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Distributional Ecology of New Guinea Birds

Recent ecological and biogeographical theories can be tested on the bird communities of New Guinea.

Jared M. Diamond

As indicated by frequent references in the syntheses of zoogeography by Wallace (1), of evolution by Mayr (2), and of ecology by MacArthur (3), the tropical island-continent of New Guinea and its birds have played a special role in advancing our understanding of animal populations. This role developed partly because birds are the best known, most easily observed and identified animals, and partly because of unique advantages of New Guinea itself. New Guinea provides a range of habitats from tropical rain forest to glaciers within distances of less than 16 kilometers, a range of elevations of over 5000 meters, and an equatorial position that minimizes seasonal migration with its associated complications. The rugged topography, which isolates populations in adjacent valleys or on adjacent mountains, has promoted speciation within small areas of a single land mass by essentially the same mechanisms that underlie speciation on large continents. In New Guinea's expanses of forest undisturbed by man, niche interrelations retain a simplicity and beauty lost in altered environments, and distributional patterns illustrating many intermediate stages in evolution and in niche displacement are readily identified. The number of breeding bird species, 513, is large enough to give rise to the complex interactions characteristic of continental faunas, but not so large as to be overwhelming. In spite of the physical difficulties of exploration in New Guinea, the distribution and taxonomy of its bird species are by now fairly well

understood. New Guinea has served as the bird colonization source for the thousands of islands of the southwest Pacific; and New Guinea itself behaves as an "island archipelago" for montane birds, since its mountain ranges are isolated from each other by a "sea" of uninhabitable lowlands. The number of bird species on these oceanic islands and mountain islands varies with area and isolation, providing innumerable "experiments of nature" whereby the niche of a given species can be studied as a function of the competing species pool.

Within the past decade, new paradigms introduced by MacArthur and Wilson and their co-workers (3-7) have revolutionized our understanding of some central questions of ecology, such as: Why do different localities support very different numbers of animal or plant species? What determines the distribution of a given species? How do related species manage to coexist? These questions are not only of basic scientific interest but are also of practical importance in formulating conservation policies. Furthermore, the concepts of MacArthur and Wilson are proving increasingly helpful in understanding human populations. In this article I discuss these questions in the light of my studies of New Guinea birds, conducted during six expeditions to New Guinea and other islands of the southwest Pacific (8-15). A recent book discusses in detail many of the examples summarized here (15). Many patterns observed in New Guinea birds are relevant to other groups of animals in other parts of the world, especially in the tropics.

If one were to count all the animal or plant species occurring within an area of 1 hectare, the result would vary greatly depending on the location of the census area. The species total would generally be much higher in the tropics than in the temperate zones, higher at the base of a mountain than at the summit, higher on a large island than on a small island, and higher on an island near a continent than on a remote island. It is important to understand this variation if, for example, one is establishing a system of national parks to ensure survival of as many native species as possible. Islands such as those of the southwest Pacific lend themselves well as test areas for a quantitative theory of species diversity, because each island represents a separate experiment, and because most insular variation in species diversity can be predicted from values of only two or three readily measured variables. We shall see that the diversity of bird species on most Pacific islands is in a state of dynamic equilibrium—that is, the diversity is determined by the island's present physical characteristics and is independent of the island's history. However, on some islands, the species diversity may also reflect the island's recent history.

The number of land and freshwater bird species coexisting on each tropical island of the southwest Pacific varies from 1 for some isolated atolls up to 513 for New Guinea itself. This variation is due partly to the greater variety of habitats present on the larger islands. However, even within a given habitat type (for example, in tropical lowland rain forest) there are great differences among islands in the number of bird species to be found. These differences are largely predictable from an island's area, its distance from New Guinea, and its elevation (13).

Figure 1 shows the number of bird species S occurring at sea level on islands between 8 and 500 km from New Guinea, as a function of island area A (expressed as square kilometers). Over a 3-millionfold range of areas the results fit the power function

$$S = 12.3 A^{0.22} \quad (1)$$

with an average error of 19 percent. Thus, a tenfold increase in area increases species diversity by somewhat less than a factor of 2. The numbered deviant points represent islands in var-

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ious stages of "relaxation," as will be explained.

In Fig. 2 I have plotted, as a function of island distance D from New Guinea, the ratio of an island's actual S at sea level to the S value predicted from the island's area and Eq. 1. This ratio decreases exponentially with distance, by a factor of 2 for each 2600 km from New Guinea. Thus, the most remote islands of the southwest Pacific (Mangareva and the islands of the Pitcairn group, 8000 to 9200 km from New Guinea) have a bird species diversity only 12 percent that of islands of similar size near New Guinea.

The mountains of the higher southwest Pacific islands harbor additional bird species not occurring at sea level. On the average, each 1000 m of elevation L enriches an island's avifauna by a number of montane species equal to 8.9 percent of its avifauna at sea level. Thus, bird species diversity on the New Guinea satellite islands may be summarized by the empirical formula

$$S = (12.3) (1 + 0.089 L/1000) \times (e^{-D/2600}) (A^{0.22}) \quad (2)$$

Similarly, species diversity in other plant and animal groups on other islands increases with island area and decreases with distance from the colonization source. These two trends constitute the fundamental law of island biogeography. The exponent of area is generally in the range 0.20 to 0.34 (4, 16).

To explain this law, MacArthur and Wilson (4), and Preston (16), suggested that insular species diversity represents a dynamic equilibrium between immigration and extinction. Islands constantly receive immigrants due to random dispersal of individuals from mainlands, and the immigration rate should increase with island area and proximity to the colonization source. On the other hand, island populations risk extinction due to competition and random fluctuations in population size, and extinction rates should be highest for the smallest islands with the smallest populations. Thus, at equilibrium, when the species immigration rate I on an island equals the species extinction rate E , there should be more species on a large island than on a small island, and more on an island near to other land than on a remote island. Furthermore, species turnover rates at equilibrium should decrease with increasing island area and remoteness.

As a test of the equilibrium theory, in 1968 and 1969 I resurveyed the land and freshwater birds of a temperate archipelago and of a tropical island whose birds had been surveyed 50 years previously: the nine Channel Islands off southern California (9), and Karkar Island off northern New Guinea (12). On each island I found that between 17 and 62 percent of the species present 50 years ago had disappeared, and an approximately equal number of species absent 50 years ago had immigrated. Thus, the species diversity had remained in dynamic equilibrium; Terborgh and Faaborg (17) obtained similar results for the birds of Mona Island in the West Indies. While a few of the extinctions and immigrations in these studies were related to effects of man, most of the changes were of the random kind expected in the absence of a human role. As predicted from colonization theory (4), most of the extinctions involved populations that were rare 50 years ago because of such factors as recency of colonization, small island size, presence of well-established competing species or small area or marginal suitability of island habitat. Among the Channel Islands the calculated minimum turnover rates, expressed as the percentage of island species immigrating or becoming extinct per year, range from 1.2 percent per year for the smallest or most barren islands down to 0.3 percent per year for the largest island.

Since the S and A values for Karkar fit Eq. 1 and lie on the general pattern of Fig. 1, it is probable that bird species diversity is near equilibrium on most southwest Pacific islands. However, there are some points in Fig. 1 that deviate conspicuously from the general pattern. These prove to be associated with islands on which natural processes (such as volcanic explosions or changing sea level) have displaced S from its equilibrium value at some approximately known recent time. On such islands S must be gradually returning to equilibrium as a result of a temporary imbalance between immigration and extinction; this process may be termed "relaxation." Analysis of the islands on which species diversity is undergoing relaxation provides further insight into immigration, extinction, and effects of island history (13).

The respective rates of immigration and extinction, I and E (expressed as species per year), depend on the instantaneous species diversity $S(t)$, where

t represents time. Let us assume constant coefficients K_i and K_e (expressed as year⁻¹), respectively

$$E = K_e S(t) \quad (3)$$

$$I = K_i [S^* - S(t)] \quad (4)$$

$$dS/dt = I - E = K_i S^* - (K_i + K_e) S(t) \quad (5)$$

where S^* is the mainland species pool. At equilibrium ($dS/dt = 0$), the species diversity S_{eq} is given by

$$S_{eq} = K_i S^* / (K_i + K_e) \quad (6)$$

Relaxation to equilibrium from an initial species diversity $S(0)$ that differs from S_{eq} is described by:

$$[S(t) - S_{eq}] / [S(0) - S_{eq}] = e^{-t/t_r} \quad (7)$$

where "relaxation time" t_r is given by

$$t_r = (K_i + K_e)^{-1} \quad (8)$$

The relaxation time is the length of time required for the departure of species diversity from equilibrium, $|S(t) - S_{eq}|$, to relax to $1/e$ (or 36.8 percent) of the initial departure, $|S(0) - S_{eq}|$, where e is the base of natural logarithms. Actually, this treatment is only a crude approximation of the real situation, because K_e and K_i prove to be functions of $S(t)$. However, by applying Eqs. 3 to 8 to island faunas we can deduce the form of these functions, stipulate some conditions for an improved model, and come to some conclusions about the distribution of bird species.

As an example of an "experiment of nature" that permits estimation of $S(0)$, S_{eq} , one pair of values of $S(t)$ and t , and hence calculation of t_r , I will describe the situation on a land-bridge island, Misol. During the most recent Pleistocene glaciation, when much water was sequestered in glaciers and sea level was about 100 m below its present stand (18), Misol was part of the New Guinea mainland and must have supported virtually the full New Guinea lowland avifauna of 325 species. Since the severing of the New Guinea-to-Misol land bridge by rising sea level about 10,000 years ago, $S(t)$ on Misol must have been relaxing toward the value expected for an "oceanic island" of the same area, as a result of extinction exceeding immigration. Figure 1 (points marked +) shows that Misol and other large land-bridge islands are still supersaturated—that is, their present $S(t)$ values are still considerably in excess of the equilibrium value for oceanic islands, although considerably less than the initial value of 325. Misol has an area of 2040 km² and should have 65

lowland species at equilibrium (from Eq. 1) but actually has 135. If we take Eq. 7 and substitute $S(0) = 325$, $S(t) = 135$, $S_{eq} = 65$, and $t = 10,000$ years, we obtain a relaxation time of 7,600 years for the avifauna of Misol.

Relaxation times can also be estimated from four other types of "experiments of nature." These are: the fission of a large island into two smaller islands because of rising sea levels flooding a low isthmus; contraction in an island's area because of rising sea levels; gradual extinction, from land-bridge islands, of relict populations of those New Guinea lowland species that never cross water gaps of more than 8 km or even 50 m (such species must have reached the islands at the time of the land bridge, and were isolated without possibility of recolonization after submergence of the land bridge) (13); and recolonization of volcanic islands such as Krakatau, Long, and Ritter, after cataclysmic eruptions totally destroyed the fauna.

From calculated relaxation times obtained by these methods for 19 New Guinea satellite islands, the following

conclusions can be drawn (13). (i) With decreasing island area, extinction rates increase (yielding shorter calculated t_r values) because of smaller population sizes. Thus, among land-bridge islands the calculated t_r for the relict populations decreases from 9000 years for an island of area 7800 km² (Aru), to 6100 years for 450 km² (Batanta), and to 2630 years for 145 km² (Pulu Adi). Species diversities on small land-bridge islands do not show an excess over equilibrium values (Fig. 1) because relaxation times for these islands are much shorter than the 10,000 years that have elapsed since severing of the land bridges. (ii) On supersaturated islands certain species are especially prone to extinction and tend consistently to disappear first. The resulting release of the remaining species from competition tends to increase their population densities and to decrease their risk of extinction. Expressed mathematically, K_e on a given island is an increasing function of $S(t)$. (iii) The species that arrive first at an initially empty island tend to be certain species with consistently superior dispersal ability, such as those that

characteristically colonize mainland "second-growth" habitats (transient vegetational stages during regrowth of a forest clearing). Subsequent immigrants are drawn from a mainland species pool comprised of progressively poorer colonists. Expressed mathematically, K_i on a given island is a decreasing function of $S(t)$. (iv) The probability of extinction is much higher for recently arrived immigrants that still have a low population density, than for established species that have saturated available island habitats.

Patchiness of Species Distributions

Among the characteristics of tropical species that distinguish them from their high-latitude counterparts are the lesser tendency of tropical species to disperse, their subjection to greater niche compression by interspecific competition, and their lower extinction and higher speciation rates. All these characteristics contribute to the striking tropical phenomenon called "patchiness" (3, 7, 15). Whereas the local presence or

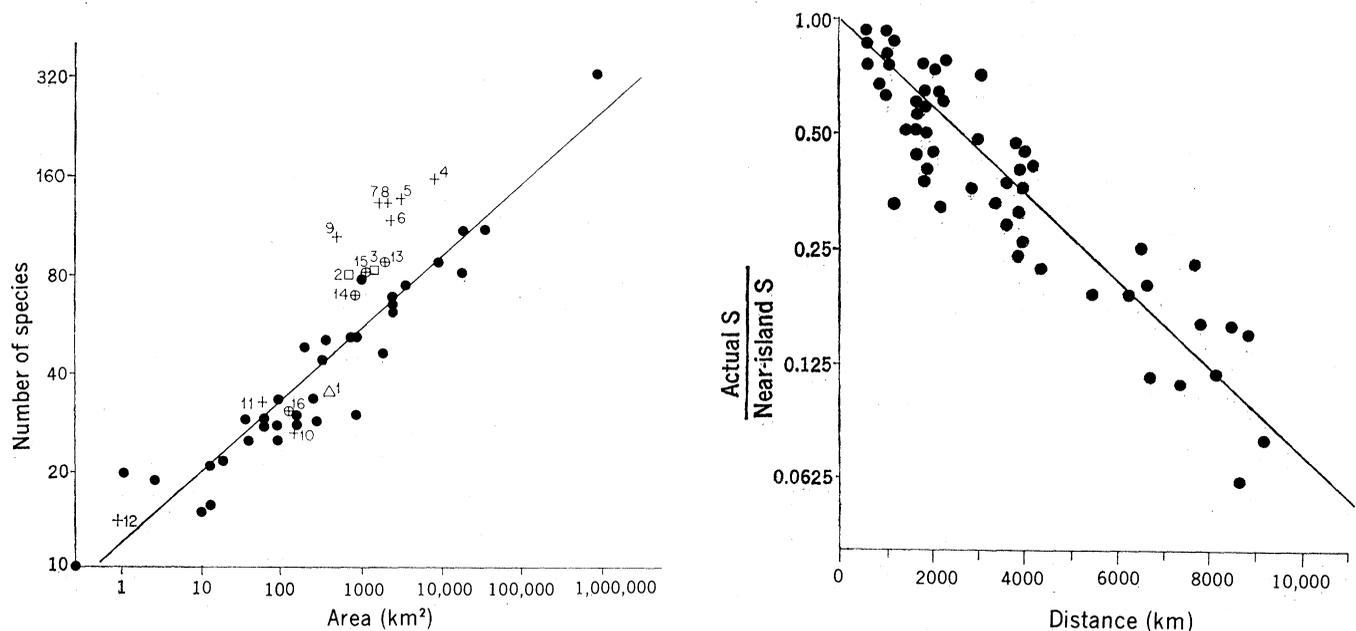


Fig. 1 (left). Number of resident land and freshwater bird species on New Guinea satellite islands, plotted as a function of island area on a double logarithmic scale. Symbols: ●, islands on which species diversity is presumed to be at equilibrium (the remaining, numbered islands are in various stages of "relaxation" after displacement of species diversity from an equilibrium value); Δ, exploded volcanic islands (1, Long); □, contracted islands (2, Goodenough; 3, Fergusson); +, land-bridge islands (4, Aru; 5, Waigeu; 6, Japen; 7, Salawati; 8, Misol; 9, Batanta; 10, Pulu Adi; 11, Ron; 12, Schildpad); ⊕, island fragments split off from a larger island by flooding of an isthmus (13, Batjan; 14, Amboina; 15, New Hanover; 16, Tidore). The straight line was fitted by least mean squares through points for all islands except the land-bridge islands. Note that the number of species increases with area; and that deviations for relaxing islands are more marked for large islands than for small islands, because of high extinction rates and short relaxation times on the latter. [After Diamond (13)] Fig. 2 (right). Ordinate (logarithmic scale), number of resident land and freshwater bird species (S) on tropical southwest Pacific islands more than 500 km from New Guinea, divided by number of species expected on an island of equivalent area less than 500 km from New Guinea (calculated from Eq. 1). Abscissa, island distance from New Guinea. The graph shows that species diversity decreases by a factor of 2 per 2600 km. [After Diamond (13)]

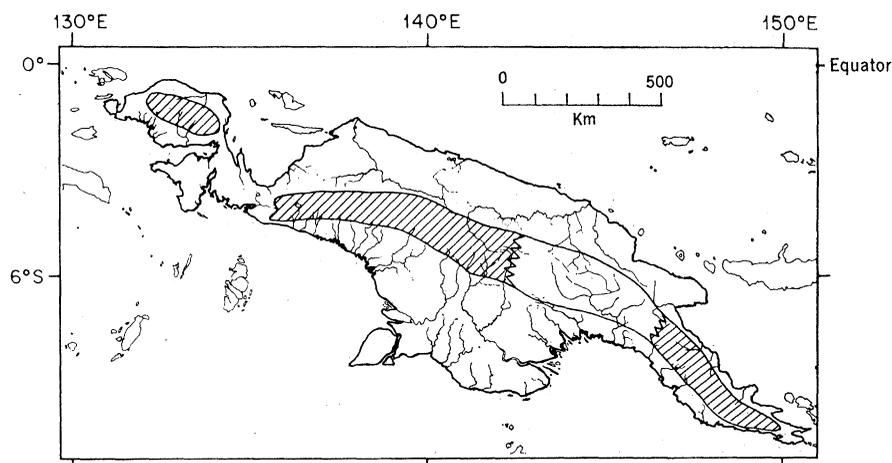


Fig. 3. Distribution of the Papuan tree creeper, *Climacteris leucophaea*, in the mountains of New Guinea. Although mountains and forests with similar tree bark extend uninterrupted for 1600 km, and although there is no other New Guinea bird in the same family, this bark-feeding species has a distribution gap (unshaded area) of 400 km in the middle of its range (hatched area). [After Diamond (15)]

absence of temperate-zone species can generally be predicted from knowledge of their particular habitat requirements, many tropical species are patchily distributed with respect to the available habitat—that is, they may be absent at a considerable fraction of the localities offering a suitable habitat for them. Temperate-zone biologists, because they are rarely confronted with examples of such patterns, often assume that the evidence for patchiness in the tropics can be dismissed as an artifact of inadequate exploration or insufficiently understood habitat requirements. To prove that a species actually is locally absent rather than just overlooked is certainly more difficult than to prove that it is present. Fortunately, the documentation of patchy distributions in New Guinea has been facilitated by many New Guinea natives who possess a detailed knowledge of local birds. Some natives were able to name (in their native languages) and accurately describe in advance all bird species that I eventually located in their areas; they could distinguish at a distance obscure sibling species in such taxonomically difficult genera as *Sericornis*; and could accurately describe other species known to them only from single individuals observed up to 10 years previously (14, 15). When such “walking encyclopedias” of bird lore confirm the permanent local absence of a species that is regularly encountered in other areas, one can have confidence that the species is actually absent and not merely overlooked. It is even more difficult to prove that a locality really does meet all of a bird’s

habitat requirements, since a skeptic can always claim that some unspecified factor has been overlooked. However, many of the examples of patchy distribution that I describe briefly below and in detail elsewhere (15) involve well-studied species which appear to have distinct and readily defined requirements, and which are ubiquitous in habitats meeting these requirements in many geographical areas of New Guinea. Since there do seem to be some generalizations emerging about patchiness, it is becoming increasingly unnecessary to invoke unspecified factors as an explanation.

There are four main types of patchy distribution.

1) *Distributional gaps in a continuous habitat.* The Central Dividing Range of New Guinea provides an uninterrupted expanse of montane forest for 1600 km. Nevertheless, 18 montane bird species that would otherwise be uniformly distributed have a distributional gap of several hundred kilometers somewhere along the Central Range (Fig. 3). For instance, the finch *Lonchura montana* occurs commonly in large flocks throughout the alpine grasslands of western and eastern New Guinea, where it is the only specialized seed-eating bird, yet it is absent in the alpine grassland of central New Guinea, which has similar grass and an otherwise similar avifauna (15). Large distributional gaps in a continuous habitat also occur in the New Guinea lowlands. The interpretation of these remarkable patterns is discussed below.

2) *Very local distributions.* The distributions of many species are patchy to

an extreme degree, such that they occur at a few widely separated localities but are absent in similar habitats over most of New Guinea (15). For instance, the flycatcher *Poecilodryas placens* is known from six scattered areas, where it inhabits rain forests with a well-shaded understory of small saplings in locally flat terrain up to 1000 m above sea level. The species is absent from hundreds of well-explored localities with similar habitat elsewhere in New Guinea. Most of these very local species in New Guinea fall into one of two categories: distinctive “monotypic genera” with no close relatives (that is, genera consisting only of a single isolated species), or members of large genera consisting of many ecologically similar species. The highly fragmented distributions of these species suggest that they are slowly becoming extinct, either because they are the last survivors of unsuccessful evolutionary lines (monotypic genera), or because they cannot compete with several ecologically similar relatives in the same genus.

3) *Complementary checkerboard ranges.* Some local absences of species are correlated with the presence of ecologically similar congeners, indicating that one-to-one competitive exclusion occurs in New Guinea mainland habitats as on oceanic islands. For example, the extensive midmontane grasslands, which are a by-product of human agriculture during the last few centuries, have been colonized in irregular checkerboard fashion by eight *Lonchura* finch species native to other habitats. Each midmontane area supports only one finch species over a considerable local range of grass types and heights, altitudes, and rainfall conditions, but the areas inhabited by a given species are often scattered hundreds of kilometers apart. Evidence indicates that in each instance the first arrival became established over a local area and was able to exclude potential subsequent colonists of the seven other species, but the identity of each locally successful colonist depended partly on chance (15). In the slightly more complex situation illustrated in Fig. 4 (“compound checkerboard exclusion”), each local area can support coexisting populations of any two species out of three potential colonists, and the identity of the locally missing third species varies irregularly.

4) *Distributional islands on a mainland.* Comparison of mountains several kilometers apart within the same range invariably reveals faunal differences

that cannot be explained by differences in habitat (15). For example, species characteristic of lower montane forest at 800 to 1100 m were compared on four peaks of the North Coastal Range. In order of decreasing area and summit elevation, the mountains and their number of lower montane species were: Menawa (1890 m high), 45 lower montane species at 800 to 1100 m; Nibo (1560 m), 36 species; Somoro (1420 m), 34 species; and Turu (1140 m), 26 species. The four mountains had structurally similar forest at 800 to 1100 m, but the smaller mountains had less area of such forest and, correlated with this, fewer bird species characteristic of this forest. Similar findings have been described for Andean birds and North American mammals (19). These patterns are reminiscent of the fundamental species: area relation of island biogeography (see page 760). Evidently, dispersal rates of birds between New Guinea mountains separated from each other by valleys a few kilometers wide are so low that the peaks behave as islands.

Significance of Patchiness

While much remains baffling about patchy distributions in the tropics, such distributions appear to be caused by the synergistic effects of two characteristics of tropical species compared to temperate-zone species. These are the lower dispersal rates of tropical species, which prolong the existence of distributional gaps as temporary or non-equilibrium phenomena; and the greater pressure from interspecific competition, which stabilizes gaps as indefinitely maintained or equilibrium phenomena.

That the mean dispersal distances of many New Guinea bird species are less than several kilometers is indicated (i) by the absences of montane species on mountains separated by several kilometers from populations of the same species on other mountains; (ii) by the numerous species absent on oceanic islands a few kilometers or even only a few meters from the New Guinea mainland (13); and (iii) by the presence of distinct subspecies or even semispecies on mountains separated by valleys several kilometers wide or on islands separated by straits several kilometers wide. Once a species has become locally extinct for whatever reason, immigration from populations in immediately contiguous areas is so slow that distribu-

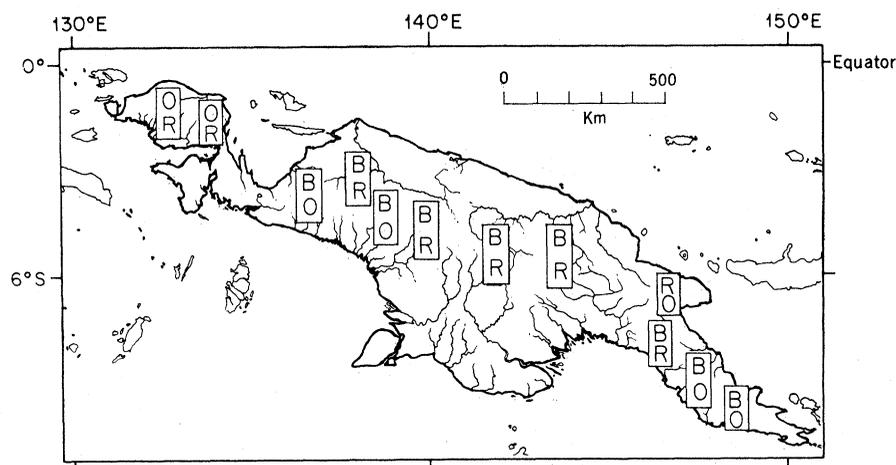


Fig. 4. Compound checkerboard exclusion: distributions of three *Melidectes* honeyeaters. O, *Melidectes ochromelas*; B, *M. belfordi*; R, *M. rufocrissalis* superspecies. Most mountainous areas of New Guinea support two species with mutually exclusive altitudinal ranges. At each locality depicted on the map of New Guinea, the letters above and below indicate the species present at higher and lower altitudes, respectively. The identity of the locally missing third species is subject to irregular geographical variation.

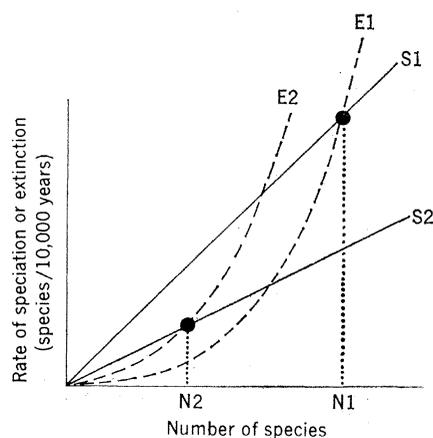
tional gaps in a continuous habitat may persist for long periods of time, albeit as nonequilibrium phenomena. For example, the finch *Lonchura montana* (discussed above) may have disappeared from the alpine grassland of central New Guinea several millennia ago, when the area of this habitat was reduced by encroachment of forest; and this finch may disperse too slowly to have refilled the whole gap since then. In the more seasonal temperate latitudes, by contrast, the annual north-south migrations, and the postbreeding wanderings of many nonmigratory species, flood suitable habitats with potential colonists of most species each year. Mortality due to climatic fluctuations in temperate latitudes places a premium on dispersal ability to recolonize vacated territories, whereas the greater stability of the tropics selects against dispersal.

Effects of interspecific competition on local distribution are easiest to recognize in the one-to-one situation of simple checkerboard exclusion, where species A, for example, occurs only in the absence of species B and vice versa, or in compound checkerboard exclusion, where species A occurs only in the absence of either species B or species C. The competitors in these situations are usually, though not always, close relatives within the same genus. It is more difficult to determine the connections in so-called diffuse competition, where the absence of a species is due to the combined effects of many species, each somewhat distantly related to the absent species and potentially overlapping it ecologically only in part (3, 10). A

decline in species B following an invasion of its close competitor A may permit B's other close competitor C to increase, depressing the population of C's competitor D and ultimately affecting species ecologically far removed from A. Correlated with the greater diversity of species in the tropics than at higher latitudes is the fact that tropical species have more closely packed niches than their temperate counterparts, such that the local survival of a given species may be critically dependent on the mix of competitors as well as on the suitability of the habitat (3, pp. 231 ff). Thus, competition may stabilize some distributional gaps indefinitely.

These considerations help us to understand the differing numbers of species on different continents. Low dispersal may allow localized populations of disappearing species to linger, relatively undisturbed by influx of competitors, for long periods of time before final extinction. Conversely, low dispersal favors high rates of speciation, since the first stage of speciation depends on the effectiveness of geographical barriers or distributional gaps (Fig. 8). Because the number of species at equilibrium on a continent depends on a balance between speciation rates and extinction rates, tropical habitats should be expected to have a greater number of species at equilibrium than habitats at higher latitudes (Fig. 5). Furthermore, with increasing continental area, extinction rates should decrease (because of larger population sizes and more local refuges), and speciation rates should increase (because of more popu-

Fig. 5. Speciation rates (solid curves) and extinction rates (dashed curves) on a single land mass, as a function of the number of species (abscissa). The ordinate is the total number of species produced through speciation or lost through extinction, per 10,000 years. The intersection of the curves ($N1$, $N2$) determines the number of species at equilibrium. The speciation curve is approximately linear, because the probability of speciation of a given species is approximately independent of the presence of other species, but extinction rates increase sharply as more species are packed together. On a large tropical land mass, high speciation rates (curve $S1$) and low extinction rates ($E1$) yield a high number of species at equilibrium ($N1$). On a similar-sized temperate land mass or a smaller tropical land mass, lower speciation rates ($S2$) and higher extinction rates ($E2$) yield fewer species at equilibrium ($N2$).



The best understood segregating mechanism among New Guinea birds depends on altitude and involves an interesting behavioral response.

Altitudinal segregation. On New Guinea mountains not disturbed by man, forest extends uninterrupted from sea level to timberline at around 3800 m. Many bird species, especially those with no closely related species in the area, exhibit gradual changes in abundance with altitude. However, in many other instances one finds sequences of two, three, or even four closely related species replacing each other abruptly with altitude (15). For example, *Crateroscelis murina* and *Crateroscelis robusta*, two abundant and very similar warblers that glean for insects near the ground, differ ecologically mainly in

lations isolated over greater distances). Thus, one should also expect more species at equilibrium in a large center of speciation, such as the Amazon Basin, than in a small center, such as New Guinea (Fig. 5).

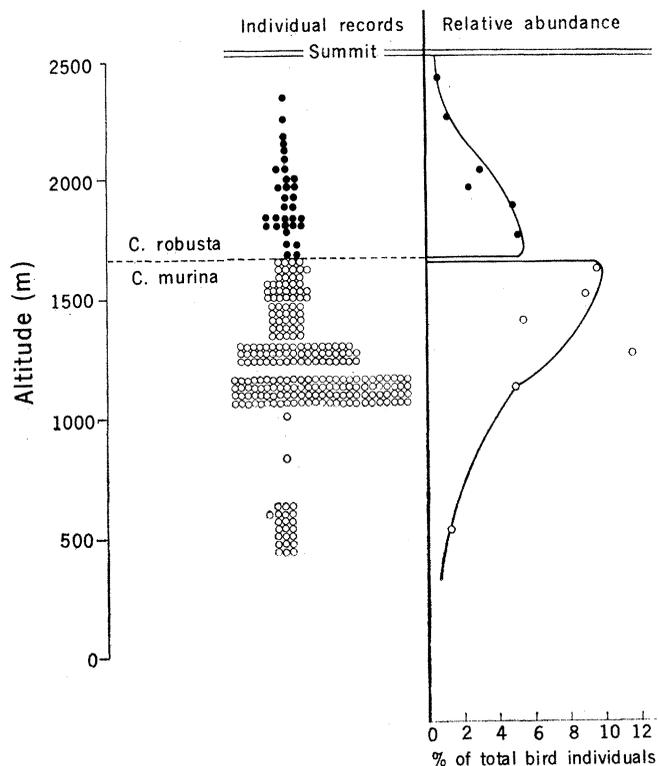
Ecological Segregation of Species

A central problem of ecology concerns community organization: How are resources divided among the species of an ecological community, and what mutual arrangements permit the coexistence of closely related species (20)?

their altitudinal range (Fig. 6). With increasing elevation *C. murina* becomes increasingly abundant until it suddenly disappears at 1643 m, an altitude not far above its altitude of maximum abundance. At this elevation *C. robusta* suddenly appears near its maximum abundance and becomes progressively less common toward Mt. Karimui's summit. Prolonged observations at the transition altitude showed that the two species are interspecifically territorial at 1643 m, and no individual of either species was ever found transgressing the range of the other. There is no change in vegetation at this altitude; the nearest "ecotone" (a border between forest types) lies 338 m higher. In all, the New Guinea avifauna contains about 45 pairs, 13 trios, and 3 quartets of related species which replace each other altitudinally with similar abruptness. For a given species pair the transition altitude shows minor local variation correlated with local conditions of rainfall, exposure, and slope, but no systematic geographical variation over New Guinea. Altitudinal sequences with sharp transitions also occur among birds in the Peruvian Andes (21) and on all large mountainous islands of Indonesia and the southwest Pacific.

Strict transitions may be violated by young birds: when one finds an individual outside the normal altitudinal range of its species, it generally proves to be a juvenile or an immature bird.

Fig. 6. Altitudinal ranges of the warblers *Crateroscelis robusta* (●) and *C. murina* (○) on the west ridge of Mt. Karimui, New Guinea. On the left, each mark represents one individual heard, seen, or collected at the given altitude (the paucity of records at 650 to 1050 m results from my having spent little time at this altitude). The right-hand side gives the relative abundance in the whole avifauna—that is, the percentage of bird individuals of all species estimated as being *C. robusta* or *C. murina*. The two species replace each other abruptly at 1643 m, and each species reaches its maximum abundance near this altitude. Many other species show equally sharp transitions, although the altitude of maximum abundance frequently differs from the altitude at which the species transition occurs.



Among New Guinea birds generally, there is a characteristic altitudinal dependence of population structure. Typically, immature birds are found in a fringe at the bottom of the altitudinal range; somewhat higher, one finds immature birds plus nonbreeding adults, with females usually appearing at lower altitudes than males; next comes the optimal part of the species' range, with breeding adults of both sexes; and, finally, another fringe of immature birds but few adults appears at the upper altitudinal limit of some but not all species. This population structure is manifested to an extreme degree by some birds of paradise, whose displaying adult males may be compressed into the top 180 m of the altitudinal range, with adult females and especially immature birds being found up to 1000 m below the lowest adult male.

Ultimately the altitudinal sequences are related to differential adaptations that are continuous functions of altitude, one species being preferentially adapted to higher altitudes, cooler temperatures, and more montane vegetation than the other species. But the very sharpness of the transitions implies that competition superimposes a special behavior pattern on these differential adaptations, since the transitions do not coincide with sharp changes in temperature or vegetation. That is, each species must be capable of surviving over a wider altitudinal range than it actually inhabits and must be excluding related species from the range in which it is competitively superior to them. To confirm this interpretation, the local population of one member of a sequence would have to be removed in order to ascertain whether the adjacent species would expand their altitudinal ranges. This test of competition arises in New Guinea under two types of naturally occurring conditions.

The first test of niche expansion associated with relief of competition occurs on small or isolated mountains or islands (8, 10, 15). Because of the dependence of species diversity on area and isolation and because of the random element in colonization, one or another member of an altitudinal sequence may be missing on such a "mountain island." As shown in Fig. 7, under these circumstances a low-altitude species may expand into the range of a missing high-altitude relative, a high-altitude species may expand into the range of a missing low-altitude relative, and a high-altitude species and a low-

altitude species may expand simultaneously into the range of a missing middle-altitude relative.

Reconstruction of the process of speciation provides the other test for competition and clearly demonstrates the origin of altitudinal sequences (15). Speciation occurs when an initially continuous population breaks up into geographical isolates, the isolates diverge, reestablish geographical contact and perfect their reproductive isolating mechanisms, and finally invade each other's geographical ranges if there are sufficient ecological differences to permit coexistence (2). While the slowness of evolution rarely permits following a given species through this process with time, the distribution patterns of different New Guinea montane species represent "snapshots" of seven different stages in a continuous speciation process (Fig. 8):

1) A single montane species extends from the western to the eastern end of New Guinea, occupying the same altitudinal range at all longitudes.

2) The local population in one area dies out, so that the east-west distribution becomes discontinuous.

3) The eastern and western populations, now isolated, diverge sufficiently that they would probably not interbreed if contact were established; hence,

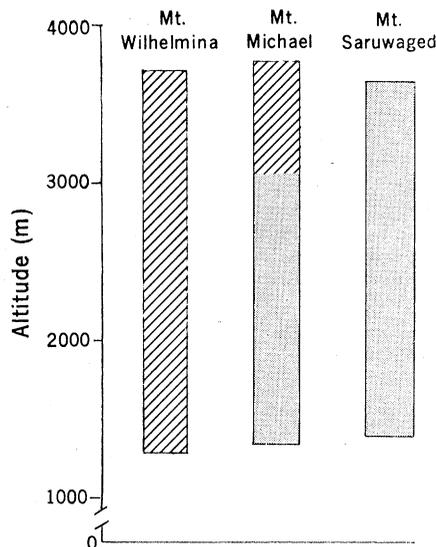


Fig. 7. Altitudinal ranges of the honeyeaters *Ptiloprora perstriata* (diagonally hatched bar) and *P. guisei* (solid bar) on three New Guinea mountains. On Mt. Michael, where both species are present, their altitudinal ranges are mutually exclusive. On Mt. Wilhelmina, where *P. guisei* is absent, and on Mt. Saruwaged, where *P. perstriata* is absent, the remaining species takes over most or all of the altitudinal range of its missing relative.

they are assumed to be distinct species. They may also develop slightly different altitudinal ranges.

4) Both populations reexpand geographically until their geographical ranges abut but do not overlap. There is no or little interbreeding, proving that the populations are in fact distinct species.

5) Each species begins to expand geographically into the range of the other, so that there is geographical overlap ("sympatric" distribution) for a short distance. Within the zone of sympatry the two species segregate altitudinally, each being confined to the altitudinal range in which it is competitively superior to the other. The narrower altitudinal range inside than outside the zone of sympatry is a clear demonstration of niche compression due to competition.

6) Expansion continues, and the western species reaches the eastern end of New Guinea and overruns the entire geographical range of its eastern sibling species. The eastern species has given up the upper (or lower) part of its altitudinal range throughout its whole geographical range, and there is no altitudinal overlap.

7) The eastern species continues to expand until it has reached the western end of New Guinea. The two species are now sympatric over the entire length of New Guinea, with mutually exclusive altitudinal ranges. Evolution may then continue in the direction of either stage 8a, 8b, or 8c.

8a) Stages 1 through 7 may be repeated one or two more times to yield series of three or four closely related species sympatric over the whole of New Guinea but occupying mutually exclusive altitudinal ranges.

8b) Two species that have become sympatric with mutually exclusive altitudinal ranges may diverge in other niche parameters besides altitudinal preference (for example, they may develop different diets or foraging techniques), so that partial altitudinal overlap as well as complete geographical overlap becomes possible.

8c) Each species becomes genetically molded to its compressed altitudinal range to a degree such that the range now reflects innate survival ability rather than competitive compression, a gap between the ranges of the two species develops, and neither species expands altitudinally on removal of the other.

This process seems to be the principal mechanism by which the rich diversity

of bird species in the mountains of New Guinea evolved out of the lowlands (15).

What is the significance of sharp altitudinal transitions? If there were no special behavioral mechanism pro-

ducing such transitions, one would expect two competing, territorial species with different altitudinal adaptations to replace each other in an overlap band which would consist of a mosaic of territories of the two species (22). In

this overlap band the neighbor of a given individual would as likely belong to the other species as to the same species, whereas in the distributions of Fig. 6 each individual is surrounded by individuals of the same species. In fact, altitudinal segregation of congeneric species on mountainous Pacific islands with fewer than 66 species always involves broad overlap bands, and sharp transitions occur only on the more species-rich islands. This contrast suggests two selective pressures underlying sharp transitions. First, in species-poor areas the niche of a given species is nearly as broad as permitted by its intrinsic adaptations and is little compressed by interspecific competition. Under these conditions the success of a dispersing juvenile in colonizing a new territory will depend mainly on visible features of the environment. In species-rich areas, however, the task of identifying a territory that offers a high probability of breeding success for a given species becomes much more difficult, since success now depends critically on the presence and abundance of many other competing species. This in effect would require a dispersing juvenile to perform a faunal survey in addition to merely judging the appearance of the habitat. Second, a selective pressure may arise from the difficulty of finding mates in a species-rich community where many species are rare. Thus, I postulate that, on species-rich islands but not on species-poor islands, dispersing young birds are programmed genetically, or they learn by early experience, to seek out habitats where their species is already established, rather than habitats where they will be surrounded by individuals of other species. The presence of individuals of their own species becomes the only reliable indicator that the habitat is suitable for them. By waiting in the juvenile fringe or "kindergarten" at the lower or upper limit of the altitudinal range, the juveniles are in a ringside position from which they can eventually seize an optimal territory vacated by an adult.

Other spatial segregating mechanisms.

Two further ecological segregating mechanisms, vertical stratification and habitat segregation, resemble altitudinal segregation in that closely related species become sorted out spatially.

Bird species are more stratified vertically in the New Guinea forest than in forests with fewer bird species but similar vegetational structure. Thus, standard bird nets 2 m in height and

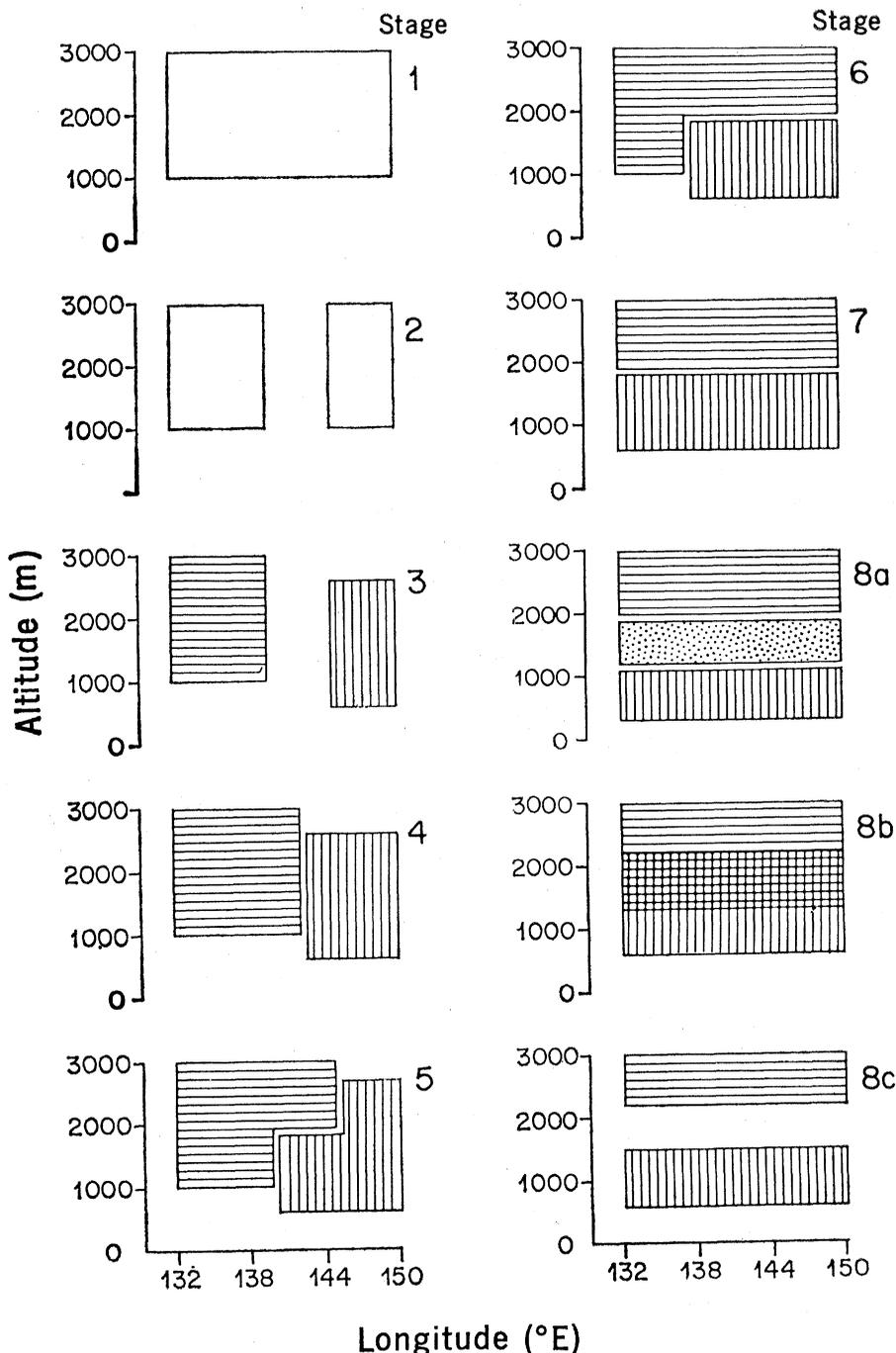


Fig. 8. Stages in the evolutionary transformation of one species into two species with mutually exclusive altitudinal ranges. See text for details. In each diagram altitudinal range is plotted as a function of longitude for some species or pairs of species in the mountains of New Guinea. Thus, in stages 1 through 4 there is neither geographical nor altitudinal overlap, in stages 5 through 8a and 8c there is geographical but not altitudinal overlap, and in stage 8b both geographical and altitudinal overlap. Each such distributional pattern represents a "snapshot" of a different stage in speciation and permits reconstruction of the whole process. Examples of species in each stage are: 1, *Irita kowaldi*; 2, *Climacteris leucophaea*; 3, *Melidectes nouhuysi* and *M. princeps*; 4, *Parotia lawesi* and *P. carolae*; 5, *Pachycephalopsis poliosoma* and *P. hattamensis*; 6, *Amblyornis macgregoriae* and *A. subalaris*; 7, *Ducula rufigaster* and *D. chalconota*; 8a, *Eupetes caerulescens*, *E. castanonotus*, and *E. leucostictus*; 8b, *Neopsittacus muschenbroekii* and *N. pullicauda*; 8c, *Meliphaga analoga* and *M. orientalis*.

resting on the ground catch only about half of the forest species locally present in New Guinea montane rain forest but all species in the species-poor rain forest of New Zealand. Some of the species in New Guinea forage only in the canopy; others forage regularly at 4 to 15 m above the ground but never descend to 2 m and hence are never caught in nets; and others forage only on the ground or up to a height of 2 m. As in the case of altitudinal ranges, vertical foraging ranges expand on species-poor mountains or islands where vertically abutting competitors are absent (10).

Some congeners become sorted by occupying different habitat types, often to the mutual exclusion of each other. For example, whereas there is only one species of barn owl (genus *Tyto*) in most parts of the world, New Guinea has three species: *Tyto capensis* in grassland, *T. alba* in partly wooded areas, and *T. tenebricosa* in forest. Among species sorting by habitat, spatial expansion is a frequent response to the absence of competing congeners on islands (10, 11). Expansion of New Guinea second-growth species into forest on islands is especially common, since New Guinea forest species are frequently absent on islands because of their poor dispersal ability.

Nonspatial Segregating Mechanisms

Spatial overlap of closely related species is possible if they separate on the basis of time, diet, or foraging techniques.

Infrequently, closely related bird species segregate by occupying the same space at different times of day or of the year. The kingfisher *Melidora macrorhina* is nocturnal, whereas other kingfishers are diurnal. The south New Guinea savanna near Merauke is alternately occupied by two marsh hawks, *Circus approximans* in the dry season and *C. spilonotus* in the wet season.

Differences in body size provide the commonest means by which closely related species can take the same type of food in the same space at the same time (15). Larger birds can take larger food items than can smaller birds, but smaller birds can perch on more slender branches than can larger birds. One can frequently see a bird foraging out along a branch up to the point where the branch begins to bend under its weight. In a tree occupied by birds of many species the larger birds are often

concentrated toward the main branches, the smaller birds toward the periphery (Fig. 9). Among congeners sorting by size in New Guinea, the ratio between the weights of the larger bird and the smaller bird is on the average 1.90; it is never less than 1.33 and never more than 2.73. Species with similar habits and with a weight ratio less than 1.33 are too similar to coexist locally (that is, to share territories) and must segregate spatially. For instance, the cuckoo-shrikes *Coracina tenuirostris* and *C. papuensis* segregate by habitat on New Guinea, where their average weights are 73 grams and 74 grams, respectively, but they often occur together in the same tree on New Britain, where their respective weights are 61 g and 101 g. New Guinea has no locally coexisting pairs of species with similar habits and with a weight ratio exceeding 2.73, presumably because a

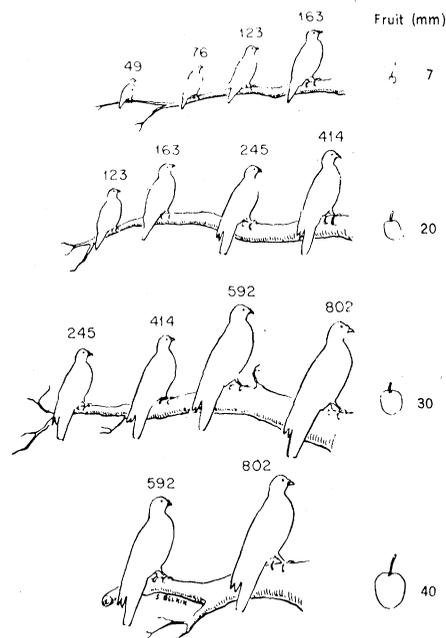


Fig. 9. Schematic representation of niche relations among the eight species of *Ptilinopus* and *Ducula* fruit pigeons in New Guinea lowland rain forest. On the right is a fruit of a certain diameter (in millimeters), and on the left are pigeons of different weights (in grams) arranged along a branch. Each pigeon weighs approximately 1.5 times the next pigeon. Each fruit tree attracts up to four consecutive members of this size sequence. Trees with increasingly large fruits attract increasingly large pigeons. In a given tree the smaller pigeons are preferentially distributed on the smaller, more peripheral branches. The pigeons having the weights indicated are: 49 g, *Ptilinopus nanus*; 76 g, *P. pulchellus*; 123 g, *P. superbus*; 163 g, *P. ornatus*; 245 g, *P. perlatus*; 414 g, *Ducula rufigaster*; 592 g, *D. zoeae*; 802 g, *D. pinon*.

medium-sized bird of relative weight $\sqrt{2.73} = 1.65$ can coexist successfully with both the large species and with the small species. Thus one finds a sequence of three or more species rather than just two species of such different sizes. For example, the eight fruit pigeons of the genera *Ptilinopus* and *Ducula* coexisting in the lowland forests of New Guinea form a graded size sequence over a 16-fold range in weight (Fig. 9).

May and MacArthur (6) predicted on theoretical grounds that species segregating along a single niche dimension in a fluctuating environment must maintain a certain minimum niche difference. This minimum spacing seems in fact to have been reached in nature by those bird species that segregate according to size. Thus, on Pacific islands with 30 to 50 bird species, the ratio between the weights of pairs of birds segregating by size is approximately 4, but this ratio has already been compressed to 2 on islands with 100 species. On New Guinea (513 species) the average value of this ratio is compressed no further, and the extra species are accommodated by expanding the size sequences to smaller or larger birds or else by finer subdivision of space or foraging techniques.

Similarly sized species that take the same food may overlap spatially if they harvest the food in different ways. For instance, small insectivorous birds differ in tactics according to whether insects are caught in midair by sallying, are pounced on and plucked off surfaces, are gleaned off surfaces, pried out of bark, taken from flowers, or are extracted from epiphytes and accumulations of dead leaves. Species with a given type of strategy further differ in the ratio between traveling time and stationary time, in the frequency of movements, and in their average rate of travel (23). Thus, the montane flycatchers *Pachycephala modesta* and *Poecilodryas albonotata* differ in that the former remains perched for an average of 2 seconds, the latter for an average of 30 seconds between moves; and in that the former travels 1 m, and the latter 12 m, per move. *Pachycephala modesta* could be described as a quick and cursory searcher, *Poecilodryas albonotata* as a slow and selective searcher.

Finally, related species may segregate by different diets. For example, the whistler *Pachycephala leucostigma* eats mainly fruit while other whistlers eat mainly insects.

Some General Features of Competition

Despite the abundant distributional evidence for competition between New Guinea bird species, one rarely sees a member of one territorial species fighting a member of another territorial species. Once territories are established, fighting simply does not pay: the winner as well as the loser may be injured, or both combatants may attract the attention of a predator. Even among migrant North American thrushes that must reestablish their territories each spring, interspecific chases and aggressive behavior disappear within a week after arrival on the breeding grounds (24). In tropical rain forest, where many bird species are permanently resident and are relatively long-lived, and where visibility inside the forest is poor, neighboring individuals may confine their aggressive behavior for years to songs and calls and simply learn to avoid each other's foraging space.

Species that colonize species-poor islands, where they are freed of competition from close relatives, often broaden the spatial parameters of the niche by immediately occupying a wider range of habitats, altitudes, or vertical foraging positions. However, the colonists rarely expand their diets or range of foraging techniques until after relatively long periods of time on an evolutionary scale (11). This combination of spatial elasticity with tactical and dietary conservatism reflects partly the degree of genetic programming underlying the stereotyped foraging strategies of birds, and partly the economics of feeding. Given a certain set of inflexible tactics, the economics of energy yield and energy expenditure in foraging dictate the diet but leave to the individual the decision about the space in which the tactics can be applied profitably (3, chap. 3).

How does the combined population density of all bird species on an island compare with the combined population density on a mainland? That is, islands have fewer species than mainlands, but the types of competitive release we have examined mean that the island colonists frequently have broader niches and higher population densities than on the mainland. How well does competitive release compensate on islands for the population densities of missing mainland species? Studies on this problem of density compensation have provided conflicting results. In the New Guinea area, total population densities in similar habitats on different islands

increase linearly or even more rapidly with species diversity, so that an island with few species also has a low density of individuals (11). However, on the Pearl Islands off Panama, total population densities of birds are even higher than on the Panama mainland (25). Part of the difference between these two sets of results may depend on whether the island colonists are as well adapted to the available habitat as are the mainland species they replace. Also, the low population densities on the New Guinea satellite islands, and on old isolated islands such as Madagascar (26) and New Zealand, may reflect genetic deterioration in their isolated populations, because of small gene pools, reduced intraspecific and interspecific competition, and (frequently) short population survival times to extinction (11).

Conclusions

The concepts by which MacArthur and Wilson have transformed the science of ecology in the past decade, and the results of ecological studies such as mine on New Guinea bird communities, have implications for conservation policies. For example, primary tropical rain forest, the most species-rich and ecologically complex habitat on earth, has for millions of years served as the ultimate evolutionary source of the world's dominant plant and animal groups. Throughout the tropics today, the rain forests are being destroyed at a rate such that little will be left in a few decades. When the rain forests have been reduced to isolated tracts separated by open country, the distribution of obligate rain forest species will come to resemble bird distributions on New Guinea land-bridge islands after severing of the land bridges. The smaller the tract, the more rapidly will forest species tend to disappear and be replaced by the widespread second-growth species that least need protection (13). This ominous process is illustrated by Barro Colorado Island, a former hill in Panama that became an island when construction of the Panama Canal flooded surrounding valleys to create Gatun Lake. In the succeeding 60 years several forest bird species have already disappeared from Barro Colorado and been unable to recolonize across the short intervening water gap from the forest on the nearby shore of Gatun Lake.

The consequences of the species-area relation (Fig. 1) should be taken into consideration during the planning of tropical rain forest parks (13). In a geographical area that is relatively homogeneous with regard to the fauna, one large park would be preferable to an equivalent area in the form of several smaller parks. Continuous non-forest strips through the park (for example, wide highway swaths) would convert one rain forest "island" into two half-size islands and should be avoided. If other considerations require that an area be divided into several small parks, connecting them by forest corridors might significantly improve their conservation function at little further cost in land withdrawn from development.

Modern ecological studies may also be relevant to the understanding of human populations. For instance, during a long period of human evolution there appear to have been not one but two coexistent hominid lines in Africa, the *Australopithecus robustus*-*A. boisei* ("Zinjanthropus") line, which became extinct, and the *Australopithecus africanus*-*A. habilis* line, which led to *Homo sapiens* (27). The need to maintain niche differences between these lines must have provided one of the most important selective pressures on the ancestors of modern man in the late Pliocene and early Pleistocene. Thus, any attempt to understand human evolution must confront the problem of what these ecological segregating mechanisms were. To what extent were contemporaneous species of the two lines separated by habitat, by diet, by size difference, or by foraging technique, and were their local spatial distributions broadly overlapping or else sharpened by behavioral interactions as in the case of the *Crateroscelis* warblers of Fig. 6? To take another example, there are striking parallels between the present distributions of human populations and of bird populations on the islands of Vitiaz and Dampier straits between New Guinea and New Britain. Some of these islands were sterilized by cataclysmic volcanic explosions within the last several centuries. The birds that recolonized these islands have been characterized as coastal and small-island specialists of high reproductive potential, high dispersal powers, and low competitive ability, unlike the geographically closer, competitively superior, slowly dispersing, and breeding birds of mainland New Guinea (10, 11, 13). It remains to be seen whether

the people of the Vitiaz-Dampier islands, the Polynesians, and other human populations that colonize insular or unstable habitats also have distinctive population ecologies.

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Humanizing the Earth

René J. Dubos

How gray and drab, unappealing and insignificant, our planet would be without the radiance of life. If it were not covered with living organisms the surface of the earth would resemble that of the moon. Its colorful and diversified appearance is largely the creation of microbes, plants, and animals which endlessly transform its inanimate rocks and gases into an immense variety of organic substances. Man augments still further this diversification by altering the physical characteristics of the land, changing the distribution of living things, and adding human order and fantasy to the ecological determinism of nature.

Many of man's interventions into nature have, of course, been catastrophic. History is replete with ecological disasters caused by agricultural and industrial mismanagement. The countries

which were most flourishing in antiquity are now among the poorest in the world. Some of their most famous cities have been abandoned; lands which were once fertile are now barren deserts.

Disease, warfare, and civil strife have certainly played important roles in the collapse of ancient civilizations; but the primary cause was probably the damage caused to the quality of the soil and to water supplies by poor ecological practices. Similarly today, the environment is being spoiled in many parts of the world by agricultural misuse or overuse, by industrial poisoning, and of course by wars.

The primary purpose of the recent United Nations Conference on the Human Environment, held in Stockholm in June 1972, was to formulate global approaches to the correction and prevention of the environmental defects resulting from man's mismanagement of the earth. I shall not discuss the technical aspects of these problems, but rather shall try to look beyond them and present facts suggesting that man can actually improve on nature. In my opinion, the human use of natural resources and of technology is compatible with

ecological health, and can indeed bring out potentialities of the earth which remain unexpressed in the state of wilderness.

The disastrous ecological consequences of many past and present human activities point to the need for greater knowledge and respect of natural laws. This view is succinctly expressed by Barry Commoner in his fourth law of ecology: "Nature knows best." I shall first discuss the limitations of this law.

When left undisturbed, all environments tend toward an equilibrium state, called the climax or mature state by ecologists. Under equilibrium conditions, the wastes of nature are constantly being recycled in the ecosystem, which becomes thereby more or less self-perpetuating. In a natural forest, for example, acorns fall to the ground and are eaten by squirrels, which in turn may be eaten by foxes or other predators; the dead leaves and branches, the excrements of animals, are utilized by microbes, which return their constituents to the soil in the form of humus and mineral nutrients. More vegetation grows out of the recycled materials, thus assuring the maintenance of the ecosystem.

When applied to such equilibrated systems, the phrase "Nature knows best" is justified, but is in fact little more than a tautology. As used in this phrase, the word *nature* simply denotes a state of affairs spontaneously brought about by evolutionary adaptation resulting from feedbacks which generate a coherent system. There are no problems in undisturbed nature; there are only solutions, precisely because the equilibrium state is an adaptive state.

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