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LITERATURE CITED

Chisholm, R. D. 1952. Nature and uses of fumigants, p. 358. *In* Insects, The Yearbook of Agriculture 1952.

Darlington, P. J. 1957. Zoogeography: the geographical distribution of animals. Wiley, New York. 675 p.

Davis, J. H. 1940. The ecology and geologic role of mangroves in Florida. Papers from Tortugas Lab., Carnegie Inst. Wash. **32**: 307–412.

French, R. A. 1964 (1965). Long range dispersal of insects in relation to synoptic meteorology. Proc. Int. Congr. Entomol. 12th (London). **6**: 418–419.

Fridriksson, S. 1967. Life and its development on the volcanic island, Surtsey. Proc. Surtsey Research Conf., 1967: 7–19.

Hermannsson, S. 1967. Introduction. Surtsey Research Progress Report, III: 1.

LaRue, D. C., and T. T. Muzik. 1954. Growth, regeneration and precocious rooting in *Rhizophora mangle*. Pap. Mich. Acad. Sci. Arts Lett. (I) **39**: 9–29.

Lauck, D. R. 1965. Chloropicrin for fast action with a Berlese funnel. Turtox News **43**: 115.

Lindroth, C. H., H. Andersen, H. Bodvarsson, and S. H. Richter. 1967. Report on the Surtsey investigation in 1966. Terrestrial invertebrates. Surtsey Research Progress Report, III: 59–67.

MacArthur, R. H., and E. O. Wilson. 1963. An equilibrium theory of insular zoogeography. Evolution **17**: 373–387.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press. 203 p.

Mainwaring, A. P. 1961. Some effects of methyl bromide on aphids and whitefly and their host plants. Doctoral thesis, London Univ., London, England.

Monro, H. A. U., and R. Delisle. 1943. Further applications of methyl bromide as a fumigant. Sci. Agr. **23**: 546–556.

Page, A. B. P., and O. F. Lubatti. 1963. Fumigation of insects. Ann. Rev. Entomol. **8**: 239–264.

Simberloff, D. S., and E. O. Wilson. 1969. Experimental zoogeography of islands. The colonization of empty islands. Ecology **50**: 278–296.

Wolfenbarger, D. O. 1946. Dispersion of small organisms. Amer. Midland Naturalist **35**: 1–152.

EXPERIMENTAL ZOOGEOGRAPHY OF ISLANDS: THE COLONIZATION OF EMPTY ISLANDS

DANIEL S. SIMBERLOFF[1] AND EDWARD O. WILSON

The Biological Laboratories, Harvard University, Cambridge, Massachusetts 02138

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Abstract. We report here the first evidence of faunistic equilibrium obtained through controlled, replicated experiments, together with an analysis of the immigration and extinction processes of animal species based on direct observations.

The colonization of six small mangrove islands in Florida Bay by terrestrial arthropods was monitored at frequent intervals for 1 year after removal of the original fauna by methyl bromide fumigation. Both the observed data and climatic considerations imply that seasonality had little effect upon the basic shape of the colonization curves of species present vs. time. By 250 days after defaunation, the faunas of all the islands except the most distant one ("E1") had regained species numbers and composition similar to those of untreated islands even though population densities were still abnormally low. Although early colonists included both weak and strong fliers, the former, particularly psocopterans, were usually the first to produce large populations. Among these same early invaders were the taxa displaying both the highest extinction rates and the greatest variability in species composition on the different islands. Ants, the ecological dominants of mangrove islands, were among the last to colonize, but they did so with the highest degree of predictability.

The colonization curves plus static observations on untreated islands indicate strongly that a dynamic equilibrium number of species exists for any island. We believe the curves are produced by colonization involving little if any interaction, then a gradual decline as interaction becomes important, and finally, a lasting dynamic equilibrium. Equations are given for the early immigration, extinction, and colonization curves.

Dispersal to these islands is predominantly through aerial transport, both active and passive. Extinction of the earliest colonists is probably caused chiefly by such physical factors as drowning or lack of suitable breeding sites and less commonly by competition and predation.

[1] Present address: Department of Biological Science, Florida State University, Tallahassee, Florida 32306

As population sizes increase it is expected that competition and predation will become more important. Observed turnover rates showed wide variance, with most values between 0.05 and 0.50 species/day. True turnover rates are probably much higher; with 0.67 species/day the extreme lower limit on any island. This very high value is at least roughly consistent with the turnover equation derived from the MacArthur-Wilson equilibrium model, which predicts turnover rates on the order of 0.1–1.0 species/day on the experimental islands.

Introduction

In the first article of this series (Wilson and Simberloff 1969) we showed how the recent formulation of mathematical biogeographic theory has both intensified the need for studies of the entire colonization process and defined the measurements required for such studies. The idea was conceived of approaching the problem experimentally by the removal of entire arthropod faunas from series of small islands. Six very small mangrove islands of the Florida Keys, each consisting of only one to several *Rhizophora mangle* trees standing in shallow water, were selected. Elimination of the faunas ("defaunation") was achieved through fumigation with methyl bromide; and techniques were worked out for censusing the arthropod species during the recolonization process.

In the present article we discuss the criteria we used for counting species and describe the recolonization process on all six islands, from the moment of defaunation to the reattainment of equilibrial numbers of species less than a year later.

Species Counts

For the species counts and discussion which follow these definitions will be used:

Propagule: the minimum number of individuals of a species capable of breeding and population increase under ideal conditions for that species (unlimited food supply and proper habitat, no predators, etc.)

Colonization: the existence of at least one propagule of a species on an island

Extinction: the disappearance of a species from an island

Invasion: the arrival of one or more propagules on an island

Immigration: the arrival of a propagule on an island unoccupied by the species

The distinction between invasion and immigration should be noted. It is incorrect to speak of an immigration rate for one species, since an immigration rate for an island is in units of species/time. A species can have an invasion rate on a given island, however; this is simply the number of propagules of that species landing per unit time.

In analyzing species counts made at discrete intervals, as in our monitorings, every species for which at least one propagule exists is designated a colonist. It is also designated an immigrant if it was not a colonist at the preceding count. Every immigrant is also, by definition, a colonist. This definition says nothing about whether food and a breeding site exist; a species whose propagule lands on one of our islands is a colonist even if it is doomed to quick extinction for purely physical reasons (e.g., the absence of a suitable nest site in the *Rhizophora* for a given species of ant).

Because of the relative nearness of our experimental islands to source areas and, to a lesser extent, their small size and ecological simplicity, ambiguities concerning the state of colonization exist that would not arise if we were dealing with truly distant and larger islands. Except for a few birds, any animal species for which a propagule is recorded either avoids leaving the boundary of the island or (much more rarely) leaves and perishes in the sea. The island, therefore, is not simply an extension in some sense of the mainland.

In our experiment a small percentage of the animal species, less than 10% of all species sighted, behave as though the distances to the experimental islands are not qualitatively different from the same distances overland. We wish to discount these species in our calculations, unless insularity becomes important in particular instances. Two classes of species can be recognized in this connection. Several kinds of insects (cicadas, odonates, foraging bees and wasps) treat small mangrove islands as part of a fine-grained foraging area, traveling readily and frequently among several islands and adjacent shore regions. A species of the wasp genus *Polistes* forages regularly over small mangrove islands but rarely nests there. When nesting does occur the wasps apparently restrict their foraging largely to the nesting island. Only an extant nest qualifies the *Polistes* as a colonist. In similar cases actual breeding, rather than just the presence of sufficient animals to breed under the most favorable conditions, was employed as the criterion for colonization. Transient adult butterflies, particularly *Ascia monuste* and *Phoebis agarithe* (Pieridae), migrating over and beyond the experimental islands, occasionally skim briefly through but do not stop to breed. These will not be considered colonists for reasons similar to those used to discount fine-grained foragers.

A second difficulty associated with the nearness of our islands concerns intermittent breeding by strong-flying insects combined with continuous foraging by adults. Females of the moth *Automeris io* (Saturniidae) fly frequently onto small mangrove islands and occasionally deposit eggs. The life cycle from egg to adult of *Automeris* on *Rhizophora* is about 2½ months, and if (as may have happened on E3) adults breed on an island at intervals greater than that, extinction rates would appear to be high. For after a brood matures, the survivors generally all disperse from the island and no new adults may breed there for a period. This is obviously not extinction in its classical sense—it is not caused by competition for food or space, predation, climatic catastrophe, etc. —but it does accord with our strict definition given above. This situation was fortunately rare, almost entirely restricted to a few lepidopterans. Species of this type will be considered colonists, with one immigration only and no extinction, until a definitive and extended absence is recorded. The behavior of the very few nesting birds would place them in this category but they were nevertheless discounted in our analysis.

A few arthropods live in and among *Rhizophora* roots at or below the water level, some foraging on mud at low tide. These include the isopod *Ligia exotica*, an unidentified amphipod, and three insects: *Trochopus plumbeus* (Hemiptera: Veliidae), *Axelsonia littoralis* (Collembola: Isotomidae), and *Anurida maritima* (Collembola: Poduridae). These will be excluded from the species counts because they are essentially part of a surface marine community and apparently do not interact significantly with the arboreal mangrove fauna. All are ubiquitous around small mangrove islands and cannot be eradicated with certainty.

The impermanent mudbanks on E8 and E9 (Wilson and Simberloff 1969, Fig. 2) that remain wet but above water for several weeks in calm weather harbor a characteristic marine arthropod community, listed in Table 1. Most of the species are concentrated in washed-up and wet debris and algae. That all but the earwig *Labidura riparia* are virtually marine and do not breed on the islands is indicated first by their never having been collected on *Rhizophora* (even when the mud is submerged and debris washed away by wind-driven high tide), second by most species having been observed swimming from one patch of mud or debris to another, and finally by the swift recolonization by large populations of most species observed after extinction caused by extended flooding. *L. riparia* is the only species found on the islands proper, and it is probably the only one whose energetic interaction with the mangrove and its arboreal fauna is significant. All the others apparently feed on seaweed or washed-up detritus, or else prey upon those which do. Consequently *L. riparia* alone is considered a colonist.

TABLE 1. Arthropod community of intermittently submerged mudbanks on small mangrove islands

INSECTS	
Collembola	
Poduridae:	gen. sp.
Dermaptera	
Labiduridae:	*Labidura riparia*
Coleoptera	
Carabidae:	*Bembidion* sp. nr. *contractum*
	Tachys occulator
Corylophidae:	*Anisomeristes* sp.
Ptiliidae:	*Actinopteryx fucicola*
Staphylinidae:	gen. sp.
Hemiptera	
Saldidae:	*Pentacora sphacelata*
OTHER	
Acarina	
Veigaiaidae:	*Veigaia* sp.
Isopoda	
Oniscoidea:	*Ligia exotica*

The tree snail *Littorina angulifera* and tree crab *Aratus pisonii* inhabit all but the upper canopy of small mangrove islands but will not be counted for the following two reasons. Neither can be removed—*Littorina* is unaffected by 50 kg/1000 m^3 of methyl bromide for 3 hr, and *Aratus* simply drops to the water and may swim under the tent—and both have planktonic larvae. Again, the interaction of these species with the remainder of the arboreal community appears superficially not to be significant.

Our definition of a propagule dictates that animals with zero reproductive value (e.g., a male ant landing on an island after a nuptial flight) not be considered colonists.

Although birds were not counted here, bird parasites which establish breeding populations on the islands rather than wholly on the birds were listed as colonists. Specifically, the hippoboscid flies *Olfersia sordida* and *Lynchia albipennis* (whose puparia are commonly found in tree crevices) and the tick *Argas radiatus* (all stages of which live under dead mangrove bark) were counted.

Finally, except for the rare larvae and pupae, all Diptera were excluded. Monitoring of flies proved too difficult to warrant faith in the accuracy of species counts, and the extreme scarcity of immature stages indicates that small mangrove islands rarely support breeding dipteran populations.

Deep-boring beetles were deemed valid colonists

in this series. The uncertainty of extinction discussed in our first report (Wilson and Simberloff 1969) notwithstanding, the data imply that the few initially surviving cerambycid larvae were destroyed by a delayed effect, and that the weevils may have succumbed in the same way. In any event there are but four species involved, and rarely were more than two found on a single island.

Acceptable colonists were counted conservatively. In all instances of uncertainty about the number of species of a given taxon present, the minimum possible number is taken. For example, occasionally the records from one census revealed two thrips, *Neurothrips magnafemoralis* and *Liothrips* sp. (both Tubulifera), as well as larval thrips identifiable only to the suborder Tubulifera. Since the larvae could conceivably be ascribed to one of the two species known present, only two species are recorded for this period. Similarly the observations on E1 (May 29, 1967) of a moth caterpillar *Bema ?ydda* (Phycitidae), and a small adult moth similar to *Bema* but seen too briefly to be so recorded with certainty yield a species count of one only, since both individuals could belong to one species.

The presence of an immature animal need not imply breeding on an island; spiderlings balloon more readily than adults, and any insect larva could be blown or rafted to an island, although for some, of course, the probability of this is quite low. Similarly, an adult female does not constitute a propagule or part of one if she has not been fertilized, is not of a parthenogenetic species, and no male is present. Nevertheless, we assume here that an adult female, an adult of indeterminate sex, and an immature animal each imply the presence of a propagule. Adult males are not so counted.

In the Appendix are given the complete recorded histories of all of the colonists on E1, E2, E3, ST2, E7, and E9, the six islands whose entire faunas were removed by fumigation (see Wilson and Simberloff 1969). These records are based on direct observation in over 90% of the cases. In certain instances (hatched bars) animals were assumed present through one or more monitoring cycles when not actually observed. To ensure consistency in such interpolations the rules given in Table 2 were followed.

TABLE 2. General rules applied in interpolation of colonists

Animal	Number of cycles interpolated	Justification
Ants: workers seen first	2 (previous)	Conservative on physiological grounds
Ants: queen seen first	indefinite	Obvious for short periods. Data of E9 support for longer periods.
Deep-boring beetles	2+	Present in relatively low density and only 10% of twigs broken at each monitoring.
Small leaf dwellers	1-2	Inconspicuous, but densities usually increase rapidly.
Bark-dwellers	1	Often become dense quickly, and habitat examined completely.
Araneids	1	Spiderlings may be minute, but webs are conspicuous.
Tetragnatha	2	Position of webs makes less conspicuous than araneids.
Salticids	2-3	Furtive, often inconspicuous, and usually present in low densities.
Anyphaenids	1	Build up relatively high densities quickly.
Small crawlers	2	Usually low densities; difficult to record.
Fliers	2	Frequently conspicuous, but may be inactive because of weather.
Caterpillars	1 (usually)	No generalization possible; large ones are conspicuous.

SEASONALITY

We must first discuss whether any aspects of the colonization depicted in the Appendix (and Figs. 1–3) are artifacts of the particular season at which defaunation was performed. That is, if all the islands were fumigated in September instead of March would the tables and derived curves be qualitatively different?

This would obviously be so in much of the United States, where dispersal stages of most insects and spiders occur at short, distinct periods (usually in the summer). The Florida Keys are subtropical, however, with the mean temperature of the coldest month (20.9°C) only 7.7°C lower than that of the warmest month. Frost has never been recorded. The mean humidity of the driest month is but 8% lower than that of the most humid. Rainfall is less homogeneous, September–October averaging about 150 mm and December–January only 38 mm. The precise amount for all months is quite variable, however, and there are obviously no extreme dry or wet seasons. Wind is also relatively constant over the year in both speed and direction: it averages about 18 km/hr from the eastern quadrant. It is not surprising, therefore, that we found most of the mangrove arthropod species active throughout the year. All life stages, including dispersal forms, of many and probably most species of insects and spiders were present during every month. We can make no

quantitative assertions, but it seemed to us that there were no striking seasonal decreases among the more abundant mangrove inhabitants in either population size or activity, including flight—except for mosquitoes, which were much more numerous in the summer.

We had the good fortune to be present February 26, 1967, when the temperature at Key West fell briefly to 9.5°C, the lowest reading in several years. Our surveys during that cold spell revealed no apparent mortality or even great lessening of activity of mangrove inhabitants other than a decrease in flight activity quite normal for the prevailing wind speed.

Finally, and most importantly, the conclusion that propagules were constantly hitting our islands is incontrovertible from the data summarized in the Appendix. Moreover, these data provide no clear indication of seasonality in the dispersal of any taxon. The colonization of E7, defaunated approximately half a year before the other islands, should certainly have manifested any strong seasonal component. Yet in both form and specifics (Fig. 2 and Appendix) it is consistent with the colonization of the other islands.

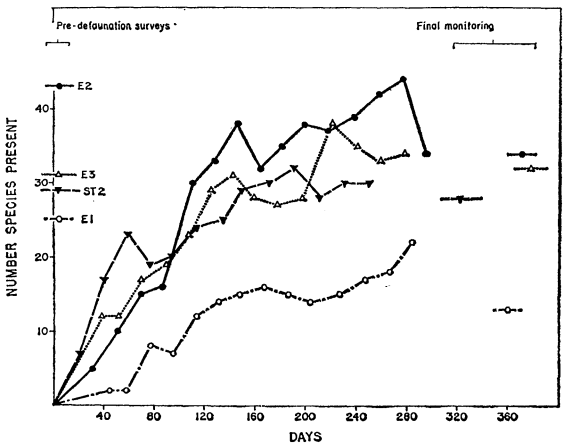

FIG. 1. The colonization curves of the experimental islands in series 1. In each curve the last and next-to-last census points are not connected by a line, only in order to stress the greater period of elapsed time compared with the times separating earlier censuses.

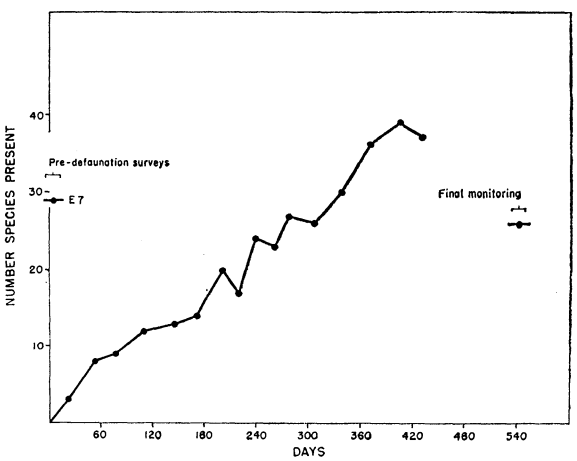

FIG. 2. The colonization curve of island E7.

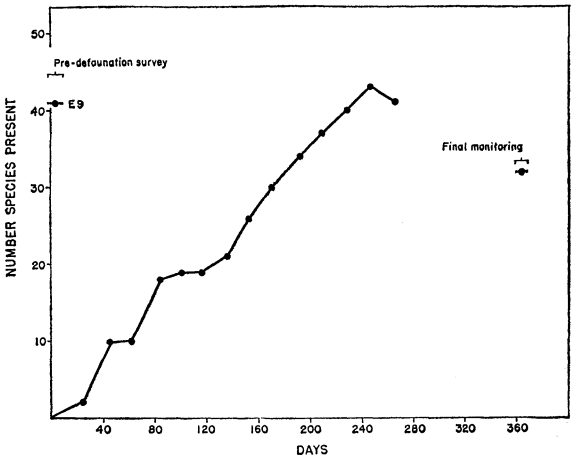

FIG. 3. The colonization curve of island E9.

PATTERNS OF COLONIZATION

As would be expected in a system involving but one plant, succession in the usual sense, a progression of discrete and relatively stable communities, did not occur. This does not imply a lack of order in the time course of colonization; indeed, the invasion of species was remarkably regular. But it was not accompanied by wholesale extinction of distinct animal associations.

Several broad patterns are nevertheless evident. First, although the earliest immigrants on all islands included both strong fliers (especially moths and wasps) and weak fliers or nonfliers (particularly psocopterans, chrysopids, and spiders), the latter built up large populations more rapidly and became numerically dominant. That wind should transport many of the early invaders is not surprising. The first animal recorded on Krakatau after its eruption was a spiderling (Cotteau 1885), while psocopterans (including wingless nymphs) and spiders are prominent in aerial plankton samples (Glick 1939). But their success in colonization deserves further comment. The food supply for psocopterans, algal and lichen growth on the mangrove itself, is evidently sufficient to allow much larger populations than one normally finds on undisturbed *Rhizophora* islands. This implies that on untreated islands there may be predation by animals not present on recently defaunated islands. In fact, we have observed the ants *Pseudomyrmex elongatus* and *Pseudomyrmex "flavidula"* (both of which colonized later) carrying appar-

ently freshly killed psocopterans to their nests. Running and jumping spiders can, of course, eat the psocopterans. *Maevia vittata* (Salticidae) was seen catching a *Psocidus texanus* adult on E7, while the webs of even small araneid spiderlings commonly trapped transient flies, especially tipulids and ceratopogonids, in the same size range as psocopterans.

Although it involves only a relatively small subset of the entire Florida Keys fauna, colonization by these early weak fliers was more variable than by other classes of arthropods, both in time of arrival on individual islands and species composition at any given time among islands. The psocopterans were particularly unpredictable; from the 2d month after defaunation there were usually 1–4 species on each island at any census period, but over the course of the experiment a total of 24 species were involved. Although certain psocopterans, especially species of *Psocidus* and *Peripsocus,* were generally more prominent than others, there was little correlation among the sets of psocopterans found on different islands. Furthermore, as can be seen from the Corrodentia (= Psocoptera) sections of the Appendix, many psocopterans persisted for less than a month. As a group they invaded and multiplied readily, and became extinct almost as readily. On E7, only 5 species of the 15 colonists remained as long as 2 months.

Spiders as a group were less variable than psocopterans in their colonization pattern but much more so than that of most later colonists. Although the majority of the 36 spider species which colonized the islands followed the pattern just described for the psocopterans—that is, they immigrated readily and were extinguished quickly, and occurred on but 1 or 2 islands—a few species behaved quite differently. *Eustala* sp., *Tetragnatha* sp., *Leucauge venusta, Hentzia palmarum,* and *Aysha velox* in particular, colonized most of the islands and usually persisted for at least several months. These include most of the spiders found on the islands before defaunation.

Wasps present a similarly heterogeneous picture of colonization, many species appearing on one or two islands and vanishing rapidly while a few, notably *Pachodynerus nasidens, Scleroderma macrogaster,* and *Calliephialtes ferrugineus,* colonized many islands and persisted for long intervals. Mites did not invade as early as did wasps and spiders, but displayed the same pattern of many short-lived species, a few persisting and recurring. Most of the 20-odd species of Acarina were recorded from one or two islands only and disappeared within a month, while *Amblyseius* sp. and *Galumna* sp. were omnipresent and their populations long-lived. An apparent correlation exists in the spiders, mites, and wasps between mean length of persistence and number of islands colonized. This relation, however, may be artifactual, for the following reason. If two species, the first with a very high, the second with a very low initial probability of extinction (long expected persistence time), invaded all six islands with equal frequency, we would expect to see the former on one or two islands only and the latter on most or all of them.

Thrips, lepidopterans, orthopterans and ants display a regularity of colonization in sharp contradistinction to the relatively unordered patterns of colonization previously described. The last three groups, particularly the ants, mount the largest populations in undisturbed mangrove animal communities.

Only five species of thrips colonized, four of which were widespread among the islands. Almost all invasions occurred 4–5 months after defaunation. Most thysanopteran colonizations endured for at least 3 months. Large populations were occasionally produced but rarely persisted—the late colonizing ants may have attacked thrips. There was no consistent order of colonization: all species commonly immigrated about the same time.

Only 8 lepidopteran species colonized the experimental islands, of about 30 species known from mangrove and a few hundred from the general Keys fauna. (This figure does not count the 2 or 3 fine-grained foragers discussed earlier.) All eight were recorded more than once, and six were widespread. Most colonizations were sustained and many involved sizable populations. There was a somewhat predictable order of invasion, with *Phocides batabano, Bema ?ydda,* and *Ecdytolopha* sp. usually the first arrivals, *Nemapogon* sp. appearing somewhat later, and *Alarodia slossoniae* and *Automeris io* usually not seen until about 200 days.

The orthopteroids colonized still more predictably. Of approximately 25 species that occur in mangrove swamps and 60 or more that occur in the Keys as a whole, only 9 invaded the experimental islands. If the two very near islands (E2 and E7) are discounted, only four species were involved and all have multiple records. These four were rarely extinguished; two, the green tree cricket *Cyrtoxipha confusa* and roach *Latiblattella* n. sp., produced large populations. All appeared capable of early invasion.

The ants displayed the most orderly pattern of colonization. These insects are also numerically,

TABLE 3. Colonization of experimental islands by ants

Island	E1	E2	E3	E7	E9	ST2
Ant species before defaunation[a]	5 6 11	3 8 9 11 13 14	5 6 9 11 13	1 2 9 11 14	4 8 9 11 12 13	5 6 9 11 13 14
Ant colonists in order of colonization	6	6 14 11 1	6 11 14 8 10 9	6 16[b] 1 10 11 14 12	12 15[b] 1 6 11 14	6 7[b] 11 14 1 13 9

[a]Species are coded as follows:
1 = *Camponotus floridanus*
2 = *Camponotus planatus*
3 = *Camponotus tortuganus*
4 = *Camponotus* sp.
5 = *Camponotus* (*Colobopsis*) sp.
6 = *Crematogaster ashmeadi*
7 = *Crematogaster atkinsoni*
8 = *Monomorium floricola*
9 = *Paracryptocerus varians*
10 = *Paratrechina bourbonica*
11 = *Pseudomyrmex elongatus*
12 = *Pseudomyrmex "flavidula"*
13 = *Tapinoma littorale*
14 = *Xenomyrmex floridanus*
15 = *Brachymyrmex* sp.
16 = *Hypoponera opacior*

[b] indicates later extinction.

and probably energetically, the dominant animals on all small mangrove islands. Of the more than 50 species found in the Keys, 20 species inhabit red mangrove swamps and about 12 of these normally occur on small islands. The pre-defaunation surveys revealed a highly ordered fall-off of ant species in two directions. First, on islands of equal size but varying distance from source area, the most distant islands contain *Crematogaster ashmeadi;* those somewhat nearer, both the *Crematogaster* and *Pseudomyrmex elongatus;* those nearer still, these two species plus *Paracryptocerus varians, Tapinoma littorale,* and *Camponotus* (*Colobopsis*) sp.; and on islands near shore, most or all of the above species plus one or more species of *Camponotus, Pseudomyrmex "flavidula," Monomorium floricola,* and *Xenomyrmex floridanus.*

If instead one fixes a distance (usually small) from the source area and examines islands of increasing size, he generally finds on the smallest bush (ca. 1 m high) *Crematogaster ashmeadi;* on slightly larger bushes, *C. ashmeadi* and/or *Pseudomyrmex elongatus;* on small trees these two with perhaps two species drawn from among *Paracryptocerus, Tapinoma, Colobopsis, Xenomyrmex,* and *Monomorium;* and on islands the size of our experimental ones, the full complement expected on an island of the appropriate distance from source. In short, the ability to colonize increasingly smaller islands parallels closely the ability to colonize increasingly distant ones.

The order of colonization by ants of the experimental islands (Table 3) provides a curious zoogeographic analog of Haeckel's biogenetic law. In almost every instance *Crematogaster ashmeadi* was the first colonist, even on the two near islands (E2 and E7) where it was not present before defaunation. On all but the most distant island (E1) *Pseudomyrmex elongatus* was an early and prominent colonist. Moreover, the small subset of the mangrove ants which comprised the remainder of the colonists was almost identical to that found on small islands as one moves nearer to the source areas. Only 3 extinctions were observed, and 2 were of species believed unable to nest in red mangrove forests. As a group, the ants colonized later than most other taxa and at the close of the first phase of our study (April 1968) few species had built up populations numerically similar to those on untreated islands.

COLONIZATION CURVES

Figures 1–3 show the original numbers of species present and the colonization curves (number of species present vs. time) for the experimental islands.

Estimation of the number of species present before defaunation and after regular monitoring had ended is complicated by two factors. First, as can be seen from the data presented in the Appendix, a few colonists are inferred present at each regular post-defaunation monitoring period without actually having been observed because they were recorded at both preceding and subsequent periods. Since there was but one pre-defaunation survey, its total species number must be increased by the mean number of species inferred present without having been observed for all regular post-defaunation monitorings after an approximate equilibrium $\hat{S}$ had been reached. The last four regular monitorings were used for this purpose, since the population structure then was probably closest to that before defaunation. A similar correction must of course be made for the final census, after regular monitorings had ended. In addition to this correction, the pre-defaunation surveys of E1, E2, E3, E6, and E7 were believed deficient for leaf fauna. Since this habitat normally harbors 3 to 5 species on all islands, it was assumed that a total of 4 such species were present on each of these islands, though the actual number seen was 1 to 4. Figures 1–3 do not include a correction for unseen short-lived species, estimated at about 2 species per monitoring period but with very high variance (Simberloff 1969).

The numbers of species recorded on the control islands before and after the experiment were:

	before	after
E6	30	28*
E10	20	23

* plus 9 spp. in bird nests only

These cannot be corrected for unseen colonists, but show conclusively that no important long-term effect was operating in the Keys that might have distorted the results from the defaunated islands. Although the numbers of species on the control islands did not change significantly, the species composition varied considerably, implying that the number of species, S, approaches a dynamic equilibrium value, $\hat{S}$.

The most apparent implication of the colonization curves and other information presented so far is that this equilibrium $\hat{S}$ does exist. Three lines of evidence are relevant. First is the fact, just mentioned, that S on the control islands did not change greatly from the beginning to the end of the year-long period in which the nearby experimental islands were being colonized. Second is the static observation that untreated islands with similar area and distance from source have similar $\hat{S}$ (note E3 and ST2 before defaunation).

Perhaps the most convincing argument for an equilibrium $\hat{S}$, however, is the increase of species present on all our islands to approximately the same number as before defaunation, and then rough oscillation about this number. This $\hat{S}$ may be only a quasi-equilibrium—that is, the curve of S versus time after $\hat{S}$ is reached may not be truly stationary—because of two long-term processes. The first is that when an approximate $\hat{S}$ is first reached the population structure of the particular set of species on the island is still changing rapidly; some species are represented by few individuals and may have large r (intrinsic rate of increase). Others may have abnormally large populations. Population sizes are generally fluctuating much more rapidly than on untreated islands. We have already indicated one manifestation of this process in our experiment: psocopterans colonized early and built up immense populations before presumed ant predators appeared in number. The effect of this extreme population fluctuation on the colonization curve is that species may be eliminated and added at a rate systematically different from that on an untreated island. The concept of a dual dynamic equilibrium—of species number and population structure—will be mentioned briefly in this paper and described more completely and formally by Simberloff (1969).

The joint evolution of the particular constellation of species on an island ought logically to raise $\hat{S}$ systematically over very long periods of time (Wilson and Taylor 1967), but we will neglect this effect because the time course of such a change is obviously beyond that of this experiment. Also, the invasion rates for most species on our islands are probably too high to allow significant genetic alteration to occur in populations on individual islands; they are not isolated in an evolutionary sense.

The curves of Figs. 1–3, except for that of E1, are believed best explained by the following equation, based on a model devised by W. H. Bossert and P. N. Holland:

$$\mathbf{E}[S(t)] = \sum_{\alpha=1}^{P} \frac{i_\alpha}{i_\alpha + e_\alpha}\left(1 - e^{-(i_\alpha + e_\alpha)t}\right)$$

where $\mathbf{E}[S(t)]$ = the expected number of colonists present at time t

P = number of species in the pool

i_α = invasion rate of species α

e_α = intrinsic probability of extinction for species α

The derivation of this equation and a discussion of the concepts involved will be presented elsewhere (Simberloff 1969). The important aspects of this theory for our immediate purpose, however, are as follows:

The variance of $S(t)$ is high:

$$\mathbf{var}\,[S(t)] = \sum_{\alpha=1}^{P} \mathbf{E}[S_\alpha(t)]\left\{1 - \mathbf{E}[S_\alpha(t)]\right\}$$

S_α is a species indicator variable, which equals 1 when species α is present and 0 when species α is absent. Also,

$$\mathbf{E}[S_\alpha(t)] = \frac{i_\alpha}{i_\alpha + e_\alpha}\left(1 - e^{-(i_\alpha + e_\alpha)t}\right).$$

Once the number of species on these particular islands is between about 75% and 90% of the equilibrium value of

$$\mathbf{E}[S(t)] \simeq \sum_{\alpha=1}^{P} \frac{i_\alpha}{i_\alpha + e_\alpha} = \hat{S}$$

the major premise of this stochastic version of the MacArthur-Wilson equilibrium theory, namely non-interaction of species, would be invalidated. From this point onward $S(t)$ declines slightly, at a slow rate which cannot yet be predicted well stochastically. It equilibrates ultimately at an enduring $\hat{S}$ partly determined by interaction and close to the number that existed before defaunation. The decrease on all islands in number of species present for the final census (after regular

monitoring had ended) is believed to be a manifestation of this decline.

E1 was so distant from its presumed source area that a few early invaders were able to build up large populations before their probable competitors arrived. Interactions thus became important before even a small fraction of the non-interaction $\hat{S}$ was achieved. We predict that on E1 the colonization curve will ascend slowly and irregularly to an equilibrium near the pre-defaunation $\hat{S}$. This enduring equilibrium will probably be the same one to which the colonization curve of E1 would ultimately have descended had interactions not become important until a large fraction of $\hat{S}$ had been achieved, as on the nearer islands.

As the distance of the island from the faunal source increases, the non-interaction $\hat{S}$ should decrease because of decreases in the i_α. Furthermore, the time necessary to reach any given percentage of the non-interaction $\hat{S}$, though not readily expressed mathematically, can be shown to increase with increasing distance from source. If this time is sufficiently long the few early colonists are able to produce large enough populations to interact significantly with later immigrants. This in fact is what happened on E1.

The colonization curve of E7 (Fig. 2) must be considered in light of the fact that 85% of the tree was killed by the fumigation (Wilson and Simberloff 1969). The dead portion did not disappear, but rather deteriorated until by the end of one year the wood was brown and dry and much of the bark was peeling. Thus the island was not a constant factor, and the relative proportions of the various microhabitats changed drastically until ultimately there was far more dead wood and bark and far less leafy canopy than on an untreated island. If a consistent measure of area existed for these islands it would probably have remained unchanged on E7, but the expected number of species would not because the different microhabitats normally support different numbers of species. In particular, dead bark shelters numerous species while mangrove leaves rarely support more than four species on a single island. Before its gradual decline, the colonization curve of E7 rose to a far higher percentage of the original $\hat{S}$ (135%) than did that of any other island. In addition, it was still rising a year after defaunation, when those of all other islands but E1 had leveled off. Arachnids (excluding orb-weavers) and psocopterans were the animals largely responsible for the higher S near the end of the experiment. Both groups are primarily bark dwellers.

All the above considerations imply that one of the determinants of the shape of the colonization curve on this island alone was variation of the island habitat, and that the enduring $\hat{S}$ which will ultimately be achieved on E7 may be very different from the pre-defaunation figure.

Dispersal

The agents of dispersal for specific immigrations can rarely be given with assurance, but the evidence implies that aerial transport, passive and active, is the major mode of invasion.

For the several parasites of vertebrates that breed on the islands proper, zoochorous transport is certain. These arthropods include the hippoboscid flies *Olfersia sordida* and *Lynchia albipennis* and tick *Argas radiatus* on E1 and E9. All three species parasitize the cormorants and pelicans which roost on these islands. A number of mite colonists could also have arrived on transient larger animals. This appears to be so for *Entonyssus* sp. on E2; it is an obligate parasite in snake lungs, and a *Natrix* was recorded sloughing on E2. The invasions of E1, E3, and E7 by the mite *Ornithonyssus bursa,* an avian parasite, were probably ornithochorous.

A more interesting possibility involves phoresy on birds, particularly by some of the psocopterans prominent among early immigrants. Mockford (1967) has hypothesized that phoresy may be a more efficient means of insular invasion than wind transport, especially for smaller species. Among four species found on Asian birds he lists *Ectopsocopsis cryptomeriae,* which has also colonized E3 and E7. Whether phoresy is a significant phenomenon in the Keys remains to be determined.

Other arthropods that may utilize phoresy are the pseudoscorpion *Tyrannochelifer* sp. found on E7, and free-living mites on all islands. These could have been transported by larger insects as well as by birds.

A related transport mechanism utilizes nesting material carried by birds. We suspect without proof that several mites in our experiment arrived in this fashion. Two beetle larvae were found in deep excavations in Green Heron nest twigs soon after the nests were built: *Chrysobothris tranquebarica* on E3 and ?*Sapintus fulvipes* on ST2 (the latter in a twig not of *Rhizophora*). It seems certain that both were in the twigs when the birds constructed their nests. Meyerriecks (1960) has observed green herons using twigs from other trees and from the nest tree itself. It is our impression that most nesting material that goes into new nests on small mangrove islands is brought from elsewhere. This was assuredly so for the non-mangrove twig on ST2.

Hydrochorous transport, either free or on rafts, was not as important as aerial transport in the invasion of our islands. Many mangrove colonists

remain afloat almost indefinitely in salt water, but only the orthopteroids seem able to achieve significant independent, oriented motion. Furthermore, most floating insects and spiders of all sizes are rapidly devoured by fingerling fishes which are immensely numerous about all mangrove islands. Even actively swimming crickets and earwigs frequently meet this fate, attracting more attackers by the very vigor of their efforts.

Nevertheless, at least one invasion (though not immigration, since the species was already present) occurred this way, and there are other pertinent observations. An adult female *Cyrtoxipha* cricket was seen floating from Upper Snipe Key to E2, a distance of only about 2 m. She successfully climbed a root and disappeared into the lower canopy. That a winged individual fully capable of oriented flight should actively choose to disperse by water is dubious, but at least over this short a distance the method is feasible in case the animal accidentally lands in the water.

Four *Automeris io* caterpillars were seen to float from one end of E9 to the other, a distance of about 8 m. Three of them lodged on roots and eventually climbed up out of the water. The weakening of leaves attacked simultaneously by several large *Automeris* caterpillars (a common occurrence) might cause them to fall into water occasionally. Also, the caterpillars release their hold readily when the branch is shaken, apparently as a defensive maneuver. It seems doubtful, however, that a high proportion of those that land in the water could successfully travel between islands. Aside from fish attack, they would be plagued by their inability to direct their motion and to climb readily from the water.

Occasionally earwigs (*Labidura riparia*) were seen swimming from one root to another within an island. We do not know how well this species flies, but its swimming ability seems adequate for aquatic travel of considerable distance, and it readily climbs out of the water. Fishes would still be a hazard, however.

Our experiments resulted in no unequivocal evidence of invasions by rafting. In fact, several considerations imply that rafting must play a minor role in mangrove colonization. There is rarely land on which rafts can lodge, since *Rhizophora* islands generally have no supratidal ground. Drifting wood usually hits an island, gets trapped temporarily among roots, and eventually floats away. Even more importantly, green *Rhizophora* wood sinks immediately and many dead twigs also fail to float, thus precluding rafting by much of the wood-boring fraction of the fauna. Finally, except during hurricanes, there is very little floating debris in Florida Bay—far less than the amount found at river mouths.

The preceding considerations lead, by elimination, to the inference that aerial transport must be an important means of dispersal to our islands. Several observations of actively flying propagules support this hypothesis. Buprestid and cerambycid beetles, lepidopterans, wasps, and a lacewing have all been seen to land on the islands after flight from an outside source. Many other mangrove colonists are evidently carried passively by wind, especially psocopterans, thrips, neuropterans, and most spiders. Many of these more or less passively dispersed organisms are minute, and direct evidence on their invasion method is therefore scarce. Occasionally spiderlings and psocopterans were found in the air around our islands. In general, they are usually important components of aerial plankton (Glick 1939), and it is known from numerous anecdotal records (e.g., Bristowe 1958) that ballooning for the distances involved in our experiment is regularly achieved by some species of spiders. So far, the small sizes of most of these animals has made it impossible to follow a flight visually from source to island. One suggestive record, however, is that of a spider dragline stretching the 2 m between Upper Snipe Key and E2.

An attempt to correlate Figures 1–3 with hourly wind data of the U. S. Weather Bureau station at Key West was inconclusive, but this piece of negative evidence is hardly damaging to the thesis of dominance of aerial transport. For such data give only timed readings at one nearby point, while dispersal depends largely on specific gusts at odd times in highly circumscribed areas about the islands. Furthermore the published wind data are from a single fixed anemometer, while the entire wind profile would be necessary to describe dispersal.

Immigration and Extinction Rates

The intermittent nature of the monitoring had the unavoidable result that many immigrations and extinctions (perhaps two-thirds) were not observed, the species involved being obligate or near-obligate transients which immigrate and are extinguished all within one interval between two monitoring periods. For this reason absolute immigration and extinction curves cannot be derived from the observational data.

The observed immigration and extinction curves for all islands were highly variable, with no apparent pattern except for generally higher immigration rates on nearer islands during the first 150 days. Rates were usually between 0.05 and 0.50 species/day. Employing a statistical method

devised by Simberloff (1969) it was determined that the very least the expected error in immigration and extinction rates could be is 0.67 species/day, and furthermore that the variance about the "expected" immigration and extinction curves is very high. The observed curves are consequently of limited interest, since they yield only an extreme lower limit for turnover rates and cannot be used to intuit shapes of the "expected" curves. On the other hand, the values of the turnover rates are of considerable interest even when they can be approximated only to the nearest order of magnitude. They are of course surprisingly high, in the vicinity of 1% of the equilibrial species number per day or higher. Yet this is at least roughly consistent with the MacArthur-Wilson (1967) model, which predicts that the turnover (= extinction) rate at equilibrium is 1.15 (mean $\check{S}/t_{0.90}$, where mean $\check{S}$ is the average equilibrial species number and $t_{0.90}$ is the time (in days) required to reach 90% of the equilibrial number. According to this formula, which is based on the simplest non-interactive version of the model, the turnover rates in our experimental islands should fall somewhere between 0.1 and 1.0 species/day. The relation between this version of the model and the more precise stochastic form of the model will be treated later at length by Simberloff (1969). The MacArthur-Wilson formulation is a special case of the many cases covered by the stochastic version and it has the advantage of permitting this first rough (and approximately correct) prediction of turnover rates.

In testing such predictions with measurements in the field there is reason to expect that the invasions not observed will occur by different means than those which are recorded. The assumption that most propagules arrived by air in the experimental keys is therefore probably valid. The evidence against a major seasonal component of dispersal was given earlier. In sum, we have a large body of information which implies that i_α (invasion rate of species α) is nearly constant through time for all α. What we lack at present is quantitative information on the sizes and distribution of the i_α.

Extinction rates, at least during most of the rise of the colonization curve from 0 to a large fraction of $\check{S}$ are adequately represented by the unchanging, species-characteristic e_α, without an additional S-dependent or density-dependent factor included. The main arguments behind this assertion are:

i) Most of the species in the Florida Keys pool are obligate transients on these small mangrove islands. For a variety of reasons not directly related to their own densities or to other species they are doomed to swift extinction.

ii) Population sizes during most of the rise of S from 0 to near $\check{S}$ are uniformly low.

The observed data from this experiment provide rough quantitative information on both the distribution and sizes of the e_α unlike with the i_α. Whatever the i_α and e_α, the expected curve of immigration rate vs. time is represented during the rise of S from 0 to a large fraction of the non-interaction $\check{S}$ by:

$$\mathbf{E}[I(t)] = \sum_{\alpha=1}^{P} i_\alpha - \frac{i_\alpha^2}{i_\alpha + e_\alpha}\left(1 - e^{-(i_\alpha + e_\alpha)t}\right)$$

$$= \sum_{\alpha=1}^{P} i_\alpha - i_\alpha \mathbf{E}[S_\alpha(t)]$$

while the expected curve of extinction rate vs. time during the same period is:

$$\mathbf{E}[E(t)] = \sum_{\alpha=1}^{P} \frac{i_\alpha e_\alpha}{i_\alpha + e_\alpha}\left(1 - e^{-(i_\alpha + e_\alpha)t}\right)$$

$$= \sum_{\alpha=1}^{P} e_\alpha \mathbf{E}[S_\alpha(t)]$$

Beyond this point accurately predicted curves are impossible. It is nevertheless clear that during the slight decline of S to an enduring $\check{S}$, $E(t)$ must be, on the average, slightly greater than $I(t)$, while after the equilibrium is reached the two must remain approximately equal. On any real island, of course, the two curves would cross and recross indefinitely. It also seems reasonable that after interactions become important, the $E(t)$ and $I(t)$ curves still do not change much, since the contribution from their common major component, the transients, does not change with time.

Whereas evidence on the specific agents of dispersal, and hence on immigration, has been plentiful during this study, observations on the causes of extinction have been meager. Obviously the probability of witnessing the death or disappearance of the last member of a population is exceedingly low. Some inferences can be drawn from observed means of population decrease.

Population decline should be most apparent when associated with interaction, especially predation, yet the small sizes of most populations during our experiment reduced interactions enormously. A few cases of predation have already been mentioned. Insectivorous birds, particularly warblers and red-winged blackbirds, were fre-

quently observed eating numerous insects of many species. Wasps, both parasitic and nonparasitic, were seen destroying several insects and spiders. Some of these attacks may have led directly to extinction, when the prey populations were small. Examples include the parasitism on *Automeris io* caterpillars by *Apanteles hemileucae* (Braconidae) and the destruction of the salticids *Hentzia palmarum* and *Stoidis aurata* by *Trypoxylon collinum* (Sphecidae).

Exclusion can also provide indirect evidence of extinction through interaction. A possible instance is the apparent predation of crickets on E9 by a large population of the centipede *Orphnaeus brasilianus*. E8, with no centipedes, had immense populations of four cricket species. After defaunation of E9 removed *Orphnaeus,* a large population of the cricket *Cyrtoxipha confusa* was rapidly established.

From observation of the pre-defaunation distribution of ant species' numbers and population sizes on the various islands, it seems probable that when one ant species is able to build up large populations before other species invade, it can exclude one or more other species. However, direct evidence of aggressive behavior among the mangrove ants is lacking; the observed exclusion may have been the result of nest site pre-emption.

Most extinctions were probably not the result of interactions, at least during the initial rise of the colonization curves, but rather resulted from the inability of most species in the Florida Keys pool to colonize these tiny mangrove islands under any conditions. Lack of proper food or nest site and hostile physical conditions are probably common causes. An example was the observation of a dealate queen of *Brachymyrmex* sp. on E9. Since this species nests in soil, which is lacking on the experimental islands, it is not surprising that no workers were subsequently observed, despite the fact that the queen landed in a totally ant-free environment.

Even species which can survive on small mangrove islands have high probabilities of extinction not related to interaction. A number of animals have been found drowned during this experiment, including entire small ant colonies, numerous lepidopterous larvae, beetles, and psocopterans. It seems probable that during the hurricanes which periodically buffet these islands such deaths would be commonplace.

Similarly, numerous mangrove colonists inhabit hollow twigs and even under normal conditions many of these fall into the water. Certainly such events are multiplied during storms. The ant *Camponotus floridanus* and the oedemerid beetle *Oxycopis* sp. seem particularly vulnerable in this respect: they typically inhabit low, weakly anchored, hollow roots.

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LITERATURE CITED

Bristowe, W. S. 1958. The world of spiders. Collins, London. 308 p.

Cotteau, E. 1885. A week at Krakatau. Proc. Geogr. Soc. Australia, N.S.W. and Victorian branches, II.

Glick, P. A. 1939. The distribution of insects, spiders, and mites in the air. U.S.D.A. Tech. Bull. 673. 151 p.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press. 203 p.

Meyerriecks, A. J. 1960. Comparative breeding behavior of four species of North American herons. Publ. Nuttall Ornithological Club, No. 2. 158 p.

Mockford, E. L. 1967. Some Psocoptera from plumage of birds. Proc. Entomol. Soc. Wash. **69**: 307–309.

Simberloff, D. 1969. Experimental zoogeography of islands. III. A theory of insular colonization. Ecology (in press).

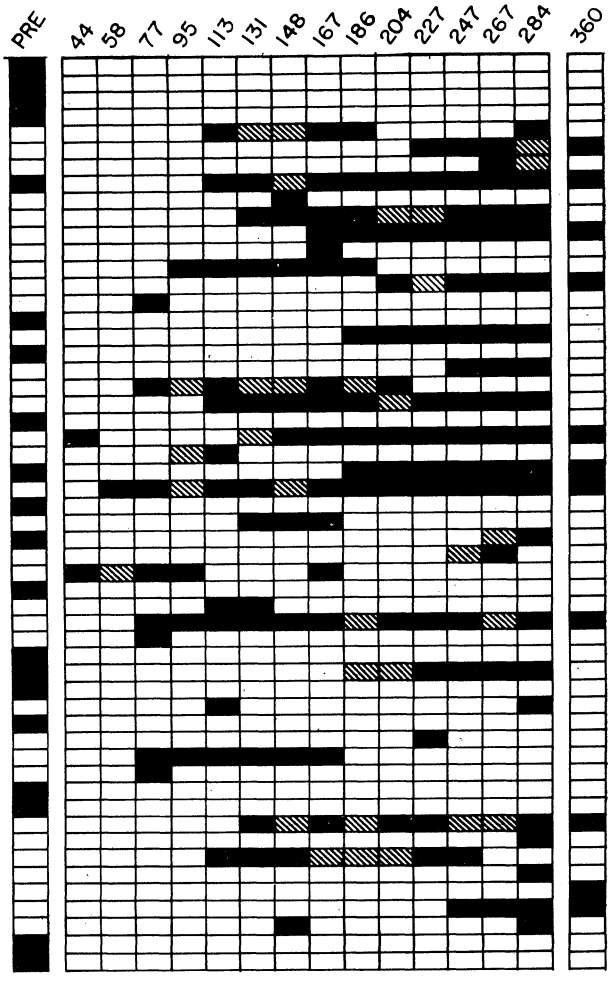
Wilson, E. O., and D. Simberloff. 1969. Experimental zoogeography of islands. Defaunation and monitoring techniques. Ecology **50**: 267–278.

Wilson, E. O., and R. W. Taylor. 1967. An estimate of the potential evolutionary increase in species density in the Polynesian ant fauna. Evolution **21**: 1–10.

APPENDIX. The colonists of six experimentally defaunated islands. Headings identify the island and give the number of days after defaunation for each census; "Pre" is the pre-defaunation census. Solid entries indicate that a species was seen; shaded, that it was inferred to be present from other evidence; open, that it was not seen and inferred to be absent.

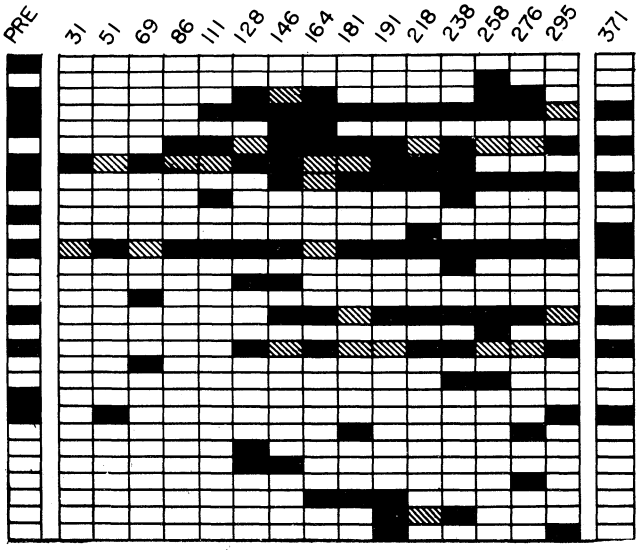
THE COLONISTS OF ISLAND E 1

THYSANURA	Lepismidae	Lepisma sp.
ORTHOPTERA	Blattidae	Latiblattella n. sp.
	Gryllidae	Cycloptilum sp.
		Tafalisca lurida
DERMAPTERA	Labiduridae	Labidura riparia
COLEOPTERA	Anthicidae	Sapintus fulvipes
	Curculionidae	Cryptorhynchus minutissimus
		Pseudoacalles sp.
		Gen. sp.
THYSANOPTERA	Phlaeothripidae	Neurothrips magnafemoraus
	Thripidae	Pseudothrips inequalis
CORRODENTIA	Peripsocidae	Ectopsocus sp. b
		Peripsocus pauliani
		Peripsocus stagnivagus
		Peripsocus sp. c
	Psocidae	Psocidus texanus
HEMIPTERA	Aleyrodidae	Tetraleurodes sp.
	Coccidae	Ceroplastes sp.
	Miridae	Psallus conspurcatus
NEUROPTERA	Chrysopidae	Chrysopa collaris
		Chrysopa rufilabris
LEPIDOPTERA	Eucleidae	Alarodia slossoniae
	Hesperiidae	Phocides batabano
	Lymantriidae	Orgygia detrita
	Olethreutidae	Ecdytolopha sp.
	Phycitidae	Bema ydda
	Ptineidae	Nemapogon sp.
	Pyralidae	Gen. sp.
	Saturniidae	Automeris io
DIPTERA	Hippoboscidae	Lynchia albipennis
		Olfersia sordida
HYMENOPTERA	Bethylidae	Scleroderma macrogaster
	Chalcidae	Brachymeria psyche
	Eumenidae	Pachodynerus nasidens
	Formicidae	Camponotus tortuganus
		Colobopsis sp.
		Crematogaster ashmeadi
		Pseudomyrmex elongatus
	Ichneumonidae	Calliephialtes ferrugineus
		Casinaria texana
ORDER UNK.	Fam. Unk.	Gen. sp.
ARANEAE	Araneidae	Eustala sp. 1
		Nephila clavipes
	Salticidae	Hentzia palmarum
	Fam. Unk.	Gen. sp.
ACARINA	Argasidae	Argas radiatus
	Ascidae	Arctoseius sp.
	Dermanyssidae	Ornithonyssus bursa
		Pellonyssus sp.
	Galumnidae	Galumna sp.
	Oribatulidae	Scheloribates sp.
	Phytoseiidae	Amblyseius sp.
ISOPODA		Rhyscotus sp.
DIPLOPODA	Polyxenidae	Lophoproctinus bartschi



THE COLONISTS OF ISLAND E 2

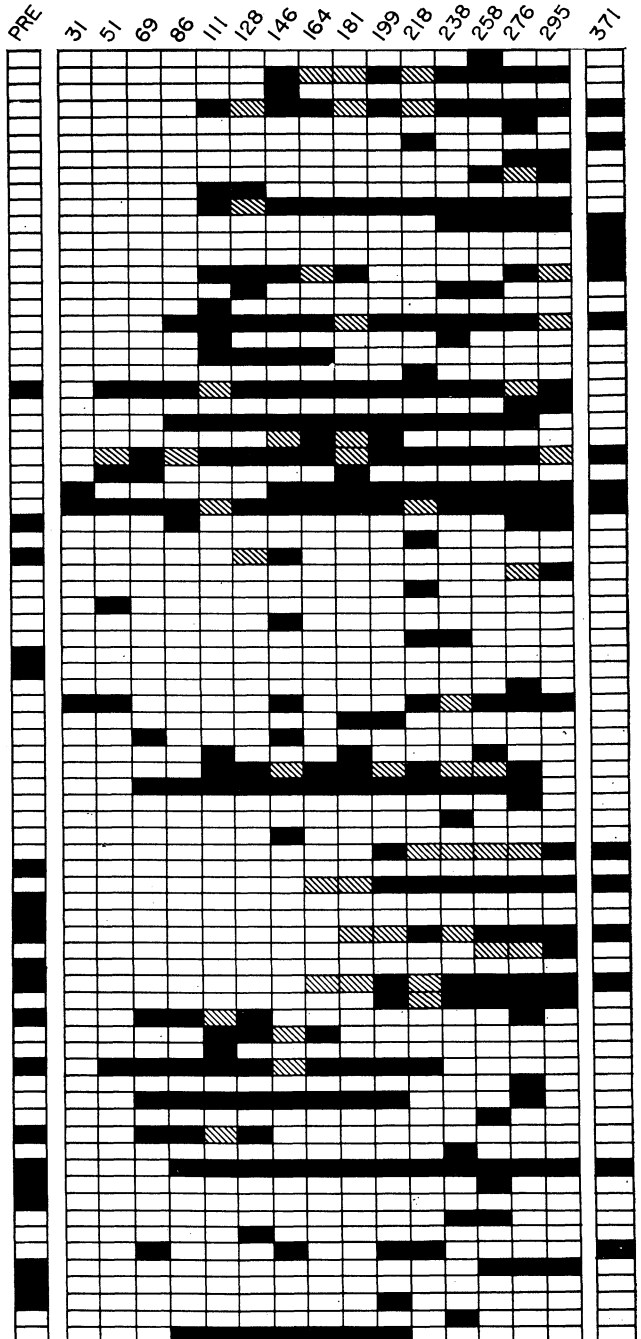
EMBIOPTERA	Teratembiidae	Gen. sp.
ORTHOPTERA	Blattidae	Aglaopteryx sp.
		Latiblattella n. sp.
		Latiblattella rehni
	Gryllidae	Cycloptilum sp.
		Cyrtoxipha sp.
		Orocharis gryllodes
		Tafalisca lurida
	Tettigoniidae	Turpilia rostrata
ISOPTERA	Kalotermitidae	Kalotermes jouteli
		Neotermes castaneus
COLEOPTERA	Anobiidae	Tricorynus sp.
	Anthicidae	Sapintus fulvipes
	Buprestidae	Actenodes auronotata
		Chrysobothris sexfasciatus
		Chrysobothris tranquebarica
	Cerambycidae	Ataxia sp.
		Styloleptus biustus
	Chrysomelidae	Gen. sp.
	Cucujidae	Gen. sp.
	Curculionidae	Cryptorhynchus minutissimus
		Pseudoacalles sp.
	Lampyridae	Micronaspis floridana
	Oedemeridae	Copidita suturalis
		Oxacis sp.
		Oxycopis sp.
	Scolytidae	Poecilips rhizophorae
		Trischidias atoma
	Fam. Unk.	Gen. sp.



APPENDIX - PART 2

THE COLONISTS OF ISLAND E 2 (cont.)

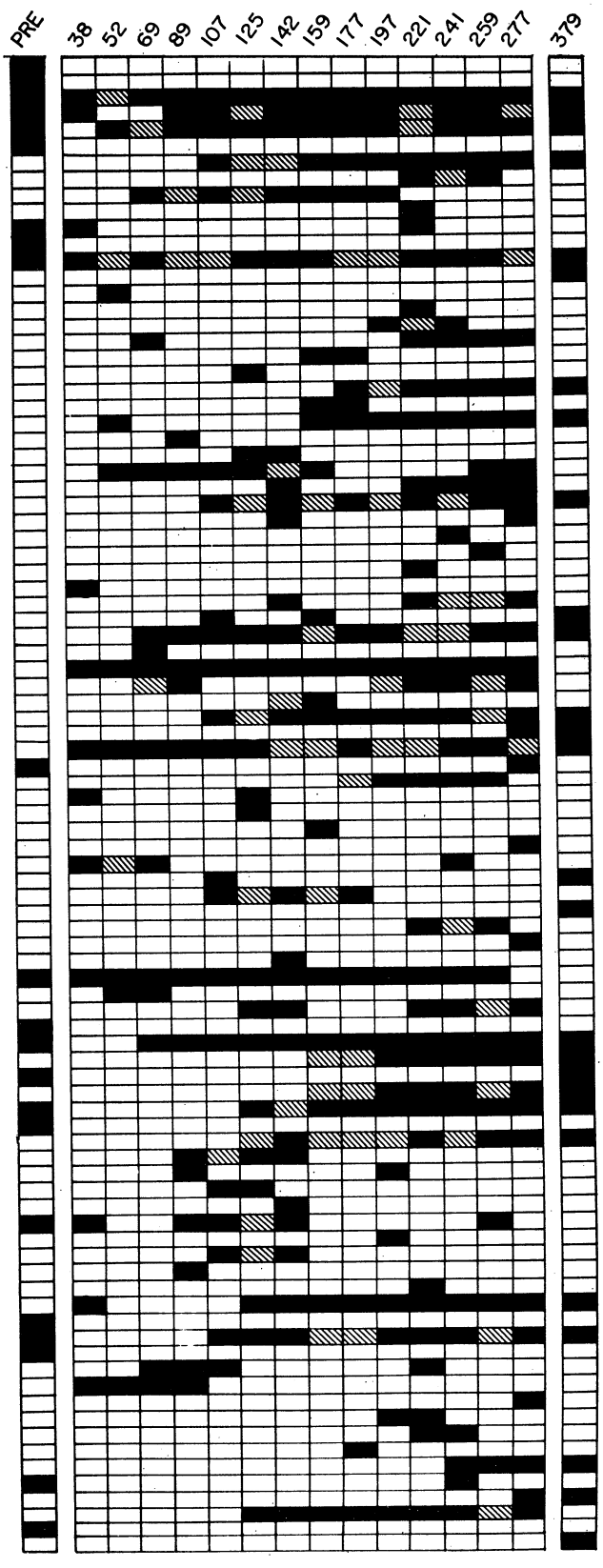
THYSANOPTERA	Phlaeothripidae	Liothrips n. sp.
	Thripidae	Pseudothrips inequalis
	Fam. Unk.	Gen. sp.
CORRODENTIA	Caeciliidae	Caecilius sp. n-b
	Lepidopsocidae	Echmepteryx hageni b
	Liposcelidae	Gen. sp.
	Peripsocidae	Peripsocus sp.
	Psocidae	Psocidus texanus
HEMIPTERA	Acanaloniidae	Acanalonia latifrons
	Aleyrodidae	Aleurothrixus sp.
		Paraleyrodes sp. 1
		Paraleyrodes sp. 2
		Tetraleurodes sp.
	Cicadellidae	Scaphytopius sp.
	Cixiidae	Gen. sp.
	Flatidae	Flatoidinus punctatus
	Miridae	Psallus conspurcatus
	Pseudococcidae	Pseudococcus sp.
	Tropiduchidae	Neurotmeta breviceps
	Fam. Unk.	Gen. sp.
NEUROPTERA	Chrysopidae.	Chrysopa collaris
		Chrysopa externa
		Chrysopa rufilabris
LEPIDOPTERA	Geometridae	Oxydia sp.
	Hesperiidae	Phocides batabano
	Noctuidae	Melipotis sp.
	Olethreutidae	Ecdytolopha sp.
	Phycitidae	Bema ydda
	Ptineidae	Nemapogon sp.
	Pyralidae	Gen. sp.
	Saturniidae	Automeris io
DIPTERA	Cecidomyidae	Gen. sp.
	Culicidae	Aedes taeniorhynchus
	Syrphidae	Gen. sp.
	Fam. Unk.	Gen. sp.
HYMENOPTERA	Bethylidae	Cephalonomia waterstoni
		Scleroderma macrogaster
	Braconidae	Apanteles hemileucae
		Callihormius bifasciatus
		Heterospilus sp.
		Iphiaulax epicus
	Chalcedectidae	Euchrysia sp.
	Chalcidae	Gen. sp.
	Encyrtidae	Ooencyrtus submetallicus
	Eumenidae	Pachodynerus nasidens
	Eupelmidae	Metapelma schwarzi
		Neanastatus sp.
		Gen. sp.
	Formicidae	Camponotus floridanus
		Camponotus tortuganus
		Crematogaster ashmeadi
		Monomorium floricola
		Paracryptocerus varians
		Pseudomyrmex elongatus
		Pseudomyrmex "flavidula"
		Tapinoma littorale
		Xenomyrmex floridanus
	Ichneumonidae	Calliephialtes ferrugineus
		Casinaria texana
	Sphecidae	Trypoxylon collinum
	Araneidae	Argiope argentata
		Eustala sp. 1
		Eustala sp. 2
		Gasteracantha ellipsoides
		Gen. sp.
		Nephilia clavipes
ARANEAE	Clubionidae	Anyphaena sp.
		Aysha sp.
		Gen. sp. 1
	Gnaphosidae	Gnaphosa sp.
	Linyphiidae	Meioneta sp.
	Salticidae	Ballus sp.
		Hentzia palmarum
		Metacyrba undata
		Gen. sp. II
	Segestriidae	Ariadna arthuri
	Tetragnathidae	Leucauge venusta
		Tetragnatha sp.
	Theridiidae	Gen. sp.
ACARINA	Acaridae	Rhizoglyphus callae
	Bdellidae	Gen. sp.
	Cheyletidae	Cheyletia wellsi
	Dermanyssidae	Gen. sp.
	Entonyssidae	Entonyssus sp.
	Galumnidae	Galumna sp.
	Oribatulidae	Scheloribates sp.
	Phytoseiidae	Amblyseius sp.
	Tetranychidae	Tetranychus sp.
		Rhyscotus sp.
DIPLOPODA	Polyxenidae	Lophoproctinus bartschi



APPENDIX - PART 3

THE COLONISTS OF ISLAND E3

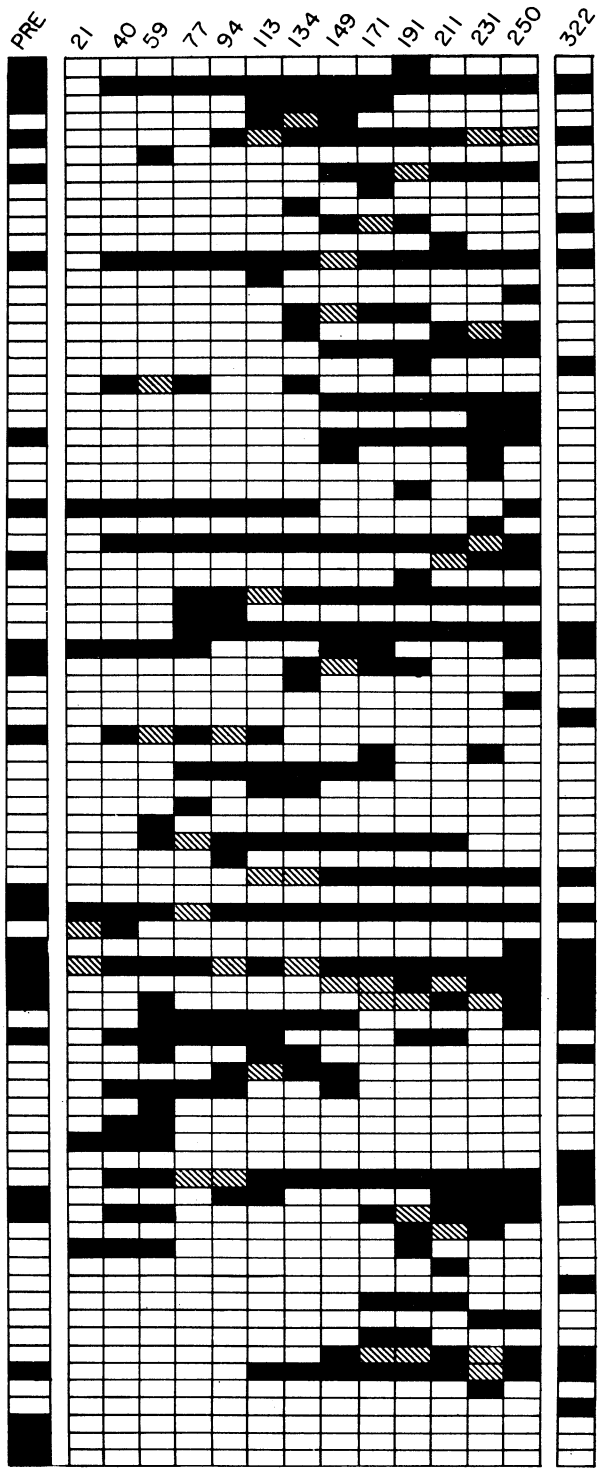
COLLEMBOLA	Poduridae	Gen. sp.
EMBIOPTERA	Teratembiidae	Diradius caribbeana
ORTHOPTERA	Blattidae	Latiblattella n. sp.
	Gryllidae	Cycloptilum spectabile
		Tafalisca lurida
ISOPTERA	Kalotermitidae	Kalotermes jouteli
COLEOPTERA	Anobiidae	Tricorynus sp.
	Anthicidae	Sapintus fulvipes
	Buprestidae	Actenodes auronotata
		Chrysobothris tranquebarica
	Cerambycidae	Styloleptus biustus
	Curculionidae	Cryptorhynchus minutissimus
		Pseudoacalles sp.
	Lathridiidae	Melanophthalma floridana
	Oedemeridae	Oxacis sp.
		Oxycopis sp.
	Scolytidae	Trischidias atoma
THYSANOPTERA	Phlaeothripidae	Haplothrips flavipes
		Liothrips n. sp.
		Neurothrips magnafemoralis
	Thripidae	Pseudothrips inequalis
	Fam. Unk.	Gen. sp.
CORRODENTIA	Liposcelidae	Liposcelis bostrychophilus
	Peripsocidae	Ectopsocopsis cryptomeriae
		Ectopsocus sp. c
		Peripsocus pauliani
	Psocidae	Psocidus texanus
HEMIPTERA	Aleyrodidae	Tetraleurodes sp.
	Anthocoridae	Dufouriellus afer
		Orius sp.
	Cicadellidae	Scaphytopius sp.
	Lygaeidae	Gen. sp. 2
	Membracidae	Gen. sp.
	Miridae	Psallus conspurcatus
	Nabidae	Carthasis decoratus
NEUROPTERA	Chrysopidae	Chrysopa collaris
		Chrysopa externa
		Chrysopa rufilabris
LEPIDOPTERA	Eucleidae	Alarodia slossoniae
	Geometridae	Oxydia sp.
	Hesperiidae	Phocides batabano
	Olethreutidae	Ecdytolopha sp.
	Phycitidae	Bema ydda
	Ptineidae	Nemapogon sp.
	Saturniidae	Automeris io
HYMENOPTERA	Bethylidae	Nesepyris floridanus
		Scleroderma macrogaster
		Gen. sp.
	Braconidae	Heterospilus sp.
		Iphiaulax epicus
		Macrocentrus sp.
	Chalcidae	Brachymeria psyche
		Gen. sp.
	Encyrtidae	Gen. sp.
	Eulophidae	Entedontini sp.
		Melittobia chalybii
	Eumenidae	Pachodynerus nasidens
	Eupelmidae	Gen. sp. 1
		Gen. sp. 2
	Formicidae	Colobopsis sp.
		Crematogaster ashmeadi
		Monomorium floricola
		Paracryptocerus varians
		Paratrechina bourbonica
		Pseudomyrmex elongatus
		Tapinoma littorale
		Xenomyrmex floridanus
	Ichneumonidae	Calliephialtes ferrugineus
		Casinaria texana
	Scelionidae	Probaryconus sp.
		Telonemus sp.
	Sphecidae	Trypoxylon collinum
	Vespidae	Gen. sp.
ARANEAE	Araneidae	Eustala sp. 1
		Gasteracantha ellipsoides
	Clubionidae	Anyphaena sp.
		Aysha sp.
	Gnaphosidae	Sergiolus sp.
	Salticidae	Hentzia palmarum
	Segestriidae	Ariadna arthuri
	Tetragnathidae	Leucauge venusta
		Tetragnatha antillana
	Theridiidae	Gen. sp.
ACARINA	Acaridae	Tyrophagus putrescentiae
	Ascidae	Asca sp.
	Dermanyssidae	Gen. sp.
	Eupodidae	Eupodes sp. nr. fusifer
	Galumnidae	Galumna sp.
	Oribatulidae	Scheloriba'es sp.
	Phytoseiidae	Amblyseius sp.
DIPLOPODA	Polyxenidae	Lophoproctinus bartschi
ISOPODA		Rhyscotus sp.



APPENDIX – PART 4

THE COLONISTS OF ISLAND ST 2

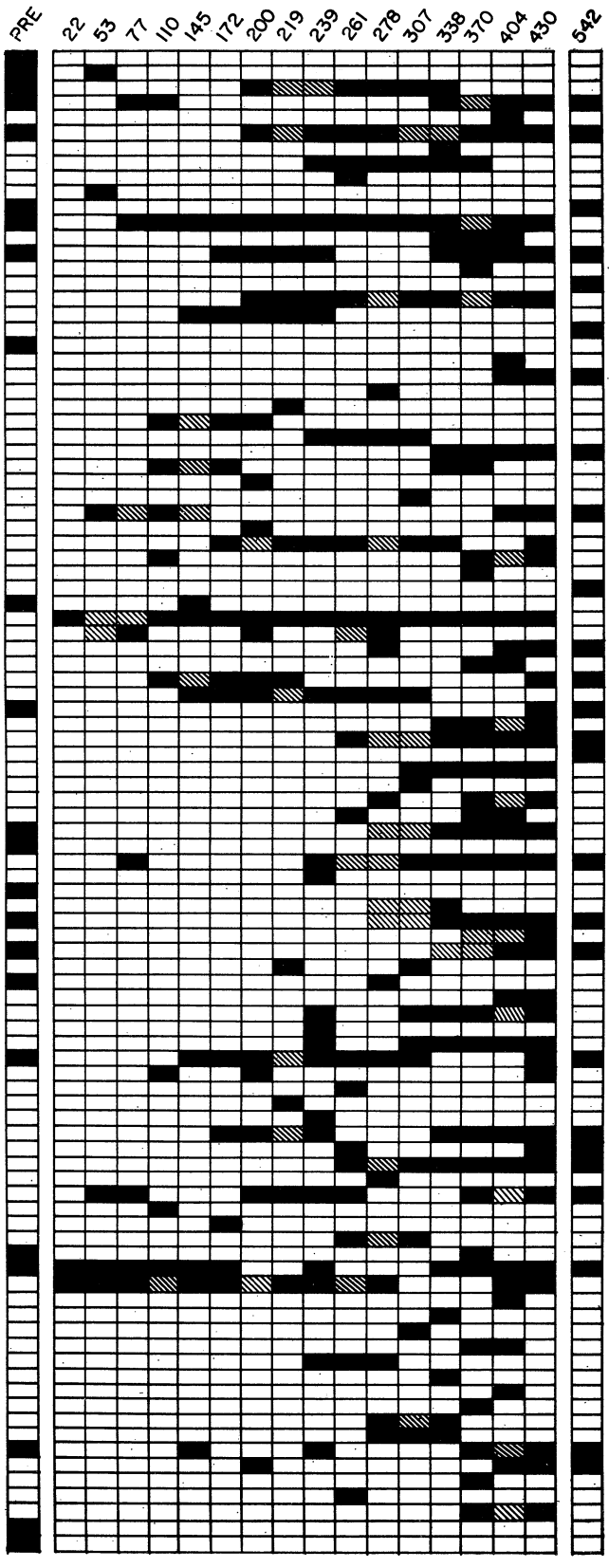
EMBIOPTERA	Teratembiidae	Diradius caribbeana
ORTHOPTERA	Blattidae	Latiblattella n. sp.
	Gryllidae	Cycloptilum sp.
		Cyrtoxipha sp.
		Tafalisca lurida
ISOPTERA	Kalotermitidae	Kalotermes jouteli
COLEOPTERA	Anobiidae	Tricorynus sp.
	Anthicidae	Gen. sp.
	Buprestidae	Gen. sp.
	Cerambycidae	Styloleptus biustus
	Curculionidae	Cryptorhynchus sp.
		Pseudoacalles sp.
	Lathridiidae	Melanophthalma floridana
	Oedemeridae	Oxycopis sp.
THYSANOPTERA	Phlaeothripidae	Haplothrips flavipes
		Liothrips n. sp.
	Thripidae	Pseudothrips inequalis
CORRODENTIA	Liposcelidae	Liposcelis bostrychophilus
	Peripsocidae	Ectopsocus sp.
		Peripsocus pauliani
		Peripsocus stagnivagus
	Psocidae	Psocidus texanus
HEMIPTERA	Aleyrodidae	Tetraleurodes sp.
	Lygaeidae	Blissus insularis
		Gen. sp. 2
NEUROPTERA	Chrysopidae	Chrysopa collaris
		Chrysopa externa
		Chrysopa rufilabris
LEPIDOPTERA	Eucleidae	Alarodia slossoniae
	Geometridae	Gen. sp.
	Hesperiidae	Phocides batabano
	Lymantriidae	Orgygia detrita
	Olethreutidae	Ecdytolopha sp.
	Phycitidae	Bema ydda
	Ptineidae	Nemapogon sp.
	Pyraustidae	Gen. sp.
DIPTERA	Fam. Unk. 1	Gen. sp.
	Fam. Unk. 2	Gen. sp.
HYMENOPTERA	Bethylidae	Scleroderma macrogaster
	Braconidae	Iphiaulax epicus
		Macrocentrus sp.
		Gen. sp.
	Chalcidae	Brachymeria psyche
		Gen. sp.
	Eumenidae	Pachodynerus nasidens
	Eupelmidae	Gen. sp.
	Formicidae	Camponotus floridanus
		Colobopsis sp.
		Crematogaster ashmeadi
		Crematogaster atkinsoni
		Paracryptocerus varians
		Pseudomyrmex elongatus
		Tapinoma littorale
		Xenomyrmex floridanus
	Ichneumonidae	Calliephialtes ferrugineus
		Casinaria texana
	Sphecidae	Trypoxylon collinum
	Apocrita	Gen. sp.
ARANEAE	Araneidae	Eustala sp. 1
		Eustala sp. 2
		Gasteracantha ellipsoides
		Nephila clavipes
	Clubionidae	Anyphaena sp.
		Aysha velox
	Salticidae	Hentzia palmarum
	Segestriidae	Ariadna arthuri
	Tetragnathidae	Leucauge venusta
		Tetragnatha sp.
	Theridiidae	Theridion sp.
ACARINA	Ascidae	Arctoseius sp.
		Asca sp.
	Bdellidae	Bdella sp.
	Eupodidae	Eupodes sp. nr. fusifer
	Oribatulidae	Scheloribates sp.
	Phytoseiidae	Amblyseius sp.
	Veigaiidae	Veigaia sp.
	Fam. Unk.	Gen. sp.
CHELONETHIDA	Cheliferidae	Tyrannochelifer n. sp.
PAUROPODA		Gen. sp.
DIPLOPODA	Polyxenidae	Lophoproctinus bartschi



APPENDIX – PART 5

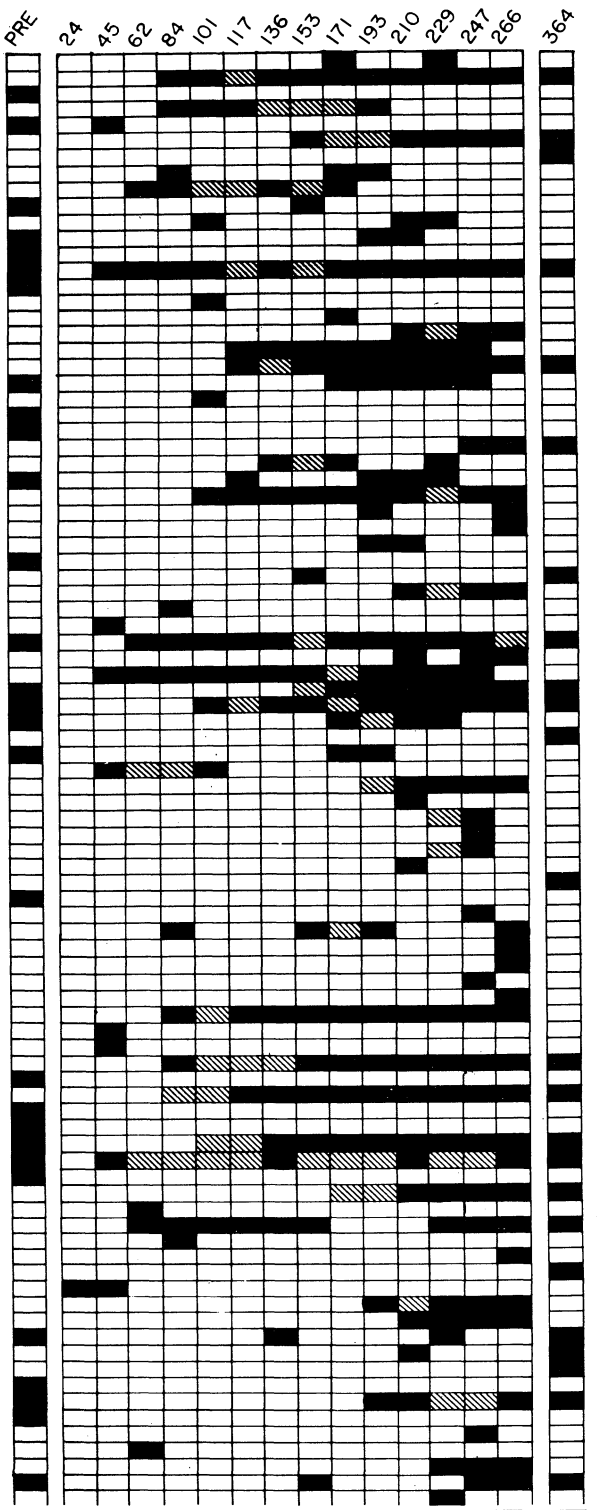
THE COLONISTS OF ISLAND E 7

EMBIOPTERA	Teratembiidae	Gen. sp.
ORTHOPTERA	Blattidae	Latiblattella n. sp.
	Gryllidae	Cycloptilum sp.
		Tafalisca lurida
DERMAPTERA	Labiduridae	Labidura riparia
COLEOPTERA	Anobiidae	Tricorynus sp.
	Anthicidae	Gen. sp.
	Buprestidae	Actenodes auronotata
		Chrysobothris tranquebarica
		Gen. sp.
	Cerambycidae	Leptostylus sp.
		Styloleptus biustus
	Cucujidae	Gen. sp.
	Curculionidae	Pseudoacalles sp.
	Oedemeridae	Gen. sp.
	Scydmaenidae	Gen. sp.
THYSANOPTERA	Phlaeothripidae	Haplothrips flavipes
		Neurothrips magnafemoralis
	Thripidae	Pseudothrips inequalis
CORRODENTIA	Archipsocidae	Archipsocus panama
	Liposcelidae	Embidopsocus laticeps
		Liposcelis bostrychophilus
	Myopsocidae	Lichenomima sp. b
		Gen. sp.
	Peripsocidae	Ectopsocopsis cryptomeriae
		Ectopsocus maindroni
		Peripsocus pauliani
		Peripsocus stagnivagus
		Peripsocus sp. b
		Peripsocus sp. c
	Psocidae	Psocidus texanus
		Psocidus sp. nr. bisignatus
		Psocidus sp. 1
		Psocidus sp. 2
HEMIPTERA	Nabidae	Carthasis decoratus
		Metatropiphorus belfragei
	Pseudococcidae	Pseudococcus sp.
NEUROPTERA	Chrysopidae	Chrysopa collaris
		Chrysopa rufilabris
LEPIDOPTERA	Hesperiidae	Phocides batabano
	Lymantriidae	Orgygia detrita
	Olethreutidae	Ecdytolopha sp.
	Phycitidae	Bema ydda
	Ptineidae	Nemapogon sp.
HYMENOPTERA	Bethylidae	Cephalonomia waterstoni
		Scleroderma macrogaster
	Braconidae	Apanteles hemileucae
		Iphiaulax epicus
	Chalcedectidae	Euchrysia sp.
	Chalcidae	Gen. sp.
	Eumenidae	Pachodynerus nasidens
	Formicidae	Camponotus floridanus
		Camponotus planatus
		Crematogaster ashmeadi
		Hypoponera opacior
		Paracryptocerus varians
		Paratrechina bourbonica
		Pseudomyrmex elongatus
		Pseudomyrmex "flavidula"
		Xenomyrmex floridanus
	Ichneumonidae	Calliephialtes ferrugineus
		Casinaria texana
	Scelionidae	Probaryconus sp.
	Sphecidae	Trypoxylon collinum
	Vespidae	Gen. sp.
ARANEAE	Araneidae	Argiope argentata
		Eustala sp. 1
		Eustala sp. 2
		Gasteracantha ellipsoides
		Mangora sp.
		Nephila clavipes
	Clubionidae	Aysha sp.
	Dictynidae	Dictyna sp.
	Gnaphosidae	Sergiolus sp.
	Pisauridae	Dolomedes sp.
	Salticidae	Hentzia palmarum
		Maevia vittata
		Paraphidippus flavus
		Stoidis aurata
	Segestriidae	Ariadna arthuri
	Tetragnathidae	Leucauge venusta
		Tetragnatha antillana
	Theridiidae	Argyrodes nephilae
		Theridion adamsoni
		Theridion atropunctatum
	Thomisidae	Misumenops sp.
	Uloboridae	Uloborus sp.
	Fam. Unk.	Gen sp.
ACARINA	Acaridae	Tyrophagus putrescentiae
	Ascidae	Proctolaelaps hypudaei
		Proctolaelaps pygmaeus
	Dermanyssidae	Ornithonyssus bursa
	Galumnidae	Galumna sp.
	Phytoseiidae	Amblyseius sp.
	Saproglyphidae	Gen. sp.
	Tydeidae	Triophtydeus sp.
CHELONETHIDA	Cheliferidae	Tyrannochelifer sp.
ISOPODA		Rhyscotus sp.
CHILOPODA	Oryidae	Orphnaeus brasilianus



APPENDIX - PART 6
THE COLONISTS OF ISLAND E9

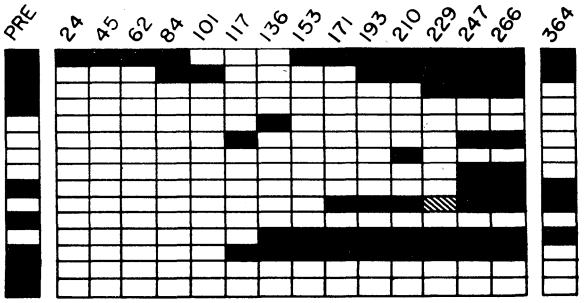
ORTHOPTERA	Gryllidae	Cycloptilum sp.
		Cyrtoxipha confusa
		Orocharis sp.
DERMAPTERA	Labiduridae	Labidura riparia
COLEOPTERA	Anobiidae	Cryptorama minutum
		Tricorynus sp.
	Anthicidae	Sapintus fulvipes
		Vacusus vicinus
	Buprestidae	Actenodes auronotata
		Chrysobothris tranquebarica
	Cantharidae	Chauliognathus marginatus
	Cerambycidae	Styloleptus biustus
	Curculionidae	Cryptorhynchus minutissimus
		Pseudoacalles sp.
	Lathridiidae	Holoparamecus sp.
	Oedemeridae	Oxacis sp.
	Fam. Unk.	Gen. sp.
THYSANOPTERA	Phlaeothripidae	Haplothrips flavipes
		Neurothrips magnafemoralis
	Thripidae	Pseudothrips inequalis
CORRODENTIA	Caeciliidae	Caecilius sp. np.
	Lachesillidae	Lachesilla n. sp.
	Lepidopsocidae	Echmepteryx hageni b
	Liposcelidae	Belaphotroctes okalensis
		Embidopsocus laticeps
		Liposcelis sp. not bostrychophilus
	Peripsocidae	Ectopsocus sp. bu
		Peripsocus stagnivagus
	Psocidae	Psocidus texanus
		Psocidus sp. 1
	Trogiomorpha	Gen. sp.
HEMIPTERA	Anthocoridae	Dufouriellus afer
	Cixiidae	Oliarus sp.
	Miridae	Psallus conspurcatus
	Pentatomidae	Oebalus pugnax
	Fam. Unk.	Gen. sp.
NEUROPTERA	Chrysopidae	Chrysopa collaris
		Chrysopa externa
		Chrysopa rufilabris
LEPIDOPTERA	Eucleidae	Alarodia slossoniae
	Olethreutidae	Ecdytolopha sp.
	Phycitidae	Bema ydda
	Psychidae	Oiketicus abbottii
	Ptineidae	Nemapogon sp.
	Pyralidae	Tholeria reversalis
	Saturniidae	Automeris io
	Fam. Unk.	Gen. sp.
DIPTERA	Hippoboscidae	Olfersia sordida
	Fam. Unk.	Gen. sp.
HYMENOPTERA	Braconidae	Apanteles hemileucae
		Apanteles marginiventris
		Callihormius bifasciatus
		Ecphylus n. sp. nr. chramesi
		Iphiaulax epicus
	Chalcidae	Gen. sp. 1
		Gen. sp. 2
		Gen. sp. 3
		Gen. sp. 4
	Eulophidae	Euderus sp.
	Eumenidae	Pachodynerus nasidens
	Eupelmidae	Gen. sp.
	Formicidae	Brachymyrmex sp.
		Camponotus floridanus
		Camponotus sp.
		Crematogaster ashmeadi
		Monomorium floricola
		Paracryptocerus varians
		Pseudomyrmex elongatus
		Pseudomyrmex "flavidula"
		Tapinoma littorale
		Xenomyrmex floridanus
		Gen. sp.
	Ichneumonidae	Calliephialtes ferrugineus
		Casinaria texana
	Pteromalidae	Urolepis rufipes
	Sphecidae	Trypoxylon collinum
	Vespidae	Polistes sp.
ARANEAE	Araneidae	Argiope argentata
		Eriophora sp.
		Eustala sp.
		Gasteracantha ellipsoides
		Metepeira labyrinthea
		Nephila clavipes
	Clubionidae	Aysha sp.
	Dictynidae	Dictyna sp.
	Gnaphosidae	Sergiolus sp.
	Linyphiidae	Meioneta sp.
	Lycosidae	Pirata sp.
	Salticidae	Hentzia palmarum
	Scytodidae	Scytodes sp.



APPENDIX – PART 7

THE COLONISTS OF ISLAND E9 (cont.)

	Tetragnathidae	Leucauge venusta
		Tetragnatha antillana
		Tetragnatha sp. 2
	Theridiidae	Gen. sp.
	Uloboridae	Uloborus sp.
ACARINA	Argasidae	Argas radiatus
	Ascidae	Lasioseius sp.
		Melichares sp.
	Bdellidae	Bdella sp.
	Carpoglyphidae	Carpoglyphus lactis
	Erythraeidae	Sphaerolophus sp.
	Galumnidae	Galumna sp.
	Phytoseiidae	Amblyseius sp.
ISOPODA		Rhyscotus sp.
CHILOPODA	Oryidae	Orphnaeus brasilianus



EXPERIMENTAL ZOOGEOGRAPHY OF ISLANDS: A MODEL FOR INSULAR COLONIZATION

DANIEL S. SIMBERLOFF[1]

Biological Laboratories, Harvard University, Cambridge, Massachusetts 02138

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Abstract. A distinction is made between immigration rate (in spp./time) for an island, and invasion rate (in propagules/time) for a species and an island. An analogous distinction is drawn between an island extinction rate and a species extinction rate (or intrinsic probability of extinction in a given time interval). It is claimed that the most objective definition for "propagule" is any animal or group capable of population increase under any conceivable circumstances. Immigration and island extinction curves are unique only if plotted against time, not against number of species.

A model for non-interactive colonization is discussed, and its equilibrium number of species, $\hat{S}$ derived. It is shown that data from the defaunated Florida Keys can be interpreted as arising from non-interactive colonization to an S near the non-interactive $\hat{S}$ (and to a point above a more enduring interactive $\hat{S}$), followed by a slow decline in S (as population sizes and interaction increase) to an enduring $\hat{S}$ near that obtaining before defaunation.

The effect on this scheme of increasing distance from source area is shown, and a simulation of the non-interactive part of the scheme was performed which corroborates that part of the model.

Explicit equations for the "expected" colonization, immigration, and island extinction curves are given for non-interactive colonization, and predictions are given about the general changes in these curves as interaction becomes significant.

SYMBOLS USED IN THE TEXT

$C(t)$ colonization rate, in species/time, at time t

$e_\tau(\alpha)$ probability that species α, if present, is extinguished in time period of length τ.

e_α species extinction rate of species α, defined analogously to i_α (q.v.); $\lim_{\tau \to 0} \frac{e_\tau(\alpha)}{\tau}$ $\tau \to 0$.

If species α were replaced immediately upon extinction, e_α would be the frequency of extinctions/time.

$E(t)$ extinction rate for island, in species/time, at time t

$E_\alpha(t)$ contribution to island extinction rate of species α; defined in text

$i_\tau(\alpha)$ probability that species α invades in time period of length τ.

i_α invasion rate of species α, in propagules/time

$I(t)$ immigration rate for island, in species/time, at time t

$I_\alpha(t)$ contribution to immigration rate of species α; defined in text

P number of species in species pool

$S(t)$ number of species on island at time t

$\hat{S}$ equilibrium number of species for island

$S_\alpha(t)$ species indicator variable for species α
$= 1$ if species α present on island during time period t
$= 0$ otherwise

INTRODUCTION

A discussion of theoretical zoogeography must be based on clear definitions of the following often ambiguous terms:

[1] Present address: Department of Biological Science, Florida State University, Tallahassee, Florida 32306