

# 14 Assembly of Species Communities

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different biogeographical regions. The working hypothesis is that, through diffuse competition, the component species of a community are selected, and coadjusted in their niches and abundances, so as to fit with each other and to resist invaders. Observations are derived from bird communities of New Guinea and its satellite islands, of which some are at, some above, and some below equilibrium in species number ( $S$ ).

From exploration of numerous islands with various values of  $S$ , so-called incidence functions are constructed for individual species. These relate  $J$ , the incidence of occurrence of a particular species on islands of a certain  $S$ -class, to  $S$ . Species are classified according to their incidence functions into six categories: high- $S$  species, confined to the most species-rich islands; A-, B-, C-, and D-tramps, present on the most species-rich islands and also on increasing numbers of increasingly more species-poor islands; and super-tramps, confined to species-poor islands and absent from species-rich islands. Since different species have incidence functions of different shapes, the fauna of any real island is a very nonrandom subset of the total species pool.

The high- $S$  category consists partly of endemic species of forest on large islands, partly of non-endemic species of scarce habitats often unrepresented or barely represented on smaller islands. Tramps, especially C- and D-tramps, are mostly nonendemic species characteristic of habitats that occur on virtually any island.

The dependence of incidence on area involves several factors, which vary from

species to species: whether the required habitat of a species occurs on small islands; minimum territory size for species in which each pair maintains an exclusive territory; minimum year-round support area for species dependent on patchy or seasonal food supplies; population size in relation to short-term and long-term population fluctuations; and the role of "hot spots" (areas of locally-high utilizable resource production) in colonization and in recovery from population crashes.

Dispersal ability of species in different incidence categories has been assessed from data sources such as recolonization of islands defaunated by volcanic explosion or tidal wave, long-term records of vagrants, and direct observations of over-water colonization. Especially in the tropics, many bird species capable of strong flight refuse to cross water barriers of even a few miles. Dispersal rates are highest for supertramps and D-tramps, followed by C-tramps, B-tramps, and nonendemic A-tramps of scarce habitats. For high- $S$  species, such dispersal as there is may be associated with rare population "blooms."

There is no obvious correlation between clutch size and incidence category. However, supertramps and D- and C-tramps have longer breeding seasons and raise more broods per year than do other species.

Supertramps have extraordinarily catholic and unspecialized habitat preferences, high reproductive potential, and high dispersal ability. They are competitively excluded from species-rich islands by "K-selected" species. However, faunas

dominated by supertramps maintain population densities up to nine times *higher* than those of *K*-selected faunas composed of the same number of species. Thus, the supertramp strategy may be contrasted with an inferred overexploitation ethic practised by high-*S* species, which are selected by competition to harvest early and overexploit. The high-*S* species thereby reduce resource levels below the point where other species can survive, even though this diminishes the rate of resource production and hence the population density of the harvesting species.

In a few instances, competition expresses itself in "simple" checkerboard distributions, by which species replace each other one-for-one. The frequent occurrence of "empty squares," however, shows that even these cases are complex. In the great majority of species groups or guilds, competitive exclusion involves so-called diffuse competition, i.e., the combined effects of several closely related species. Detailed examination of four guilds reveals the following types of assembly rules for species communities:

If one considers all the combinations that can be formed from a group of related species, only certain ones of these combinations exist in nature.

These permissible combinations resist invaders that would transform them into a forbidden combination.

A combination that is stable on a large or species-rich island may be unstable on a small or species-poor island.

On a small or species-poor island a combination may resist invaders that would be incorporated on a larger or more species-rich island.

Some pairs of species never coexist, either by themselves or as part of a larger combination.

Some pairs of species that form an unstable combination by themselves may form part of a stable larger combination.

Conversely, some combinations that are composed entirely of stable subcombinations are themselves unstable.

The forbidden combinations do not exist in nature because they would transgress one or more of three types of empirical rules: compatibility rules banning the coexistence of certain closely related species under any circumstances; incidence rules, implicit in incidence functions; and combination rules, which cannot be predicted from incidence functions.

Most of the evidence for these assembly rules is drawn from comparison of communities on different islands. However, examples are also drawn from communities at different localities, or in different habitats, or at different altitudes, or at different heights above the ground, on the same island. In some cases one can recognize simple effects of one-to-one competition. In other cases, one can recognize assembly rules describing more complex competitive effects and permitted combinations of several related species. In still more complex cases, competitive effects must be described by incidence functions relating the occurrence or niche limits of one species to diffuse competition from many other species. Thus, recognition of assembly rules may help us understand competitive effects on the spatial niche limits of a given species, and the puzzling tropical phenomenon of patchy distributions.

Much of the explanation for assembly rules has to do with competition for resources and with harvesting of resources by permitted combinations so as to minimize the unutilized resources available to support potential invaders. Communities are assembled through selection of colonists, adjustment of their abundances, and compression of their niches, in part so as to match the combined resource consumption curve of all the colonists to the resource production curve of the island. Members of permitted combinations must also be "companions in starvation"—i.e., must be similar in their tendencies to overexploit and in their tolerances for lowered resource levels, thereby starving less tolerant species off the island. Thus, consumer species form hierarchies with respect to exploitive strategy. The conditions under which overexploitation becomes a useful strategy for its practitioners are examined by loop analysis. Also relevant to the origin of assembly rules are two further factors: dispersal abilities, which permit only certain species to have a high incidence on small islands with high extinction rates; and transition probabilities, i.e., ease of assembling a species combination in one or a few steps from other permitted combinations.

Major unsolved problems include: the development of mathematical models for incidence functions; extensions to habitat communities and to locally patchy communities; the relative roles of chance and of predestination (i.e., detailed matches of different species combinations to slightly different local production curves) in the build-up of alternate communities; and applications to conservation problems.

## Introduction

The understanding of alternate, stable, invasion-resistant communities of co-adjusted species poses a major current problem in ecology. Sets of such communities occur in similar habitats in different biogeographical regions, in similar habitats on different islands colonized from the same species pool, in similar habitats at different localities on the same large island or continent, and in different adjacent habitats. The theoretical basis for the existence of alternate stable communities was brilliantly explored by Robert MacArthur (1972) in *Geographical Ecology*. A conceptual framework is now available within which field observers can approach such unsolved problems as the following:

To what extent are the component species of a community mutually selected from a larger species pool so as to "fit" with each other?

Does the resulting community resist invasion? If so, how?

To what extent is the final species composition of a community uniquely specified by the properties of the physical environment, and to what extent does it depend on chance events (e.g., the question of which colonists arrive first, possibly also affecting which subsequent arrivals are compatible with the successful first colonists)?

The present chapter discusses such problems in the light of observations on bird communities of New Guinea satellite islands. It will be shown that (a) the probabilities or incidences of occurrence of particular species in a community bear

neat empirical relations to the total species number in the community; (b) these so-called incidence functions can be interpreted in terms of island area plus a species' habitat requirements, dispersal ability, birth and death schedule, exploitation strategy, and competitive relations; (c) the various species in a guild can co-exist only in certain combinations; (d) these permitted combinations resist invaders that would result in forbidden combinations; and (e) lowering of resource levels by coadjusted constellations of species, to below the point where invaders can survive, may be an important mechanism of competitive exclusion.

### Statement of the Problem

The structure of a species community may be described in terms of its species composition, together with the resource utilization, and distribution and abundance in space and time, of each component species. Comparison of different communities at any one of four levels generally reveals some differences in structure:

1. Differing but adjacent habitats differ in community structure, even though there may be no physical barriers preventing species of one habitat from invading another habitat (cf. Cody, Chapter 10).

2. Differences in community structure may exist between similar habitats in different areas of the same continent or large island, or even between similar habitats in areas that are in immediate contact and constitute artificially defined sections of a continuum. This phenomenon is es-

pecially marked in the tropics. The result is often that tropical species are patchily distributed with respect to the available habitat. Figures 33-38 will present examples of these baffling distributional patterns.

3. Communities on similar islands colonized from the same species pool may differ. For example, the islands Sakar and Tolokiwa lie 29 miles apart in the Bismarck Sea near New Guinea, differ in area by only 13%, are geologically similar, support similar forest, have derived their birds from the same sources, and support similar numbers of lowland bird species (36 and 40, respectively). Yet Tolokiwa lacks three of the seven most abundant species of Sakar, Sakar lacks eight of the 15 most abundant species of Tolokiwa, and only 23 species are shared. In the Pearl Archipelago off Panama, MacArthur, Diamond, and Karr (1972) cite equally striking differences in bird species composition between Chitre and Contadora islands, which are only 1 mile apart. Furthermore, a species that is shared between similar islands may still occupy different habitats and have different abundances. For example, the fruit pigeon *Ptilinopus insolitus* is present both on Sakar and on Tolokiwa, but on Sakar it is widespread whereas on Tolokiwa it is confined to mid-montane forest. Its congener *Ptilinopus solomonensis* is present both on Sakar and on Tolokiwa and occupies similar habitats on the two islands, but is approximately six times more abundant on Tolokiwa than on Sakar.

4. The examples mentioned so far involve communities formed from the same species pool and lying within the same

biogeographic region or faunal province. Much larger differences are observed between more distant communities lying in different faunal provinces. For more than a century, from the time of Sclater and Wallace until the publication of *The Theory of Island Biogeography* by MacArthur and Wilson (1967), these differences formed the principal subject matter of biogeography. Although similar habitats in South America, Africa, and Australia may share few species in common, these communities may exhibit remarkably detailed convergent similarities in structure (Cody, Chapter 10; Karr and James, Chapter 11). The borders of the world's major faunal provinces are formed by present and past barriers to movement of organisms. These barriers have not served to eliminate colonization, but rather to reduce it to a level where great differences are maintained indefinitely between the communities on opposite sides of the barrier. If the communities did not possess some resistance to invasion, colonization across the barriers for millions of years would have smoothed many of the differences between even the major faunal provinces. Thus, the differences between the Australian Region and the Oriental Region present many of the same problems, albeit in more marked form, as the differences between Sakar and Tolokiwa islands in the Bismarck Sea.

These examples suggest (but do not prove) that the species in a community are somehow selected, and their niches and abundances somehow coadjusted, so that the community possesses some measure of "stability." Stability implies the existence of several different properties, some of

which are easier to demonstrate than others. The most obvious thing we mean in describing a community as "stable" is that its present species composition is likely to persist with little change if there is no change in the physical environment. This property is easy to assess by comparing historical surveys with recent surveys. For instance, faunal surveys of a given New Guinea satellite island a century ago and today yield much more similar species compositions than do surveys of several different islands of similar size at the same time. The property of stable species composition suggests the existence of an additional property, namely, ability of a community to resist invasion by new species. This property is more difficult to document, because one needs much more than two faunal surveys at different times. A particular species may be absent from a particular island because the existing community prevents colonizing individuals of the new species from establishing themselves, or merely because colonizing individuals of the species may never reach the island at all. To document resistance to invasion requires sufficiently extensive observations so that arrivals of colonizing individuals, and their failures to establish stable populations, are detected. Finally, the property of resistance to invasion suggests a further property, which is still more difficult to document as well as to formulate, namely, that the existing community utilizes available resources in some optimal manner (MacArthur, 1970; MacArthur, 1972, pp. 231-234).

It seems likely that competition between species plays a key role in the integration of species communities. Real or potential

utilization of some of the same resources could be an obvious explanation for why similar species do not occur in the same community, unless their resource utilizations are somehow coadjusted. Numerous recent studies have provided clear-cut distributional evidence for competition between members of a pair of related species. These examples are valuable in documenting the existence of competition, but by themselves they do not account for much of the real world. Far more often, the presence or absence of a given species, and intercommunity variation in its abundance or spatial distribution, cannot be understood predominantly in terms of a correlated distribution of any single other species. It is then a logical extension of simple two-species distributional checkerboards to invoke "diffuse competition"—i.e., the complex situations resulting from the sum of competitive effects from many other somewhat similar species (Diamond, 1970a, p. 530; 1970b, pp. 1716–1717; MacArthur, 1972, pp. 43–46 and 249; Pianka, Chapter 12). The power of this concept is that, in principle, it can explain anything. Its heuristic weakness is that, if it is important at all, its operation is likely to be so complicated that its existence becomes difficult to establish and impossible to refute. Such a concept deserves to be greeted with skepticism until its importance can be documented. A profitable biogeographic approach to documenting diffuse competition would seem to be, first, to seek evidence whether variation in the incidence, niche, or abundance of a given species is correlated with variation in total species number; then, to

seek to trace out cases in which the distribution of a given species can be clearly related to the distribution of certain *combinations* of a few other species, yielding patterns that are analogous to two-species distributional checkerboards but more complex.

Such a test of the hypothesis of alternate, stable, invasion-resistant communities integrated by diffuse competition requires a field situation or experimental situation with the following properties: (a) a large number of communities that provide a similar physical environment and habitat structure; (b) a large species pool, varying fractions and combinations of which occur in the available communities; (c) availability of evidence that a species absent from a given community actually has had access, and that its absence is not simply due to a total lack of immigrants; (d) availability of evidence that the community does resist invasion, and that failure of attempted colonizations is not simply due to unsuitable habitat; (e) availability of cases in which a community has been displaced from equilibrium, so that relaxation towards equilibrium can be studied.

The avifauna of New Guinea and its satellite islands provides a favorable test situation. Considerable ecological and evolutionary information exists about the New Guinea species pool of 513 breeding nonmarine bird species. Surrounding New Guinea, and colonized by varying fractions of this species pool, are thousands of islands of varying sizes and at varying distances, providing numerous sets of replicate communities. Ornithological ex-

Species

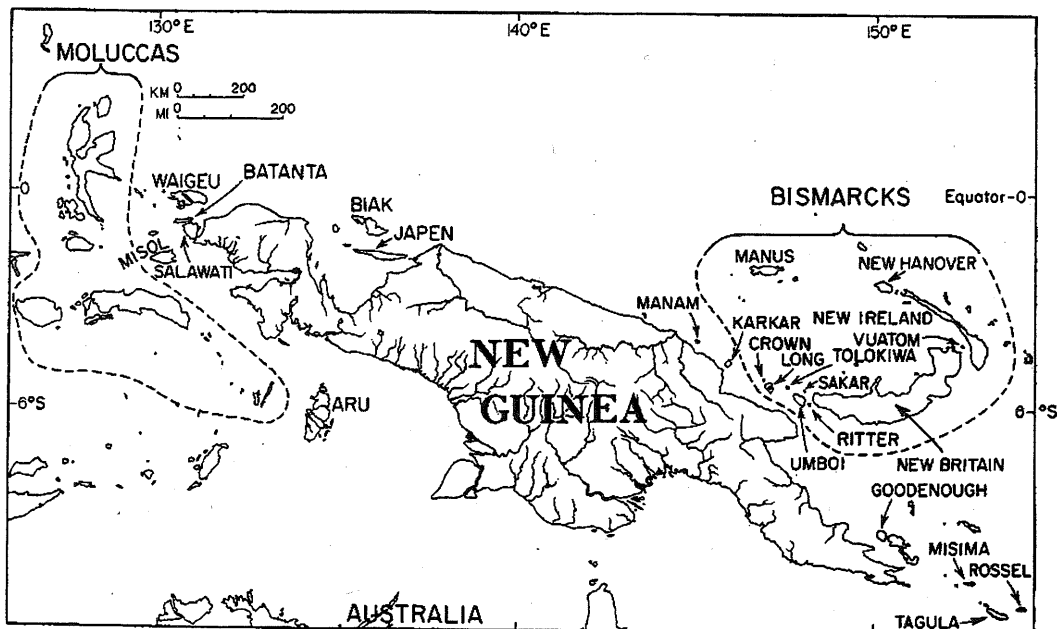


Figure 1 Map of the New Guinea region with names of some of the islands to be discussed.

ploration has been sufficiently intensive to provide not merely species lists but, for some islands, instances of successful and unsuccessful colonizations. Species numbers on some islands have been displaced above what would be their present value at equilibrium by Pleistocene episodes of lowered sea level, which joined some islands to New Guinea, joined other islands to each other, and expanded still other islands in area. Species numbers on other islands have been displaced below equilibrium by Krakatoa-like volcanic explosions or by tidal waves. Some species called supertramps are particularly useful in studying community integration, be-

cause of their high colonization rates and sensitivity to competition. We shall see that the distributions of most species can be neatly related to total species number in a community; and that, in a few cases, it is possible to relate species distributions to diffuse competitive effects from specific combinations of related species.