced an equation relating the observed rate of turnover to the interval of time between censuses, an expression which described fairly well the data from the Farne islands, but not those of Jones & Diamond (1976). Diamond & May suggested that the latter failure was due to the fact that they had not included in the equations the effects of competition, population changes, or variations in the rates of immigration and extinction. It could be argued that the model

of MacArthur & Wilson suffers from the same omissions. However, support for Diamond & May's interpretations was provided by Abbott (1978), who found that the rate of turnover of passerines on Carnac Island off Western Australia was significantly correlated with the time in weeks between censuses. The annual rates of turnover for this and other islands nearby remained low, and some show no changes at all with time.

The above studies have all sought to find a turnover in the composition of species, and have claimed to have shown that it has occurred. Other studies have found the opposite, and Abbott (1978) found both cases. For example, it has been contended that there has been no turnover at all of the birds of the Tres Marias Islands (Grant & Cowan, 1964) or Cocos Island (Slud, 1976). Heller (1976) found that the distribution of Aegean Enid snails was closely related to the topography of the sea bed, suggesting a relict continental pattern. Brown's (1971) work with mammals on mountains suggested that there was no immigration to the islands, and that the rate of extinction was extremely low. Johnson (1972) pointed out that of forty-one bird species found on the Californian Channel Islands, thirteen are represented by eighteen endemic subspecies, concluding that eleven of these could have resulted from a single colonization, and that two species have apparently colonized twice. Two of the subspecies have reinvaded the mainland. This argues, he maintained, for the relative stability of these insular populations through long periods of time (but see Johnson & Selander, 1964).

A lack of constancy of the 'equilibrial' number of species was found for the birds of islands near Australia and New Zealand by Abbott & Grant (1976) and Abbott (1978). Using the usual technique of searching the literature for 'thorough' surveys of the islands, they found that although all islands had undergone faunal change, the details of these changes did not support an equilibrial interpretation. Taking three categories of 'constancy', exactly the same, 10% and 20% change, then five, eleven and twelve out of fifteen islands, respectively, had 'constant' numbers of non-passerine species. Whilst these species might be regarded as approximately in

equilibrium, the passerines could not be described in this way: only two, five and six out of seventeen islands, respectively, had 'constant' numbers of species (the probability that this is due to chance is 0.097, 0.016 and 0.013 respectively). Abbott & Grant found no inverse relationship between the rate of immigration and the distance from the mainland, and the correlation was positive for the passerines. For the non-passerines, seven of the islands, and for the passerines, ten of the islands, had extinction rates of zero, and most of the extinctions that had occurred could be attributed to the activities of man. Abbott & Grant reviewed the studies published up to 1976, and found no significant regression of the rate of immigration on the distance to the mainland; a significant relationship was found for the rate of extinction and the area of the island. The authors concluded with an examination of the figures for breeding birds on Skokholm (Lack, 1969), where figures are available for the period 1928–68. They found that the 'equilibrium' number of passerine species varied by more than 150%, with enormous variation in the rates of extinction and immigration. Lack gave the figures for all birds, and the total number of species also varied greatly, by as much as 100%. Abbott (1978) studied the islands off the west coast of Australia, and suggested that natural rates of turnover were low, only augmented by the hand of man.

Similar reports have been published dealing with continental situations. Culver *et al.* (1973) tried to show that there was an equilibrium in the numbers of species of arthropods in limestone caves, but they were forced to conclude that immigration rates were 'probably very low' or non-existent. They stated that the major cause of extinction of the terrestrial species was heavy flooding, but could find no evidence of the disappearance of any species after a hurricane struck the area in 1969 with its concomitant flooding. Smith (1974) misapplied the equilibrium theory to the numbers of individuals of one species, the pika *Ochotona princeps*. This species is territorial, and it is therefore not surprising that some sort of dynamic equilibrium exists. The boreal mammals of the Great Basin are not at equilibrium (Brown, 1971), and probably never had been since at least the end of the

Pleistocene because there can be no immigration of new species. Whitcomb *et al.* (1976) claimed that on average there was a 13.6% change in the composition of the birds breeding in Trelease Woods, but the evidence for an equilibrium is equivocal (see above). An equilibrium was re-established, it was claimed by Brown & Kodric-Brown (1977), on 'defaunated' patches of thistles, but their evidence for this is questionable: one patch had an average of 1.67 before and 3.78 species after defaunation. They further claimed that the rate of turnover of the species of arthropods was related to the distance away from the 'source' and inversely to the number of species; in neither case do they provide any detailed figures to justify these claims.

Very high rates of turnover were calculated for chironomids inhabiting prairie ponds (Driver, 1977), but the number of species fluctuated wildly. Beaver (1977) showed that dead snails eaten by the larvae of flies could not be regarded as islands at equilibrium.

Lassen (1975) studied freshwater snails in Denmark, where there are thirty-four species, and used surveys conducted in 1899, 1958 and 1971. He calculated the Variance/Mean ratio for the number of species occurring in various classes of sizes of lake, claiming that the figures lent 'strong support' to the equilibrium model. The model predicts that the ratio should be 0.5 if the lakes are at equilibrium, and between 0.5 and 1.0 if they are 'undersaturated'. Four of Lassen's seven figures were 1.22, 0.93, 0.81 and 0.77. He regarded one particular pond as 'oversaturated' because it had seven species, and the species-area relationship predicted that it should have six.

Therefore none of the continental situations, and very few of the insular ones, warrant the application of MacArthur & Wilson's model. Only the studies of Simberloff & Wilson (1969, 1970) and Jones & Diamond (1976) show good support for the equilibrium theory.

Conclusions

The equilibrium theory was accepted long before there was adequate evidence to indicate that it was valid. Simberloff (1974)

seemed at first to support the view that the theory was proven: '...the equilibrium hypothesis has been experimentally confirmed for oceanic islands, proved useful in interpreting many other situations, and spawned a mass of research which was given biogeography general laws of both didactic and predictive power.' However, he then appeared to retract this view (e.g. Simberloff & Abele, 1976a; Simberloff, 1976b), and wrote (Simberloff, 1976b): '...[the theory] has achieved the status of a paradigm... a theory so widely accepted as an accurate description of nature that failure of an experiment to yield the result deduced from the theory leads *not* to a rejection of the theory but rather to attempts to fault the deductive logic or experimental procedure, or simply to wilful suspension of belief in the experimental result'. He had decided that 'the models may or do not incorporate potentially biologically important facts' (Simberloff & Abele, 1976a), and that applications were premature. He was led to these conclusions partly by the use of the theory in the realm of nature conservation. Terborgh (1974) has suggested that certain principles for the design of nature reserves could be derived from the equilibrium theory, and Diamond (1975a) produced a set of geometrical principles, repeated in several subsequent papers (Diamond, 1976b; Diamond & Mayr, 1976; Terborgh, 1976; Wilson & Willis, 1975). The concepts were reviewed by Sullivan & Schaffer (1975). Simberloff & Abele (1976a, b) pointed out that the theory was not sufficiently validated to allow such an extension, suggesting that there was a certain 'taxal idiosyncrasy' in the model's applicability. Their views were hotly disputed by Diamond (1976a), Terborgh (1976) and Whitcomb *et al.* (1976).

That extinctions occur in reserves or otherwise is not in question (Galli *et al.*, 1976; Willis, 1974), but there is no need to label these places as 'failures as faunal preserves' (Terborgh, 1974) merely because some birds have died out. There is no evidence that any extinctions in reserves have been due directly to any decrease in area; Miller & Harris (1977) could not attribute any disappearances in the East African National Parks to this cause. The occurrence of immigrations is also not in doubt. However, a turnover of species at an

equilibrium has only been unequivocally demonstrated by Simberloff & Wilson (1969, 1970) in their studies on experimentally defaunated islands.

The apparent lack of conformity of the model when any taxon other than that of the birds is considered points to a major flaw in its derivation: indeed, Sauer (1969) thought that 'the whole approach smacks of ornithology'! Natural turnover rates appear to be extremely low, if not non-existent (Simberloff, 1974; Abbott & Grant, 1976; Brown, 1971; Slud, 1976; Abbott, 1978; etc.), if man's influence is slight or can be assessed. The proponents of the model seem to have gone to inordinate lengths to fit the available evidence to the bed of Procrustes that constitutes the hallowed tenets of the theory, and I believe it is necessary to cut out those parts that are contradicted by experiment. For example, it would seem that many, if not all, insular continental situations are at best badly described by the equilibrium model.

Sauer (1969) and Lack (1970) believed that an 'idiographic' approach to insular biogeography is valuable, where 'each island can be regarded as a unique locus of species assembled for idiosyncratic reasons that can tell us little about other islands'. Sauer in particular criticized heavily the MacArthur-Wilson theory on the basis of its simple nature: 'In short the equilibrium model and its derivatives suffer from extreme oversimplification by treating islands as functional units with no attention to internal habitat diversity and by treating species as interchangeable with no allowance for genetic or geographical diversity. This is not even good as a first approximation, because it filters out the interpretable signal instead of the random noise... In a field as complex as biogeography, pure deduction that starts with gross assumptions and a few casually selected variables is unpromising, however skilfully done... (such a model) is essentially absurd'.

The qualitative use of the equilibrium concept has stimulated a great deal of valuable research, and is clearly of use as a way of approaching an appropriate problem; in particular, Janzen's (1968, 1973) proposals have an intuitive value in the study of the colonization of plants by phytophagous insects. Quantitatively, however, it would seem that

the model has little evidence to support its application to any situation.

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Addendum

Several papers have come to my attention since completing the review and which I list below. Others have only recently been published, and I would like to draw particular attention to the work of Connor & McCoy (1979). These authors agree with the assessment that I have outlined above of the species–area relationship as interpreted by the followers of MacArthur & Wilson. An ingenious attempt to use the model of insular biogeography to explain the nature of the process of extinction has been published by Stenseth (1979), but I am not qualified to comment upon its validity. Apart from these two exceptions, the other papers listed below do not alter the opinions expressed in the main body of the review.

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