

ASSEMBLY OF MANGROVE ANT COMMUNITIES: PATTERNS OF GEOGRAPHICAL DISTRIBUTION

By BLAINE J. COLE

Department of Biology, Princeton University, Princeton, New Jersey 08544

SUMMARY

- (1) The mechanisms by which communities of mangrove ants develop are examined.
- (2) Eighty-one small mangrove islands in the Florida Keys were surveyed for ant species. Islands varied four orders of magnitude in size.
- (3) Each of the five major species was found only on islands of a certain minimum size (MSR) or larger.
- (4) For two species, termed Primary species, experimental introductions showed that the MSR was due to island unsuitability. For two other species, termed Secondary species, the MSR was shown to be the result of competitive interactions with the Primary species.
- (5) Experiments involving the two Primary species showed that either was capable of preventing the invasion of the other species. Simultaneous introduction experiments showed that one species invariably invaded while the other invariably became extinct.
- (6) Behavioural interactions between all pairs of the species were tested in arena experiments. The patterns of aggression and avoidance were consistent with, and presumed to be the cause of, the experimental results and patterns of geographical distribution.

INTRODUCTION

One of the most popular themes in community ecology of the past 20 years has been the study of ecological resource partitioning (e.g. MacArthur 1959; Schoener 1974). In studies of this kind a guild (Root 1967) of ecologically similar species is examined, the behavioural traits, resource utilization patterns, habitat use and activity patterns of the species are assessed and the pattern of community organization is thus elucidated.

The present study is concerned with a qualitatively different question. Rather than ask, how is a complex community organized, I ask the question, how does a community come to be complex? What processes take place in the course of achieving complexity?

I use the term community assembly to describe the process whereby species are added to communities. The topic of community assembly has been the subject of some controversy since Diamond (1975) used the term in his study of birds of the Bismark archipelago (Connor & Simberloff 1979). My usage of the term community assembly differs somewhat from that of Diamond in that emphasis is placed on the dynamics of dispersal, colonization and competition rather than in formulating a set of phenomenological assembly rules to account for geographical distribution.

The mangrove islands of the Florida Keys are in many respects an ideal testing ground for theories on island biogeography of community structure (Wilson & Simberloff 1969; Simberloff & Wilson 1969, 1970; Simberloff 1969, 1974, 1976a, 1976b, 1978). Literally

Present address: Department of Biology, University of Utah, Salt Lake City, Utah 84112, U.S.A.

thousands of islands exist which vary in size over an enormous range. At one's disposal are a number of communities which differ mainly in the size of the habitat into which the species are cast. Such confounding factors as structural diversity or vegetational composition of the islands themselves vary in relatively trivial ways.

The purpose of the present work is to examine the process of community assembly in the guild of ants that inhabit small mangrove islands. The process of community assembly may be divided into several subunits: dispersal, colonization and interspecific interaction. These processes together contribute to the patterns of geographical distribution. The geographical patterns are the concrete manifestations of the processes and I will first look at the patterns of co-occurrence. After presenting the static distribution patterns that result from dispersal, colonization and interspecific interactions, I shall then characterize the types of interactions that contribute to the geographical distribution.

MATERIALS AND METHODS

Ants are the most abundant and the dominant arthropod on red mangrove (*Rhizophora mangle* L., Simberloff & Wilson 1969). All species nest within the abundant hollow twigs of red mangrove. Five major species of ants are discussed in this study. The major species are of three subfamilies, *Crematogaster ashmeadi* Mayr, *Xenomyrmex floridanus* Emery and *Zacryptocerus varians* (F. Smith) of the Myrmicinae, *Camponotus (Colobopsis)* sp., of the Formicinae and *Pseudomyrmex elongatus* Mayr of the Pseudomyrmecinae.

Small islands in the Lower Florida Keys near Sugarloaf Key, the Saddlebunch Keys and Big Coppitt Key were censused. Islands in direct contact with other mangrove trees were not censused. Trees which were close enough to permit aerial or wind transport of workers or which were not separated from other mangroves by water during the lowest tides were not censused. An island composed of both red and black mangrove (*Avicennia nitida* Jacq.) was excluded from study. This was done in order to exclude any possible effects of differential use of mangroves by different ants. On a few of the largest red mangrove islands a very few seedlings of black mangrove were present. These never made up more than 0.05% of the total island volume and were certainly of little consequence to the ant species found on the islands.

An effort was made to examine as many dead twigs as possible on each island. For islands with only 0, 1, 2 or 3 ant species this meant that all dead twigs on the tree were examined. For the largest islands it was not feasible or even desirable that all dead twigs on the island be broken and examined. In the monitoring techniques of Wilson & Simberloff (1969) approximately 10% of the hollow twigs were broken in each sample period. Confidence of the completeness of the ant species list for a large island is attained well before the twigs are sampled exhaustively. Any species that could have been missed must have been very rare and therefore ecologically insignificant.

The size of the island was estimated by measuring its long axis and the axis at right angles to it. The height of the mangrove island at its central, highest point was also measured. The volume of the island, given in cubic metres, is the length \times width \times height. Mangrove islands are, to a very good approximation, either circular or elliptical basally, and overall shaped like a half-ellipsoid. The size of the island given in Fig. 1 is an overestimate of the actual volume, but differs only by a constant transformation. For a typical shape of half-ellipsoid all values must be multiplied by $\pi/6 = 0.52$.

Forty-six experimental introductions of ant species were performed on small mangrove islands. Several points must be made about the techniques for experimental introduction.

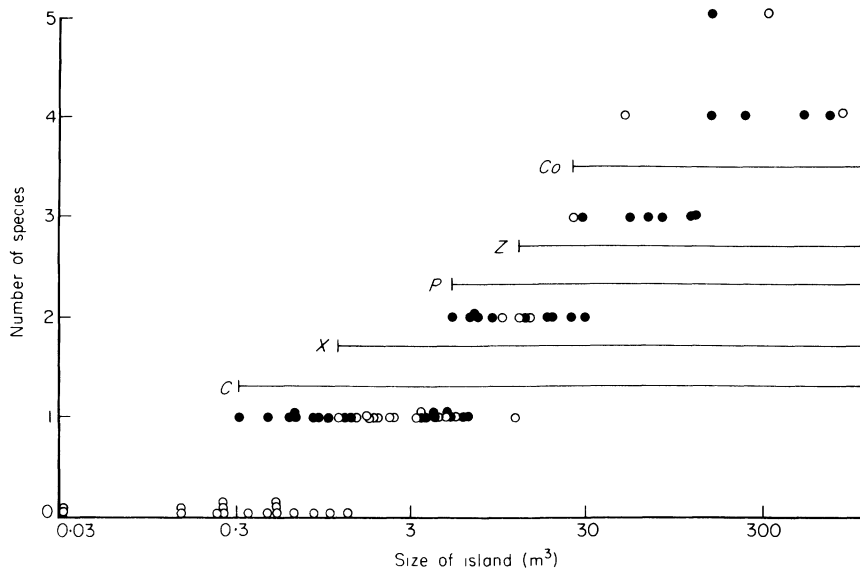


FIG. 1. Species number-island size relation for mangrove ants. The 81 points represent individual mangrove islands. ● indicates the presence of *C. ashmeadi*. ○, excluding islands without species, indicates the presence of *X. floridanus*. The bars indicate the range of island sizes on which the five major species of mangrove ants are found.

Some experiments required ant-free islands of a certain size. If an island of proper size had a colony of ants, the colony could be destroyed by breaking off a number of the dead twigs. This was done only on islands which were small enough to ensure that all ants were removed from the islands. During a period of 2 weeks between the first attempt to remove ants and the introduction of a new colony, the island was monitored to be certain that all pre-existing ants had been removed.

Colonies of the experimental species were collected from other red mangrove trees. In most experiments the colony, containing the queen, was transferred to a new nest twig. The twigs used were hollow saw grass stems. At least two of the species (*P. elongatus* and *Z. varians*) used these twigs as nests in upland areas and none of the ants were apparently affected by the change of nest. The colonies were then introduced to the island simply by wiring the nest twigs onto a branch of the experimental mangrove. An effort was made to standardize the size of the colony introduced to the island. Colonies containing twenty to thirty workers and whatever brood was present were introduced.

The experiment was scored on the basis of persistence. If the introduction was a failure it died out within 3 weeks. A successful introduction persisted at least 8 weeks. Failed introductions, with a single exception, died out within 1 week. Successful introductions, with one exception, lasted at least until the completion of field work (average of at least 27 weeks). Experiments were monitored once per week and thus the minimum persistence time is 1 week. Unfortunately, the size of the colony could not be monitored weekly. To do so would have required breaking into nests, possibly influencing the final outcome of the experiment.

The behavioural reaction of one species to another was tested in a series of arena experiments. Workers of two species were placed in arenas with an area of 87 cm². Initially five workers of each species were used. The number of one or both species was often

increased. The effect of increasing numbers was to increase the rate of interaction; qualitative aspects of the interaction were unaltered. The ten possible pairs of the five species of ants were tested in arena experiments.

RESULTS

Figure 1 summarizes the census results of eighty-one mangrove islands. Islands ranged in size from 0.03 m³ to 877 m³, a span of four and one-half orders of magnitude in size. The best fit to the standard species number-island size relation, $S = cA^z$, is given by $S + 1 = 1.62 A^{0.21}$ ($n = 81, r = 0.90, P < 0.001, A$ is the volume in cubic metres). The value of the exponent is in line with other such measurements (MacArthur & Wilson 1967, Sugihara 1981). $S + 1$ is used because of values of S equal to zero.

The very smallest islands are uninhabited by any species. Until a size of 0.31 m³ is attained, no ants are found. Between 0.31 and 1.25 m³ zero or one species may be found, and above 1.25 m³ all islands have at least one species. Starting at 5.09 m³ some islands have two species. The smallest island with three species had a size of 25.4 m³. Apart from a few points (12.1 m³, one species; 50.4 m³, four species) there is very little overlap between islands with incrementally larger faunas. In Fig. 1 the range of island size on which the five major species are found, is shown by the horizontal lines. Each species is found only on islands above some characteristic minimum size. I have termed this size the Minimum Size Requirement for the species. Table 1 shows the MSR for species encountered in this study.

To:

	<i>C</i>	<i>X</i>	<i>Ps</i>	<i>Z</i>	<i>Co</i>
Reaction of:	<i>C</i>	aggression avoidance	aggression	aggression	aggression
	<i>X</i>	aggression avoidance	aggression	aggression	aggression
	<i>Ps</i>	avoidance	avoidance	avoidance	avoidance
	<i>Z</i>	avoidance	avoidance	avoidance	ignore
	<i>Co</i>	avoidance	aggression	aggression	ignore

FIG. 2. Behavioural response of a given species (listed vertically) to the presence of another species (listed horizontally) in arena experiments.

TABLE 1. Minimum Size Requirement for mangrove ants (m³)

<i>Crematogaster ashmeadi</i>	0.3
<i>Xenomyrmex floridanus</i>	1.2
<i>Pseudomyrmex elongatus</i>	5.1
<i>Zacryptocerus varians</i>	12.6
<i>Camponotus (Colobopsis) sp.</i>	25.4

TABLE 2. The relation of island size to the ability of a species to persist. The numerator of the entry shows the number of times that an introduction resulted in persistence (average residence at least 27 weeks). The denominator gives the number of times that the experimental introduction was performed. Failed introductions persisted an average of no more than 1½ weeks

Introduction of	To islands	
	Smaller than MSR	Larger than MSR
<i>C. ashmeadi</i>	0/3	1/1
<i>X. floridanus</i>	0/3	2/2
<i>P. elongatus</i>	1/1	—
<i>Z. varians</i>	2/2	—

The question asked experimentally was: does the existence of an MSR for each species mean that an island is, in some way, uninhabitable, or does it reflect competitive interactions between species? Experimental introductions were performed with *C. ashmeadi*, *X. floridanus*, *P. elongatus* and *Z. varians* to test the effect of island size of the species' ability to persist. Table 2 summarizes the results of twelve experimental introductions.

When *C. ashmeadi* and *X. floridanus* were introduced to islands smaller than their MSR, they did not persist. The length of time until the colony failed varied from less than 1 to 3 weeks. For the colony that persisted for 3 weeks, the colony was reduced to the queen and a single worker for two of those weeks. When *C. ashmeadi* or *X. floridanus* were introduced to islands smaller than their MSR the average time to extinction was no greater than 1½ weeks. In both *C. ashmeadi* and *X. floridanus*, failure to persist is not due to the inability of the island to supply food resource sufficient for colony maintenance. The speed of colony die-out is too rapid to be explained by starvation of the workers. The important factor is certainly the exposure of the island. Islands in the range of 0.3 m³ (for the *C. ashmeadi* experiments) are very exposed to wind and possibly wave and tidal stress.

When *C. ashmeadi* or *X. floridanus* are introduced to islands larger than their MSR they persist apparently indefinitely. The difference in persistence ability with size is clearly a feature inherent in the relationship between ant and island. *C. ashmeadi* and *X. floridanus*, at the lower limit of their island size range, are facing the difficulty that the islands themselves are not suitable. The transition from an island with zero species to an island with one species relies on the transition of an island from an inhospitable to a hospitable environment.

For *P. elongatus* and *Z. varians* the picture is different. These species were introduced to islands smaller than their MSR, which had had all other ants removed. They persisted apparently indefinitely. For these species the island itself is suitable, however the species are not found on these smaller islands. At the lower limit of their island size range *P. elongatus* and *Z. varians* are not limited by the quality of the islands.

Because of the natural dichotomy between two groups of species, *C. ashmeadi*, *X. floridanus* and *P. elongatus*, *Z. varians*, I have designated the two groups Primary and Secondary species, respectively. The Primary species are those species that are found on single species islands and are limited at the lower range of island size by the fact that the islands themselves are not suitable. The Secondary species are those that are found on two species islands along with a Primary species. The MSR for this group of species is not simply a property of the islands themselves. This raises the question of whether interactions between Primary and Secondary species influence the size of islands on which Secondary species are found.

TABLE 3. Relation of species composition to the ability of a species to persist. Entries are read as in Fig. 2. \emptyset indicates an empty island

Introduction of	To island containing			Simultaneous C and X introductions
	C	X	\emptyset	
<i>C. ashmeadi</i>	—	0/4	1/1	5/5
<i>X. floridanus</i>	0/4	—	2/2	0/5
<i>P. elongatus</i>	0/4	0/4	1/1	
<i>Z. varians</i>	0/4	0/1	2/2	
<i>Colobopsis</i>	0/2	—	—	

Table 3 shows the results of twenty-seven experimental introductions which tested the effect of the presence or absence of a Primary species on the ability of other species to persist on an island. Colonies of *P. elongatus* and *Z. varians* were introduced to islands which were already occupied by colonies of *C. ashmeadi* or *X. floridanus*. Such introductions did not result in persistence. When introduced to islands with no other ants present, they persisted until the completion of field work. The presence of *C. ashmeadi* or *X. floridanus* on islands smaller than 5.09 m³ precludes the invasion of either *P. elongatus* or *Z. varians*.

Experiments to test whether or not the presence of *P. elongatus* or *Z. varians* precluded invasion by *X. floridanus* or *C. ashmeadi* were not performed. Islands which contained naturally-occurring colonies of either *P. elongatus* or *Z. varians* also contained colonies of either *X. floridanus* or *C. ashmeadi*. The problems of removing the existing colony of *C. ashmeadi* or *X. floridanus* without disturbing the colony of *P. elongatus* or *Z. varians* could not be surmounted. Because all islands above a minimum size were occupied, *P. elongatus* and *Z. varians* either never dispersed to these islands (exceedingly unlikely) or were unable to prevent invasion by either *C. ashmeadi* or *X. floridanus*.

The results of two introductions with *Colobopsis* were consistent with the pattern shown by *P. elongatus* and *Z. varians*. These introductions cannot be considered conclusive due to the fact that very few experiments could be performed with less abundant species.

Although each island contains one of the Primary species, I never found an island which had colonies of both *C. ashmeadi* and *X. floridanus*. Table 3 shows the results of introductions of colonies of one of the Primary to islands containing the other Primary species. In all cases the introduced colonies failed to persist. When either of the Primary species is introduced to an island without other ants, it persists indefinitely. The presence of one species makes impossible the foundation of a colony of the other species by dispersing queens.

The last set of experimental results concerns another facet of the relationship between Primary species. Given the fact that either Primary species can invade an empty island, and neither can invade an island on which the other is already established, there is a single remaining non-trivial combination. What is the result of simultaneous invasion of an empty island by both species? The results of simultaneous introduction of colonies of *C. ashmeadi* and *X. floridanus* are given in Table 3. *C. ashmeadi* successfully invades each island, *X. floridanus* never persists.

* Figure 2 summarizes the results of the arena experiments. The reaction of *C. ashmeadi* and *X. floridanus* to either *P. elongatus*, *Z. varians* or *Colobopsis* was aggressive. The reaction of the latter three species to either of the Primary species was almost strictly one of avoidance. The exception was a mildly aggressive response of *Colobopsis* towards *X. floridanus*. However, aggression by *X. floridanus* toward *Colobopsis* precipitated a rapid

withdrawal by *Colobopsis*. The reaction of the two Primary species to one another was a mixture of both aggression and avoidance. In some cases the response was aggressive, in other cases individuals of one species avoided individuals of the other. In aggressive interactions an individual *C. ashmeadi* worker was capable of killing *X. floridanus*, whereas a single *X. floridanus* could not injure *C. ashmeadi*.

DISCUSSION

Examination of the geographical distribution of ants on mangrove islands revealed two significant patterns. First, each species was found only on a range of island sizes and not below a certain Minimum Size Requirement (MSR). Second, *C. ashmeadi* and *X. floridanus* were never found on the same island. Experimental introductions elaborated the geographical distribution patterns and confirmed that the patterns were not due to chance effects. For the Primary species the MSR was a characteristic of the island, while *P. elongatus* and *Z. varians* could exist on islands smaller than their MSR. The presence of a Primary species was found to be the critical factor preventing the invasion of an island by a Secondary species.

Introduction experiments showed that the presence of either *C. ashmeadi* or *X. floridanus* precluded the invasion of the other species to the island. Mangrove islands thus have two alternative stable states (Sutherland 1974), *C. ashmeadi* present or *X. floridanus* present. An additional pattern of coexistence that was not revealed by looking at the static distribution alone was the fact that in cases of simultaneous invasion *C. ashmeadi* successfully colonized and *X. floridanus* became extinct.

A mechanism to account for the patterns of geographical distribution that is consistent with the results of the introduction experiments must explain three observations: (i) the presence of a Primary species prevents the invasion of small islands by Secondary species; (ii) the Primary species form mutually uninvasible islands; (iii) *C. ashmeadi* is the victor in cases of simultaneous invasion with *X. floridanus*.

The results of introduction experiments are consistent with the pattern of aggression in behavioural interactions. Certainly aggressive interactions between ant species are well known and can be responsible for patterns of spatial organization (Pontin 1961, 1963; Brian 1956; Greenslade 1971). Primary species are uniformly aggressive to Secondary species, whereas Secondary species uniformly avoid Primary species. Primary species are capable of preventing the invasion of Secondary species but Secondary species should not be capable of preventing the invasion of Primary species. The mutually aggressive response of Primary species indicates that they should form mutually uninvasible islands. Since this is the only case of mutual aggression and avoidance among the five species, this should be the only case of alternative stable states involving these five species.

Because of the size difference between the two Primary species (*C. ashmeadi* is $1\frac{1}{2}$ times the length of *X. floridanus*) the outcome of mutual aggression is biased. *C. ashmeadi* is capable of killing *X. floridanus* in one-to-one encounters: the reverse is not true. This bias in the effectiveness of successful aggression is mirrored in the invasion of *C. ashmeadi* in simultaneous introduction experiments with *X. floridanus*.

Figure 3 summarizes the contingencies, processes and interactions that take place in the assembly of mangrove ant communities. The importance of behavioural interactions to this scheme is emphasized by the fact that a single arrow leads to extinction without behavioural interaction. For Primary species the two important factors are: (i) the size of the island, if very small and (ii) the presence of another Primary species. For Secondary

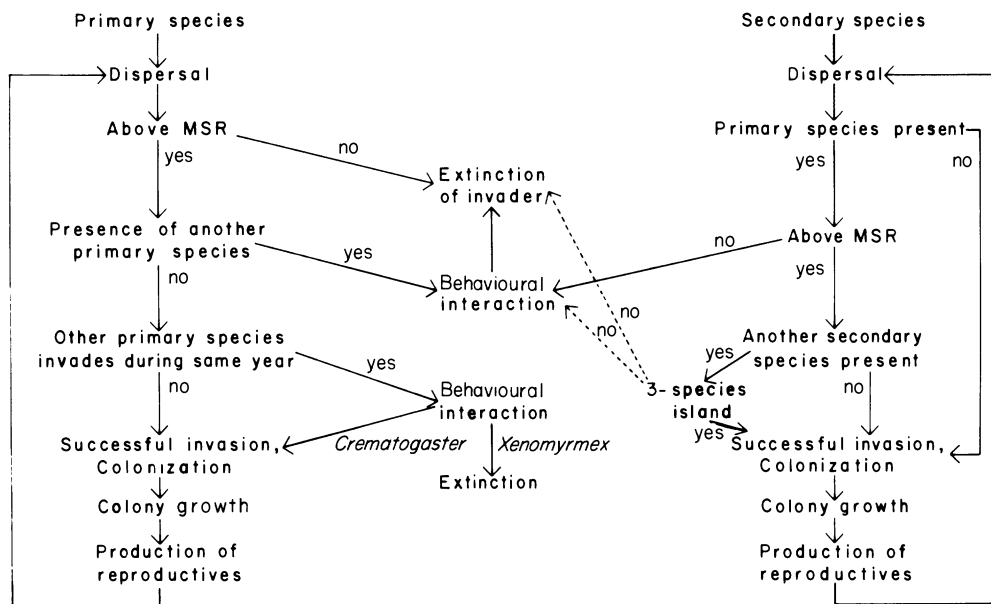


FIG. 3. Assembly of mangrove ant communities. Primary and Secondary species have different pathways leading to eventual colonization and colony growth.

species the single important factor is whether the island is large enough to permit coexistence with a Primary species.

The mangrove ant communities that result from the process of assembly are neither random assemblages of species drawn from a pool nor a perfectly predictable and repeatable set of species which conform to a suite of rules. There is a deterministic element; behavioural interactions, interference competition, proscribes the coexistence of certain pairs of species. There is a stochastic element; prior invasion of one of the Primary species precludes invasion by the other of the pair.

ACKNOWLEDGMENTS

I thank Dan Simberloff for many helpful suggestions and encouragement. E. O. Wilson provided useful recommendations. Bob May and Henry Horn provided invaluable advice and guidance. I profited greatly from discussions with Diane Davidson, John Terborgh, John Endler, Douglas Green, Bruce Beehler, Cathy Bristow, Diane Wiernasz, John Schneider, Tony Janetos, John Fitzpatrick, David Duffy, David Tonkyn, Kathy Schneider and Rich Kiltie.

REFERENCES

- Brian, M. V. (1956). The natural density of *Myrmica rubra* and associated ants in West Scotland. *Insectes Sociaux*, **3**, 473–487.
- Connor, E. F. & Simberloff, D. (1979). The assembly of species communities: chance or competition? *Ecology*, **60**, 1132–1140.
- Diamond, J. M. (1975). Assembly of species communities. *Ecology and Evolution of Communities* (Ed. by M. Cody & J. M. Diamond), pp. 342–444. Belknap/Harvard Press Cambridge, Mass.
- Greenslade, P. J. M. (1971). Interspecific competition and frequency changes among ants in Solomon Islands coconut populations. *Journal of Animal Ecology*, **40**, 323–352.

- MacArthur, R. H. (1959).** Population ecology of some warblers of northeastern coniferous forests. *Ecology*, **39**, 599–619.
- MacArthur, R. H. & Wilson, E. D. (1967).** *The Theory of Island Biogeography*. Princeton University Press, Princeton.
- Pontin, A. J. (1961).** Population stabilization and competition between the ants *Lasius flavus* (F.) and *L. niger* (F.). *Journal of Animal Ecology*, **30**, 47–54.
- Pontin, A. J. (1963).** Further considerations of competition and the ecology of the ants *Lasius flavus* (F.) and *L. niger* (F.). *Journal of Animal Ecology*, **32**, 565–574.
- Root, R. B. (1967).** The niche exploitation pattern of the blue-gray gnatcatcher. *Ecological Monographs*, **37**, 317–350.
- Schoener, T. W. (1974).** Resource partitioning in ecological communities. *Science*, **185**, 27–39.
- Simberloff, D. S. (1969).** Experimental zoogeography of islands: a model for insular colonization. *Ecology*, **50**, 296–314.
- Simberloff, D. S. (1974).** Equilibrium theory of island biogeography and ecology. *Annual Review of Ecology and Systematics*, **5**, 161–182.
- Simberloff, D. S. (1976a).** Species turnover and equilibrium island biogeography. *Science*, **194**, 572–578.
- Simberloff, D. S. (1976b).** Experimental zoogeography of islands: effects of island size. *Ecology*, **57**, 629–648.
- Simberloff, D. S. (1978).** Using island biogeography distributions to determine if colonization is stochastic. *American Naturalist*, **12**, 713–726.
- Simberloff, D. S. & Wilson, E. D. (1969).** Experimental zoogeography of islands: the colonization of empty islands. *Ecology*, **50**, 278–295.
- Simberloff, D. S. & Wilson, E. D. (1970).** Experimental zoogeography of islands: a two-year record of colonization. *Ecology*, **51**, 934–937.
- Sugihara, G. (1981).** $S = CA^2$, $Z \approx 1/4$: a reply to Connor and McCoy. *American Naturalist*, **117**, 740–793.
- Sutherland, J. P. (1974).** Multiple stable points in natural communities. *American Naturalist*, **108**, 859–873.
- Wilson, E. D. & Simberloff, D. S. (1969).** Experimental zoogeography of islands: defaunation and monitoring techniques. *Ecology*, **50**, 267–278.

(Received 28 July 1981)