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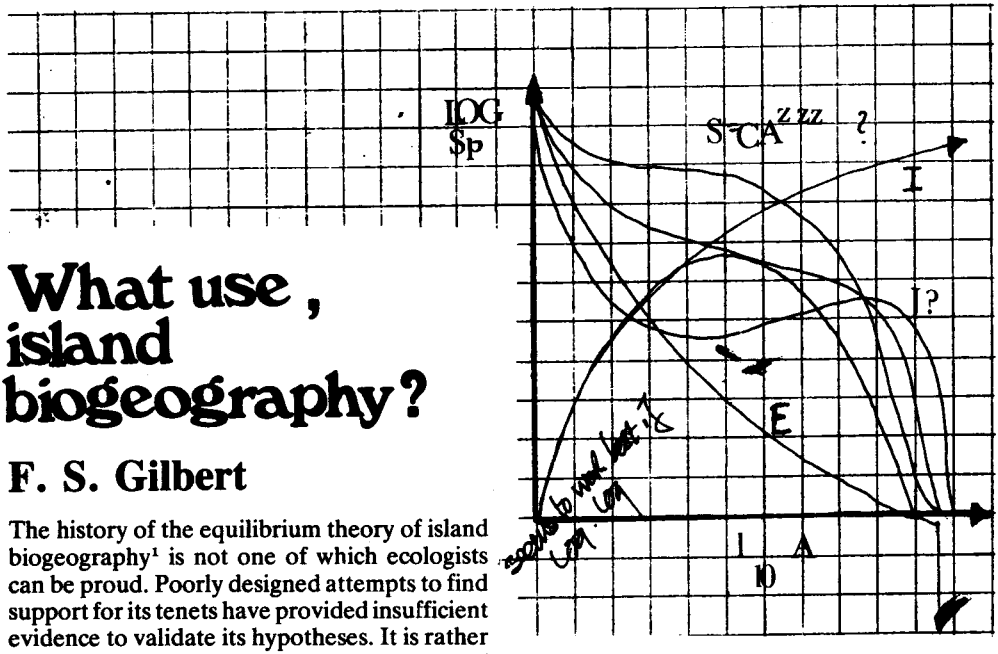

What use, island biogeography?

F. S. Gilbert

The history of the equilibrium theory of island biogeography[1] is not one of which ecologists can be proud. Poorly designed attempts to find support for its tenets have provided insufficient evidence to validate its hypotheses. It is rather embarrassing therefore that the principles of the model have been applied so widely in the realm of nature conservation with apparently no real assessment of their value. One may argue[2] that the puritanical rigour of the physical sciences is not relevant to ecological theory and that one must therefore tolerate a number of anomalies in the theoretical development of ecology. This view may be valid in the rarefied atmosphere of the academic world, but falsified hypotheses are hopeless in the practical application of ecological models, where rigour and accuracy may be vital.

What is the Equilibrium Theory?

It has been known for a long time that, in general, more species are found on large than small islands. It is important to realise that this is only a general observation since the method normally used to demonstrate this phenomenon, double-logarithmic regression, turns almost anything into a straight line.[3,4] The equilibrium theory is an attempt to explain the species-area relationship in terms of a dynamic balance between immigration and extinction of species, the rates being set by the area and position of the 'island' (i.e. not only oceanic islands, but also habitat patches). One consequence of this hypothesized relationship is that the identities of the species should change through time, evident as an appreciable turnover of species. Any change in the area of the 'island' (usually a decrease) should cause an imbalance between these processes of immigration and extinction, which in turn should lead to a change in the number of species on the island. *Ad hoc* modifications of the theory have been proposed to account for numerous anomalies.[5] The essence of the theory concerns the numbers of species and not their identities, treating species as ecological equivalents. The only recognition of differences between species included in the theory was in terms of the shapes of the immigration and extinction curves (versus distance and area).

The main interest of island biogeography theory to nature conservationists, is the prediction that a recently isolated patch of habitat, such as a reserve, will inevitably lose species because of the reduced rate of immigration, and that the number of species will therefore decline to a new equilibrial level; this process is labelled 'relaxation'.[6] It is claimed that the principles of the equilibrium theory indicate a method of minimizing the number of species lost, and a set of design criteria have been proposed [6]: reserves should be as large as possibe, of certain shapes, and situated in certain configurations with respect to one another.

What evidence can we muster to support the predictions of the theory? Criticism of studies purporting to provide such support has been growing.[3,5,7] We need consider here only two aspects, the species-area relationship and the process of relaxation.

Problems with the theory

The species-area relationship actually predicts that two small areas will probably contain more species than one large one of the same total area [3]; often it is the case that one small area has a greater number of species than a large area. Recognition of the inadequacy of large area *per se* as a design criterion[6] has led to several recent theoretical papers: these modify the theory somewhat, and naturally demonstrate that subdivision of reserves will often be of greater value than a single large reserve.[9,10] When this principle was originally proposed in 1976, some of the authors who now provide theoretical justification, hotly disputed the case.[11] Other design criteria obtained from the equilibrium theory have similarly been challenged on both empirical[8] and theoretical[12] grounds.

It is therefore clear from nearly all studies of the species-area relationship that the correlation between species number and area is not good enough to justify using the regression to predict the species richness of other areas.[4] However, this is exactly the procedure adopted by those who have tried to show that 'relaxation' occurs. These oft-cited studies have been heavily criticized in recent publications.[3,5] Knowledge of the present-day species richness and area of an island, and of the former area (also often inadequately estimated) does not entitle one to calculate the former number of species inhabiting it. Even if this procedure were valid, the calculated 'relaxation times' in most cases are well in excess of a thousand years, so while no one would deny that the problem of extinctions in reserves is a real one, the process of relaxation as predicted by the equilibrium theory seems essentially irrelevant to its prevention.

Some authors have predicted a dramatic "faunal collapse" in East African national parks by these methods,[13] with the loss of up to 23 per cent of the mammalian fauna within fifty years. Whilst they could prove to be correct, the technique of arriving at this prediction seems open to question. A species-area regression for oceanic islands in the Far East was used to predict the number of species there "10 000 years ago", and from this relaxation coefficients were calculated. These were then applied to the habitat islands in East Africa, the parks and reserves, to predict a huge loss of species. Many other applications of the theory seem equally imprecise.

Island Biogeography in Perspective

Over and above criticisms of method, one of the main reasons why the equilibrium theory has little relevance to conservation is that it ignores the identities of the species concerned. Conservation is only possible where public opinion dictates and economic considerations allow; very few people would be upset if an obscure species of mite were to disappear from the earth, but no one desires the total disappearance of the tiger. Thus the sheer number of species contained within a reserve is often likely to be of subsidiary importance; management strategies designed to preserve the maximum species richness are seldom totally acceptable and are frequently inherently unattainable.

A recent conference on conservation biology had several participants speaking about the equilibrium theory. One of these was critical of the theory as applied to conservation; his paper was not accepted for the conference report, recently published.[14] Likewise several important but critical papers were not cited by any speaker concerned.[15,16] It is hardly surprising that the equilibrium theory has gained such wide acceptance if only confirmatory studies are presented, and never those refuting it.

Historically, animal ecologists have still to make a major contribution to the preservation of nature; conservation may make use of science, but it has very much more to do with economics, politics and sociology. It is time we realized that uncritical acceptance of simplistic theories can only make matters worse.

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Dr. F. S. Gilbert is a member of the Department of Applied Biology, University of Cambridge. Oliver Prŷs-Jones and Hilary Gilbert helped with the article.

The implications of GEDNEY

Stuart E. Crooks

The future conservation of Britain's estuarine habitats received both a boost and a setback with the announcement by the Secretary of State for the Environment of his decision about the application for planning permission for saltmarsh reclamation at Gedney Drove End (Lincolnshire). His decision — widely welcomed by those campaigning for a new deal for estuaries — was to refuse planning permission, but the report of the Inspector appointed to direct the Public Inquiry together with the detailed findings of the Secretary of State leave an ambiguous and wholly unsatisfactory situation.

Public Enquiry

The Gedney Drove End Public Inqury held in February 1980, was a significant event in the history of estuarine conservation: it gave the conservation bodies an opportunity to advance their arguments in favour of conservation and to present publicly their evidence for the value and importance of such wildlife habitat. It was doubly significant because of the ruling by the Department of the Environment that evidence as to the importance of the Wash as a whole would be admissable. The Inquiry also marked the first occasion on which the voluntary conservation bodies had joined with the Nature Conservancy Council to present a co-ordinated case, under the guidance of a barrister, at a Public Inquiry.[1]

Gedney Drove End, in the south of the Wash, is situated next to the outfall of the River Nene. It is in Lincolnshire, but lies not far from the boundary with Norfolk. An application was made for the agricultural reclamation of 81 hectares of saltmarsh by the construction of sea banks. Reclamation of saltmarshes is nothing new, but for a variety of reasons this application became the focus of attention for the conflict between conservation of estuarine habitats and agricultural reclamation. Interestingly the Public Inquiry was called, not on appeal against the refusal of planning permission, but by the referral of the application first by the District to the County Council, and then by the County to the Department of the Environment, as a matter raising issues of national and international importance in view of competing demands.

The Inquiry lasted for several days and much detailed evidence was heard from interested parties. The basic conflict was, however, quite simple. The applicants wished to turn a large area of agriculturally poor land into highly valuable and profitable arable land. In their eyes they were proposing a business venture which would provide employment and help to offset the loss of agricultural land elsewhere. The resulting agricultural produce would, it was