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Excerpt
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PART I

Theoretical and experimental
studies

CHAPTER ONE

Introduction

It is clear that at present the peoples of this planet, in general, do not treat it as a single superhabitat for all its life forms, including its human population. There is little evidence that even the so-called developed countries have this global philosophy. The reluctance of nations such as the USA and Australia to come to terms with clear danger signs of global warming is a striking example of the priorities adopted by ‘developed’ nation states in the third millennium. They are unwilling to forfeit some economic well-being by taking precautionary steps that would reduce the rate of human-induced climate change. The argument that the change has not been proved beyond doubt to the satisfaction of the political leaders is a shallow excuse. So widespread are the repercussions of climatic change, and so potentially detrimental to human welfare generally, that the safe global strategy would be to begin taking preventative steps now, and argue about the validity of scientists’ warnings later. But the bottom lines of national economies take precedence over global concerns, and in democracies these choices must reflect the wishes of the majority, or governments that espoused such approaches would fall. In the end, the people of the ‘leading countries’ of the world must bear the responsibility.

But I am an optimist. I believe that the overriding philosophy within the next century will be framed within a truly global outlook. More and more countries will come to regard their plant and animal species, and the ecosystems that they help to form, as part of their nation’s and the world’s natural wealth. A few, notable among them such small countries as Iceland and Costa Rica, already appear to do so. Perhaps at the time that a world government is accepted, and possibly as a prelude to that development, considerations of first continental, and then global, ecology will gradually override nationalistic economic rationalism. People generally may then come to regard the degree of disturbance to Earth’s ecosystems that is involved in the exploitation of some of its resources as an unacceptable price to pay for the use of them. Until then, it is likely that the large-scale, rapid consumption and destruction of some of Earth’s non-renewable or slowly renewable resources will continue, and at an accelerating rate. This rapid destruction of resources is already endangering complex ecosystems such as tropical forests, about which we still know very little, and which

4 INTRODUCTION

may yet be found to harbour untold wealth, for example in the form of biotic components with economic and medical applications.

Upon the future dawning of what may be viewed as the Age of Global Management, mankind may have to intervene on a large scale in order to maintain some natural ecosystems at levels that permit the normal functioning of global ecological processes. Not only will those ecosystems that have survived need to be conserved, but those that have been seriously damaged or destroyed may have to be repaired or restored. The large-scale restoration of complex ecosystems such as tropical rainforest would be an enormous challenge to our descendants, but one that would be accepted by ecologists if they were given supranational political support. Any such undertakings would need to be as accurate restorations of the natural systems as possible; mere rehabilitation, such as is now often practised following relatively small-scale industrial, mining or agroforestry disturbance, would not suffice. Daniel Janzen and his team of biologists in Mesoamerica have already made a start in the large-scale rehabilitation of a tropical forest ecosystem. They are the pioneers, and their project will surely be followed by others in the decades and centuries to come.

Crucial to any attempts to restore, or re-create a natural ecosystem, will be some knowledge of its 'embryology', how it has arisen and developed naturally. What might be called the science of 'developmental ecology' would combine some of the rapidly fledging applied subsciences of restoration and rehabilitation ecology with much of present community ecology and island biogeography, including studies on the origins and development of ecosystems and communities. For this last, it is obvious that study ecosystems are needed that are at or near the beginning of their development, so that we may follow, and attempt to understand, the natural processes of species' colonization and biotic assembly and succession that characterize the making of functioning communities.

These study systems may be theoretical models, of course, or experimental systems in the laboratory or in the field, and there have already been studies along these lines, notably in the United States. Rarely, however, geological events provide us with large-scale natural situations that involve the creation of new ecosystems. These events usually involve the production of a *tabula rasa*, or 'clean slate', by total devastation of a previous ecosystem by some natural catastrophe. More rarely, they involve the creation of a completely new, pristine substrate, on which an ecosystem is assembled *de novo*, from scratch.

The processes involved in ecosystem and community assembly are likely to be shown most clearly when the new system is distinctly separated from its source, or reservoir of potential participants, so that colonizing events and their ecological repercussions are clearly recognizable. This means that work will focus on the study of isolates, whether they be real or simulated, ecological or geographical, natural or artificial.

Theoretical, model systems have the advantage that certain basic assumptions may be incorporated into the model, and the consequences of changing these or various parameters of the developmental process can be studied in computer simulations. But convincing models must be founded in biological reality rather than solely in conceptual perspectives.

'Real' island colonization situations can be created in the laboratory, and the effects of changing various factors, in terms of the composition of the resultant community, can be determined – a subsistence that may be called 'experimental developmental ecology'. For practical convenience such experimental systems have usually involved the controlled introduction (both rate and sequence may be altered) of freshwater bacteria, algae, protozoans and other microbiota to artificial aquatic island microcosms on the laboratory bench.

Experimental work that is necessarily less precise but closer to the natural situation than laboratory studies involves the colonization of artificial substrate 'islands' in natural conditions. Some early pioneer studies of this kind have been the monitoring of colonization by aquatic microbiota of glass slides placed in streams (Patrick 1967), the build-up of aquatic communities in dishes of sterile water placed in natural situations (Maguire 1963), and the growth of populations of settling ('fouling') communities of marine organisms on settlement plates placed in the sea (Osman 1982). Examples of isolated physical habitats or critical resources (such as the isolated hostplants needed by insect specialist herbivores in diverse stands of vegetation) could be multiplied ad nauseam. Many have acknowledged value in disciplines such as biological control, in which an 'island plant' or 'island host' may be exploited by consumers. They collectively demonstrate the need for many organisms to continually disperse and colonize, in order to 'track' their needs as conditions change. The term 'island habitats' was used, for example, by Beaver (1977) in referring to dead snails, sought by the carrion-feeding flies which use them as breeding sites. As for more conventional islands, such substrates or discrete units can be the foundation for community development, with the course of that development subject to processes such as succession and stochastic events (such as the snail carcass being eaten).

As another example, 'phytotelmata' is the collective name for natural plant-held water bodies, such as those in hollows at the junction of branches, in the axils of leaves or in tree holes. These very small natural rainwater pools, of course, are habitat islands for their inhabitants. Individual phytotelmata support relatively simple, isolated microcosms, and these are available in multiplicate (Kitching 2000). Such natural mini-islands are study units that have much to offer the student of island biotas, not least because they are sufficiently abundant for experimental manipulations to be made. Thus, variations and deviations from the 'standard microcosm' can be interpreted and, to some extent, explained in terms of community changes. Moreover, modelling

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6 INTRODUCTION

approaches to these studies, such as that of Post and Pimm (1983), have relevance not only to community ecologists studying water-filled tree holes, but also to island ecologists and biogeographers.

Natural restoration may be studied on land on a larger scale following the devastation of an ecosystem by purposeful or accidental human activity, such as clear-felling or fire. More rarely, nature herself provides the whole 'experiment', including the 'new' substrate, for example following natural events such as fire, hurricane, flood, glacial action or volcanic activity involving lava flows or tephra falls. Such cases, however, are not always isolated from adjacent areas that have been spared destruction, from which colonists may arise. They are thus less instructive, in the context of this book, than cases that involve islands. Moreover, the destruction is usually incomplete. Almost invariably, a 'foundation community' (usually incompletely documented) is already present – soil biota, surviving plants and others – and the processes then involve aspects of succession, with the trajectories determined in part by these source communities. The base-line from which restoration of a community or the assembly of a new community must proceed is thus not absolutely clear or uniform; recolonization can proceed from remnant foci of survivors, and often does so. To a large extent each such case is unique in detail, although the underlying principles driving change may be more widespread.

Very occasionally, biologists have the chance to follow the natural assembly of an isolated ecosystem on a macro-scale, and from a base-line that is known to be zero or very near to zero. Isolated sterile substrates, or at least substrates from which all macrobiota (animals and plants) have been extirpated, may be formed by the destruction of an existing island community by a natural cataclysm. For example, a terrain that has been scraped clean by the slow, inexorable action of a glacier may be exposed when the glacier retreats, providing a new substrate, almost literally a cleaned slate, on which new communities may now develop. Or following explosive volcanic activity, the subsequent reassembly of a community may be monitored by periodic biological surveys. Where the volcano happens to be an island, the monitoring is facilitated because the sources of organisms are discrete from it and colonists more easily identified.

Perhaps the best natural situation of all for the study of the origins of ecosystems is the emergence of a new volcanic island from the sea or from the crater lake of an existing volcano. Such an event provides a rare opportunity to monitor the assembly of a terrestrial community on a substrate that is undoubtedly originally devoid of terrestrial life, and, moreover, clearly separated from possible sources of colonists. From tree holes to emergent volcanic islands may seem like a giant leap, but island biogeographers need to keep a wide perspective. In seeking to understand the processes that operate in the colonization of 'real islands', of whatever size, we need to be aware of, and where appropriate

make connection with, the work of theoreticians and of both laboratory and field community ecologists.

However, an important point to appreciate in seeking analogy is that laboratory island studies can provide relatively rigorous and controlled information on the basis of adequate replication and statistical analyses, whereas real world islands are each unique. We may seek, and to some extent reveal, parallels between different islands, but each is a single unreplicated experiment in ecological development.

Types of islands
Continental islands

Unlike an oceanic island, which emerged from the sea as an isolated land mass, usually by volcanic activity, and has received all its biota from outside sources, a continental island is formed by the isolation of a piece of land that was formerly part of a larger land mass. Many continental islands were formed as a result of rising sea levels following lowered levels in the Pleistocene glaciations, when much of Earth's water was locked up in the form of ice. The rocks of continental islands may be sedimentary, metamorphic or igneous, or any combination of these, but are similar to those of their parent mainland. In some cases the island is separated by a shallow narrow strait, such as the separation of Bali from Java in Indonesia; in other cases, such as Fiji or the Seychelles, the continental shelf may be so extensive and so far below sea level (perhaps 200 m) that the islands appear to be oceanic. At the time of their creation by separation from the larger land mass, continental islands contained a portion of the latter's biota. Over time, the diversity (species richness) of the newly created fragment usually declines as an adjustment to what is now a smaller and isolated environment.

Ecological 'continental islands' may also be formed naturally. For example, when lava flows around a piece of higher ground, often round the same piece of ground in successive eruptions, the biota of the isolated area, or *kipuka*, is spared destruction for a long period and becomes surrounded by a sea of barren lava or, at least, by a community at a very much younger stage of development. Mountain tops also become 'continental' ecological islands when climatic change changes the tree-line, leaving areas of montane biota as ecological islands, surrounded by lower lands within which many mountain organisms cannot survive and through which they cannot pass. Many such areas thus support taxa long isolated from their closest relatives on other, sometimes nearby, mountain peaks. As Carlquist (1965) elegantly put it, 'Mountain tops are like islands in the upper air', which he contrasted with the deep ocean trenches as islands for organisms coping with very different extreme environments. Lakes, geographical islands in reverse, may be 'continental' if they are formed by the entrapping and isolation of part of a once more extensive water body.

Continental islands may also be formed by human activity. Every piece of remnant woodland left in an agricultural landscape, and every natural reserve preserved in an urban area, is a ‘continental’ ecological island of natural vegetation surrounded by a sea of modified habitat. Two such natural reserves in urban areas that have been studied in this context are the famous 84-ha Botanical Gardens in the town of Bogor, Java (Diamond *et al.* 1987) and the 400-ha Kings Park Reserve in the centre of Perth, Australia (Recher and Serventy 1991). The 72-ha Bukit Timah rainforest reserve on Singapore Island and Barro Colorado Island, Panama, are other well-known examples of continental islands formed as a result of human activity. Barro Colorado Island, a former hilltop, was isolated early in the twentieth century by the construction of the Panama Canal.

Oceanic islands

Oceanic islands, in contrast, are those that have originated from a lake or from the ocean bed, usually as a result of subaquatic volcanic activity, and were never connected to a mainland. They are usually, but not necessarily, extremely isolated. They may be the result of submarine volcanic activity at a geological ‘hot spot’ in the middle of a tectonic plate (e.g. Hawaii, Fig. 1.1), at the mid-ocean

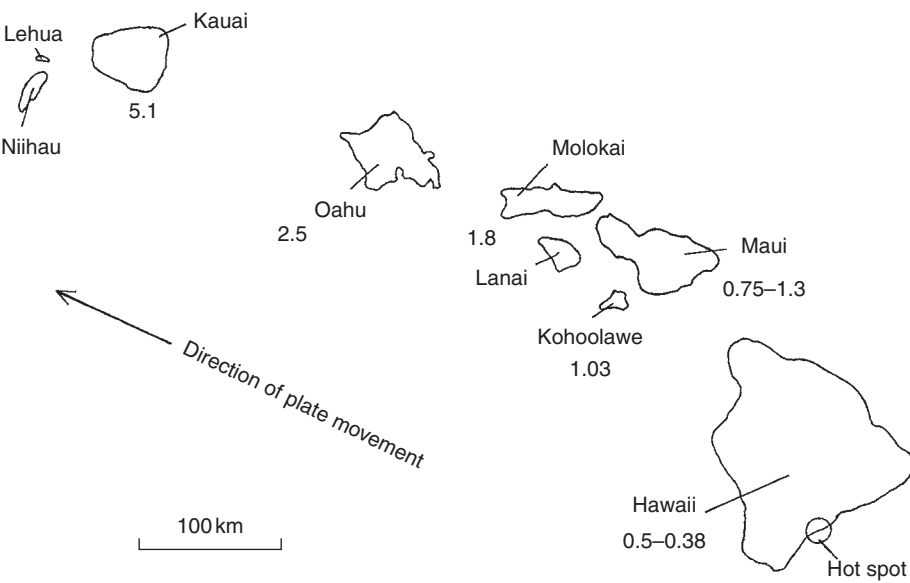


Figure 1.1 The Hawaiian archipelago, indicating the progressively older sequence of islands as the Pacific tectonic plate moves westward over the hot spot currently near the southeastern part of Hawaii. No other oceanic archipelago supports such an array of endemic species, and studies of major radiations of insects (such as drosophilid flies) have done much to illuminate patterns of speciation in such isolated environments. The islands shown are the most recent (ages shown in millions of years) in an island chain that extends for some 5800 km across the Pacific.

ridge where new plate material is being formed (Iceland, Tristan da Cunha), at the junction of two or more ocean ridges (Galapagos), or beyond a subduction zone, where the movement of the subducting plate results in magma reaching the surface usually along an arc (e.g. the Solomon Islands). Subsidence and erosion may transform oceanic islands into low atolls (e.g. Wake), or subsequent uplift may result in 'raised atolls' of limestone (like the Lau group of the Fiji archipelago), but originally they were all high islands with volcanic mountains. Very occasionally, a freshwater lake may arise *de novo*, as when a volcanic caldera fills with rainwater. From the point of view of aquatic organisms a new island has been formed, and, by our definition, an 'oceanic' one.

There are a number of examples of very young oceanic islands that are not particularly isolated. Anak Krakatau emerged initially from Krakatau's submarine caldera between Java and Sumatra on the Sunda island arc in 1930. Surtsey emerged in 1963 from the subatlantic mid-ocean ridge, off Iceland. The new Fijian island, Lomu, named after a famous rugby player, emerged in 1994. Motmot is an islet that emerged, probably in the late 1950s, from the freshwater caldera lake of Long Island. Rakaia Island was formed in 1878 when the Vulcan volcano erupted in the Rabaul caldera, New Britain, and became joined to the mainland during a subsequent eruption in 1937. The nascent island Loihi, off the east coast of the big island of Hawaii, is still developing below sea level – as an oceanic island not yet 'born'.

Island biogeographers have studied all these types of islands and their biotas. The ways in which their ecological communities have developed, and the pathways of their assembly and evolution, are of particular interest on oceanic islands. There, they illustrate processes that are of much wider importance in seeking to understand the dynamics and restoration of natural ecosystems. Together, these studies contribute much to our understanding of change in the natural world. This book is an attempt to explore and integrate studies on oceanic and continental islands, and to see what features, if any, are common to the growth and development of different kinds of island communities.

CHAPTER TWO

Theoretical and experimental colonization

Theoretical models

The colonization of islands can be studied in theory by constructing models on the computer. Such models require that certain assumptions be built into the model, and, although these are necessarily simplified (and always fail to take into account all the parameters relevant to natural situations), insights can be gained from their use. As an example, one of the questions that can be investigated in this way is the relative roles of chance (stochasticity) and determinism in the colonization process. This question has been debated vigorously by island biogeographers, and an understanding of the different points of view is important in introducing the topics.

Chance and determinism

In the process of assembly of a functioning community from a number of species of living things, both stochastic and deterministic elements are almost always involved. Several biologists have attempted to assess the interplay of these two elements of the process. After using a very simplified model, Seamus Ward and I concluded that, on theoretical grounds, in the early stages of colonization stochasticity (in the sense of the likelihood that in a population of similar islands the communities that are assembled will be different from one another) will be low. Pioneer colonizers are invariably species with good dispersal powers and/or establishment characteristics. Their arrival rates will be high and very similar to one another, and the intervals between colonizing events (colonizing intervals) will be short. Also, later in the colonization process, when arrival rates and colonizing intervals of the species concerned are considerably more variable, as with pioneers versus late-successional species, stochasticity will again be low.

Still later, when the colonizing species have fairly similar, but low, arrival rates (for example, pairs of species on distant islands), priority (the order of arrival) will vary a great deal between cases, and because the presence of the first arrival may enhance or decrease the chances of establishment of later arrivals, the particular sequence of arrival will greatly influence the final community outcome. At this stage, stochasticity will be high (Ward and Thornton 2000).

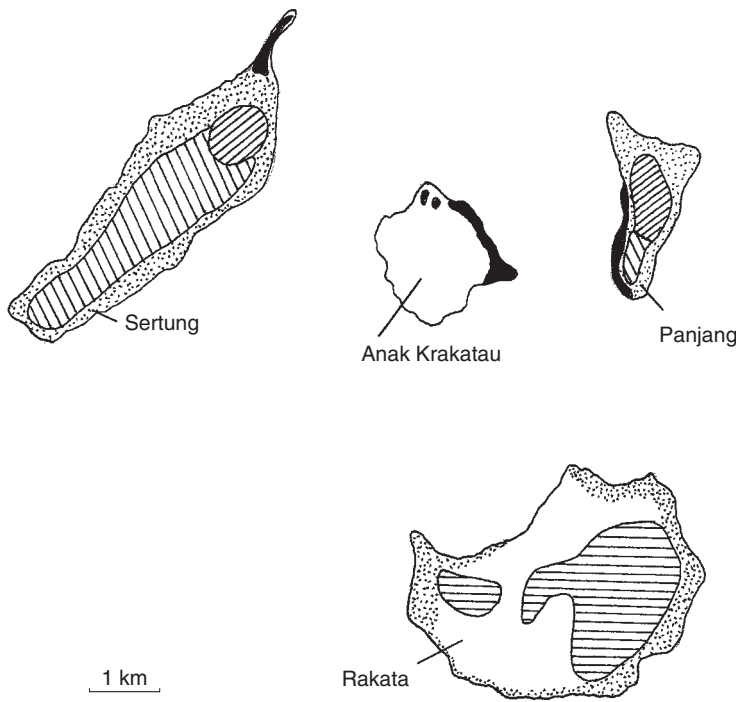


Figure 2.1 The islands of the present Krakatau archipelago, indicating the major forest categories present on each island. Black, *Casuarina*; horizontal hatch, *Neonauclea*; dots, *Terminalia*, coastal; left-right diagonal, *Timonius*; right-left diagonal, *Dysoxylum*; blank, none (Anak Krakatau) or unexplored (Rakata). (After Whittaker *et al.* 1989, as modified by Thornton 1992a.)

When the colonizing species differ considerably, but not extremely, in dispersal ability, our model showed that stochasticity may still be high, but variation in colonizing interval, rather than variation in priority, may be the main contributor to the stochasticity (Ward and Thornton 1998). This theoretical finding is supported by the known course of colonization of the Krakatau islands by plants.

The three older Krakatau islands (Fig. 2.1), some 4 km apart, have been recolonized by plants and animals since Krakatau’s great devastating eruption of 1883. The course of development of mixed forest on the islands diverged after the 1920s, so that on two of them, Panjang and Sertung, but not on the third, Rakata, areas of forest were dominated by one of two animal-dispersed trees, *Timonius compressicaulis* and *Dysoxylum gaudichaudianum*. On Rakata, however, the forest came to be dominated by the wind-dispersed tree *Neonauclea calycina*, which has a dispersal rate higher by perhaps two orders of magnitude than those of the two zoochorous species.

On Rakata the colonizing intervals between *Neonauclea* and *Timonius* and between *Neonauclea* and *Dysoxylum* were at least 24 and 34 years respectively (Table 2.1), but on Panjang, where *Timonius* and *Dysoxylum* became the dominants, the corresponding intervals were zero and at most 3 years, and *N. calycina* forest was not able to develop when its competitors followed so quickly.