Coral Islands as Ecological Laboratories[1]

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The ecology of the tropics is an incredibly complex subject, probably far too complex to be grasped in its entirety by the human mind. Yet it is of the greatest urgency that it should be sufficiently understood so as to help man utilize the tropical lands without utterly destroying the region eventually as a human habitat.

In physiology, a great deal has been learned by the essentially trial-and-error method of analyzing individual factors and their action, leading, of course, to the obviously sounder method of formulating hypotheses and testing them by experiment. The "single factor approach" has been traditional, also, in ecology, with the difficulty that it is not usually feasible to test the resulting hypotheses by experiment. When experiment is possible, it frequently must be carried out under abnormal conditions, so that one is, in fact, not studying the system intended, but an artificial one created by the experiment.

These difficulties have led in very recent years to a great and increasing preoccupation with the holistic, or ecosystem, approach where entire, functioning ecosystems are studied, instead of only partial systems or the individual components of which they are built. Living systems can be compared by studies involving as little disturbance as possible.

The problem with this approach, especially in the tropics, is the enormous complexity referred to above. In any ordinary tropical forest tens of thousands of species of organisms are involved, the most numerous groups being insects, soil biota, and microbiota. Even to identify them, let alone to understand what they are doing, is an almost impossible task. It is significant that far more understanding has been achieved of simpler ecosystems, such as desert, temperate grassland, and tundra. A reasonable approach to tropical systems would then seem to be to search out the simplest possible functioning tropical ecosystems and study them as an entering wedge. After some grasp of such systems is attained, it will be possible to go on to somewhat more complicated situations, with the ultimate aim of understanding how the highly evolved tropical rain-forest, perhaps the real "mono-climax," works.

A logical candidate for such a study is the low coral island or atoll. This is a low, flat area of limestone of organic origin surrounded by the tropical seas—an accumulation of the skeletons of calcium-carbonate-secreting plants and animals, derived from the complex marine biotic communities commonly called coral reefs. The dry-land portion of such an island seldom shows an elevation of more than several meters above sea-level, and consequently little topographic diversity. The limestone may be in the form of the original reef structure, or

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of an accumulation of loose debris, or of secondarily consolidated debris cemented by calcium carbonate or calcium phosphate, or more commonly a mosaic of all of these. Fringing such an island is almost invariably a living reef community which continually supplies additional calcareous debris in the form of dead skeletons, tests, or shells. Typically, an atoll consists of an irregular ring of reef topped by some small islets and enclosing a relatively shallow lagoon or body of water, usually connected with the surrounding sea by channels or passages through which tidal currents flow. Occasionally these may be filled up or cut off, in which case the lagoon may be less salty than sea-water, or even fresh. Some coral islands, however, have no lagoons, or only small ponds.

This paper, partly because of the limited time available for presentation, was deliberately limited to the terrestrial ecosystems of coral islands. I am, of course, well aware of the fact that the islands owe their very existence to the sea around them, and that the marine ecosystems of the lagoon and reefs contribute incessant exchanges of "materials and energy" (Fosberg 1961) to the terrestrial communities. However, one has to circumscribe one's object of study somehow, or else take on the whole universe. For the purposes of this discussion, I believe that the circumscription adopted here is at the same time fairly natural and useful.

The land vegetation is composed of a very few species, most of which are of extremely wide distribution on tropical strands. The terrestrial fauna is likewise very impoverished, compared with that of a continental area of equivalent size, topography, and climate, in the tropics. The temperature range, both diurnal and annual, is only a few degrees.

There is, of course, some ecological variation even within the land area of a single island or atoll. The texture and consolidation of the calcareous substratum varies greatly from place to place, ranging from silt or sand to boulders, and from absolutely loose to thoroughly cemented or even recrystallized.

The soil ranges from dry in well-drained sites to marshy in low spots, and from pure calcium carbonate to pure accumulated organic matter or to phosphate. The salinity of the ground water, a lens floating on the heavier sea-water, varies from that of the sea, around the edges, to completely fresh at a little distance inland in places where the texture is reasonably fine so that mixing is retarded (Arnow 1954, 1955). The vegetation, within the limits of the few species in the flora, differs greatly from place to place, depending on local environmental conditions such as salinity, drainage, texture of soil, exposure to wind, or even pure chance, and may be anything from a crust of blue-green algae on bare sand to bunch-grass savanna, or dense scrub or forest to 30 or 40 m tall (Fosberg 1953). Seabirds tend to inhabit local colonies rather than being evenly distributed (Fosberg 1966). Differences in vegetation resulting from man's activities may be enormous.

Perhaps more significant from our viewpoint here are certain well-defined variations from atoll to atoll. Some of them are linked to geographical position. In 1953 Bryan listed about 400 low coral islands or atolls, and more could be added now. They occur mostly in the tropical seas, but range between 28°25′N latitude (Kure, Leeward Hawaiian Islands) and 30°S (Elizabeth Reef in the Coral Sea), and extend from the vicinity of Madagascar all the way across the Indian and Pacific Oceans, the Gulf of Mexico and the Caribbean Sea to Rocas Atoll in the Atlantic (3°52′S, 33°49′W). Outstanding among the differences between atolls over these vast areas is that in rainfall. Even in an area as restricted as the Marshall Islands, extending about 600 miles from north to south, the mean annual precipitation ranges from an estimated 600 mm in the northernmost, Pokak, to about 5000 mm at the south end of the archipelago. The indigenous floras of atolls range in size from three species each in Vostok and Johnston Islands to a hundred or more species in islands that are either very wet or very close to continental sources of plant colonists. The sizes of the land area may vary from a few square meters to well over 100 square km (Christmas I.). Great contrasts in the character of the biota exist, depending on the geographical location of the island, and the origin of the plant and animal colonists.

Geographical differences, such as between Pacific, Indian Ocean and Caribbean atolls permit a different kind of comparison—differing biotas and climatic regimes, and perhaps subtler differences depending on the tectonic history of the areas (see Fosberg 1962, Stoddart 1962).

A striking phenomenon in evidence on atolls in different seas is that of vicarious species. On Wake Island, or Pokak, *Tournefortia argentea* scrub covers the beach ridges, extending sometimes far inland. The same landscape, in Pedro Cays south of Jamaica, is achieved with *T. gnaphalodes*. Similarly, different species or varieties of seabirds occupy what seem to be identical niches on these widely separated coral specks.

Contrasts between lagoon and non-lagoon islands (Napuka vs Tepoto), between freshwater and salt water lagoon (Washington vs Fanning), between islands in typhoon belts and those where such storms are lacking (Ulithi vs Kapingamarangi), and between mangrove islands and non-mangrove islands (Stoddart 1962; cf. Caroline Atolls versus Tuamotus) are all instructive.

Since many atoll islets, at least, are very young or newly formed, initial stages in biological colonization, as well as various stages in primary vegetational succession, may be studied to advantage. The effects of typhoons and the recovery from these occurrences are most interesting (Stoddart 1962, 1963, Blumenstock, ed. 1961). In places where the floras are small, one can follow what happens without being swamped by sheer numbers of plants. For example, on Pokak, with a vascular flora of nine species, the dynamics of invasion by *Pisonia grandis* seems quite clear.

A logical development after some grasp of the working of the atoll ecosystem is achieved, is to extend the studies to elevated coral islands, such as Henderson, Cayman Islands, Aldabra, Rennell, and Makatea, where other phenomena are added to the simple low island picture. Leaching out of salt, pitting and karstic erosion of the limestone, different soil-forming processes, leading to rendzina and terra rossa soils, all provide additional complexity. Also, the biota, with even small amounts of elevation, are very conspicuously augmented. One can determine if an atoll has even slight elevation by a glance at a list of its flora. A number of species will be added as on Anaa and Niau, in the Tuamotus, probably because of a combination of less salinity, greater habitat diversity, and longer exposure above sea level. These elevated coral atolls, as a class, seem unquestionably to be the least known of all oceanic islands. They are also so few in number as to be high on the threatened list.

Still further complexity may be added by studying the various stages intermediate between atolls and volcanic islands. These are volcanoes ringed by fringing (Maupiti) or barrier reefs (Borabora, Truk), worn down volcanic peaks with remnants of old raised reefs on their flanks (Rurutu, Rimatara), and atolls with pinnacles of volcanic rock sticking up above reef or lagoon (Clipperton, French Frigate Shoals). Some of the volcanic islands, such as the Marquesas, have no reefs, and may be high enough to carry a cloud forest, rich in endemic plants and animals on their misty summits. Finally, the highest degree of complexity may be reached in islands such as New Caledonia, with its complex substrate including volcanic, sedimentary and old continental rocks, and its unique vegetation including many strange-looking endemics. Each of these stages adds complexities and more varied habitats, and additional biota. And, of course, islands occur in all sizes from tiny rocks or sandbars up to those approaching continents in their dimensions (New Guinea). Size adds variability, stability, numbers of species, general complexity, greater evolutionary opportunity, and likelihood of interaction between different factors.

Contrasting situations such as these series of islands, similar in many features but differing in others, may be likened to laboratory experiments. Selection of examples located at different points along a gradient may illuminate the ecological significance of this gradient. Study of islands differing in a particular feature may clarify the influence of that feature (e.g. climate). These comparisons, of course, lack the precision of experimental work where the situations are arranged to order. However, the additional time dimension as well as the fact that the systems are living, naturally functioning ones, may more than compensate for the lack of laboratory exactness.

Not the least interesting features of coral islands are the changes produced by man. Men of different cultures have occupied islands for varying lengths of time. Man has brought additional plants and animals; he has destroyed many indigenous forms. He has added new habitats and niches, but generally has tended to simplify the whole situation and to break down many of the previously existing relationships. Man tends to introduce instability into these systems. The degree of resistance to disturbance of systems of varying degrees of complexity is a subject of great interest and enormous practical importance. We are only dimly beginning to perceive what we are doing to the ecosystems in which we live and their resistance to what we are doing is a matter on which our future may depend.

In 1950, a program of research on coral atoll ecology was initiated in the Pacific Science Board of the National Academy of Sciences sponsored by the Office of Naval Research. Originally our idea was to select atolls with contrasting aspects: a dry one, a humid one; a small one, a large one; one densely inhabited, a desert one, and so on. Difficulties in logistics changed this plan somewhat, but the core of the program remained: to gather all available published information on atolls and to make detailed and complete studies of the selected few as time and personnel permitted. We like to think that this beginning phase of a tropical ecology study was successful. We have accumulated not only large collections of organisms, of soil samples, of photographs, but also observations on the way in which biota and landscape interact. A preliminary model has been proposed to relate some of these data (Fosberg 1961) to form a living community. However, we have no illusions that we know all these is to know about low coral islands, or even about one of them.

Much could still be done, and indeed should be done, to study the coral island terrestrial ecosystems. They are valuable tools in an approach to tropical systems because they offer some of the simplest situations available in the tropics. I hope to have shown how they can be used as ecological laboratories, because along with their simplicity and similarity, they offer diversity along a number of gradients, with varied biota including some vicarious, and some endemic, species. One can choose a number of atolls and study them as "stages" in a classical experiment. Comparison of the results can then perhaps elucidate the functioning of these ecosystems and eventually be extrapolated to deal with more complicated situations.

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