EXPERIMENTAL ZOOGEOGRAPHY OF ISLANDS. A TWO-YEAR RECORD OF COLONIZATION[1]

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Abstract. In 1966–1967 the entire arthropod faunas of six small mangrove islands in the Florida Keys were removed by methyl bromide fumigation. In earlier articles we described the process of recolonization through the first year, during which the numbers of species in five of the six faunas rose to what appear to be noninteractive equilibria and then slumped slightly to interactive equilibria. The sixth, that of island E1, we believed to be climbing more slowly because of its greater distance from the source area. It had not reached the predefaunation (interactive) equilibrium by 1 year. Here we give the results of censuses taken at the end of the second year on the four islands in the group located in the lower Keys (E1, E2, E3, ST2). The numbers of species were found to have changed little from the previous year, providing further evidence that they are in equilibrium. Species immigrations and extinctions have continued at a high rate, and the species compositions on three of the four islands appear to be moving slowly in the direction of the original, predefaunation states.

In the first two articles of this series we described an experiment in which the entire arthropod faunas of six small mangrove islands in the Florida Keys were exterminated by methyl bromide fumigation and the process of recolonization was monitored thereafter by frequent censuses (Wilson and Simberloff 1969, Simberloff and Wilson 1969). The experiment was designed both to test and to extend certain aspects of species equilibrium theory (MacArthur and Wilson 1967, Simberloff 1969, Wilson 1969) and to observe the actual processes of immigration and extinction. At the end of the first year following defaunation, the numbers of species had reattained approximately the original (prefumigation) levels on five of the six islands. The most distant island (E1) supported the fewest species, just as it had prior to defaunation; it alone had not approached the original species number. Intermediate islands (E3, ST2) reattained intermediate numbers of species. The time-colonization curves appeared to have assumed the logarithmic forms predicted by basic equilibrium theory. Moreover, higher levels of species numbers were reached prior to the buildup of the populations belonging to the constituent species. These numbers then dipped slightly as the densities of the constituent populations approached the predefaunation levels. The decline occurred near the end of the first year following defaunation (see Fig. 1). We interpreted the first, higher levels to represent "noninteractive species equilibria," that is, species equilibria reached before the extinction rates could be greatly influenced by interspecific interactions such as

predation and competition; the second, lower levels were considered to represent "interactive species equilibria," in which species interactions contributed significantly to species extinction rates. The colonizations had thus been followed to the mere beginnings of the interactive equilibria. It was clearly desirable to continue monitoring the islands to watch for subsequent developments.

Censuses at the end of the second year

Near the end of the second year following defaunation, we visited the islands again. Time permitted the examination of only the four islands in the Sugarloaf area of the lower Keys, namely E1, E2, E3, and ST2. We employed the same procedures for censusing as described in our earlier reports (Wilson and Simberloff 1969, Simberloff and Wilson 1969). The results are summarized in Figure 1 and in Tables 1 and 2.

From Figure 1 it can be seen that the estimated species numbers have not changed greatly since the end of the first year—and therefore since the period just before the entire original fauna was destroyed by fumigation. The equilibrial numbers continue to be an inverse function of the distance of the islands from the nearest mangrove islands and swamps that can serve as a source of fresh immigrants. Only E1 has failed to reattain fully the original predefaunation level. We do not know the reason for this exception. Our best guess is the following: basic equilibrium theory predicts that distant islands approach equilibrium more slowly than near islands, and it is possible that E1 is still in the process of climbing toward equilibrium. This purely statistical effect, caused

TABLE 1. The colonists of four experimental islands 2 years after defaunation

E1 March 8, 1969	E2 March 6-7, 1969	E3 March 9, 1969	ST2 March 10-11, 1969
			Embioptera *Diradius caribbeana*

	Orthoptera
	  Latiblattella n. sp.
	  Latiblattella rehni
	  Cyrtoxipha sp.
	  Tafalisca lurida
		Orthoptera
		  Latiblattella n. sp.
		  Cycloptilum sp.
		  Tafalisca lurida
			Orthoptera
			  Latiblattella n. sp.
			  Tafalisca lurida

Coleoptera
  Sapintus fulvipes
  Tricorynus sp.
  Cryptorhynchus
    minutissimus
  Pseudoacalles sp.
	Coleoptera
	  Tricorynus sp.
	  Styloleptus biustus
	
	  Chrysobothris sp.
	  Pseudoacalles sp.
	  Trischidias minutissima
		Coleoptera
		  Tricorynus sp.
		  Pseudoacalles sp.
			Coleoptera
			  Tricorynus sp.
			  Styloleptus sp.
			
			  Pseudoacalles sp.

	Thysanoptera
	  Barythrips sculpticauda
		Thysanoptera
		  Liothrips sp.
		  Pseudothrips inequalis
			Thysanoptera
			  Haplothrips sp.
			  Pseudothrips inequalis

Corrodentia
  Psocidus texanus
  Peripsocus sp.
	Corrodentia
	  Caecilius subflavus aff.
	  Caecilius flavidus aff.
	  Psocidus texanus
		Corrodentia
		  Liposcelis bostrychophilus
		  Psocidus texanus
			Corrodentia
			  Liposcelidae gen. sp.
			  Caecilius subflavus aff.
			  Psocidus texanus

	Hemiptera
	  Paraleyrodes sp.
	  Pseudococcus sp.
	  Anthocoridae gen. sp.
	  Gen. sp.
			Hemiptera
			  Miridae (Phylinae) gen. sp.

Lepidoptera
  Alarodia slossoniae
  Ecdytolopha sp.
  Bema ydda
  Phocides batabano
	Lepidoptera
	  Bema ydda
	  Nemapogon sp.
	  Phocides batabano
		Lepidoptera
		  Ecdytolopha sp.
		  Phocides batabano
			Lepidoptera
			  Alarodia slossoniae
			  Ecdytolopha sp.
			  Nemapogon sp.

Diptera Hippoboscidae gen. sp.			

Hymenoptera
  Pseudomyrmex elongatus
  Crematogaster ashmeadi
	Hymenoptera
	  Ichenumonoidea gen. sp.
	  Pseudomyrmex elongatus
	  Xenomyrmex floridanus
	  Crematogaster ashmeadi
	  Paracryptocerus varians
	  Paratrechina bourbonica
	  Camponotus floridanus
		Hymenoptera
		  Calliephialtes sp.
		  Pseudomyrmex elongatus
		  Xenomyrmex floridanus
		  Monomorium floricola
		  Crematogaster ashmeadi
		  Paratrechina bourbonica
			Hymenoptera
			  Scleroderma macrogaster
			  Pseudomyrmex elongatus
			  Crematogaster ashmeadi
			  Paracryptocerus varians
			  Tapinoma littorale
			  Camponotus floridanus

Araneae
  Ayscha sp.
	Araneae
	  Ayscha sp.
	  Hentzia grenada
	  Salticidae gen. sp.
	  Nephila clavipes
	  Ariadna arthuri
		Araneae
		  Ayscha sp.
		  Hentzia grenada
			Araneae
			  Ayscha sp.
			  Hentzia palmarum
			  Ariadna arthuri

Acarina
  Scheloribates sp.
  Gen. sp.
	Acarina
	  Gen. sp. 1
	  Gen. sp. 2
		Acarina
		  Scheloribates sp.
		  Eupodes sp.
		  Gen. sp.
			Acarina
			  Gen. sp.

		Diplopoda
		  Lophoproctinus sp.
			Diplopoda
			  Lophoproctinus sp.

Total seen = 16 Estimated present = 18	Total seen = 34 Extimated present = 39	Total seen = 23 Estimated present = 28	Total seen = 26 Estimated present = 30

by a uniform lowering of invasion rates with increasing distance, may have been enhanced by abnormal population growth of the few early colonists (Simberloff 1969).

A comparison of the species lists in Table 1 with those provided from earlier censuses by Simberloff and Wilson (1969) shows that a high rate of species turnover occurred during the second year, resulting in a significant alteration of species composition, even though the species numbers remained nearly the same. In fact, 35–52% of the species making up the total lists from individual islands at the ends of the first and second years were encountered during both censuses (Table 2, section C).

A question of major significance that continued monitoring should answer is whether the species compositions will eventually converge toward those prevailing before defaunation. Wilson (1969) has suggested the general proposition that as new

TABLE 2. Percentages of species that were present at both of two given censuses on four of the experimental islands

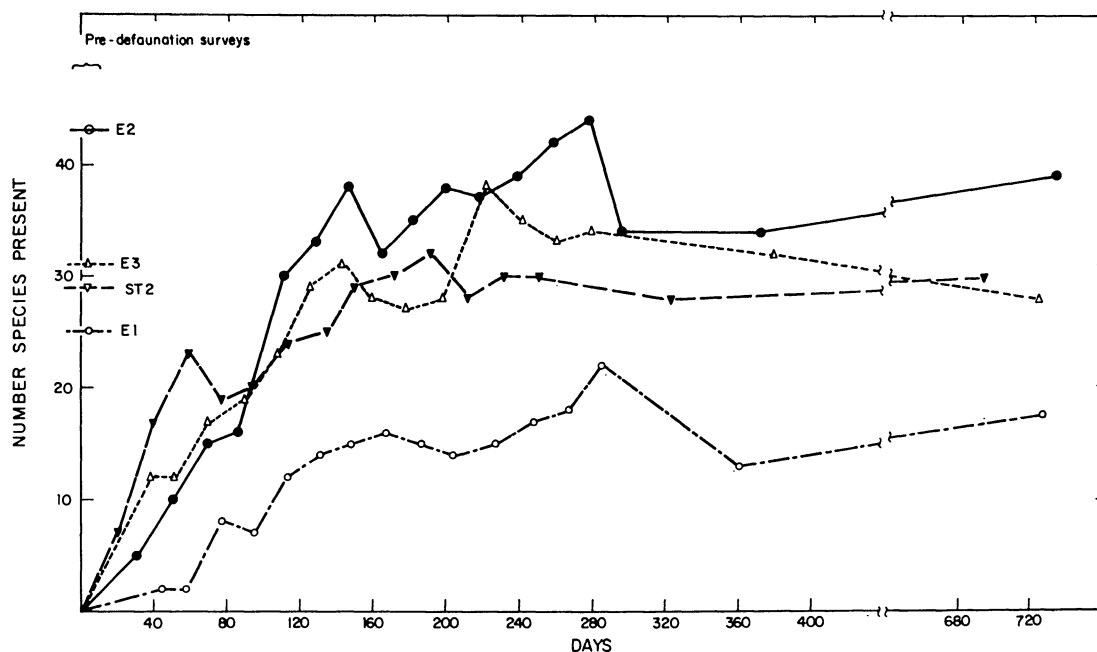| Name of experimental island	A. Censuses: just before defaunation and one year later			B. Censuses: just before defaunation and two years later			C. Censuses: one and two years after defaunation		
	No. spp. in common	Total no. in both censuses	Per cent in common	No. spp. in common	Total no. in both censuses	Per cent in common	No. spp. in common	Total no. in both censuses	Per cent in common
E1........	2	29	6.9%	5	26	19.2%	7	18	38.9%
E2........	10	54	18.5%	13	51	25.5%	16	34	37.2%
E3........	8	40	20.0%	7	35	20.0%	16	31	51.6%
ST2.......	11	37	29.7%	17	31	54.8%	12	34	35.3%

FIG. 1. The colonization curves of four small mangrove islands in the lower Florida Keys whose entire faunas, consisting almost solely of arthropods, were exterminated by methyl bromide fumigation. The figures shown are the estimated numbers of species present, which are the actual numbers seen plus a small fraction not seen but inferred to be present by the criteria utilized by Simberloff and Wilson (1969) and Simberloff (1969). The number of species in an inverse function of the distance of the island to the nearest source of immigrants. This effect was evident in the predefaunation censuses and was preserved when the faunas regained equilibrium after defaunation. Thus, the near island E2 has the most species, the distant island E1 the fewest, and the intermediate islands E3 and ST2 intermediate numbers of species.

combinations of species are generated by turnover, combinations of longer-lived species must eventually accumulate. Such species persist longer either because they are better adapted to the peculiar physical conditions of the local environment or else because they are able to coexist longer with the particular set of species among which they find themselves. Thus in time an "assortative equilibrium" will succeed the original "interactive equilibrium." Because the individual survival times of the resident species populations are greater on the average, while the total propagule invasion rates of the faunas remain about the same, the

numbers of species in an assortative equilibrium should be higher. It is also true that the numbers of possible assortative equilibria are fewer, and therefore under similar conditions the species compositions should converge to some degree. Our data are still too few to be conclusive, but they do suggest that the faunas of the experimental islands are drifting in the direction of the original compositions. By comparing section A and B in Table 2 it can be seen that on three of the islands the faunas were closer in composition to the predefaunation faunas at the end of the second year than they were at the end of the first year. In one of

the four islands (E3) there was no change. We regard these trends as being suggestive only. Time should tell us with certainty whether convergence has really been occurring.

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