LAND ECOLOGY OF CORAL ATOLLS

Ecology is rather an approach than a subject-matter. Factual information from almost all other sciences makes up the raw material utilized by the ecologist, and, in its highest expression, ecology is an integration of all of these subject-matters around the central idea of their interrelationships, with special emphasis on those involving living things.

A natural consequence of this diversity of subject-matter is a tendency for the vast accumulation of information to swamp and obscure the basic patterns of relationship, and to delay the emergence of principles. At the same time, without the enormous amount of information, the actual true patterns of relationship cannot be determined or verified, and the essential complexity of natural situations is not realized.

To lessen this dilemma, it may be useful, as ecological information and thought on a given area or situation develops, to construct, from time to time, tentative or theoretical patterns of relationships and processes embodying and expressing what appears to be likely from the information actually at hand. These patterns can form frameworks around which new data may be assembled as they accumulate, and which may be modified, torn down and reconstructed as the facts demand. They serve to keep the basic relationships in their proper place of importance as information piles up and the picture becomes more complex. One of the most outstanding examples of this was the formulation of Darwin's theory on the formation of coral atolls. This, though dealing largely with a geological subject-matter, was one of the outstanding ecological generalizations of all time. It has been assailed mightily, modified as new data were secured, but has provided a framework for the thinking in an important segment of both marine geology and marine ecology.

It is proposed here to outline briefly a tentative historical ecological approach to terrestrial problems on atolls. Arbitrarily, because it provides a satisfactory geological framework, simplifying the time relationships to where they do not obscure the problem, and because it provides an automatic solution for certain otherwise difficult biological problems before they can even be raised, one of the several alternative geological theories on the origin of land on atolls is adopted. This does not imply acceptance of this theory or loss of sight of its purely tentative nature, and if it were to be abandoned, the only aspect of the pattern here proposed for the land ecology that would have to be modified would be the time relations. Certain other problems, also, would then arise and need solution.

This geological framework postulated, during the post-glacial xerothermic period, an all-time maximum sea-level two or three meters higher than the present one. Postulated also, as a logical consequence, is a wide distribution, in tropical seas, of sea-level banks, living reefs, awash, with no permanent land, excepting possibly occasional isolated dry-land atolls resulting from local elevation.

It postulates, also, a subsequent world-wide lowering of sea-level to the present one, possibly coincident with the accumulation of the Greenland and Antarctic ice-caps.

This would have produced a large series of relatively uniform examples of a new habitat, the atoll islet, available for colonization by plants and animals and for primary vegetation development.

The outstanding characteristics of this habitat were as follows: physically it was flat exposed reef-rock, probably partially covered by rock debris, foramniferal sand, and shells of mollusks. Its drainage was practically perfect down to sea level, its relief very low or none at all. It had a high instability of substratum under influence of wind, storms, and waves, an extremely high insolation, and high surface temperatures. Chemically it was very saline, calcareous, basic, low in iron, high in magnesium and nitrogen, with a little organic matter but no humus. This makes up, on the whole, a highly inhospitable environment for most organisms.

Immediately upon emergence from the sea certain processes commenced which gradually altered this habitat, the alteration being more marked or more rapid in some examples than in others, depending on the climatic and geographic area in which they were situated. The more obvious of these processes may be itemized, with remarks on their effects:

1. Leaching out of the salinity by rainwater, but its continual renewal to some extent by spray and storm waves, as well as diffusion from below sea-level. The more this process proceeds the more species of plants are able to gain a foothold.

2. Piling up of clastic material on seaward sides of islets by storm waves,

3. Piling up of foramniferal sand and finely divided fragments of all kinds of organic calcium carbonate on the lagoon side, and their shifting by wind.

4. Establishment of individuals of the most extremely halophytic of strand plants from seeds cast up by waves or brought by seabirds - such species as Scaevola frutescens, Messerschmidia argentea, Ipomoea pes-caprae, Boerhavia diffusa, Triumfetta procumbens, etc.

5. Visits of sea birds, augmenting the phosphorus and nitrogen content of substratum.

a. Colonization by land-crustacea with planktonic larvae.

6. Gradual building up of a thin lens of fresh or brackish water in the substratum.

7. Weathering of rock by solution and by physical abrasion, resulting in some compaction of soil. Materials exuded from roots of plants, or released by their decomposition might augment this process, as might the actual physical penetration by the roots of porous fragments.

8. Accumulation of fine wind-blown material, caught by plants, resulting in the formation of small dunes and in the gradual assorting of the material from coarse fragments on the windward side to finer and finer sediments to the lee or usually the lagoon beach.

9. Formation of "beach-rock" by cementation of sediments under influence of fresh water, resulting in increased stabilization of substratum.

10. Development of simple plant communities by increase of first colonists and the addition of others with time, possibly several grasses, Fimbristylis, Pandanus tectorius, Suriana maritima, Tribulus cistoides, Wedelia biflora, Ipomoea tuba, and in wetter atolls, Pisonia grandis, Ochrosia parviflora, Barringtonia asiatica, Terminalia samoensis, etc. Most of these are current borne, but the grasses and sedge may be carried by wind and Pisonia certainly by sea birds. These would bring about increased stability of the substratum, which would, in turn, permit increased integration of the communities.

11. Occasional arrival and establishment of terrestrial animal colonists, also fungi, with consequent slow development of a soil biota, and terrestrial biotic communities.

12. Production, over long periods of time, of depressions in the centers of islets, possibly by solution and removal or redeposition in finer form of coarser calcareous material by rainwater and tidal and temperature fluctuations of freshwater lens. If the tidal fluctuation is slight and the material fairly compact, the depressions are muddy; if the fluctuation and water movement is greater, they will be clear and rock-lined.

13. Development and multiplication of the plant communities and their gradual integration into a vegetation. This involves the modification of the environment toward a more stable and more favorable type, also the arrival and establishment of additional species, particularly those whose existence is made possible by the operation of the various processes that help modify the environment, and environmental factors that are dependent on these processes. Some of these are the addition of humus, shade, accumulation of sand, accumulation of guano, stirring by land-crabs, decrease of salinity, protection from wind, formation of muddy depressions, etc. Community development would culminate, theoretically, in the establishment of a more or less mesophytic forest of Pisonia, Ochrosia, Ficus, Calophyllum, Guettarda, Pandanus, Hibiscus, with epiphytic and terrestrial herbs, ferns, mosses, and wood-destroying fungi.

14. Development, under influence of mesophytic forest and soil biota, of a brown forest soil.

15. Gradual development, under the influence of varying salinity, slight variations of surface and elevation, gradation of size of materials from seaward boulder-rampart inward, and distribution of wet depressions, of a pattern in the arrangement of the plant communities that, while subject to much local variation, as well as regional variation due to climate, is rather characteristic of atoll vegetation.

The development of a normally complex flora and fauna, and consequently, of a normally complex vegetation and mosaic of biotic communities, is drastically controlled by a series of limiting factors inherent in the atoll environment and situation. These may be enumerated, noting such of their effects as may not be obvious.

1. Barrier of sea water and distance from sources of suitable species. This would vary in intensity with location, but would certainly be at least somewhat of a retarding factor to every group of organisms except sea birds and land crustacea with planktonic larvae.

2. Proximity of sea, with consequent high average level of salinity. A great many organisms simply cannot tolerate, physiologically, this condition.

3. High temperature, preventing much humus accumulation except under saturated conditions. The soils take a long time to become fit for the growth of most plants.

4. Uniformity of topography, original substratum, and early biotic colonization, limiting the number of ecological niches available.

5. Iron deficiency, due to high pH and possible lack of iron in original material. Many plants cannot thrive without more available iron.

6. High average incidence of typhoons and hurricanes with attendant destruction of biotic communities and frequently destruction or severe alteration of the substratum itself.

7. Probable short length of geological life of any given land surface. This lessens or eliminates the gradual accumulation, with time, of suitable species by chance, and greatly lessens the chance of local endemic species developing.

8. Relative youth of this habitat as a whole. This, also, would preclude any complexity that is dependent on great lengths of time.

The next era in the history of atolls started with the arrival of man. He came needing food and space in which to live, as well as materials for his arts and manufactures. These had to be supplied by the environment. A certain amount of direct alteration of the environment was inevitable.

With him came rats, lizards, flies, coconuts, breadfruit, Morinda, Eugenia, taro and taro-like plants, and possibly Tacca, and, at least in some regions, pigs and dogs. The introduction of these dependents of man undoubtedly resulted in the rapid destruction of many colonists which were precariously near the limits of their tolerance of this environment, or which were the natural prey of the animals, as well as the possible increase of certain ones for which the conditions were improved by the changes.

There was a gradual destruction of the most mesophytic vegetation on the most fertile soil, and substitution for it of forest of coconut palms or of a coconut-breadfruit forest with a sparse understory of Pandanus, Morinda, etc. Taros were planted in the muddy depressions, and gradually these were enlarged and elaborated into excavations.

The sea bird populations were reduced by the rats, hogs, and dogs, and their breeding areas were restricted to certain islets. This resulted in a reduction of the flow of phosphates and nitrogen to the soils of most islets.

As populations increased, the taro excavations were enlarged and their muddy soil turned into a muck by throwing in coconut refuse and other organic materials to increase the humus content. Other plants are brought to the atolls from nearby high islands and cultivated in these swamps. They become, in many regions, a basic part of the food supply, though in drier atolls, this method of taro culture did not prove feasible.

The populations tended to increase and exert pressure on the environment, but there was much fluctuation because of wars, typhoons, and other disasters.

Many of the driest atolls could not support a human population and were never successfully colonized or were later abandoned.

The arrival of European man brought on another era. Human diseases and disease carrying insects were introduced, and the native populations decreased rapidly in most areas. More aggressive species of rats were introduced, resulting in further reduction of native biota. Insects that attacked coconuts arrived in some places.

There was a rapid increase in coconut plantations and destruction of the native forest on the less fertile soils. Both this forest and the native coconut plantation were replaced in many areas by more orderly and efficient commercial plantations. The practice of burning organic refuse was introduced in some places, resulting in a less fertile soil. The diet and requirements of the natives began to undergo a change, with substitution of foods that could be bought with the proceeds of the sale of copra for those produced by the people or caught in the sea. The same occurred to an even greater extent in articles manufactured for other uses than food.

The series of world wars accentuated these tendencies in some areas, retarded them in others, and on many islands converted large areas into barren, unproductive air-strips or bases.

Ecological relationships on atolls are now in the midst of changes whose direction and probable effects must be studied to be understood.

This generalized picture of atoll ecology, from a historical slant, suffers most seriously from underemphasis of the regional differences resulting from variation in amount and seasonal distribution of rainfall and from distance from large land masses which serve as a source of colonizing plant and animal species.

These differences may be epitomized by saying that in drier regions the development of communities cannot go on to the stage attained on the wetter atills, that the faunas and floras are much smaller, the vegetation sparser and more scrubby, human influence is usually less or negligible, sea birds are much more numerous; the farther an atoll is from large land masses the smaller will its fauna and flora be in comparison with otherwise similar atolls that are closer to such land areas.

Though the picture presented here may seem to some to represent adequate knowledge and understanding, it must not be forgotten that it is purely theoretical, based, to be sure, on observations on many atolls, but on no direct historical evidence. Research is needed on all points of it to confirm or alter the propositions made here. The most urgent needs seem to be more complete inventories of the biotas and descriptions of the vegetation of most of the atolls, and a few strategically placed detailed and thorough studies of all aspects of atolls of widely different types and geographic areas.

It must be reiterated that atoll ecology is dependent on data from all other fields of atoll research, and that deficiencies in the information on any other aspect will reflect themselves in less reliable understanding of the ecology.

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