

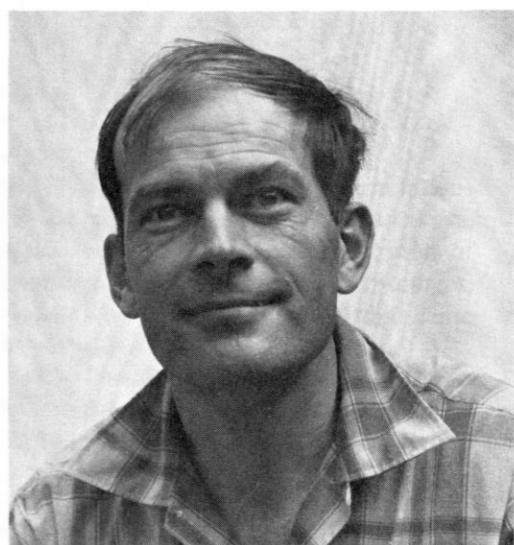
Ecology
and
Evolution
of
Communities

*Martin L. Cody
and Jared M. Diamond,
Editors*

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Dedicated
to
Robert MacArthur



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Ecology and Evolution of Communities

This book presents a broad range of topics in community ecology and evolution. It includes contributions from some of the leading authorities in the field, including Robert MacArthur, G. Evelyn Hutchinson, and Jared Diamond. The book covers a variety of topics, including the development of species diversity, the assembly of communities, and the evolution of ecosystems. It also explores the relationship between community ecology and other fields, such as genetics and paleontology. The book is intended for students and researchers in ecology, evolution, and environmental science. It is a valuable resource for anyone interested in the study of communities and their dynamics.

The Evolution of Communities

The book begins with an introduction to the basic concepts of community ecology, including the principles of competition and the role of environmental factors in community structure. It then delves into the evolution of communities, examining the forces that drive change over time, such as mutation, selection, and migration. The book also explores the relationship between community ecology and other fields, such as genetics and paleontology. It concludes with a discussion of the future of community ecology research.

The Diversity Ethic

In a world of shrinking faith and uncertain trumpets, very few precepts are any longer accepted as absolute. We can nevertheless hope that one of them will be the ethic of organic diversity—that for an indefinite period of time man must add as little as possible to the rate of worldwide species extinction and where possible he should lower it. This precept, which is based wholly on rational considerations, can also be the guiding principle of applied biogeography. It emerges from a recognition that man is the self-appointed but still profoundly ignorant steward of the world's natural resources, that the living part of the environment is still mostly unknown to him, and that he has therefore scarcely begun to conceive of the possible benefits that other organisms will bring in economic welfare, health, and esthetic pleasure. To sense the depth of that ignorance, consider that biologists do not even know to the nearest order of magnitude how many species exist. Ten years ago the popularly accepted figure for animals was C. B. Williams' estimate of three million, based on extrapolations of species abundance curves. Now some authors use the figure ten million, an order-of-magnitude conjecture advanced in the manner of physics. The reason for the upward revision is twofold: the dis-

covery that whole faunas, such as the marine annelids, abyssal benthos, and many insect taxa, are still in the earliest stages of Linnaean exploration; and the growing realization that large complexes of poorly defined sibling species are common even in the better-known animal and plant groups.

All this lack of information must be balanced by an equal amount of caution. Our best strategy is a holding operation, by which diversity is preserved through any reasonable means until systematics, ecology, and evolutionary theory work their way up from the stone age toward some degree of mastery of the essential subject matter. As an example of the worst thing that biologists might let slip by them, consider the possibility that the Atlantic and Pacific biotas could be mingled by migration through the new Panamanian sea-level canal proposed for construction in the 1980s. Three to five million years ago the emergence of the Panama Isthmus cut the straits that connected the Pacific Ocean and the Caribbean Sea, isolating the marine populations on either side. The existing ecological differences between the inshore habitats are substantial. The Atlantic coast has moderate tides, sandy beaches, mangrove swamps, and rich coral reefs. The Pacific side is characterized by strong tides, more silty water, periodic upwellings

of cold nutrient-rich water, rocky shores created by extensive lava flows, and limited, depauperate coral reefs. Accelerated no doubt by such differences in the physical environment, evolution has proceeded mostly to the species level and beyond. Of the roughly 20,000 species of marine animals and plants that occur on both sides of the Panama Isthmus, perhaps no more than ten percent are held in common (Newman, 1972). In the extreme case of the fishes and mollusks, fewer than one percent are held in common. What would happen if free exchange of these faunas were permitted through a sea-level canal? On this point biologists have fallen into total disagreement. The following diversity of opinions has been expressed in various articles, seminars, and government hearings during the past ten years:

1. There would be only limited exchange of species, mostly from the Pacific to the Atlantic. The ecosystems would not be seriously disturbed (Topp, 1969; Voss, 1972).

2. The Atlantic marine biota is richer in species and hence possesses superior competitive ability. If allowed to invade through a sea-level canal, it would cause widespread extinction in the Pacific biota. The combined extinction rates of the Pacific and Atlantic elements might reach 5000 species (Briggs, 1969).

3. The Briggs argument (just cited) is based on the postulate that the greater the number of species, the greater their individual competitive ability. An alternative hypothesis that cannot be excluded with existing knowledge is that the greater fluctuation of the Pacific inshore environ-

ment induces the evolution of a higher proportion of opportunistic species, capable of wedging their way into existing biotas, especially within areas disturbed to some extent by man's activities. If this model is correct, and Briggs' conjecture wrong, the biotic flow would be predominantly from the Pacific to the Atlantic. In either case, the total impact on the two ecosystems cannot be predicted.

4. An exchange of biotas would be generally unpredictable and dangerous. Species could be removed not only by competitive replacement but also by overwhelming degrees of hybridization with imperfectly isolated geminate forms on the other side of the Isthmus (Rubinoff, 1965).

In fact, biogeography has neither the theory nor the previous experience to predict the outcome of an unimpeded exchange of faunas across the sea-level canal. This incapacity has become increasingly clear to concerned scientists who have tried to evaluate the evidence dispassionately, including Aron and Smith (1971). Therefore, a strongly cautious approach seems mandatory. It is necessitated not just by the very real possibility of widespread species extinction. The introduction of only one wrong species, such as the yellow-bellied sea snake from the eastern Pacific into the Atlantic Ocean (see Graham, Rubinoff, and Hecht, 1971), could inflict enough direct economic or ecological damage to justify the attempt to prevent any migration at all. Furthermore, changes in just a few species in a tightly integrated community could have widespread indirect effects by destabiliz-

ing the community (Levins, Chapter 1). Previous experience with the careless mixing of aquatic biotas, for example in the Great Lakes via the Erie and Welland canals, indicates that to permit the mixing of the rich tropical Pacific and Atlantic biotas would be playing ecological roulette with all cylinders loaded. Moreover, a unique biogeographic experiment of global proportions would thereby have been performed, without adequate preparation and in the wrong century. The natural setting for the experiment took millions of years to develop and cannot be repeated. Biology should be fully prepared before allowing it to proceed even piecemeal. For these reasons two groups of biologists, the University of Miami team supported by the Battelle Memorial Institute and the Committee of Ecological Research for the Interoceanic Canal (CERIC) of the National Academy of Sciences, have independently recommended that some kind of biological barrier be constructed across the canal before it is opened (Voss, 1972; Newman, 1972). The barrier can take any one or a combination of several forms: bubble curtains, ultrasonic screens, intrusions of heated or fresh water, and others. The details will be a straightforward exercise in engineering, infinitely simpler than the one biologists and the rest of humanity would face if the mixing is allowed to proceed.

The Design of Nature Preserves

Biogeographers cannot predict the outcome of mixing the Pacific and Atlantic biotas, except to say that it is dangerous,

for the reason that this is one of the most complex problems they can ever conceivably face. Similarly, molecular biologists do not understand how metazoan tissues develop, and behavioral biologists cannot explain conscious thought, because these problems are also the Mount Everests of their respective disciplines. Like the rest of biology, however, biogeography is far from helpless when dealing with smaller, better-circumscribed units. The quantitative theory of island biogeography in which Robert MacArthur was so involved can be brought to bear on several kinds of problems of diversity maintenance. Preston (1962), Willis (1971), Wallace (1972), Diamond (1975), and Terborgh (1974a) have pointed out that the most straightforward application is in the design of natural preserves. Natural habitats have always been fragmented into island-like enclaves. With certain exceptions, such as the forests of New England, man has intensified this process, reducing the fragments in size and increasing their degree of isolation. The number of species belonging to a single taxon such as birds, ants, or flowering plants, equilibrates on a given island at a level that is a function of the area and the degree of isolation of the island (MacArthur and Wilson, 1967). Similar effects are seen on "habitat islands" within continents (Cody, Chapter 10). When the distance to the principal source area is held constant, whether that area is a continent, a set of islands, or just a similar habitat nearby, the number of species S increases approximately as a simple power function of the area, as follows: $\log S = a + z \log A$, where A is the

area and a and z are fitted constants. When the independent parameter of isolation is increased, z rises at a rate characteristic of each taxon and the part of the world in which the relation is observed. In most cases z falls somewhere between 0.2 and 0.4 (cf. May, Chapter 4, Table 5; Diamond, Chapter 14, Figures 2 and 3). A very rough rule of thumb is that a ten-fold increase in area results in a doubling of the number of species at equilibrium.

When a nature preserve is set aside, it is destined to become an island in a sea of habitats modified by man. The species number will shift from its original equilibrium because of the area and distance effects just cited. As years pass the diversity will decline, eventually reaching a new, lower steady state. An estimate of the loss can be made by comparing the reserve with the area-species curve of older systems, providing that appropriate systems exist under comparable conditions of isolation. Diamond (1972, 1973, and Chapter 14) has developed an elegant technique to estimate the relaxation rate and secondary equilibrium values in the case of island birds. He made use of land-bridge islands that were disconnected from New Guinea at known times in the recent geologic past. His results have been confirmed and extended by Terborgh (1974b) in parallel studies in the West Indies and Central America. Both Diamond and Terborgh discovered that significant drops in the number of species in newly disconnected islands take place over a period of decades in the smallest islands, which are comparable in area to small natural reserves on continents, and

during centuries in islands comparable in size to our largest national parks.

Barro Colorado Island in Panama provides both a test of the theory and an alarming example of the high potential decrement rate on small islands. Barro Colorado actually consists of a hilltop of 15.7 km² of lowland tropical forest, which was isolated from surrounding forests about 1914 when Gatún Lake rose around it as part of the formation of the central part of the Panama Canal. Since 1923 the island has been a protected biological reserve, and its forests have been growing to maturity. Inserting the area of the island and its known period of isolation into an extinction model based on the West Indian studies, Terborgh (1974a) estimated that the number of resident bird species should have declined by nearly 10 percent. This is in close agreement with the decline actually observed. Let us examine the history of extinctions in some detail.

The birds of Barro Colorado, fortunately, have been well studied over the years. Chapman (1938) and others worked there during the 1920s and 1930s, Eisenmann (1952) and others visited from 1947 to date, and Willis studied there two to eleven months per year from 1960 to 1970. Of 208 species of birds breeding on the island in Chapman's time, 45 had disappeared by 1970. Several other species were down to one or a few individuals. A grebe and a gallinule have colonized the lake, and three species of the forest edge (two tanagers and a wren) are currently attempting colonization. Other species of the forest edge have attempted colonization but failed. No forest species has

reached the island, although points on its edge are only about half a kilometer from sites on the mainland where the species occur.

For two reasons the record of extirpations must be interpreted with care. Early workers probably missed several species, including several tiny flycatchers and an elusive forest dove now present. Several sight records by early workers have to be doubted as possible vagrants or misidentifications. If some of these forest species, notably difficult to detect, were actually breeding earlier, there may have been a higher original avifauna and more extirpations than we think. On the other hand, if other species such as the tiny flycatchers have been successful colonists, the original avifauna may have been lower than we think. We regard a higher figure for the original avifauna to be the more likely, but neither possibility materially affects conclusions of this chapter.

The second reason for careful interpretation presents more of a problem. Barro Colorado was not just a tract of mature forest that became an island of mature forest. Rather, it was a mixture of mature forest and patches of second-growth forest, the latter now growing to maturity. Some 32 of the lost species of birds, or perhaps a few less, are birds of second-growth or forest edge (Willis, 1974). These species lost their habitats as the forest grew. They are "weed" species, abundant on the mainland and easily capable of colonizing patches of secondary forest there. Such opportunistic forms are in little danger of extinction even where cutting of the forests has reduced forests

to fragments. Thirteen lost species (Table 1), or perhaps a few more, regularly occur in extensive tracts of tall forest elsewhere, sometimes at lower density than in less mature forests. They can be expected to disappear as the forests are cut.

The particular, idiosyncratic causes of extinction are nearly impossible to pinpoint and are probably varied (Willis, 1974). Several of the lost species nest or feed on the ground. Perhaps leaf litter is reduced as monolayer trees take over the forest (see Horn, 1971), and very likely the sparser ground cover in mature forests provides relatively poor protection from predators. However, ground-living birds are also the ones that are least able to emigrate to the island. High densities of certain mammals, in part due to losses of large predatory mammals, could lead to destructive levels of predation on the nests and of some birds. Finally, because the range of habitats is limited, refugia do not exist during exceptional wet or dry years (cf. discussion of "hot spots" by Diamond, Chapter 14).

Two lost species belong to a group studied most intensively, the birds that follow army ants to feed on the arthropods flushed by these insect predators. Of the original seven species in this guild, the largest (*Neomorphus geoffroyi*, a ground cuckoo) was gone before Willis arrived in 1960. The second largest (*Dendrocolaptes certhia*, a woodcreeper) was down to two pairs in 1960 and disappeared by 1970. The third largest (*Phaeostictus mcleannani*, an antbird) decreased from 15 pairs to one female and a few males by 1970. The fifth species (*Gymnopithys bi-*

Table 1. Forest birds extirpated from Barro Colorado Island

Species	Large for guild	Ground nester	Ground forager	Low density in tall forests	Immigra- tion
Harpy eagle (<i>Harpia harpyja</i>)	++			a	f
Barred forest-falcon (<i>Micrastur ruficollis</i>)*	+			b	
Red-throated caracara (<i>Daptrius americanus</i>)*	+			c	f
Great curassow (<i>Crax rubra</i>)	++			a	e
Marbled wood-quail (<i>Odontophorus gujanensis</i>)	+	+		b	e
Rufous-vented ground-cuckoo (<i>Neomorphus geoffroyi</i>)	++		+	a	e
Barred woodcreeper (<i>Dendrocolaptes certhia</i>)*	+		+	b	e
Buff-throated Automolus (<i>Automolus ochrolaemus</i>)	+	+		b	e
Black-faced antthrush (<i>Formicarius analis</i>)	+		+	b	e
Sulphur-rumped flycatcher (<i>Myiobius sulphureipygius</i>)				d	e
White-breasted wood-wren (<i>Henicorhina leucosticta</i>)		+	+	b	e
Nightingale wren (<i>Microcerthulus marginatus</i>)					
Song wren (<i>Leucolepis phaeocephalus</i>)*			+	b	e
			+	b	e

Species marked with an asterisk disappeared during the 1964–1973 decade. Probably other species disappeared during 1971–1973. a, low density because large for the ecological guild. b, higher densities reached in less mature or dry forests. c, wasp-eating, wanders widely. d, nests over streams, which are uncommon on Barro Colorado. Several other flycatchers that nest over or near streams in second-growth have also been extirpated. e, immigration to Barro Colorado from the mainland unlikely. f, birds not now present on mainland, but could immigrate.

color, an antbird) decreased from some 50 to 20 pairs. Only the fourth, sixth, and seventh species, medium to small birds that often forage apart from the ants as well as near them, maintained substantial populations. Even over a ten-year period, reasons for declines were not evident; it can only be said that high predation on nests kept replacements below fairly high losses of adults despite frequent renestings.

Several other losses fit a pattern of early loss of large or specialized species, a pattern to be discussed later as "ecological truncation." The harpy eagle was the largest local raptor of Barro Colorado, the

great curassow the largest local frugivore, the barred forest-falcon the largest insect-eater, the caracara the only wasp-eater, and the black-faced antthrush the largest litter insectivore. Some small and generalized birds are doing better than in similar mainland forests nearby, an example of the usual island pattern of "density compensation" (MacArthur, Diamond, and Karr, 1972) by which a large number of individuals of a few small species replace missing species (cf. Cody, Chapter 10; Brown, Chapter 13). The most abundant species on the island has been studied closely (Oniki, in preparation) and has high nest and adult losses

but a wide range of foraging behaviors. Maturation of the forest has led to success for several large fruit-eaters and arthropod-eaters; average bird weights are higher in the half of the island covered by tall forest than in the remaining medium forest. Since losses of large species and density compensation go against this trend, small size of the island rather than forest growth is likely to be the main reason for losses. However, losses of small wrens may have followed from reduction of the isolated populations due to maturation of the forest.

Loss rates on Barro Colorado have remained steady or increased slightly, at about ten species per decade. Of these, about three have been forest inhabitants. The latter estimate is close to the one that Diamond (1971) made for losses on Karakar Island off New Guinea and Santa Cruz Island off California. Coiba, an island connected to Panama by a Pleistocene land bridge about 10,000 years ago, is much larger than Barro Colorado but has retained many fewer of the mainland species near it than has Barro Colorado (Wetmore, 1957). One can therefore predict that many more species will ultimately be lost from Barro Colorado.

All of this new information from island biogeography shows that planners and managers of national parks and other natural preserves will be prudent to take the spontaneous extinction rate into account and to choose appropriate measures to minimize it. The following basic procedures should be included:

1. Individual preserves must be made

as large as possible. Since the areas of preserves will always be fixed by political compromise, estimates should be made of the extinction rates, as a function of time and area, of the most vulnerable taxa such as the birds and mammals. Then the minimal areas demanded should be the ones at which the initial and consequently highest extinction rates will be reasonably low. The projected rates should be such that only large increments of reserved land will lower them significantly further. In other words, land acquisition must reach the point of diminishing returns with respect to the most extinction-prone groups.

2. Unique habitats and biotas are best contained in multiple preserves, and these isolates should be located as closely together as possible. The reason is that extinction has a strong random component. Species seldom become extinct in every part of their range simultaneously. They tend to persist because ecologically suitable localities that lose them can be recolonized from other localities that are still occupied. Reciprocal intercolonization of preserves can proceed indefinitely through time and, if aided by deliberate transplants, might extend the life of species well beyond what it would be under natural circumstances.

3. Because of the peninsula effect discovered by biogeographers, preserves of a fixed area should be as round in shape and as continuous as possible. (This principle and those embodied in the first two recommendations are illustrated in Figure 1.)

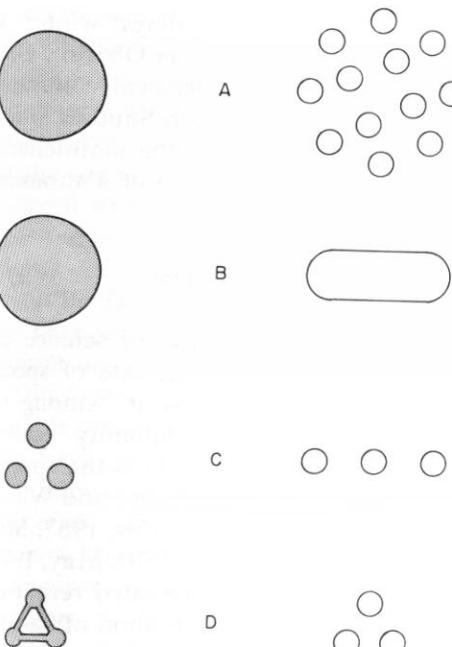


Figure 1 The geometrical rules of design of natural preserves, based on current biogeographic theory. The design on the left results in each case in a lower spontaneous extinction rate than the complementary one on the right. Both the left and the right figures have the same total area and represent preserves in a homogeneous environment. A: a continuous preserve is better than a fragmented one, because of the distance and area effects. B: a round design is best, because of the peninsula effect (cf. MacArthur and Wilson, 1967, pp. 115–116 and Figure 37). C: clumped fragments are better than those arranged linearly, because of the distance effect. D: if the preserve must be divided, extinction will be lower when the fragments can be connected by corridors of natural habitat, no matter how thin the corridors (Willis, 1974). Another principle, not incorporated in this figure, is that whatever the design of a given preserve, its extinction rate can be greatly lowered if similar preserves are located nearby.

4. Extinction models of the kind invented by Diamond and Terborgh should not be restricted to the most conspicuous or vulnerable organisms but should eventually be developed for all taxa. Those displaying the highest degrees of endemism and vulnerability (the two phenomena are generally correlated) deserve first attention. No group, not even the humblest and most obscure among invertebrates and microorganisms, should be ignored. Thus, in addition to the full taxonomic surveys that are just getting underway in natural preserves, biologists should begin studies of species dynamics and species equilibria.

The Special Problem of Ecological Truncation

Truncation of ecological guilds, the well-known but seldom-emphasized early loss of specialists and of large species, is probably mainly due to the fact that most such species occur at very low densities, require large areas for sustenance, or both (see discussion of so-called incidence functions, the dependence of an island's species composition on its species number or area, in Chapter 14 by Diamond). "Density compensation" for truncation may lead to increased numbers of individuals of generalized small species (MacArthur, Diamond, and Karr, 1972). However, species diversities and biomasses will still be lower.

The ant-following birds of Barro Colorado show ecological truncation clearly, as shown earlier. Diamond (Chapter 14)

found a large eagle (*Harpyopsis novaguineae*) and a distinctive kingfisher (*Clytoceyx rex*) gone from all the formerly connected islands off New Guinea. An even better example of truncation is presented by the disastrous extinctions of Hawaiian birds during the past century. These losses were evidently due at least in part to human cultivation of the lowlands and to the introduction of disease-vector mosquitoes (Warner, 1968). The first species to go were such large or specialized species as the big Kioea (*Chaetoptila angustipluma*) and both long-beaked Mamos (*Drepanis* spp.). Many of the species now approaching the end are characterized by intermediate size, distinctive adaptations, or both—the half-beaked *Hemignathus*, for example, the parrotbill *Pseudonestor*, and others. Few members of the endemic Hawaiian family Drepanidae other than small warbler-like species such as the Amakihi (*Loxops virens*) are doing well.

Truncation creates a particular difficulty for the planning of natural reserves, because multiple refuges of a given habitat tend to lose the same specialized species. Diamond (1972) found that the largest (3000 square miles) of the formerly connected islands off New Guinea has retained only 45 out of the 134 land-bridge bird species. Even if parks in the New Guinea of the future should be huge like these offshore islands, many species would still be lost.

The island effect and truncation, taken to their extremes, result in the domination of small parks by rats, cockroaches, sparrows, and similar invaders from nearby human areas. Practically no birds other

than pigeons and starlings winter in wooded Tappan Square in Oberlin, Ohio (Margaret F. Smith, personal communication). A thousand such Squares would be far less valuable for the maintenance of biotas than one refuge of a thousand Square units.

Planned Biotic Enrichment

It is within the power of science not merely to hold down the rate of species extinction but to reverse it. Among the principal topics of community ecology now under intensive study is the species-packing problem (MacArthur and Wilson, 1967; MacArthur and Levins, 1967; MacArthur, 1972; Schoener, 1970; May, 1973). One of the more sophisticated recent developments is the specification of "assembly rules" by Diamond (Chapter 14). A central goal of this research is the identification of those traits that allow certain sets of species, but not others, to be fitted together in the same ecosystem without markedly increasing the species extinction rate. During colonization by undisturbed biotas, such congenial sets are gradually assembled by chance alone, raising the steady-state species number to what has been called the assortative equilibrium (Wilson, 1969). Theoretically, assortative equilibria can be planned that exceed any occurring in nature. Species might even be drawn from different parts of the world—not willy-nilly, as in the careless importations of the past, but after careful ecological analysis has identified them as candidates for insertion into new faunas. Some of the first and most important intro-

ductions would surely be "orphan species," those on the brink of extinction in their native range but capable of being fitted into certain alien communities elsewhere. We do not suggest that the state of the art is advanced enough for us to proceed with planned biotic mixing, only that species packing is one of the techniques of applied biogeography that seems likely to become practicable within the next several decades, on the basis of current and projected research.

Optimism is further justified by the favorable outcome of a few biotic mixtures that have already occurred haphazardly, indicating a degree of flexibility on the part of species that will provide biogeographers with some margin for error. The Kaingaroa Forest of New Zealand, for example, contains 250,000 acres of exotic conifers, including *Pinus radiata*, *P. ponderosa*, *P. contorta*, and *Pseudotsuga taxifolia* from North America, and *Pinus nigra* from southern Europe. Introduced birds mingle with endemic New Zealand species in this synthetic environment. Ecological differentiation is well marked; no two species have the same feeding habit, and the insectivorous birds exploit all of the major feeding niches except that of woodpeckers. The really surprising fact, however, is that some of the native species are now as abundant in the Kaingaroa Forest as in almost any native forest, and some are more abundant than in most of the remainder of their range (Gibb, 1961; personal communication, 1973). Furthermore, the invertebrate fauna of the forest consists mostly of native species (Rawlings, 1961). Two circumstances are special

in the case of the birds. First, the number of species is still small, largely because the New Zealand fauna was depauperate to start with, and the mixed community has probably not yet encountered many of the difficulties in packing that would be routine in large continental faunas. As discussed by Cody (Chapter 10), species of depauperate faunas are better able to colonize exotic habitats than are species of rich faunas. Second, forest birds are differentiated to a large degree by foliage height and profile rather than by the species of trees in which they live. Monophagous and oligophagous insects, particularly those specializing on hardwoods, would in most instances find it impossible to penetrate the Kaingaroa conifers. Yet the lesson is clear: what works in part by accident can be brought closer to perfection through design.

Ultimately, design might also include the artificial selection of strains, or even the creation of new species, for the purposes of biotic enrichment. If theory and experiment indicate that an orphaned species cannot be fitted into any existing communities, strains might be selected within captive populations of the species that could eventually be inserted into one or more communities. We do not seriously suggest that such a procedure will be followed in the foreseeable future for any but a very few of the organisms most valued by man. Furthermore, the genetic molding of communities is a technology that cannot be seriously contemplated until the inchoate discipline of population ecology has moved closer to a full solution of the species-packing problem.

The Creation of New Communities

Many of the earth's major habitats are biological deserts: the open sea, the ice caps, some of the trace-element barrens, and the real deserts, the extremes of which are virtually abiotic. Quite by coincidence, technology is at this moment striving toward two major goals that could transform these areas: an unlimited or at least vastly greater source of energy, and, as one of the principal benefits of the first, the cheap desalinization of sea water. With the achievement of these goals, men will move increasingly onto the land deserts, carrying communities of organisms with them. We will not be satisfied, it is hoped, with limiting ourselves to a baggage of domestic animals, houseplants, pests, and commensals. It lies easily within our power to create wholly new parks and reserves where nothing existed before in historical times. But what will go into these *de novo* communities? Thought about this subject sharpens one's vision of the future of applied biogeography.

In fact, the deliberate creation of new biological communities has already begun. Large areas of desert-like barrens in Australia have been transformed into agricultural land by the simple addition of zinc, copper, or molybdenum, "trace" elements required for life that were previously present in abnormally low quantities (Anderson and Underwood, 1959). Marine biologists have discovered that artificial reefs, with rich complements of reef organisms, can be created just by dumping concrete rubble, abandoned automo-

biles, used automobile tires, and similar inert refuse onto the mud or sand floors of shallow marine waters. Successful experiments of this nature have been conducted off the shores of Florida and California (see Turner, Ebert, and Given, 1969). What these efforts engender are in effect habitat islands, the biotas of which grow and equilibrate according to the same laws of biogeography governing wholly natural islands. The communities are not likely to be as diverse as those that have evolved for millions of years in the natural islands, yet the process of enrichment can be speeded by the deliberate importation of compatible species to reach new and higher assortative equilibria. This is another aspect of biogeographic technology that ongoing basic research might render practicable during the next few decades.

Ecosystem Manipulation: The Ultimate Game

The greatest misfortune that awaits the human intellect is to be no longer faced with something commensurate with its capacity for wonder. If the golden age of science really ends, and research shrinks to a few remote and arcane frontiers accessible only to specialists, the wonder will indeed be gone. By that time even the prescientific myths that sustained our ancestors, and intrigue us still, would have largely evaporated—having been accounted for in full, perhaps by the right kind of neurophysiological analysis of the limbic system and hypothalamus. But this possibility will not materialize during the

lifetime of anyone now living. The ultimate complexity, offering an unexplored terrain of virtually infinite extent, lies in biology. Even after the cell has been torn down and put together again, and the labyrinthine mysteries of metazoan development followed to their ends, there lie ahead much more extensive challenges of ecology and biogeography. The full exploration of organic diversity is a prospect that suits the biocentric human brain, especially those emotive centers that evolved to make us superior hunters and agriculturists. The same instincts that motivate the birdwatcher, the butterfly collector, and the backyard gardener can indefinitely sustain the scientifically curious segment of a more sophisticated human population in the pursuits of ecology and biogeography. The very size of the world's biota, comprising millions of species, is itself a challenge that only generations more of study will encompass. The possibilities for ecosystems manipulation, outlined in this essay on applied biogeography, offer creative work that is orders of magnitude even more extensive.

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