INDEPENDENT DISCOVERY OF THE EQUILIBRIUM THEORY OF ISLAND BIOGEOGRAPHY

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A correlation of this kind [between number of species and logarithm of area of island] *is as interesting as it is unexpected, for it suggests the existence of an equilibrium value for the number of species in a given island, a value which acts as a limit to the size of the fauna. The processes which determine the equilibrium value for an island of given size must be, on the one hand, the extinction of species, and, on the other hand, the formation of new species within the island, and the immigration of new species from outside it.*

The above quotation does not come from one of MacArthur and Wilson's (1963, 1967) two seminal publications on the equilibrium theory of island biogeography. It was written 15 yr earlier by another author. It appears on page 117 of Eugene G. Munroe's (1948) doctoral thesis on the distribution of butterflies in the West Indies.

The earlier and independent discovery of the equilibrium theory by Munroe is more than one of those amusing little incidents in the history of science. It warrants further examination for two reasons. First, unlike some purported cases of prior discovery of important ideas, Munroe did not have just some vague, poorly articulated notion of the species equilibrium. He clearly presented the empirical species-area relationship that stimulated his inductive discovery, investigated the generality of this pattern, and developed detailed verbal and mathematical models to explain it (Munroe 1953). Munroe's concept of the species equilibrium was identical in all important respects to MacArthur and Wilson's. Second, given the striking similarity of the two models, it is worthwhile to ask why Munroe's discovery went unrecognized (but see Gilbert 1984) while MacArthur and Wilson's has been hailed as one of the successes of the evolutionary ecology of the 1960s.

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Convergent Origin and Development of the Equilibrium Theory

Species-area relationships and the concept of equilibrium. It is clear that the inspiration for both Munroe and MacArthur and Wilson came from the very regular correlation between the number of species inhabiting different islands within certain archipelagoes and the area of the islands. Thus Munroe writes:

Observed figures show that the numbers of the better known animal groups inhabiting certain islands within the same archipelago bear an approximately linear relationship to the logarithms of the surface areas of the respective islands. This is true, with some exceptions, for the birds and butterflies in the West Indies, and for birds in certain Malayan and Pacific island groups. —Munroe 1953: 52

It is clear that this semi-logarithmic relationship is dependent on the rate of extinction of species, which must in turn be governed in some way by the area which they occupy: i.e., by their population numbers. Restriction of the population number, more severe the smaller the island, must increase the hazard of extinction of each species, whether through accidental reduction of already small population, through contest with other species for the essentials of life, or through deterioration of the population genotype, due to the Sewall Wright effect. We can, then, think of an equilibrium value for the number of species in a given island fauna, depending on the one hand on the probability of extinction, correlated inversely with island size, and on the other hand on the probability of reinforcement, correlated directly with proximity to an area of richer fauna. Any tendency to differentiation of new species within islands would work in the same direction as reinforcement, i.e., against extinction. —Munroe 1948: 118–119

And MacArthur and Wilson:

Theories, like islands, are often reached by stepping stones. The "species-area" curves are such stepping stones. . . . There exists within a region of relatively uniform climate an orderly relation between the size of a sample area and the number of species found in that area. Darlington (1957) expressed it as follows for the particular case of the herpetofauna of the West Indies: "division of area by ten [in going from one island to the next] divides the fauna by two." A more general first approximation for the number of species in island faunas as a whole is given by the equation $S = CA^z$, where S is the number of species of a given taxon found on the island and A is the area of the island. C is a parameter that depends on the taxon

and biogeographic region, and in particular most strongly on the population density determined by these two parameters. z is also a parameter but one that changes very little among taxa or within a given taxon in different parts of the world.
                                                 –MacArthur and Wilson 1967: 8–9

The strikingly orderly relation between island area and species diversity has elicited several attempts to identify and to measure the contributing factors. . . . Preston (1962) and MacArthur and Wilson (1963) independently suggested that there might be a balance of immigration by extinction so that the diversity of at least some biotas could be understood as an equilibrium. A perfect balance between immigration and extinction might never be reached, . . . but to the extent that the assumption of a balance has enabled us to make certain valid new predictions, the equilibrium concept is useful. . . .
                                                 –MacArthur and Wilson 1967: 19–21

Both Munroe and MacArthur and Wilson appreciated not only the significance of the tight correlation between species richness and island area, they also recognized that it was possible to explain deviations from the relationship in terms of insular characteristics that would affect either immigration or extinction rates. Munroe:

> *The exceptions to the rule are: The Virgin Islands and Hispaniola, in which the faunas are too large, and Barbados, in which it is too small; as we shall see, it is possible in each case to find an hypothesis to account for the departure. . . . In Barbados, a small island, situated a considerable distance to the windward of the nearest sources of immigration, themselves small islands, the immigration rate must be unusually small. In the Virgin Islands, on the other hand, an abnormally high rate of immigration may be expected, owing to the proximity of the relatively large fauna of Puerto Rico. In Hispaniola there is no reason to expect an abnormal immigration rate, but here the rate of speciation has been higher than elsewhere, due to the expansion of the genus Calisto, which, as we have seen, has taken place largely within the island; and in fact, if all but one species of Calisto are subtracted from the total, the corrected value for the size of the fauna falls much closer to the semilogarithmic line.*   –Munroe 1948

And MacArthur and Wilson:

> *Deviations from the theoretical value z [slope of the regression of log S on log A] are to be expected, and should be subject to biological explanation. . . . In comparing archipelagos, we would expect that as a rule z will increase with increasing degree of isolation,*

both of the islands from each other and of the archipelago as a whole from the nearest neighboring archipelago or continent. Hamilton and Armstrong have pointed out that this is true for land birds of the West Indies, East Indies, and East-and-Central Pacific, which are increasingly isolated in that order. . . . As islands become large, their topography becomes more complex, especially if they are mountainous. . . . The result is an enhancement of species accumulation that will account for some, and perhaps most, of the observed increment of insular z values above the predicted number.–MacArthur and Wilson 1967: 16–17
See also MacArthur and Wilson 1963: 373 and Fig. 2.

Mathematical models.   Had Munroe stopped with his doctoral thesis, the similarities to MacArthur and Wilson's later work would have been striking enough. However, Munroe (1953) developed his equilibrium theory of island biogeography in a subsequent paper, but only the abstract was published, and this appeared 4 yr after it was presented at a meeting in 1949. This tantalizing abstract contains only three paragraphs. The first, quoted above, points out the generality of the semi-logarithmic species-area relationship, but then Munroe goes on to present a mathematical model.

The actual form of the curves is that of a shallow sigmoid, with the equation

$$F = \frac{iL}{i + kp} k'A$$

where F = *number of species in the fauna at equilibrium,* L = *number of species in surrounding lands capable of immigrating into the island,* i = *the probability of any one of these species actually immigrating,* p = *the probability of extinction of a single pair of one species, and* A = *the area of the island, to which the population number of each species is assumed to be directly proportional.*
                                                 –Munroe 1953: 53

MacArthur and Wilson (1967: 26, Fig. 11 and Eq. 3-1) use a similar, but somewhat simpler, expression in their first mathematical model:

$$S = \frac{IP}{(E + I)}$$

(where S = the equilibrium number of species, I = the initial immigration rate if the island were empty of species, P = the number of species in the species pool available to colonize, and E = the extinction rate if P species were present on the island).

The above quotes demonstrate that Munroe developed a concept of species equilibrium nearly identical to that derived later and independently by MacArthur and Wilson. Munroe clearly recognized that the equilibrium number of species represented a balance be-

tween opposing rates of extinction, which varied inversely with island size, and origination by both immigration, which varied directly with distance from a source of colonizing species, and speciation within the island, which varied with island size, environmental heterogeneity, and other factors (Munroe 1948: 118–119). Thus in the abstract he writes:

Where speciation is important, as in large islands and continents, the expected size of the fauna is exceeded, but the relationship between area and size of fauna is not lost, but accentuated.–Munroe 1953: 53

In addition to speciation, Munroe recognized the importance of historical events, operating on geological time scales, that have since been shown to influence the size and composition of insular biotas (e.g., Brown 1971, Diamond 1972). Thus Munroe writes:

Islands might come temporarily to have faunas above the equibrium level in one of two ways: either through an unusually rapid accession of species, or through sudden reduction of their area. The latter process appears to have been important in the Greater Antillean area.   –Munroe 1948: 119

Conceptual Advances and Scientific Progress

Why didn't Munroe promote his ideas? Despite the remarkable similarity of their ideas, Munroe's prior discovery had no apparent impact and went virtually unrecognized to this day (but see Gilbert 1984), whereas MacArthur and Wilson's later, independent development of the same concept has been enormously influential.

It is not surprising that Munroe's concept of species equilibrium remained unknown to MacArthur, Wilson, and virtually all biogeographers and ecologists. Munroe's ideas were presented in five pages, one table, and one figure in a large unpublished doctoral dissertation devoted primarily to the systematics and descriptive biogeography of Caribbean butterflies, and in a one-page abstract in a relatively obscure regional publication.

In another sense it does seem surprising, especially with the clarity afforded by decades of hindsight, that Munroe did not make a greater effort to publicize his discovery. This is especially true considering that Munroe did not retire from productive science after receiving his degree, but went on to enjoy a distinguished career as a lepidopteran systematist. Munroe clearly devoted considerable time to developing his ideas of faunal equilibrium and recognized at least some of their important implications. Thus Munroe wrote (in a letter to J.H.B. dated 16 February 1988):

I did write a paper called "The Size of Island Faunas"

when I was at the Institute of Parasitology at McGill University shortly after I finished at Cornell. This was one of two papers read for me by my director, T. W. M. Cameron, at the Seventh Pacific Science Congress in Aukland in 1949. The other one, on the biogeography of papilionid butterflies, was published in full in the Proceedings of the Congress in 1953, but the island fauna paper was evidently considered of less interest, as it was published in abstract only. Even at the time I thought that ironical. Subsequently I gave oral presentations at the International Congress of Zoology in Copenhagen in 1953 and at a meeting of the Entomological Society of America in 1958 or 1959. Having competing interests and pressures I didn't write either of these up, but the second led to an invitation from Bob Usinger to spend the winter term of 1959–60 at Berkeley leading a seminar in biogeography, in which my ideas were developed and exposed to graduate students. He encouraged me to write a book on biogeography, but I found difficulty in getting it together in the months that I was there.

It is not hard to understand why a young scientist with "competing interests and pressures" did not aggressively pursue ideas that apparently elicited interest from only a few colleagues. In the late 1940s biogeography was dominated by descriptive and taxonomic approaches. This was not a propitious time for injecting mathematical theory and ecological concepts.

Why were MacArthur and Wilson so successful? Even two decades later, in an intellectual climate much more favorable to mathematical models and ecological theories, MacArthur and Wilson's book was severely criticized (e.g., Sauer 1969, Lack 1970, Carlquist 1974, Gilbert 1980). Nevertheless, the equilibrium theory weathered this criticism, and by 1974 Simberloff, in a major review, cited 121 references to document how "Preston and MacArthur & Wilson revolutionized biogeography with the suggestion that the biota of any island is a dynamic equilibrium between immigration of new species onto the island and extinction of species already present." In fact, the equilibrium theory has emerged as one of the few enduring contributions of the theoretical evolutionary ecology of the 1960s and 1970s. MacArthur and Wilson's theory and the vicariance approach to reconstructing the history of biogeographic distributions are jointly largely responsible for the revitalization of biogeography that has occurred in the last two decades. In addition, the idea that the number of species represents a dynamic equilibrium between opposing rates of origination and extinction has had a major impact on other areas, such as the species composition of small patches of habitat, the coevolution of phytophagous insects and

their food plants, and the turnover of phylogenetic lineages in the fossil record.

MacArthur and Wilson's success can probably be attributed to three factors. First, by the 1960s ecologists and evolutionary biologists were much more receptive to mathematical models than they had been a decade earlier. The genetic models of Fisher, Wright, and Haldane had not only endured, but proven their value in initiating a major synthesis of evolutionary theory. Cole, Preston, Hutchinson, MacArthur, and others had achieved considerable success in reviving the mathematical approach to ecology pioneered by Lotka, Volterra, and Pearl. There was an increasing dissatisfaction with purely descriptive studies, and a growing optimism that it would be possible to develop mathematical theories that would help explain the complex organization of the natural world.

The second reason for MacArthur and Wilson's success was that, like Darwin before them, they not only published their ideas in a seminal paper, but they followed up quickly with a much more substantial development in a major monograph. Although the 1967 book was rather spare by monographic standards, it enabled them to assemble and synthesize a significant body of theory and supporting data. It also certainly helped that by the time the book appeared, its authors were well on their way to establishing excellent reputations, MacArthur as a theoretical ecologist and Wilson as an insect systematist and biogeographer.

Undoubtedly the greatest reason for the success of MacArthur and Wilson's theory, however, was the elegantly simple and robust graphical form in which it was presented. The graphical model made the essential elements of the theory immediately accessible to a wide audience, including those with minimal mathematical training. More importantly, because it did not depend on equations of a specific form, the theory made robust, qualitative predictions about how measurable quantities such as species richness, species turnover rate, and rate of colonization of empty islands should vary with island size and distance from a source of new species.

The lessons.   It is unfortunate that Munroe did not get more recognition for his discovery. One of the purposes of this essay is to rectify this. This case is strangely reminiscent of the independent discovery of the theory of evolution by natural selection by Wallace and Darwin. It shows that, as important as new ideas are in the progress of science, they are often not the unique inspirations of genius that are portrayed in the textbooks. On the one hand, scientific revolutions usually do depend on major conceptual innovations. On the other hand, in order for these insights to have impact they must be promoted cogently at a receptive stage in the development of a discipline. It is not sufficient to have a good idea, it is even more important to develop and publicize it. Munroe and MacArthur and Wilson had the same basic idea. Munroe, distracted by other interests and perhaps frustrated in his initial attempts to publish, allowed it to languish. MacArthur and Wilson vigorously pursued and advocated it, and had a major impact on their science.

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