

EXPERIMENTAL ZOOGEOGRAPHY OF ISLANDS: EFFECTS OF ISLAND SIZE¹

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Abstract. A controlled experiment performed on 8 small mangrove islands constituted an exact test of several biogeographic hypotheses which had rested largely on unsatisfying statistical treatments. The islands were censused for arboreal arthropods; each contained a different subset of a species pool of ≈ 500 . Sections of the islands were then removed and censuses retaken after a waiting period; this procedure was repeated on four islands a second time. The results were consistent with a model which posits the islands as originally in a state of dynamic equilibrium between immigration and extinction, then re-equilibrating quickly when forced into an oversaturated condition. It was specifically demonstrated that: (1) species number increases with island size alone, independent of habitat diversity; (2) the increase with area is faster on separate islands than on increasing subsections of one island; (3) the area effect and the underlying dynamic equilibrium are not due only to an increased sample of transients and vagrants on larger islands, though there are a number of species which are particularly prone to quick extinction and which contribute disproportionately to the observed high turnover rates; and (4) predictions of the effects of decreased area on species composition can be stochastic at best, not deterministic. The equilibrium theory prediction of higher turnover rate on smaller islands could not be conclusively tested because of small sample size. Several species interactions suggested by the distributional data are so subtle that it is apparent that much more intensive work will be required to demonstrate even the existence of interactions, let alone whether they are important. It is clear that much of the dynamic equilibrium and its associated turnover in this system can be ascribed to individual species characteristics and the effects of a rigorous physical environment.

Key words: Area; equilibrium biogeography; Florida; mangrove islands; species interaction; species number; species turnover.

INTRODUCTION

The effects of island size on biotic richness have been exhaustively discussed over the last two decades; in recent reviews of the relevant literature (Simberloff 1972, 1974) I have depicted two independent hypotheses, and supporting evidence for each, which dominate current thought on this phenomenon. First is the notion, associated with the more general and much older consideration of the effects of area on species number, that larger islands tend to have more habitats than smaller ones. Because each habitat contains its own set of species, larger islands have more species.

Restricted habitat preferences are so fundamental a part of any biologist's working view of nature that habitat diversity was widely presumed to account for the entire area effect until the last decade. At that time MacArthur and Wilson (1963, 1967) suggested that island biotas are dynamic equilibrium entities, with species composition at any instant the result of continuing island-wide extinction balanced by immigration from the species pool of the mainland and/or surrounding islands. This hypothesis has attracted such wide attention that further general

discussion might be likened to flogging a dead horse; suffice it to say that some direct experimental evidence supports the concept of a dynamic equilibrium biota and much observation appears consistent with it (Simberloff 1974). On the other hand, Lynch and Johnson (1974) attack this interpretation of some observations, particularly the inference that local extinction is a common event for birds.

With respect to the effects of area, the equilibrium view suggests that larger islands should have more species independent of habitat diversity, simply as a consequence of decreased extinction rates (Fig. 1). If, in addition, larger islands have increased immigration rates, this would also contribute to higher species numbers. MacArthur (1972) gives a probabilistic interpretation of the immigration and extinction rates of Fig. 1, partially responding to the observation (Simberloff 1969) that these rates are not ordinary single-valued functions of species number. So a direct effect of area on species number independent of habitat diversity, but possibly acting simultaneously with it, is posited: all species on an island have finite extinction ("turnover") probabilities. The smaller the island, the smaller are population sizes, therefore, the higher these "species-extinction" rates (Simberloff 1969), which, of course, comprise the island-wide extinction rate of Fig. 1.

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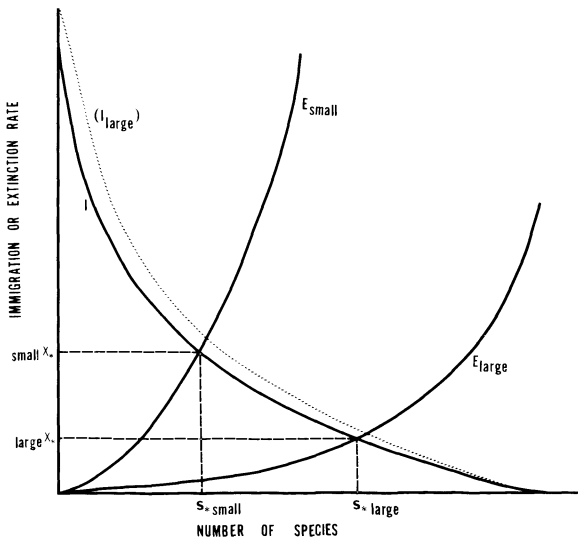


FIG. 1. Relationship of equilibrium species number (S_*) and turnover rate (X_*) to island size. Dotted line depicts possible effect of area on immigration rate; large island may have higher immigration as well as lower extinction rate.

If the increase in species-extinction rates with decreasing population size were not linear, but rather reflected a critical population size below which extinction would be exceedingly likely (MacArthur and Wilson 1967), the independent effect of area on species number would be exaggerated. Direct experimental evidence on this proposition is lacking (Simberloff 1974), but so long as species-extinction rates were monotonic decreasing functions of population size, area would affect species number directly. Depending on the shape and distribution of the species-extinction vs. population size curves, one might even propose species-area curves resembling the allometric ones which are dictated (Johnson and Raven 1973) by the probability statistics of habitat addition with increased area. For this reason, as well as the limited information on local extinction in the general literature, we may question how we could detect the independent effect of area on species number and, even if it must exist, whether it would be nearly as important for most islands as the effect of habitat diversity.

Equilibrium theory also suggests that, of two islands identical except for area, the smaller should have the higher equilibrium turnover rate X_* (Fig. 1); this is what produces the lower equilibrium number of species S_* . If immigration, as well as extinction rates are affected by area, no clear prediction can be made about turnover rates; perhaps one could surmise in the absence of exact data on the shapes of the curves that if extinction is more sensitive than immigration to area, smaller islands would probably still have higher extinction rates.

TABLE 1. Parameters of experimental islands

Island name	Area (m ²)	D1 = distance (m) from nearest island	D2 = distance (m) from nearest large (> 1,000 m ²) island
CR1	343	2	2
G1	519	5	120
IN1	264	110	110
J1	1,263	432	432
MUD1	990	38	82
MUD2	942	5	5
R1	721	336	336
SQ1	1,082	139	139
WH1	380	84	84

Species and area data for island archipelagoes are automatically confounded by habitat diversity differences, many of which may be difficult to measure or even too subtle to recognize. For this reason multiple regression techniques which tend to emphasize the importance of habitat diversity as opposed to population sizes are not too compelling. Furthermore, the high correlation of habitat diversity (however it is measured) and area makes stepwise regression interpretations subjective; we could as well ascribe most of the variability in species number to area as to habitat diversity in many published studies (Simberloff 1974). Because of the high intercorrelation of the independent variables, an experiment is needed that changes one variable, enabling us to distinguish between the effects of area and habitat diversity. This paper reports an experiment designed to separate the intercorrelated variables and to examine whether faunal turnover is significant in sizable communities or whether it is a quaint, mathematically tractable, but usually minor effect observable only in systems smaller than those of interest to most ecologists.

MATERIALS AND METHODS

Nine red mangrove (*Rhizophora mangle*) islands were chosen in Florida Bay near Sugarloaf Key (Figs. 2 and 3). Areas, distances from nearest island and distances from nearest large island (> 1,000 m²), are listed in Table 1. Islands R1 and SQ1 had small satellite islands (diam < 4 m, distance < 5 m) not listed; each satellite consisted of a single *Rhizophora mangle* tree, which in no instance contained animal species not present on the larger island. A general description of mangrove islands is provided by Wilson and Simberloff (1969), who fumigated several of them to ascertain that each island did, in fact, have an equilibrium number of species. The islands of this experiment differ physically from those primarily in their greater area, up to 5 × that of the largest fumigated island. A consequence is the greater frequency of black mangrove (*Avicennia germinans*)

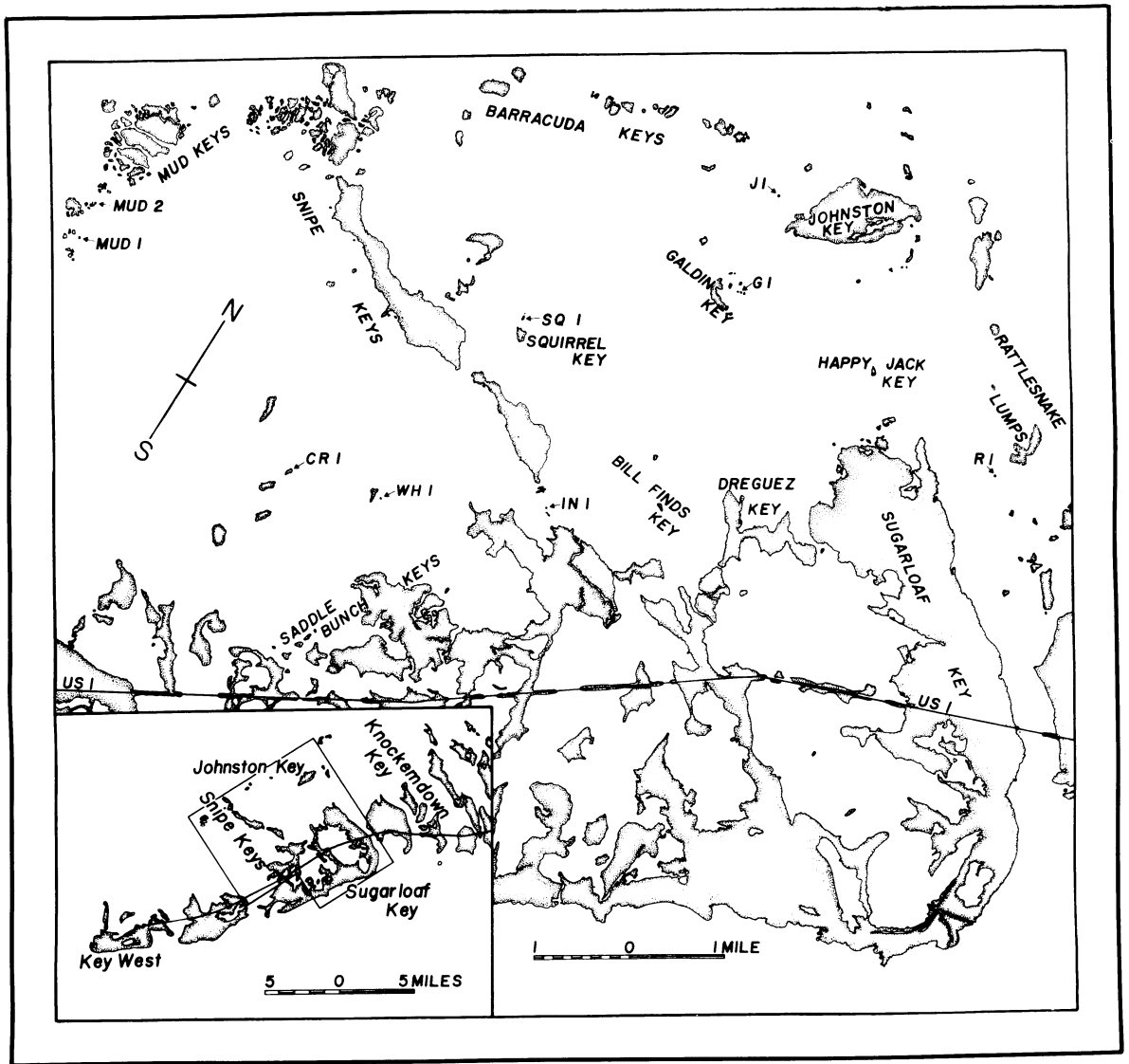


FIG. 2. Experimental and control islands in Florida Bay.

and even white mangrove (*Laguncularia racemosa*) on these larger islands. The nine islands were chosen partly to minimize the presence of these other trees, but small *Avicennia* bushes were present on IN1, SQ1, G1, and MUD1; the latter two islands each had one small *Laguncularia* bush, while R1 had a larger dead *Laguncularia* tree. In no instance was an animal found on these other plants which was not also recorded from *Rhizophora* on the same island. Few animals generally were found on these small plants; neither species supports an entomofauna as large as that of red mangrove.

The nonmarine fauna of small *Rhizophora* islands consists almost entirely of arboreal arthropods (Wilson and Simberloff 1969); the intertidal substrate is covered by seawater twice daily, effectively elimi-

nating a ground fauna. A few insects are found on the intertidal mud when the water recedes, and retreat onto mangrove roots when the tides come in (Table 2). Those which are never found on the island proper and do not appear to feed on the mangrove or to interact with its other inhabitants are excluded from further consideration. The intertidal algae around the roots contain several arthropods (Table 2); again, most of these are never found above the algae and so will be discounted. The tree snail *Littorina angulifera* and tree crab *Aratus pisonii* are ubiquitous but are omitted from subsequent census data. The snail rasps lichens from the bark and its fortunes are probably unrelated to those of other colonists. The crab has been observed to rasp and thereby severely to damage mangrove leaves and

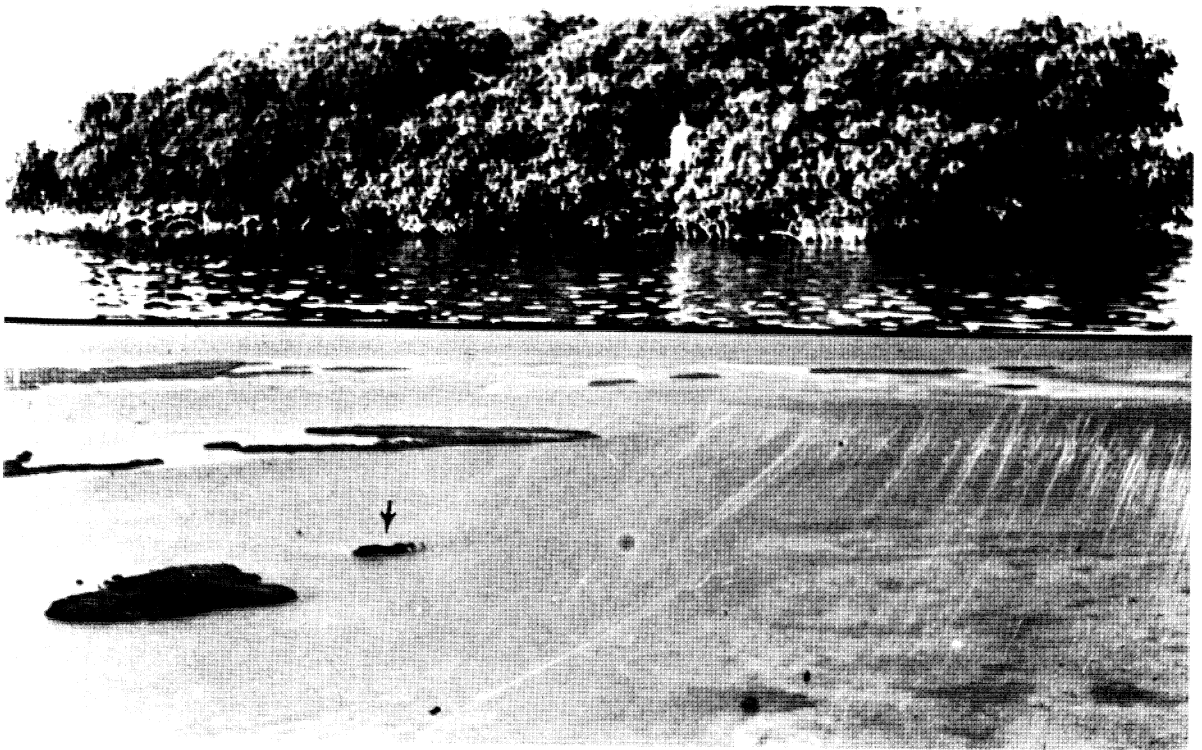


FIG. 3. *Upper*: Control mangrove island IN1. *Lower*: Experimental mangrove island SQ1 (arrow), near Squirrel Key. Tiny fumigated island E1 is in foreground.

also to catch and consume a large cricket (*Tafalisca lurida*); it may be an important faunal component. Even if extinction (disappearance of every individual) should occur for either of these species, recolonization would be qualitatively different from that of other colonists inasmuch as both species have planktonic larvae and the adult crab swims well.

I omitted dipterans because censusing was too inaccurate; larvae or pupae were discovered only 14 times in this experiment, anyway. There are many species of mites on mangrove islands (Simberloff and Wilson 1969, 1970), but the size of these islands precluded certain species counts, so these too were omitted. Finally, I did not count vertebrates, although breeding cormorants (*Phalacrocorax auritus*) were present on R1 and SQ1, breeding green herons (*Butorides virescens*) at one time or another on most islands, nesting white-crowned pigeons (*Columba leucocephala*) on SQ1, breeding water snakes (*Natrix sipedon*) on R1, and a transient cotton rat (*Sigmodon hispidus*) on J1. None of these animals are insectivorous, so it is unlikely that they contribute to population decline of other island colonists. Simberloff and Wilson (1969) showed that birds may carry small arboreal arthropods to mangrove islands in nesting material, while phoresy must occasionally occur. A number of small insectivorous birds fre-

quent small mangrove islands, although only the gray kingbird (*Tyrannus dominicensis*) commonly nests there. Available data do not permit an assessment of how important these birds are in the population dynamics of resident insects, but it is suggestive that more than half the time that investigators were on the islands of this experiment, none of these birds were present. Abandoned birds' nests were found on all islands; their significance will be discussed.

This leaves a large community of arboreal insects, spiders, centipedes, millipedes, isopods, pseudoscorpions, and scorpions as potential colonists of these islands. In this study 254 species were encountered, while 351 species have been collected on small *Rhizophora* islands I have visited. There are probably about 500 species routinely found in large Florida Keys *Rhizophora* swamps, and perhaps 4,000 in all the Keys.

Species were considered present on an island if individuals were observed that were potentially capable of population increase (reproduction); presumably this would be a pair or a fertilized female for sexual species, or just a female for species capable of parthenogenesis. If only males were observed (as occasionally happened for ants, for example) the species was considered absent, while an immature individual was considered evidence of reproduction.

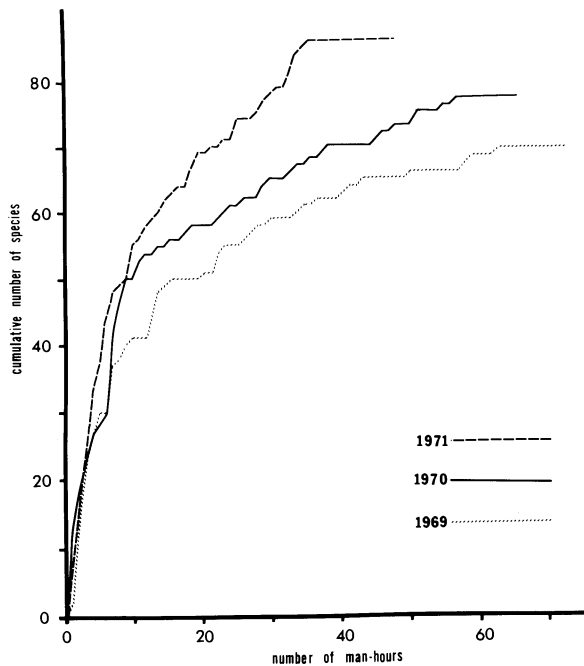


FIG. 4. Cumulative counts of species vs. time spent collecting on island G1 in 3 successive yr. Each year an asymptote was reached.

With this criterion for presence or absence, at least 99% of all individual organisms encountered during this study could be either unambiguously identified in the field or collected and subsequently identified by specialists. In rare instances collection was impossible, and in others an immature form could not be certainly referred to a species (though often it could be placed to family and all but once to order). In such situations the most conservative possible accounting was made: if the doubtful individual could conceivably belong to any species recorded from its island, it was placed in that species.

The basic technique for censusing these islands, described by Wilson and Simberloff (1969), involves exhaustive examination of all microhabitats which comprise the mangrove: dead hollow twigs and branches, dead bark and tree holes, leaves, flowers, fruits, and green shoots. Because these islands are larger than the fumigated ones it was impossible to examine as great a fraction of most of these microhabitats as in the earlier experiment, but the islands are still sufficiently small and simple that it was possible to examine virtually the entire island. In addition, entire abandoned birds' nests, small parts of active nests, bracket fungi, and litter and duff from tree holes and under bark were collected and subjected to light-powered Berlese funnels. Collections were continued until an asymptote was reached in cumulative number of species collected vs. time: 40–82 man-hours of collection not counting Berlese

funnels (which were always operated within the first 20 man-hours). Figure 4 depicts these curves of cumulative numbers of species vs. time spent sampling for island G1 during 3 successive yr. Of course the islands did not all yield identical curves: weather, condition of collectors, and size of island all caused differences, but the shape of the curve, with negative second derivative and a clear asymptote, was universal.

In the summer of 1969 all nine islands were censused. Island IN1 served as a control throughout the experiment. In November 1969 fractions of the other islands were removed. In the summer of 1970 all islands were censused again, after which four of them (CR1, G1, MUD1, and WH1) had further fractions removed. In autumn of 1971 these four islands plus IN1 and MUD2 were censused once again. A crew of workmen, under the author's supervision, using gasoline-powered saws on the canopy and hand-tools on the roots removed fractions of islands (Fig. 5). All removed areas were leveled to below the highest algal growths on the roots, so that they were totally submerged by high tides twice daily. Repeated subsequent examination of the remaining dead algae-encrusted roots (as many as possible were simply pulled out) revealed no colonists. The removed section of each island was loaded onto a barge, towed at least 300 m from the island to deep water, and dumped overboard to sink (green *Rhizophora* and most dead wood do not float). Areas of all islands were determined by planimetry of aerial photographs. Throughout the remainder of the experiment no regrowth of the removed sections was observed, and the few newly established *Rhizophora* seedlings were continually pulled out. However, by 1975 significant growth from new seedlings was observed on islands J1, MUD2, and R1, with lesser establishment on all other experimental islands except for SQ1. It should be emphasized that these islands were chosen from among thousands of similar islands in the Keys, that such islands frequently are devastated naturally by hurricanes and high seas, and that the animals on these islands are all distributed at least throughout the Keys and are not in any sense rare or endangered.

Because the validity of all results and conclusions rests on the censuses, evidence for their completeness is presented first; it consists of seven kinds:

- 1) That the cumulative species vs. sampling effort curves each reached an asymptote suggests that if there is a faunal component which these censuses fail to record, it must be forever hidden and not subject to discovery by greater effort (more time). Furthermore, one may infer that if such species exist, they would be missed on all islands and so at least the error is uniform.

- 2) In no instance did the Berlese extraction re-



FIG. 5. *Upper*: Island R1 as tide comes in when removal of right-hand section is nearly complete. *Lower*: Removal of roots on island R1; process was continued until water covered tops. Note satellite island in background.

veal more than four species which had not been recorded by the normal census procedure; the maximum addition to any census was 5%. Even small, agile, secretive species like collembolans, psocoptera, and thrips are generally discovered *in situ*.

3) As in the fumigation experiment (Wilson and Simberloff 1969), several dusk and night censuses were performed, and in no instance was a species recorded that had not been counted already. Crepuscular and nocturnal species are discovered in their daytime microhabitats in a system as simple physically as this one.

4) When one island (J1) was cut, $\approx 5\%$ of the cut vegetation ($< 2\%$ of the total size of the island) was placed on a stage constructed inside a covered canvas raft. The raft was then sealed and the contents fumigated with chloropicrin (tear gas), which works as a noxious agent for insects, driving out even woodborers (Wilson and Simberloff 1969); in effect, a giant floating Berlese funnel was created. The vegetation and raft floor were then examined for insects; 49 species (68% of the total census) were recorded from this small fraction, but none that had not been collected already. Woodborers can be discovered easily by hand in mangrove, but they must be one of the more difficult groups to census with certainty.

5) On three islands (MUD2-1969, R1-1969, and

WH1-1969), the island fraction which was to be removed was initially uncensused; only after an asymptote was reached for the remainder of the island was examination extended to the whole island. One goal of this censusing procedure was to test whether differential effort in different island sections, which I tried to avoid but which must nonetheless have occurred to some extent, could bias the results. Major differences would have dictated even more intensive collecting. But the censuses of the three islands minus the fractions to be cut revealed 91%, 96%, and 95%, respectively, of the species in the full censuses, while the censused fractions comprised only 35%, 66%, and 69%, respectively, of the island areas. These results imply that precisely equal sampling effort over all parts of an island is unnecessary and that most species, although they may have stringent microhabitat needs, are not particularly localized geographically within an island. These conclusions apply *a fortiori* to the census results from the tiny fumigated fragment of J1.

6) On all islands except for the 1969 versions of CR1, MUD1, MUD2, R1, SQ1, and WH1, records were kept of the number of species found more than once vs. those found but once. The rationale behind these data was that a high percentage of species recorded from one individual would indicate the existence of a correspondingly high percentage of

TABLE 2. Animals of intertidal mud and algae. 1 = Found on mud, 2 = found in algae, × = not counted in censuses

Order	Species
Collembola	<i>Anurida maritima</i> ^{1, 2, ×}
	<i>Axelsonia littoralis</i> ^{1, 2, ×}
	<i>Seira bipunctata</i> ¹
Orthoptera	<i>Hygronemobius alleni</i> ^{1, ×}
Dermaptera	<i>Labidura riparia</i> ¹
Hemiptera	<i>Pentacora sphacelata</i> ^{1, ×}
Coleoptera	<i>Actinopteryx fucicola</i> ^{1, ×}
	<i>Anisomeristes</i> sp. ^{1, ×}
	<i>Bembidion</i> cf. <i>contractum</i> ^{1, ×}
	<i>Micronaspis floridana</i> ²
	<i>Tachys oculator</i> ¹
	Gen. sp. (Staphylinidae) ^{1, ×}
Lepidoptera	Gen. sp. (Unknown) ^{2, ×}
Araneida	<i>Clubiona littoralis</i> ^{2, ×}
	<i>Pirata arenicola</i> ^{2, ×}
	<i>Stenoconops minutus</i> ²
Isopoda	<i>Ligea exotica</i> ^{1, ×}

the true species complement which were unrecorded at all (cf. Preston's [1962] discussion of the "veil line" in lognormal species abundance curves). The range for fraction of species recorded more than once was 0.645–0.836, with a mean of 0.742. Only one major group, the small parasitic wasps, contributed disproportionately to the fraction of records consisting of just one individual, and this is the group for which, by nature of its small size, position in the trophic web, and active habits, the censuses are most likely to be deficient. But even for this group the majority of records are for more than one insect.

7) Finally, on island SQ1-1970 all individuals up to 200 per species were counted and then killed. For the 80% of species represented by more than one individual, usually many more than one were seen ($\bar{x} = 52$). This supports the claim that if a species is present at all, it is likely to be present in number and to have been recorded.

A second question which may be raised is whether the time allotted for re-equilibration (7 mo, then 1 yr) was sufficient. The results of the fumigated island experiment (Simberloff and Wilson 1969, 1970) imply that for smaller mangrove islands with this degree of isolation 4–8 mo is sufficient for re-establishment of the equilibrium number of species, although the composition may still be peculiar (e.g., lacking millipedes, centipedes, and certain ants). In the experiment reported here, island MUD2 served as a control in the matter of whether enough time elapsed for re-equilibration; it was reduced only in 1969. That the number of species fell by 17 in the 7 months following area reduction, then by only 1 in the following year supports the claim that suf-

TABLE 3. Changes in parameters on experimental islands

Island name	Year	Area (m ²)	Total species	Special ^a species
CR1	1969	343	74	0
	1970	104	65	5
	1971	54	62	2
G1	1969	519	86	0
	1970	327	77	0
	1971	169	69	0
IN1	1969	264	63	0
	1970	264	63	0
	1971	264	68	0
J1	1969	1,263	75	4
	1970	779	71	3
MUD1	1969	990	79	0
	1970	565	76	0
	1971	320	71	0
MUD2	1969	942	79	4
	1970	327	62	0
	1971	327	61	0
R1	1969	721	103	0
	1970	478	85	4
SQ1	1969	1,082	88	0
	1970	731	82	5
WH1	1969	380	86	0
	1970	261	73	0
	1971	123	72	1

^a In Berlesates of birds' nests or bracket fungi.

ficient time was allowed. However, it may be noted that MUD2 was the second most severely reduced of the original group, down to a third of its original area, which ought to have exaggerated the difference between the initial species number decline and the subsequent one.

RESULTS

Areas and species numbers of all islands are listed in Table 3; compositions are in the **Appendix**. To begin to assess the effects of area on species number, an attempt was made to regress species number of the original nine islands on the variables listed in Table 1. Because "stepping stone" islands were present for G1 and MUD1 only, variables D1 and D2 were highly correlated ($r = 0.97$) and the stepping stone data could as well have been omitted. In any event, no significant simple or multiple regression was produced with all possible combinations of log-transformed and untransformed variables.

MacArthur and Wilson (1967) suggest that on very small islands high area-independent extinction rates may eliminate an area effect, but mangrove islands clearly do not fit this pattern. The smaller fumigated islands always had fewer species than did these islands (Simberloff and Wilson 1969), and tiny *Rhizophora* islets consisting of a single bush, 1 m or so high, typically have even fewer species. However, a much larger island (Bill Finds Key), which

is a virtual *Rhizophora* monoculture, has yielded 120 species in only 24 man-hours of collection.

One reason why these nine islands do not show a clear area effect upon regression is their narrow span of areas; the largest is $< 5 \times$ the size of the smallest. Darlington (1957) suggested that for island herpetofaunas, a tenfold area increase is usually associated with only a doubling of species number; a similar rule can be extracted from Preston's bird data (1962). Particularly with such a small sample of islands, species number variance not associated with area variance would likely obscure any statistical dependence of species number on area over this narrow range of areas.

It was impossible to increase sample size for these regressions beyond nine islands by including the decreased versions of the eight experimental islands because the successive species sets on these islands were not independent, even though the numbers may have re-equilibrated. If each fauna were viewed as an independent draw from a collection of 254 equiprobable colonists, the number of ways in which two islands with n and m ($\leq n$) species, respectively, could share exactly $(m - i)$ species (with $i \leq 254 - n$) is $\binom{254 - n}{i} \binom{n}{m - i}$. The expected number of shared species under this hypothesis is then

$$\sum_{\substack{i=0 \\ i \leq 254 - n}}^m \binom{254 - n}{i} \binom{n}{m - i} (m - i) / \binom{254}{m} = mn / 254.$$

Because species are not equally likely to colonize (discussed below), the observed number of species held in common between two islands is always much greater than this expected number; because the expected number is heavily dependent on the sizes of the faunas (m and n), the probability of a number as large as or larger than the actual number is a better measure of the nonrandomness of two faunas than is the deviation of actual number from expected number. For all 36 possible pairs of the original nine islands, the mean excess of actual number of shared species over expected was 22.2, and the median probability of a deviation as large as observed was 4×10^{-10} . For all 15 possible pairs of islands where one island was simply the other (modified physically or not) during the next census period, the mean excess of actual number of shared species over expected was 31.8, and none of these deviations was as probable as 10^{-13} . As time passes an island fauna becomes successively more different from (and independent of) the original composition: for the six possible pairs of islands where the first differs from the second by two census periods (19 mo), the mean excess was 27.4 species (always less than the deviation between successive censuses on the same island), and two of the deviations were as probable as 100^{-13} . But over the course of this experiment

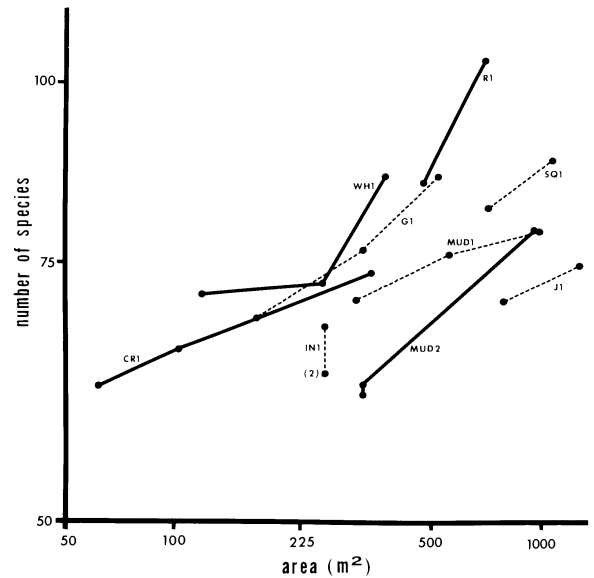


FIG. 6. Individual species number vs. area curves for the experimental islands in a log-log plot.

the composition revealed at each census period was largely determined by the original composition.

The second reason, in addition to the combination of narrow area range and small sample size, that these nine islands do not show a clear area effect upon regression is the reason why regression is not quite suitable for elucidating area effects generally: the presence of other, possibly unrecognized, independent variables affecting species number. On an island-by-island basis (Fig. 6) the importance of area is clear: there were 12 decreases and no increase. Such an extreme result, if the null hypothesis of no area effect were correct, would occur just $(0.5)^{12} = .0002$ of the time. The rise in species number on control island IN1 is probably no more than random variation about an equilibrium, particularly in light of the concurrent decrease in species number of the partial control island MUD2. But the control changes in no way suggest that the observed effect of area is an artifact.

It was not possible to modify just the one parameter of area. For example, perimeter could not be held constant without also changing shape. But, as has been said earlier, no colonists have been observed to prefer a geographic location like the edge (as opposed to a microhabitat like the canopy of leaves). Mangrove islands are remarkably homogeneous; a fraction of one is truly just like an entire one except for area because all *Rhizophora* microhabitats are present in all sections, probably in similar proportions with the possible exception of dead bark. However, the effects of microhabitat diversity may be very subtle; on CR1, J1, MUD2,

R1, SQ1, and WH1 a few species were found only in abandoned birds' nests, while *Berlesates* of bracket fungi on R1 and SQ1 produced species not observed elsewhere during the appropriate census. Numbers of these special colonists are given in Table 3. In no instance is the independent effect of area brought into question.

That these islands are behaving like islands for this biota should be emphasized. The data indicate that most or all of the species do not treat these islands as part of a fine-grained foraging system; invasion of one of these islands from without is much more difficult than dispersal within a large island. If this were not so, the higher equilibrium number of species on larger islands could be viewed simply as a consequence of a higher immigration curve, rather than of a lower extinction curve. Osman (1975) has been able to separate, for small marine rocks, the contributions of decreased extinction and increased immigration, respectively, to an observed area effect and has demonstrated that the latter predominates. In effect, the rocks are acting as different-sized sampling devices collecting settling marine organisms in proportion to their sizes. As stated earlier, for three islands in 1969 (MUD2, R1, and WH1) censusing was first restricted (until an asymptote was reached) to the section which was to be left after the subsequent area-reduction. The censuses of the three islands minus the fractions to be cut yielded 116%, 116%, and 112%, respectively, of the subsequent censuses 7 mo later, when the same territories comprised entire islands instead of parts of larger islands. This suggests that the mangrove islands, unlike marine rocks, are not just sampling, proportionally to their sizes, a constantly active pool of propagules.

Looked at another way, this result shows that species number increases more slowly with area when successively larger quadrats within a large system are examined than when successively larger discrete islands are taken. This is the same phenomenon depicted by MacArthur and Wilson (1967) when they pointed out that the exponent in the allometric species-area relationship is lower for mainland sections than for an archipelago of true islands; this experiment has produced the first completely appropriate test of this proposition, for precisely the same territory was first a section of a larger island, then a discrete island. MacArthur and Wilson suggest that the reason for the lower exponent for quadrats within a large island or mainland is that species which cannot maintain themselves in a small area may be frequent transients if the small area is embedded in a larger one which can support breeding populations. Such transients would be rarer if the area were a separate island with no nearby source for these species. Whether this is the true explanation for the

result on MUD2, R1, and WH1 cannot be determined from the numerical information alone. That > 90% of the species present were found in 35%–69% of each island is certainly consistent with MacArthur and Wilson's hypothesis. There is no reason to think that all observed species were actually breeding in the censused fragment, and in this sense at least some were likely transients from the uncensused part of the island.

As explained below, the best one can conceivably do to predict the compositional nature of the species number increase on larger and larger islands is to state probabilities that given species will be present given a certain area, and the mangrove insect data do not yet permit even this kind of stochastic prediction. I can summarize the numerical species-area data by saying that they are in accord with the hypothesis of higher probabilities of extinction on smaller islands for all species, resulting in fewer species present at any given time.

All other things being equal, and assuming that immigration rate is much less affected by area than is extinction rate, a small island ought to have a higher turnover rate than a large one (Fig. 1). In this experiment the number of immigrations may serve as an estimate of the equilibrium turnover rate; the excess of extinctions over immigrations may be viewed as the additional extinction wrought by the decreased area. Of course the observed immigrations and extinctions underestimate the actual numbers, because species which immigrate and go extinct (or vice-versa) between monitorings will not contribute. For the fumigated mangrove islands with 18-day intervals between monitorings I suggested (Simberloff 1969) that perhaps half of all turnover would go unrecorded for this reason; Gilroy (1975) feels that this is unduly pessimistic and that 10% might be a more realistic figure. The much longer intervals between censuses on the area-modified islands ought to increase the unobserved turnover at the same time as the generally larger island size ought to decrease actual turnover rates. Which one will affect observed turnover more cannot be guessed, but it is the observed rates with which we must work, and we must assume they are correlated with the actual rates.

In Fig. 7 the turnover rates thus defined are plotted against number of species, with single island values connected. Three rates rose upon decrease in area, in accord with the prediction, and two declined. For all points, the correlation coefficient is -0.252 ($n = 15$, NS). That the control (IN1) turnover rate changed (increased) more than any other contributes to the insignificance of this result. If the same data are examined as percent turnover vs. species number (as in Diamond 1969) four rates rise and one falls on the modified islands; only 19%

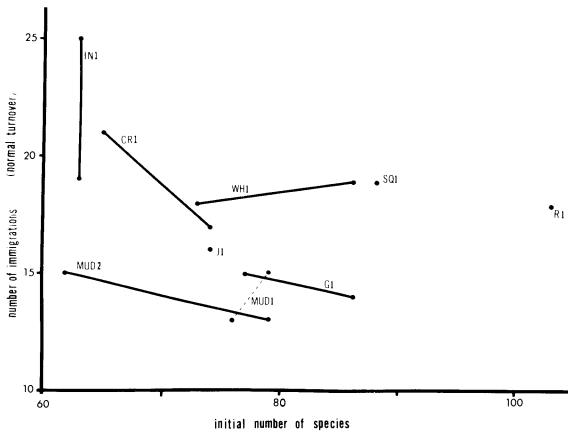


FIG. 7. Turnover rate vs. area curves for the experimental islands.

of the time would a result this extreme be observed if the null hypothesis of no effect of area were true. Furthermore, for these data $r = -0.687$ ($P < 0.01$), but this nearly monotonic decrease in percent turnover vs. S , similar to that published by Diamond (1969) for Channel Island birds, must surely be an artifact. Species number, the denominator of percent turnover, decreases when area is reduced, so there is a bias for percent turnover to increase on smaller islands. It is the actual value of the turnover, not the percentage, which is important.

DISCUSSION

I have interpreted this experiment as a disturbance of islands from an equilibrium condition, followed by a re-equilibration similar to that of the fumigated mangrove islands (Simberloff and Wilson 1969). Here, of course, equilibration will be occurring from an oversaturated rather than undersaturated condition. If one assumes constant coefficients of immigration and extinction (Diamond 1972), the curve for fall from oversaturation to equilibrium would be $S_t = S_* + (S_0 - S_*)e^{-(K_i + K_e)t}$, where S_t = number of species at time t , S_0 = number at time of area change, S_* = equilibrium number for new area, and K_i and K_e are the coefficients of immigration and extinction, respectively. This asymptotic curve is a mirror image about S_* of the expected curve for an undersaturated (e.g., fumigated) island (Fig. 8). The time to fall any fraction x of the way to S_* for the oversaturated island (or to rise a fraction x of the way to S_* for an undersaturated one) would be given for this model by $t_x = -\ln(1-x)/(K_i + K_e)$. The presence in the denominator of K_e , which one might expect to be a decreasing function of area, suggests the intuitively obvious: that large islands should take longer to re-equilibrate from oversaturation (where extinction is the rate-limiting event).

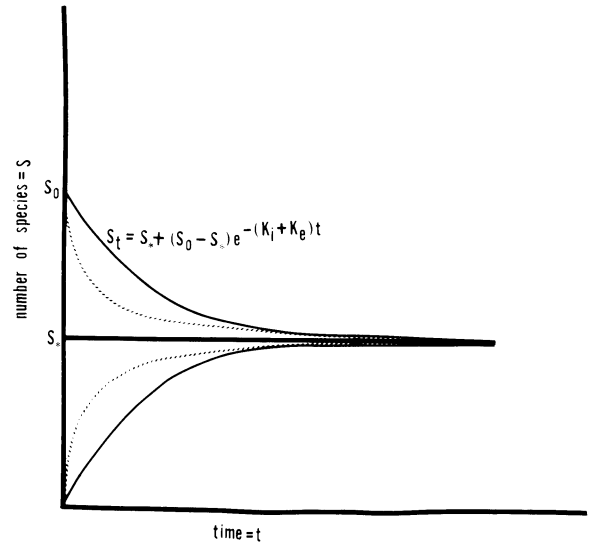


FIG. 8. Predicted "relaxation" curve of species number vs. time for an island out of equilibrium, given constant coefficients of immigration and extinction (K_i and K_e). Dotted lines represent more realistic model where coefficients are functions of S , the number of species present.

(K_i in the denominator implies that distant islands should take longer to re-equilibrate from undersaturation, where immigration is the rate-limiting event.) Diamond (1972) found exactly this trend—larger islands remaining oversaturated for longer—for birds on islands off New Guinea. I have already noted that immigration rates might be higher for larger islands, which would increase K_i and therefore the denominator of the equation for t_x , lowering the "relaxation" time required for re-equilibration to be substantially complete. There is no corresponding expected effect of distance on K_e .

The I_S and E_S curves are likely concave in nature, as indicated in Fig. 1 (MacArthur and Wilson 1967); the reason is that certain species will be good dispersers and others (possibly some of the same ones) will be good at persisting on islands. As the former invade, they lower the immigration curve disproportionately; as the latter are added to the biota, they raise the extinction curve disproportionately (i.e., subsequent species will have higher species-extinction rates). So K_i and K_e are functions of S , not constants; in the same vein, Terborgh (1975) treats K_e as a constant but uses a factor of S^2 . This restricts the shape of the extinction curve in Fig. 1, but the effect on return to equilibrium from perturbation is similar: to make the return quicker than it otherwise would be (Fig. 8). The precise equation for re-equilibration analogous to the equation already given for t_x depends on the functional relationship of K_i and K_e to S .

The interpretation of the area effect in this experiment as predominantly an increase in the extinction rate which lowers a dynamic equilibrium deserves further comment. Lynch and Johnson (1974) point out that much claimed avian turnover could actually be construed as "pseudoturnover": either an artifact of incomplete censuses or passage of transients, migrants, and vagrants which, if studied carefully, would be found never to breed on an island and so ought not to be regarded as contributing to immigration or extinction rates. Their second concern is that turnover attributable to human modification of the environment cannot tell us much about the workings of nature. In the Keys mangrove, aside from the area modification, it is hard to conceive of another secular environmental change, man-induced or otherwise.

With respect to their first contention, I have already listed evidence for completeness of my censuses. Whether or not actual breeding occurred usually cannot be proven, although the frequent presence of immature individuals of most of the species suggests that we are dealing here with breeding populations. Certainly there must be some species in the **Appendix** (such as herbivores which cannot reproduce on *Rhizophora*) which, although they fulfill the technical definition of "propagule," are unlikely ever to breed on such islands or to constitute a major component of the trophic web. The infinitesimal probabilities described in the previous discussion of similarities of island faunas are largely due to the presence in the species pool of such obligate transients. But the majority of species recur again and again in this system; 171 of 254 species encountered in this study (67%) were counted in more than one census, and I have recorded at least another 45 (18%) on other *Rhizophora* islands. Furthermore, 48 (58%) of the species recorded just once in this study are either parasitic wasps or predators, which ought to have low population densities on thermodynamic grounds alone and might be expected to have high species-extinction rates. A few of the larger ones, such as the vespid *Polistes* and braconid *Iphiaulax*, may not be treating these islands as islands, but rather as parts of larger "home ranges" or fine-grained foraging areas. Although sample sizes are too small for a chi-squared contingency test and differences often rested on just one or two species, it may be noted that in 10 of 12 situations where area was decreased the proportion of predators and parasites decreased; this happened in two of three control situations.

On the other hand, there were a number of extinctions recorded of species whose individuals are largely restricted to one island where it seems highly unlikely that the species could have been missed in 40 or more man-hours of observation. The ants

Camponotus abdominalis floridanus, *Crematogaster ashmeadi*, and *Paratrechina bourbonica* all have large colonies of active foragers and became extinct 4 times in this experiment. The adult spiders *Nephila clavipes*, *Gasteracantha ellipsoides*, *Allepeira lemniscata*, and *Tetragnatha antillana* are large and have highly visible webs; even the spiderlings are easily discovered, particularly by their webs. Together they accounted for 16 extinctions. *Micronaspis floridana*, a lampyrid beetle, is large and usually appears to be present in number if at all; it disappeared five times. Because of its microhabitat requirements and sizable colonies the termite *Cryptotermes cavirostris* is easily discovered; six extinctions occurred. These are just some of the more striking species recorded as going extinct; in the final analysis assessment of the amount of turnover must rest on faith in the census methods, and for the reasons already stated I feel that the great majority of listed extinctions are real. Furthermore, because most of them involve "valid" mangrove colonists, the area effect described here is not simply the uninteresting phenomenon of larger sample sizes turning up more transients and vagrants.

This is not to say that even among species which regularly colonize *Rhizophora* islands there are not some species which are particularly good dispersers and others which are especially persistent. The defaunation experiment (Simberloff and Wilson 1969) provided evidence particularly on differences in dispersal capabilities; this experiment sheds additional light on extinction. A measure of a species' ability to persist is the ratio of its observed number of extinctions to the potential number of extinctions. (Presence in 1970 on J1, R1, and SQ1 and 1971 on the other islands of this experiment could not have been followed by observed extinction.) There were 1,148 extinctions which could conceivably have been observed, but only 349 actual extinctions. One group of 96 species (38% of all those observed) contributed 111 of these extinctions out of only 121 possible; these species are poorly adapted to survival in this habitat and it is among them that transients in the sense of Lynch and Johnson (1974) must be sought. At the other end of the gradient, a group of 22 species were present at all censuses or absent only once, and produced only 11 extinctions of a potential 320. Among these are four ant species which are typically common and among the ecological dominants; two weevils, a termite, and a moth which contribute a large fraction of the woodboring which produces the favored microhabitat of many mangrove species (including ants); and two crickets and two roaches which are ubiquitous and numerous. Finally, three of these species, the nonballooning spider *Ariadna arthuri*, the polyxenid millipede *Lophoproctinus bartschi*, and the oniscid isopod *Rhyscotus* sp., combine poor dispersal ability (Sim-

berloff and Wilson 1969) with extremely good persistence once present. This contrasts with several spiders (such as the orb-weavers already mentioned) and bugs which seem to be adept at reaching islands but are quite likely to be extinguished once there.

Extinction is a stochastic rather than deterministic event in this system, and the increase in extinction caused by decreased area did not have precisely predictable components. Certain species (e.g., the ant *Camponotus abdominalis floridanus* and the scorpion *Centruroides keysi*) are much more frequently found on large islands than small ones, and among the ants, in particular, there is a quite ordered succession of nested subsets on larger and larger islands. But there are exceptions to all these rules (e.g., the presence of scorpions on the small remaining fraction of CR1 in 1971), and aside from the weak rule that predators and parasites are more likely to suffer extinction from decreased area, no generalizations can be made. Any species is more likely to disappear on a smaller island.

Finally, a word is in order about the nature of the biological processes or phenomena that organize mangrove island insect communities and allow numerical, and rarely compositional, predictions to be made. Heatwole and Levins (1972) suggest that the trophic web of these communities is such an organizing force and that a species' trophic position and interactions with other species determine in large part whether or not it will be found at some time on some mangrove island. I have questioned (Simberloff 1976) whether the data from the fumigated islands support this claim and proposed that interactions determining presence or absence, if they exist, are likely to be subtle and complex and to require detailed observation to confirm their importance. I would extend this principle to the area-modified islands as well; the presence-or-absence data do not permit many inferences to be made about interactions. Four suggestive patterns are now described which indicate the sort of additional information required.

First, the nearly omnipresent roach *Latiblattella* sp. nov. has black nymphs with two thin white bands crossing the abdomen. These bands appear to give the roach a waist, and these roaches are occasionally seen running in files of the black ant *Crematogaster ashmeadi*. Furthermore, they have been observed to elevate the rear of their abdomen not unlike the characteristic way in which *Crematogaster* raises its gaster when disturbed. *Crematogaster* dominates red mangrove islands, except when large colonies of *Camponotus abdominalis floridanus* are present, everywhere except the Mud Keys, where it is rare or absent. In this experiment *Crematogaster* was present and abundant everywhere but IN1 (it was absent in 1970, rare the other 2 yr) and the two

Mud Keys, MUD1, and MUD2, which are in an archipelago distant from all other islands of this experiment. *Latiblattella* sp. nov. was recorded everywhere except the Mud Keys, where it was never observed. The similarity between MUD1 and MUD2 transcends this pair of species but is subtle enough that it could not be detected by cursory inspection of the **Appendix**. The deviation between expected and actual overlap, given the assumptions described above, is larger (31.2 species) and less probable ($< 10^{-13}$) than for any other pair of islands.

Second, *Camponotus abdominalis floridanus* is a very large, active ant whose size precludes it from nesting in the thin hollow twigs used by all other mangrove ants. It is forced to use special microhabitats: large, low, hollow aerial roots, the space between two large, appressed branches, or tree holes. The roots are labile, frequently falling into the water, and probably are too small to support large colonies. The other two microhabitats are rarer, but when a *Camponotus* colony establishes itself in one of them it may grow very large, the workers swarming all over the branches and even being visible from a boat. This situation occurred once in this experiment, on IN1, and on a nearby fumigated island, ST2. On the former *Crematogaster* has always been absent or present just as tiny new colonies consisting of a queen and a few undersized workers, probably new colonies (E. O. Wilson, *personal communication*). On the latter *Crematogaster* was originally extremely abundant but has become progressively rarer. The nature of the interaction, if one exists, cannot yet be guessed.

Third, the waxy scale insect *Ceroplastes rubens* is not seen on many mangrove islands. In this experiment it occurred very frequently on IN1, tended by *Camponotus abdominalis floridanus*, and in 1971 on CR1, also tended by *Camponotus*. One may imagine that *Ceroplastes* has a much higher species-extinction rate in the absence of the ant.

Fourth, the centipede *Orphnaeus brasilianus* is a common mangrove island inhabitant and quite possibly its predation on crickets helps to control cricket population sizes (Simberloff and Wilson 1969). It was found in great abundance on two of the original fumigated islands, seven of the islands in this experiment, and five other small mangrove islands. A second centipede, *Cryptops* sp., which also lives in hollow twigs and under dead bark, is about the same size and is also probably a generalized predator (R. Crabill, *personal communication*). It was observed only on CR1, where *Orphnaeus* was absent, and WH1, where *Orphnaeus* disappeared after 1969. For *Orphnaeus*, at least, dispersal to small mangrove islands is a problem; it never recolonized the two fumigated islands E7 and E9. There is no reason

to think that *Cryptops* is more adept at overwater dispersal. From the distributions and the disappearance of *Orphnaeus* on WH1 one might tentatively postulate that these centipedes exclude one another competitively or by predation. (Crabill suspects that they are even cannibalistic.) The wider distribution of *Orphnaeus* may be due either to better dispersal powers or to a stochastic competitive superiority.

CONCLUSIONS AND SUMMARY

This experiment demonstrates conclusively that a smaller island will support fewer species than a larger one, all other things being equal. In particular, if we equate microhabitats of the mangrove island system with habitats of larger archipelagoes, it is clear that habitat diversity differences are not a sufficient explanation of the widely observed effect of area on species number. That population sizes of most species on these islands are large suggests that the independent effect of area on species number is not restricted to microcosms of little interest to most ecologists. The area effect in this experiment was a consequence of the dynamic equilibrium on any island between immigration of new species and extinction of those already present. It supports the notion that any species is more likely to become extinct on a smaller island. Because of unobserved immigration and extinction it is impossible to measure turnover rates exactly, but they must have a minimum of about 15 species per year for an island with a standing equilibrium fauna of about 75 species and are likely much larger. Some species are exceptionally prone to extinction, but some of this turnover is not generated by the fluke arrival and swift subsequent extinction of species unsuited for mangrove island colonization.

The results of this experiment are consistent with an hypothesis of fast asymptotic approach to equilibrium from an oversaturated condition, the precise curve resting on the functional relationship between immigration and extinction rates and number of species. Equilibrium theory predicts that turnover rates should be higher on a smaller island; this is neither confirmed nor refuted by these data, probably because sample size was too small and turnover rates on untreated islands of this type are too high and variable. A comparison of percent turnover with island size has an inherent statistical bias which makes it uninteresting.

The processes underlying the observed turnover and its relation to area remain obscure. It is clear not only that there are distributions of dispersal and colonization abilities among potentially colonizing species but also that there is a large historical component in the determination of an island biota. In this experiment 19 mo was not a sufficient in-

terval to render two successive censuses of the same island independent of one another, or at least as independent as contemporaneous censuses of two different islands. It is my hypothesis that the characteristics of individual species—invansion and species-extinction rates—adequately explain most of the observed pattern of species number vs. area. Proof of this hypothesis will be difficult, resting on the demonstration that interactions between species are less important factors in population dynamics in this system than are aspects of the physical environment. Even the interior of these islands is exposed to wind-driven waves, and violent rainstorms characterize the Keys. Even ordinary rains and moderate wind and seas frequently cause damage such as broken branches and leaves killed by mud-splattering. Drowned individuals are often seen, but to prove that such physical factors are dominant causes of population decline would be a formidable task. The distributional data alone cannot be used either to prove or to disprove the hypothesis, and the paucity of evidence on four subtle interactions suggested by the data imply that even a description of most interactions between species, let alone an assessment of their importance, will be a monumental undertaking.

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