vegetation variation and the single variable, annual solar radiation, suggests that the
continuum associated with slope, aspect and altitude might be jointly related to insolation,
and that the degree of insolation could be used as a general predictor of vegetation type
with surface geology and drainage held constant. However, in areas with considerably
higher precipitation than experienced at Risdon the influence of solar radiation on
evapotranspiration and thus moisture availability would lose its significance. In
this situation differences in solar radiation would influence the vegetation mainly through
their effects on soil temperature and light conditions. Thus, with high precipitation
the vegetation biomass could be expected to be greater on the more insulated sites, in
marked contrast to the situation at Risdon and in other Australian areas that have been
studied (Pook & Moore, 1966; Ashton, 1976).

References

Ecol. 64, 463-483.

Bray, J.R. & Curtis, J.T. (1957) An ordination of

the upland forest communities of southern
Wisconsin. Ecol. Monogr. 27, 325-349.

Cantlon, J.E. (1953) Vegetation and microclimates on north and south slopes of Cubbit Tank Mountain,


Hobart.

Tasmanian eucalypt forests and woodlands. J. Biogeog. 1, 227-245.

Holland, P.G. & Steyn, D.G. (1975) Vegetational
responses to latitudinal variations in slope angle and aspect. J. Biogeog. 2, 179-183.

McNaughton, K.G. & Black, T.A. (1973) A study of
evapotranspiration from a Douglas Fir forest
using the energy balance approach. Water
Resources Res. 9, 1579-1589.


Oke, T.T. (1977) Boundary layer climates. Methuen,
London.

aspect on the composition and structure of dry

Specht, R.L. (1976) The vegetation of South


Introduction

The object 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 extensive definitions (see
Poppier, 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
that 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 unpunished; 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

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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 conclu-
sion that a logarithmic series could be fitted,
and Preston (1962) showed that, by con-
verting the abundances to canonical form (i.e.
the geometric scale), one could obtain a normal
distribution. The relationship between the
number of species and their canonical abun-
dances 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 con-
venient 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 popu-
lations in the Arctic has been superseded by
other demonstrations of cycling numbers
from both temperate and tropical environ-
ments.
When faced with a highly complicated
phenomenon where the observed effects
result from an interaction of many factors,
which are 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 knowl-
ledge because it may not satisfy the criteria
to which I have referred.
The 'very special case of island species'
(Krebs, 1972) results from being a trap
that collects successfully dispersing and colo-
nizing species. In the words of Slud (1976),
reviewing the literature dealing with adivasas
of islands throughout the world: '... islands
come closest to constituting discrete inde-
pendent ecosystems or natural laboratories;
this makes islands desirable for the study of
geographical variation'.
Preston (1962) pointed out that a relation-
ship could be derived from his canonical abun-
dances of species if one assumed that the
number of individuals in a taxon on an land
could be represented by the product of
the density of those individuals and the area.
The relationship is:

$$S = ce^z$$

where $S$ is the number of species inhabiting an island of area $A$, and $c$ and $z$ are con-
s tant. Latitudinal gradients in the diversity
of species were construed to be 'due to vari-
tions in the value of $c$, taken to represent the 'biot
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 coloni-
sation' (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
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 by
MacArthur & Wilson (1963, 1967) to propose
their equilibrium theory, combining these
factors with the basic phenomena of immi-
 nation and extinction, to suggest that the
number of species on an island, $S$, tends
wards an equilibrium number, $S_e$. This
equilibrium is the result of a balance be-
bet
the rate of migration and the rate of extinc-
tion, and the equilibrium number is deter-
mined by the island's area and position.

The variance ($\sigma^2$) at equilibrium is:

$$\sigma^2 = S(1 - e^{-Gt})$$

where $G$ is a constant, $S$ is the equilibrium
number, $S_e$ 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 'stepp-
ing 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 equili-
brum number over long time spans. As
required, the theory generated several falsifi-
able predictions:

(i) that the observed turnover in the com-
position of species is considerable;
(ii) that log $S_e$ 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,

$$\text{variance } (\sigma^2) < \frac{S\sigma^2}{S}$$

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 equili-
brum number ($T_{90}$), using the equation:

$$T = 1.165/t_{90}$$

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:

\[
\text{Mean} = \frac{P}{\sum \frac{I_a}{E_a + E}}
\]

\[
\text{Variance} = \sum \frac{I_a E_a}{(I_a + E)^2}
\]

where \(I_a\) and \(E_a\) 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 \(I_a\) and \(E_a\) 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 pooling 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 (Vullemier, 1970) and apparently indiscriminately (Terborgh, 1973a). Jansen (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),

\[
S = a + b \log A \exp \left(-D^2/4A^2\right)
\]

where \(D = \text{dispersal distance}, a = \text{pool of colonists}, b = \text{lower case letters denote litter constants}.\) Their claim will be examined later. Finally, Taylor & Regal (1978) consider '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 pan mony': but there is an epistemological problem associated with this conception simplicity that is philosophically insoluble (Popper, 1968). Practically it is possible to pick out simpler theories from the more complex ones; however, the danger lies in equating a simpler explanation with that which is more aesthetically pleasing. Although one may believe in the 'austerely beautiful simplicity of the world' as revealed by 'nature 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 that the Heuristic value of the model is duced. The task in hand is to produce simplification that is not itself necessary simple, and which involves the smallest practicable number of elements. T MacArthur–Wilson model is certainly parsimonious, and that capacious Nature shot
The equilibrium theory of island biogeography

The strictly delimited boundaries of oceanic islands, and the comparative ease of making counts of the total numbers of species, have made it possible to demonstrate a species-area relationship over a wide range of islands, and to make rigorous tests of the theory. The theory is based on the idea that the total number of species on an island is a function of the island's size. This relationship is often expressed as a power law of the form:

\[ S = kA^z \]

where \( S \) is the number of species, \( A \) is the area of the island, \( k \) is a constant, and \( z \) is the species-area exponent. The value of \( z \) is typically around 0.25 for oceanic islands.

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(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 seven soil types, the log of the latitudinal range, 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 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 ten variables 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 area and latitude 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 ($R^2 = 0.97$ 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 Amazonic (Müllerberg et al., 1977). Lillegren (1972) found no relationship between area and the diversity of orders and families of Cenozoic mammals, in contrast to the later find 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 is of the theoretical level and the birds are fit 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 the birds of the Solomon Islands carried out by three co-workers (Diamond et al., 1976; Mayr, 1976; Gilpin & Diamond, 1976). Their studies produced a complex equation (see above) that it is claimed, describes an accuracy of 98% the number of species on any one of their 'core islands', but that 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 source of information were censuses carried out in 1959–60 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 $\log A$ 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 at least, then 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 25% 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 combinations are each the unique result of interplay among many factors that are peculiarly diad to islands: this makes islands ecologically noninterchangeable' (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 not almost universally ignored or explained away, often in a very impressionistic and dubious manner. The values of $z$ obtained from these regressions are very often, 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 the results in Zuckerman, 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 $S = \log (0.18) +$
The equilibrium theory of island biogeography

F. S. Gilbert

0.72 log A. The manner in which they did this is far from convincing, since it was necessary
in a slightly less 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, S and A were not significantly correlated for the aquatic species, but the authors still produced
the equation ($c = 2.14, z = 0.19$). The Tesen 'caves' of southern Switzerland were studied by
Vuilleumier (1973), who compiled from the
'scientific literature' list of species of arthropods
for forty-eight caves. He then performed 'stepwise multiple regression analyses' with various
indices of area, environmental vigour, and isolation, as the independent variables. He
found significant correlations in the case of 'area' (the combined length of all the galleries),
accounted for 47% of the variance in species. However, for any measure of isolation, 57%
of the variance in the number of species was accounted for by five independent variables,
and three consistently high contributors were
'area', a water source, 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 of
fast and slow-moving birds were used. But Maiuriello and 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.

Simmon (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
mountain tops 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, $0.25$ is close to the theoretical value of $0.263$,
these 'restored' populations are 'probably near
the biological equilibriunm 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 not
attempt to discuss several of the studies again, in the
case 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 m$^2$, 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 sampling, and found that an equation of the form $S = 0.81 + 4.45 A$ can
be applied. Here area had no effect on the
'foliage height diversity' (supporting del
tro, 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
$S = 0.68$, 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
Trelawne 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 'eims were dying from Dutch elm disease',
and the average number of species increase to
32.5 (SD = 2.6; $P < 0.01$) 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'.

Hellwelli (1976), like Moore & Hooper,
examined breeding data of birds from British
woods, and disagreed with their findings. His
analysis suggested that the validity of the $c$ 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 flora. However,
Harman & Harvey (1975) claimed that 98% of
the number of species 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 fish of
ponds and lakes, but Lassen (1975) claimed
that his figures showed that $S = 0.37$ for small eutrophic lakes, 0.05 for large eutrophic lakes, and 0.25 for oligo-
trophic lakes, in the case of Danish freshwater
small. 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 tech-
iques were used by Sepkoski & Rex (1974) to
claim that coastal rivers were biogeographic
island small. However, like Gilpin & Diamond
(1976), they thought that this was
merely because they had shown that a
criteria existing, which meant
that their complicated modelling of immi-
grant 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) and
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 coloni-
ized 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 increas-
ing distance between patches! but, because
of the figures to substantiate these claims, it is difficult to assess the validity of
them. Seifert (1975) studied insect
communities on Heliconia blossoms, and
found that there was a highly significant
relationship between the number of flow-
ers and the number of species, with
smalling 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 & Lackenhoff (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 (1974, 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 the 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 California violets and their legumes. Opler has been 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.

Finally, the number of mites living or being carried on North American cicadoid 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.
(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 invertebrates 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 _K_ is defined as the probability of establishment once the island has been reached) is (μ/K), where n is the size of the island 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 each case).

As stated above, Crowell could not demonstrate any natural immigration or extinction of populations of either voles, 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_ is:

\[ K = \frac{\lambda}{\mu} \left( \frac{1}{1 + \frac{\lambda}{\mu}} \right) \]

where

\[ \lambda = \frac{1}{\mu} \left( \frac{1 + \lambda}{2\mu} \right) \]

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

Schaefer & Schaefer (1978) found an inverse relationship between the survival of _Anolis_ lizards and the size of an island, contrary to the assumption of the MacArthur–Wilson theory.

Janzén (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 plant species of trees were distributed about the regression line no differently from native species. Van Veen (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 dates for Birkenhead 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 conclusion 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). Focusing on one detail, their regression line seemed to be determined in slope and significance by just two points, those for _Eugenia_ and _Säliz_.

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 the 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 colonization 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 irreproachable 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). Heastwole & 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, 1978c) 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 there to be no effect 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 fauna 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 colonization 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
distribution of West Indian birds on small or intermediate islands, and 80% on larger islands, was explicable deterministically, was effectively dismissed by Simberloff (1976a). 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 'associative 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 very small islands may be bad examples from 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 considerable support for the equilibrium theory because the 'relaxation times' (defined in Diamond, 1971) calculated by Diamond are so long that by the time 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 cannot be used to predict the 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 mammal biota (see below).

Wilcox (1978) purported to find a relationship between the time of isolation of various 'land-bridge' islands in the region of Baja California 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, the results are dependent upon the controversial estimates of the timing and magnitude of eustatic rise 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 systems. 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. Heliwell, 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, located in 1910-11 by the rising waters of Gatun Lake, on 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 forest is not reoccupiable in the area (no species recolonized from the mainland, only 500 yards away near the latest 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 for smaller data sets. 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 Peninsular Triangular 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 and families.

A recent example of the way in which the idea 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 method of demonstrating the equilibrium proposition, whereby actual turnover among insular populations is documented whilst the total 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 for smaller populations. At this point, extinction 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 organizing 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 results 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 breeding avifauna of the 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 number of species breeding on each island (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 did not construct 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 surveys and one to 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 at 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 that ‘linearly perfect inverse correlation’ betwixts islands 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 dispersion. 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 the 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 paper, without any attempt to construct a new 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 these 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 earlier deforestation 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 this would be difficult to disprove, unless a population drop was documented into question (Stud, 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 'seemed to have been exhaustive', had seen in 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 'immigrants' have similarly been called into question (see Lynch & Johnson, 1974). Stud (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 claim that roughly 95% of the species on this island was comparable with Guanica Reserve in south-west Puerto Rico, claiming that all the land birds resident on Mona constituted a subset of those of the reserve and that therefore the latter could be regarded as the immigrant pool. Their claim, however, is false (Stud, 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 66% of the complement of species changing in identity. This was the reason for the experimental 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 have shown that man's activities 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 Abogado, a shifting sand cay of average area 650 m² and 'Dianium' diameter of 10 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 equilibrant number. Coastal birds of the Kunit Islands in the Gulf of Bothnia were the subjects of a study by Lack (1973) and a very high turnover (ca. 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 avian
faunas of the temperate islands was
conducted by Jones & Diamond (1776)
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 1.2–3.8% per
year for the smaller ones; values calculated
from yearly censuses were even higher (0.9–
1.9% per year, 0.1% 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 California birds, 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 ‘equilibrium’ numbers of
species, and others for which various explana-
tions are deemed necessary to convince the
readers that these islands would have been at
equilibrium but for some traumatic experience
in their history. The authors also fail to
real-score the predictions of the model
on this point, especially in the
apparent high turnover for the
passenger pigeons. 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 a significant reduction of the rate
of immigration on the distance to the main-
land; a significant relationship was found for
the rate of extinction and the area of
the island. The authors concluded with an exami-
nation of the figures for breeding birds on
Skokholm (Lack, 1967), where figures are
available for the period 1926–68. They found
that the ‘equilibrium’ numbers 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 &
Grant (1976) believed that the area 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. (1976)
showed that there was an equilib-
rium in the number of species of butterflies
in limestone caves, but they were forced to
conclude that immigration rates were ‘prob-
bly 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. Later, a hurricane struck the area
in 1969 with its concomitant flooding. Smith
(1974) misapplied the equilibrium theory to
the number of individuals of one species, the
pika Ochotona princeps. This species is terri-
torial, and it is therefore not surprising that
Smith failed to produce the equations that
describe the dynamics of equilibrium. The
breeding season of the species was not at
equilibrium (Brown, 1971), and probably
never had been since at least the end of the
Pleistocene because there can be no immi-
grantation of new species. Whittaker et al.
(1976) claimed that on average there was a
13.6% change in the composition of the birds
breeding in Trelase 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 ‘de-
faunation’ of the island’s birds, but one
extinction of one species; one extinction of
island has been well described by Hamilton &
May’s interpretations was provided by Abbott
(1978), who found that the rate of turnover
of passerines on the Carnarvon Island off Western
Australia was significantly correlated with
the time in weeks between censuses. The annual
rate of turnover for this and other islands
nearly remained low, and some show no
changes at all with time.

The above studies 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 oppo-
site, and Abbott (1976) was an example,
having been contended that there
had 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 Aegae Enid
snails was closely related to the topography
of the island, according to a classic geographical
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
individuals, concluding that eleven of
these could have resulted from a single
colonization, and that two species have
apparently colonized twice. Two of the sub-
species have invaded the mainland. This
argues, he maintained, for the relative stability
of the insular populations through long
periods of time (but see Johnson & Selander,
1964).

A lack of constancy of the ‘equilibrium’
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 dates at which the birds were
first recorded, they found that although all islands had
undergone faunal change, the details of these
changes did not support an equilibrium inter-
pretation. Taking three categories of ‘con-
stancy’, exactly the same, 10% and 20%
change, then five, eleven and twelve out of
fifteen islands, respectively, had non-passnerine species. Whilst these
species might be regarded as approximately in
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 appears to retract this (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 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 recent conservation, Terborgh (1974) has suggested that certain principles for the design of nature reserves could be derived from the equilibrium theory, and Diamond (1973a) produced a set of geometrical principles, repeated by Diamond & May (1977) and Wilson & Willis (1976a). The concepts were reviewed by Sullivan & Schafter (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 idiocy' in the model's applications, and were hotly disputed by Diamond (1976a), Terborgh (1976) and Whittcomb et al. (1976).

That, extinctions occur in reserves or elsewhere 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, 1976) merely because some birds have died out. There is no evidence than 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 de-faunated 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 is a biological fallacy'. 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 force 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 experience. 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 insular reasons. Sauer, in particular criticized heavily the MacArthur-Wilson (1967) and several subsequent studies: '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 inter-changeable 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. In a genuine 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.


Holland, P.G. (1978) Species turnover in deciduous forest vegetation. Vegetatio, 38, 113—118.


Abbott, L. (1978) Factors determining the number of land bird species on islands around South-Western Australia. Oecol. (Berl.), 33, 221—233.


