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AN ESTIMATE OF THE POTENTIAL EVOLUTIONARY INCREASE IN SPECIES DENSITY IN THE POLYNESIAN ANT FAUNA¹

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An exceptionally high proportion of the ant species of Polynesia are "tramps," that is, species carried about the world by human commerce. A truly native fauna is present as well on the islands of western Polynesia. In the eastern and northern archipelagoes, however, there may be in fact no truly native species at all, the faunulae here consisting of synthetic aggregations of tramp species. Some of these species originated ultimately in the Indo-Australian area, some in Africa, and some in the New World tropics. Most have been carried accidentally to the Pacific islands on European ships, certainly within the last 400 years and probably no earlier than the time of Cook's first voyage (1768-1771). This tramp fauna, despite its heterogeneity and youth, has achieved an orderliness of sorts. In particular, the number of species on an island is well correlated with the island's area, and some related species have acquired complementary (mosaic) inter- and intra-island distributions that can be explained easily only as the outcome of competitive exclusion. In the course of current studies on the Indo-Australian fauna we have come

to recognize that the Polynesian ants offer an unusual research opportunity; namely the chance to compare the synthetic, poorly coadapted faunulae of the eastern and northern archipelagoes with the older, native, and better coadapted faunulae of the western archipelagoes. A detailed account of the taxonomy and distribution of individual species is being given elsewhere (Wilson and Taylor, 1967). In the present article we will describe certain particular phenomena which might be of general interest.

RELATIONSHIPS OF THE POLYNESIAN FAUNA

Our survey has included all of the islands from the Ellice group, Rotuma, Samoa, and Tonga, eastward to and including the Marquesas and Easter Island, and north to Hawaii. New Zealand was excluded from the current analysis, since it is faunistically very distinct, most or all of its few native species having been drawn directly from Australia (Brown, 1958). The Wallis Islands and Futuna have been intensively collected only recently by Mr. George Hunt, and their ant faunulae will be the subject of a later separate report by Hunt and Wilson.

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TABLE 1. *A classification of the Polynesian ant species according to origin.*

1. Endemic to one or more Polynesian archipelagoes:

Ectomomyrmex insulanus, *Ponera loi*, *P. woodwardi*, *Strumigenys mailei*, *Pheidole aana*, *P. atua*, *Vollenhovia pacifica*, *V. samoensis*, *Rogeria exsulans*, *Adelomyrmex samoanus*, *Camponotus navigator*, *C. rotumanus*, *C. flavolimbatus*, *C. conicus*, *C. nigrifrons*, *Polyrhachis rotumana*.

2. Continuously distributed from Indo-Australian area into Polynesia:

Prionopelta kraepilini, *Platythyrea parallela*, *Ponera incerta*, *P. tenuis*, *Hypoponera confinis*, *H. punctatissima*, *Cryptopone testacea*, *Odontomachus simillimus*, *Anochetus graeffei*, *Eurhopalothrix procera*, *Smithistruma dubia*, *Strumigenys szalayi*, *Pheidole fervens*, *P. oceanica*, *P. umbonata*, *P. sexspinosa*, *Solenopsis papuana*, *Oligomyrmex atomus*, *Monomorium talpa*, *Tetramorium pacificum*, *T. tonganum*, *Rogeria sublevinodis*, *Iridomyrmex anceps*, *Tapinoma minutum*, *Technomyrmex albipes*, *Paratrechina minutula*, *Camponotus chloroticus*.

3. "Tramp species": certainly distributed by recent human commerce:

Hypoponera opaciceps, *H. zwaluwenburgi*, *Trachymesopus stigma*, *Leptogenys maxillosa*, *Syscia typhla*, *Trichoscapa membranifera*, *Strumigenys godeffroyi*, *S. lewisi*, *S. rogeri*, *Quadrstruma emmae*, *Pheidole megacephala*, *Solenopsis geminata*, *Monomorium destructor*, *M. latimode*, *M. floricola*, *M. fos-sulatum*, *M. minutum*, *M. pharaonis*, *Triglyphothrix striatidens*, *Tetramorium caespitum*, *T. guineense*, *T. simillimum*, *Cardiocondyla emeryi*, *C. nuda*, *C. wroughtoni*, *Iridomyrmex humilis*, *Tapinoma melanocephalum*, *Anoplolepis longipes*, *Plagiolepis alluaudi*, *P. exigua*, *Paratrechina bourbonica*, *P. vaga*, *P. longicornis*, *Brachymyrmex obscurior*, *Camponotus variegatus*.

4. "Tramp species" intercepted in quarantine at Honolulu but not yet established in Polynesia:

Brachyponera solitaria, *Tetramorium caespitum*, *Wasmannia auropunctata*.

5. Uncertain status:

Amblyopone zwaluwenburgi, *Ponera swezeyi*, *Smithistruma mumfordi*, *Oligomyrmex tahitiensis*, *Chelaner antarcticum*.

of Hygiene and Tropical Medicine Expedition were studied by Santschi (1928). In the period 1938–1962, five other entomologists, O. H. Swezey, E. C. Zimmerman, T. E. Woodward, G. Ettershank, and R. W. Taylor, made additional collections. A five-week tour by Taylor and his wife in 1962 was devoted wholly to collection and study of the Samoan ants.

Classification of the 83 known Polynesian species according to biogeographic origin is given in Table 1, and the composition of the faunulae of the better known islands is given in Figures 1 and 2. Two conclusions of immediate relevance can be drawn on the basis of these partitions, and on some additional considerations of particular species presented elsewhere by Wilson and Taylor (1967).

First, it is apparent that, prior to the coming of man, few if any native species ranged east of Rotuma, Samoa, and Tonga. The evidence is as follows:

No certain endemics are known to occur in Polynesia beyond these islands. Five species which prior to 1950 were considered to be peculiar to the peripheral areas of the Pacific [namely *Ponera swezeyi* (Wheeler), *Syscia typhla* Roger (= *Cerapachys silvestrii* Wheeler), *Quadrstruma emmae* (Emery) (= *Epitritus wheeleri* Donisthorpe), *Chelaner antarcticum* (White) (= *Monomorium rapaense* Wheeler), and *Plagiolepis alluaudi* Forel (= *P. mactavishi* Wheeler = *P. augusti* Emery)] are now known to occur elsewhere. Three others, *Amblyopone zwaluwenburgi* (Williams) of Hawaii, *Smithistruma mumfordi* (Wheeler) of the Marquesas Islands, and *Oligomyrmex tahitiensis* Wheeler of Tahiti, are still unknown elsewhere but belong to poorly collected and taxonomically little-known genera. Moreover, *O. tahitiensis* is known solely from the sexual castes and cannot even be compared with most of the other Indo-Australian members of the genus, which are known only from the worker caste. Thus, the status of these three remaining "endemics" is very dubious. Also, despite a plethora of subspecific and varietal names applied in the literature to populations of species now living in the central and eastern Pacific, we have detected only a single example of true geographic variation in these populations. The case is furthermore a rather trivial one involving color and the thickness of propodeal spines in samples of *Pheidole sexspinosa* Mayr from the Marquesas and Society islands.

About 20 Indo-Australian ant species range to some point east or north of Rotuma, Samoa, and

The Polynesian ant fauna is now relatively well known. Samoa, the archipelago of principal interest to us, has been especially well surveyed. Large collections made in the 1920's by the London School

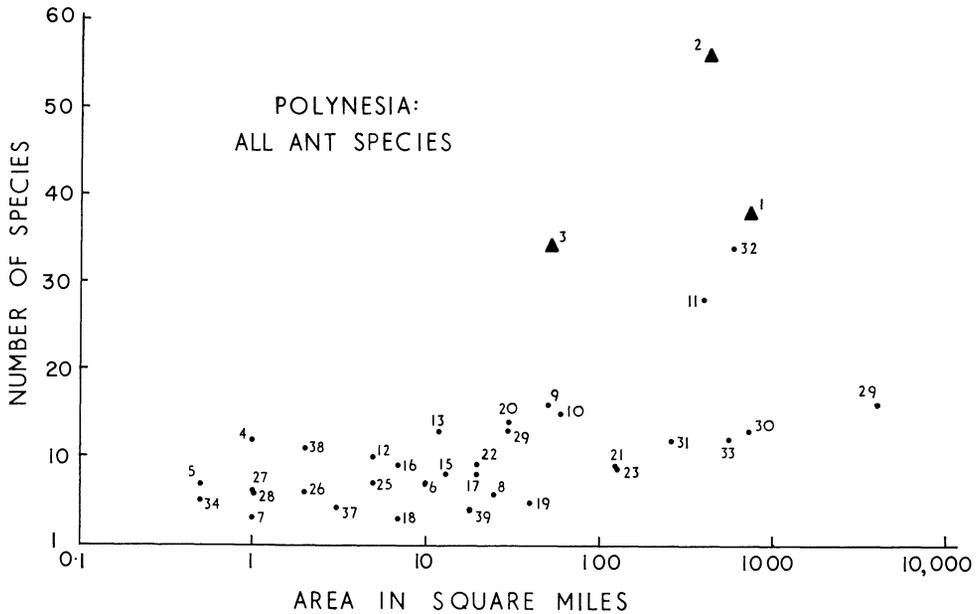


FIG. 1. Total number of ant species plotted against island area for each of the better collected Polynesia islands. Note the high values for the three large Samoan islands (1–3), this is due to the presence of a substantial native fauna in addition to the tramp species. SAMOA: (1) Savai'i, (2) Upolu, (3) Tutuila. TOKELAU: (4) Fakaofu. DANGER ISLANDS: (5) Motu Kotawa. SOCIETY ISLANDS: (6) Bora Bora, (7) Mehetia, (8) Huahine, (9) Moorea, (10) Raiatea, (11) Tahiti. AUSTRAL ISLANDS: (12) Rimatara, (13) Raivavae, (14) Maria Island, Northeast islet, (15) Rapa. GAMBIER ISLANDS: (16) Mangareva. MARQUESAS: (17) Eiao, (18) Hatutu, (19) Ua Pu, (20) Ua Huka, (21) Hiva Oa, (22) Tahuata, (23) Nuku Hiva, (24) Fatu Hiva, (25) Mohotane. PITCAIRN: (26). HENDERSON: (27). FLINT: (28). HAWAII: (29) Hawaii, (30) Maui, (31) Molokai, (32) Oahu, (33) Kauai, (34) Nihoa, (35) French Frigate Shoals, (36) Laysan, (37) Wake, (38) Midway, (39) Kure (Ocean).

Tonga, but these might easily have been transported there by man. For example, *Iridomyrmex anceps* (Roger), one of the most widespread of the Indo-Australian dolichoderines, was unknown until recent years from east of the Solomon Islands. In 1955 it was collected on Aitutaki in the Cook Islands, and in 1956 at Nandi, the international airport community of Viti Levu, Fiji. Intensive collecting has not yet revealed it in the intermediately situated Samoan islands, and the case for its transport to Aitutaki by human commerce is therefore strong. Several others of the Indo-Australian elements in the central and eastern Pacific are certainly known to be tramp species, having become established in the New World as well. Three others—*Odontomachus simillimus* Fr. Smith, *Tetramorium pacificum* Mayr, and *Pheidole fervens* Fr. Smith—have been intercepted at quarantine stations in Hawaii, and the last two have been taken in quarantine in New Zealand.

Second, the native species of western Polynesia are drawn almost exclusively

from the Indo-Australian area. Almost all of the endemics have close relatives in Australia or Melanesia, mostly the latter. The single exception is the Samoan *Rogeria exsulans* Wilson and Taylor, which apparently belongs to a group otherwise known only from the Neotropical Region.

STABILIZATION OF THE NEWLY ASSEMBLED FAUNULAE

The central and eastern archipelagoes have thus been populated, in large part or even entirely, by species carried there by human commerce. Some of the Indo-Australian species might have been stowaways on the canoes of the early Polynesian voyagers. But others, originating ultimately in native populations in Africa and the New World, must have come with European ships no earlier than 400 years ago. The

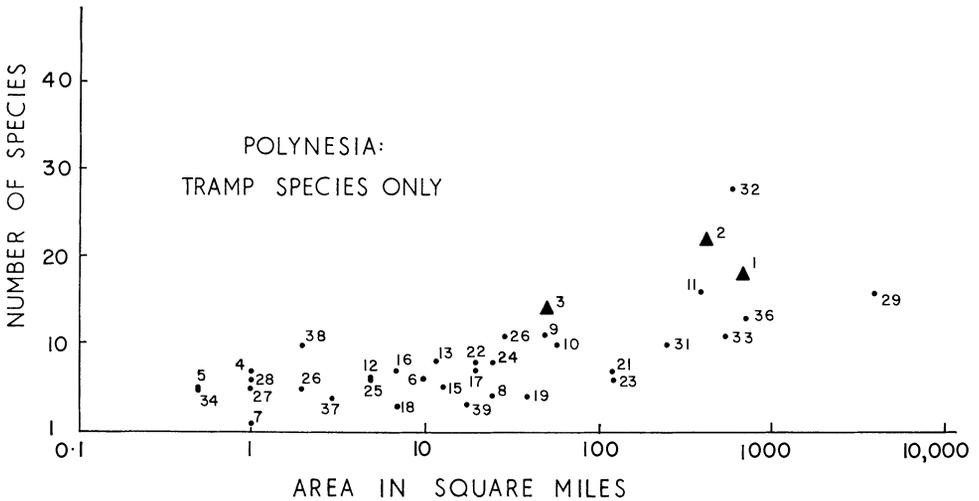


FIG. 2. Number of tramp species plotted against island area for each of the better collected Polynesian islands. The number code is the same as in Figure 1. With the native species removed, the Samoan islands are more consistent with the remainder of Polynesia.

question arises then: Are the islands continuing to fill up as quickly as new species reach them, or are the species densities stabilizing through competitive interactions? Several lines of evidence suggest that some degree of stabilization has occurred:

1) Although the 38 tramp species have been widely and—judging from Hawaiian and New Zealand quarantine records—repeatedly carried through the Pacific, only a fraction inhabit any given island at one time. Twenty-eight occur on Oahu, an island which is both relatively large and which has the most active foreign trade of all the Pacific islands and, with it, probably the highest immigration rate of tramp ant species. Most islands have fewer than nine species, or one-fourth the number in the available pool. As seen in Figure 2, there is a good correlation between the area of each island and the number of tramp species on it. The slope of the log-log plot of the same data is approximately 0.22. This compares favorably with the value of 0.14 obtained for native ant species of the Solomon Islands from the data of Figure 4. It is intermediate between the low (and probably underestimated) value of the Solomon Islands and the values of 0.4–0.5 obtained

for land and freshwater birds in the same part of the world (MacArthur and Wilson, 1963). Thus, numbers of species seem to have been limited, and this seems to have occurred in an orderly fashion.

2) One of the more convincing forms of evidence of competitive displacement is a detailed mosaic complementarity of distribution between ecologically similar species. This phenomenon occurs in several sets of the Polynesian tramp species. The clearest example involves the large, aggressive species of *Pheidole*. *P. fervens* Fr. Smith, a widespread Indo-Australian element, is unknown from Samoa at the present time, but it is a dominant ant in the Society Islands. *P. megacephala* (Fabricius), a pantropical species of African origin, well known for its competitive interactions with other ant species, is dominant on Upolu in Samoa, but it is rare or absent in the Society Islands. *P. oceanica*, another Indo-Australian element, replaces *megacephala* on Savai'i, Samoa, and occurs on Upolu only on the western side facing Savai'i; it is relatively uncommon in the Society Islands. Elsewhere in Polynesia the complementarity among the three species is maintained. *Fervens* occurs in Tonga and Pitcairn; it is

only occasional in the Marquesas and is quite unknown in Hawaii. *Megacephala* is unknown from Tonga and Pitcairn, but it is dominant on the Marquesas and in Hawaii.

Similar complementary patterns also occur between *Cardiocondyla emeryi* Forel and *C. nuda* (Mayr) and, less clearly, between *Paratrechina bourbonica* (Forel) and *P. vaga* (Forel). In Hawaii *Solenopsis geminata* (Fabricius) is displaced to drier habitats by *Pheidole megacephala*. On small islands in the Dry Tortugas, Florida, and around Puerto Rico, these two species replace one another almost entirely, so that both are seldom found on the same island. Our data are not yet sufficient to determine whether this is also true in Polynesia, though it is strongly implied by records from smaller islands outside the Hawaiian group. Finally, *Iridomyrmex humilis* (Mayr) is proceeding to eliminate all but a few ant species within its restricted area of distribution in Hawaii, a habit it has exhibited in other parts of the world where it has been introduced.

Not all ant genera have developed complementary distributions or shown other obvious signs of competitive interaction. The four species of *Tetramorium*, for example, are often sympatric, as are the five species of *Ponera* found in Samoa.

3) Some of the tramp species have quite unstable populations, a fact which has been nicely demonstrated by E. S. Brown (1958) in his studies of the coconut grove species of the Solomon Islands. There is some evidence that fluctuations, perhaps great enough in magnitude to produce occasional extinction, have also occurred in Polynesia. In the earlier years of this century, *Tapiinoma melanocephalum* (Fabricius) was common enough to be a house pest in Honolulu but apparently had disappeared, at least temporarily, by 1949 (Clagg, 1957). *Trachymesopus stigma* (Fabricius) was apparently common in Samoa up to and including 1940, but has not been encountered by collectors since 1956. *Pheidole fervens* was collected in Samoa in 1926 and 1940, but has not been found since 1956; while

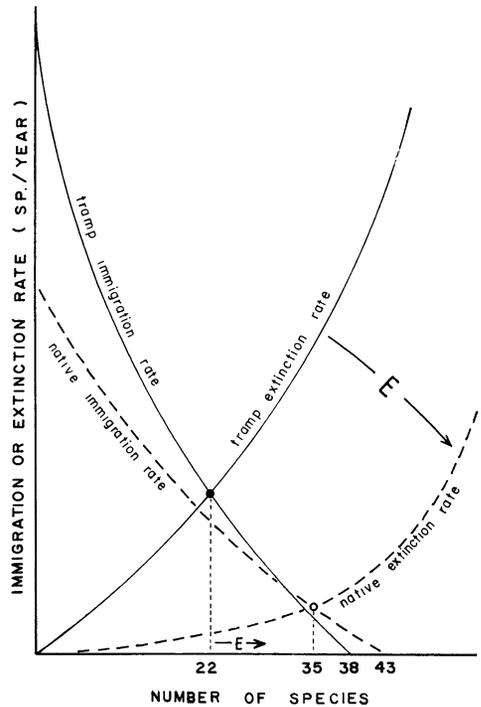


FIG. 3. An equilibrium model (based on MacArthur and Wilson, 1963) of the ant fauna of Upolu, Samoa. An attempt is made to estimate the probable increase in the number of species of tramp origin from the present "quasi-equilibrium" (at 22 species) that would result if the extinction rate were lowered, by means of evolution ($E \rightarrow$), toward the native level. The number of known native species on Upolu is 35, and this number is taken as the minimum to which the tramp quasi-equilibrium could move if given enough time.

its apparent nemesis *P. megacephala* has increased in abundance on Upolu since the 1920's.

To summarize, the numbers of tramp species on individual Polynesian islands have remained well below 38, the number available from the total species pool. The stabilization has evidently been effected in part by competitive replacement within at least two or three groups of related species. Conspicuous population fluctuations have occurred in some species in this century, probably resulting in a few extinctions; the role of competition in the fluctuations is suspected but not proven. Detailed histories of most individual species in Poly-

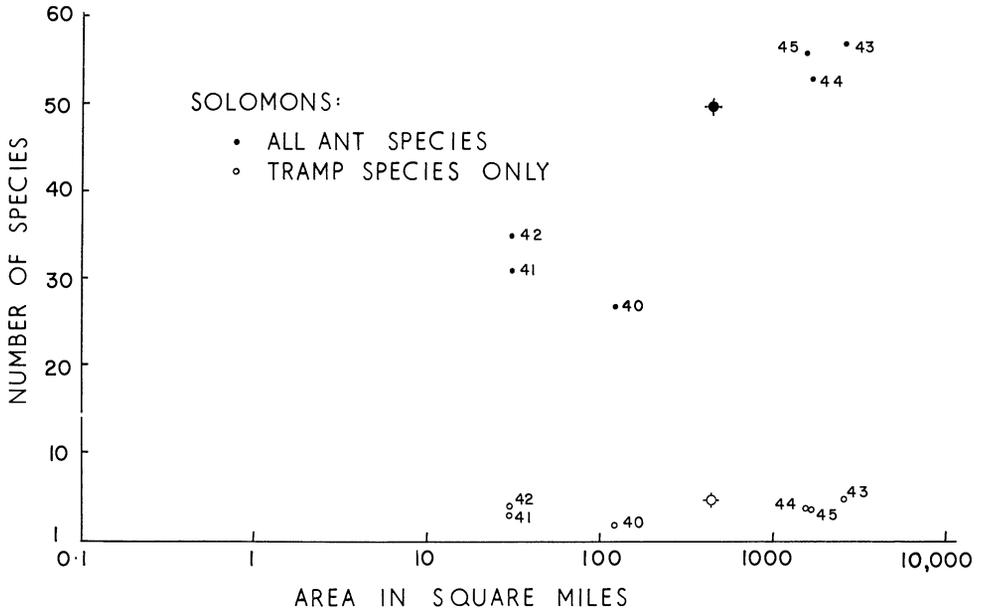


FIG. 4. Numbers of ant species plotted against island area for the better known of the Solomon Islands; based on the data of Mann (1919). The large closed circle represents the estimated total number of species that would occur on an island with the same area as Upolu (430 square miles). The large open circle represents the estimated number of these species of tramp origin on the same island. (40) Florida, (41) Malapaina, (42) Ugi, (43) Malaita, (44) San Cristoval, (45) Santa Ysabel.

nesia are not yet available. The account by Wilson and Taylor (1967) is intended as a first chapter of a record to be carried on in the future.

THE POTENTIAL INCREASE OF SPECIES DENSITY THROUGH EVOLUTION

The data just presented can be applied to the following abstract problem. Suppose a new faunula were assembled on an island from a pool of species chosen at random from various parts of the world and hence relatively ill-adapted to each other. Immigrants are placed on the island continuously from the beginning of the episode. As the number of species is increased, the rate of extinction will increase until in time it comes to equal the rate of immigration (in species per year). At that point of course the number of species will cease to change. Let us assume that the number on the island reaches the equilibrium at some value less than the number in the species pool.

Now suppose the faunula is allowed to remain at equilibrium long enough for evolution to occur. In evolutionary time the species become better adapted to the local island environment and to each other. As this happens, population stability should increase, since those species unable to achieve it will be preferentially eliminated. As a consequence the species extinction rates will decrease and, providing that immigration rates are not altered, species density will increase.

Hence, in evolutionary time, our imaginary newly assembled fauna is not in a true equilibrium but rather in a *quasi-equilibrium*. Over a period of a few generations, such as might be observed in a human lifetime, the rate of species extinctions would appear to equal the rate of species immigrations. But followed through a much longer period of time, it could be seen to have been almost imperceptibly less. The species density at quasi-equilibrium was gradually increasing in this time by means of evolution.

Presumably the quasi-equilibrium number would go on increasing indefinitely (but at an ever decreasing rate) if the pool of immigrant species were large enough and the environment remained otherwise stable. Indeed, since the pool is finite, the ultimate determinant must be environmental stability. As we expand our time scale from that of evolutionary time, during which evolution is effective, to that of geological time, in which geographic and climatic changes are also effective, environmental stability must become decisive. To digress momentarily, it follows that since tropical regions are more stable than temperate ones, higher quasi-equilibria can be obtained in them. This factor alone might account for most or all of the difference in species diversity between the tropical and temperate zones.

Returning to the concrete case, it would be of general interest to obtain some estimate of the amount of increase in species numbers that can occur through evolution. The Polynesian ant fauna appears to provide at least an entrée into the problem. In Figure 3 is presented the quasi-equilibrium on Upolu, Samoa, as it might be viewed by means of the equilibrium model of MacArthur and Wilson (1963). The following facts and postulates are introduced into the model:

1) There are 38 species of tramp origin known from Polynesia (Table 1, Classes 3-4). These constitute the pool of available immigrants. If all the 38 species were established on Upolu, the immigration rate would of course be zero because no further species would be available as colonists. We have therefore drawn the *tramp immigration rate curve* to intersect the species axis at 38 species.

2) Actually, only 22 tramp species are known to occur on Upolu. For reasons already given we are postulating that this is a short-term "equilibrium" value, or nearly so. In Figure 3 the *immigration rate curve* and *extinction rate curve for tramp species* on Upolu are therefore drawn to intersect the species axis at 22 species.

3) Forty-three native species are known for all of Polynesia. They represent the pool of Melanesia-based species that have successfully crossed the water gaps to Rotuma, Samoa, or Tonga by presumably natural means. Since Upolu is centrally located and close to eastern Melanesia, all of the 43 species that occur in Polynesia are actual or presumably potential colonists on Upolu. The *native immigration rate curve* for the island is therefore drawn to intersect the species axis at 43 species.

4) Actually, only 35 of the 43 native species occur on Upolu. This is taken as the minimum short-term "equilibrium" number for native species and in Figure 3 the *immigration rate curve* and *extinction rate curve for native species* are drawn to intersect the species axis at 35 species.

5) Since most of the tramp species of the world have spread through Polynesia in less than 400 years, the tramp immigration rates can be taken as higher than the native immigration rates, and the curves have been drawn accordingly. The precise differences are unknown but are not necessary for the solution of the problem we have posed.

6) From evidence already given, the extinction rates of tramp species appear to be high. They are almost certainly higher on the average than those of the native species, in which survival has often been prolonged enough to allow geographic differentiation and even full speciation. The two extinction rate curves are drawn accordingly. Again the precise differences are not needed for the solution to the problem.

A fortunate circumstance that permits the model to be applied in this case is that the number of species in the tramp pool, 38, and the number in the native pool, 43, are nearly the same. The immigration curves of the two groups thus descend to nearly the same point on the abscissa. Also, by definition, the two extinction curves ascend from the same point, the origin. By taking advantage of the circumstance it should be possible to make predictions concerning changes that would occur in the equilibrium numbers if the slopes of the

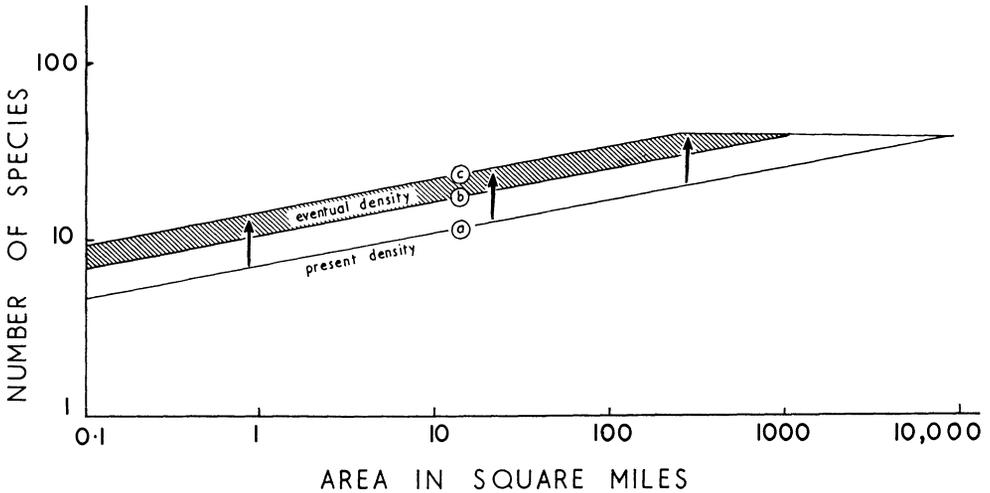


FIG. 5. The Upolu estimate extended to islands of differing area, at least for the Samoa region. It is assumed that the species pool remains at 38 and that the slope of the species-area curve does not change in evolution. (a) The present curve based on the relatively high values for Upolu and Fakaofu. (b) and (c), increases of $1.5 \times$ and $2 \times$ respectively.

immigration and extinction curves were altered.

The particular alteration of interest is the lowering of the tramp extinction curve from its present high level through evolution (indicated in Figure 3 as vector *E*) toward the lower, native species level. Notice that in a newly assembled fauna, in which imperfectly adapted species were drawn from a much larger but constant pool, immigration rates would tend to remain unchanged, since the recipient island (or continent) is not apt to influence the makeup of the source fauna in any significant way. [In the Indo-Australian ponerine fauna, for example, the ratio of exchange of species in older islands is approximately equal to the ratio of the areas, with the result that a continent or large island will dominate a small island in reciprocal influence (Wilson, 1965).] On the other hand, the extinction rates in the newly assembled fauna can be expected to be sensitive to evolution, since the rates would tend to be lowered by character displacement and other forms of local adaptation.

The question we wish to pose and try to answer is: In the case of an island like Upolu, by how much would the equilibrium

species number be increased through evolutionary lowering of the extinction curves? This is a specific case of the more general problem—by how much will species density increase as evolution occurs in a newly assembled fauna? First, it can be affirmed parenthetically that the equilibrium number, or more precisely quasi-equilibrium number, in the newly assembled tramp fauna must be about 22, the number actually occurring there. This is a number quite consistent with the species-area curve presented by the eastern Polynesian faunulae, which are made up more purely of tramp species (Fig. 2). In addition to these tramp species, there are on Upolu 33 native species and one additional species of uncertain classification. These species have stood up to the onslaught of the tramp species by living in the extensive tracts of native vegetation extant on Upolu. Because the great majority of the same species also occur on Savai'i, a larger and even less disturbed island about 11 miles to the west, we conclude that not many extinctions have occurred among the native species of Upolu due to competition from tramp species. The tramp species are concentrated in the cultivated areas and the native species in

the native forests, with the two groups overlapping widely in their habitat choices. Thirty-three is the minimum quasi-equilibrium number for native Upolu ants, and we take it to be not far from the true figure. We conclude that if the newly assembled fauna of tramp species were allowed to evolve on an island such as Upolu, without competition from natives and with the immigration rate held constant, the number would increase from about 22 to at least 33, or by a minimum factor of about 1.5.

What is the maximum to which the quasi-equilibrium would increase over a very long time? The answer of course must be no greater than 38, the number in the entire tramp species pool, or by a factor of approximately 2, unless species multiplication occurred. There is another, nontrivial line of evidence that suggests this upper limit to hold even in the presence of a much larger pool of immigrant species and higher immigration rates. In the Solomon Islands, the fauna is much closer to the very rich source fauna of New Guinea and contains correspondingly higher numbers of stocks and species. Even so, the expected number of native ant species on an island the size of Upolu (whose area is 430 square miles) is only about 45, as shown in Figure 4.

To summarize, it is to be expected that species density of a fauna in quasi-equilibrium will increase to some extent as local evolution occurs. In the case of a tropical island the size and position of Upolu, as the faunula changes specifically from a newly assembled, poorly integrated condition to one in which it is adapted enough to produce some species endemic to the island, the number of species can be expected to increase by a factor of between 1.5 and 2. If the newly assembled faunula is better adapted, as it would be if it were drawn entirely from species native to a nearby area, the lower limit would probably be less. In any case, it is hard to imagine a situation in which the species number would be more than doubled, unless the initial assemblage were deliberately chosen for incompatibility among the species.

Estimates can be made for increase in density for the whole range in island areas, at least for the Samoa area, if it is recalled that the species-area curves vary little among different faunas. Such an extended set of estimates is given in Figure 5.

SUMMARY

1. Few if any ant species are native to Polynesia east of Rotuma, Samoa, and Tonga. The central and eastern archipelagoes have been populated in large part by 35 "tramp" species carried there from various parts of the tropics by human commerce. Several other tramp species are known to have been carried to the Pacific but are not yet established in the center and east. The tramp species also occur, along with native ones, in western Polynesia and outside the Pacific area.

2. No one island contains all of the tramp species, and most contain less than one-fourth of them. Several lines of evidence suggest that the species densities have stabilized. Competitive replacement has evidently played a role in the stabilization.

3. The species numbers are considered not to be resting at perfect equilibrium but rather to be at most at a "quasi-equilibrium." If the immigration rates of the 38 tramp species (35 established and 3 others available) were held constant, and after all the species had an opportunity to colonize a given island, the number at quasi-equilibrium could still be expected to increase slowly as local adaptation proceeded through evolution.

4. By comparing the newly assembled tramp faunulae with older native faunulae of Indo-Australian origin in Samoa, an estimate of the potential increase in species numbers through evolution was made. On an island with the size and history of Upolu the factor of increase should be between 1.5 and 2.

5. Estimates can then be made for islands of all areas if the slope of the changing species-area curve holds constant (Fig. 5).

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