

Species Turnover and Equilibrium Island Biogeography

Critical field studies are needed to ascertain
the frequency of local population extinction.

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The equilibrium theory of island biogeography (1, 2) has found wide acceptance as a description of the organization of communities on oceanic and habitat islands (3). The basic premise is that the biota of any island is in dynamic equilibrium between immigration of species new to the island and local extinction of those already present. Extinction rates are believed to have a stochastic component, probabilities of local extinction presumably being inversely proportional to population size. Despite occasional data-based studies that appear not to demonstrate an immigration-extinction equilibrium (4-6), the equilibrium theory as just expressed has achieved the status of a paradigm, as used by Kuhn (7): a theory so widely accepted as an accurate description of nature that failure of an experiment to yield the result deduced from the theory leads *not* to rejection of the theory but rather to attempts to fault the deductive logic or experimental procedure, or simply to willful suspension of belief in the experimental result. As one example, equilibrium biogeography theory has been held to be important in vertebrate conservation planning (8) despite the fact that Lynch and Johnson (6) have severely impugned the primary avian basis for acceptance of the theory. Their result, however, is relegated to the status of "technical criticisms" by Sullivan and Shaffer (9) rather than used in a reexamination of the underlying theory.

I shall attempt here to express the theory of equilibrium biogeography as a testable (falsifiable) hypothesis within the usual framework of hypothesis and deduction that has served the physical sciences (10) but has been often neglected in community ecology (11). I suggest also the kinds of evidence that could

falsify the hypothesis, with some reference to the significance of partial or complete falsification. I also present new evidence from the mangrove island experiment (12-14) that was performed to test the theory of island biogeography.

Status of the Theory

In the first place, a theory ought not to be elevated to the rank of paradigm or rejected as a hypothesis on grounds of either taste or experimental convenience. Smith (15) argues that

Fluctuations may bring a species to extinction in a system. I can accept a moderate amount of this but not very much. Obviously, extinction is more frequent in smaller systems. At a ridiculous extreme every death or movement creates extinction at that exact point. Robins become extinct in an apple tree many times each day whenever they fly elsewhere. To me, frequent extinction is a signal that the system under study is not large enough to include the processes being studied. Move the system boundaries out until extinction becomes rare. This ensures that the organizing forces of the system lie within the system, and also solves the problem of frequent extinction.

Although Smith's point that we ought not to focus on unimportant transients is well taken, rigorous application of his procedure could mask interesting biology. We desire an accurate picture of how nature works, and, for example, if nature were actually organized into rather discrete ecosystems with little biotic movement between them but with relatively high within-ecosystem extinction rates, Smith's approach would preclude our recognizing this organization, and subsequent treatment of its ecological and evolutionary consequences. Instead we must decide first what actually constitutes meaningful biological extinction and then what actually constitutes an independent, functional ecosystem, and then attempt to obtain field data to give

actual numerical values to statistics describing both phenomena. Only then can we say whether local extinction is frequent or not.

If we restrict our consideration of criticisms of the theory to those based on data, we find substantive issue on both points of the theory, continuing immigration and continuing local extinction in ecological, as opposed to geological, time. With respect to local extinction, we can deduce that, if it occurs at all for stochastic reasons, it must occur more frequently for small populations because the probability of death or breeding failure of individuals in a population is at least partly multiplicative. Furthermore, we might deduce (although less firmly, because we must assume untested population mathematics) that the increase in local extinction rate on small islands should be more than linear (2, 16) and therefore easy to affirm. However, there is no way in which we can deduce that local extinction occurs at all in ecological time from stochastic population factors rather than secular environmental change; we must actually observe local populations. For mangrove island arthropods I discuss such observations below, but it is disturbing that the other main support for the notion that local extinction occurs frequently in ecological time, Diamond's analysis of Channel Island birds (17), has been heavily criticized by Lynch and Johnson (6) on three main grounds. First is that the censuses were not sufficiently complete to demonstrate absence of given species, and that apparent turnover from this source (part of Lynch and Johnson's "pseudoturnover") greatly inflates turnover rates. This contention is at least arguable if evidence can be adduced that the censuses were comprehensive.

The second criticism is that long- and short-term changes in the environment have been so great that they alone are sufficient to account for observed biotic change. Whether or not this is true probably cannot be determined from the Channel Island data alone; it is conceivable, for example, that there are both stochastic and deterministic (environmentally based) elements in all observed changes in the bird composition of the Channel Islands. How is one to distinguish their relative importance? But at the least, Lynch and Johnson have cataloged an impressive amount of secular environmental change that could potentially affect birds. They suggest (6) that other claims of frequent equilibrium turnover of birds are subject to these two classes of criticism and that the minimum rates described are therefore great-

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ly inflated. Subsequent related work (18) on the birds of Barro Colorado Island, concerning a remarkable match between observed species number and that predicted by a stochastic extinction model must be viewed in the context of major ecological change over the period in question. Before the island was formed in 1910–1914, the area was partly farmed; much of the present forest is, therefore, less than a century old (19).

Lynch and Johnson's third claim regarding avian turnover in the Channel Islands is that much of it can be ascribed to normal annual inter-island movement and does not really correspond to local extinction of breeding populations; in short, it conforms to Smith's model of robins in apple trees. This constitutes the remainder of Lynch and Johnson's "pseudoturnover", and will be taken up in the next section.

Frequent immigration has also been doubted. As with local extinction, amount of immigration cannot be deduced, but must be determined by observation. Mangrove island evidence is presented below; clearly, if early Channel Island bird censuses were very deficient, then subsequent immigration cannot be demonstrated. Brown (4) examined mammals on an archipelago of mountaintop islands and concluded that stochastic extinction occurred occasionally, and was indeed a function of population size, but that immigration in ecological time was rare or absent.

What Constitutes Extinction?

Local extinction, as defined by Simberloff (20), occurs when we first observe a sufficient number of individuals of some species so that reproduction is possible (that is, a propagule), and then subsequently find that the species is absent or reduced to nonreproductives (for example, a single male) in the region of interest; it is a population phenomenon, in contrast to the global extinction of an entire species. This definition appeared, and still appears to me, to be the only objective and clear one, as opposed, say, to one in which a minimum probability of initial population increase is arbitrarily defined. Lynch and Johnson (6) suggest a slight change: that local extinction be limited to disappearance after breeding has actually occurred. With respect to why we want to know about extinction in the first place, actual breeding might be a good criterion, but for some animals (like arboreal arthropods) such data would be difficult to get, and I believe that the presence-absence data can be useful in

conjunction with dispersal information.

Why, in fact, is there interest in local extinction at all? In a strictly ecological sense we would like to understand the population dynamics and dispersion, and the relationship between the two, of all species comprising some community of interest. If species were distributed in space and time as conceived in the theory of equilibrium biogeography, recurrent local extinction would be a third organizing force in community ecology, as important as the two listed by Smith (15): trophic interaction and space competition.

But I suggest that the interest in local extinction is engendered as much by evolutionary as by ecological considerations. This is precisely why breeding seems to be more fundamental to a definition of local extinction than does mere presence of a species. In the mangrove island experiments, Simberloff and Wilson (12–14) explicitly eliminated from consideration a few strongly flying species, such as some wasps and bees, which appeared not to breed on mangrove islands but to forage freely over these islands and the mainland as if they were all part of a homogeneous, fine-grained foraging system. This distinction is perhaps artificial, since such species could conceivably have a strong influence on the population dynamics of "valid" colonists and on energy flow through the island communities, whereas certain species (for example, the mangrove skipper *Phocides pygmalion*) which breed exclusively in red mangrove move freely as individual adults throughout a group of islands. Fortunately, in the mangrove ecosystem species of either type are rare; most animals once on an island are largely restricted to it and breed there if they breed at all. But for birds on continental islands and on habitat islands such as apple trees, this situation of presence without breeding, and frequent inter-island movement of individuals, forces us to reconsider the meaning of local extinction.

If recruitment to local populations is primarily by reproduction within the populations, and only rarely by invasion from without, preconditions are satisfied for the operation of classical group selection by population extinction (21). For this is exactly the situation in which local populations, with genetic differences induced by either selection or drift, can maintain sufficient genetic isolation to succeed or fail as discrete populations. Success by one population, and subsequent dispersal to areas vacated by populations that have failed and become locally extinct, provides a different mode

of gene frequency change and evolution from the one given by the neo-Darwinian paradigm of selection acting on individuals. The more generations, on the average, which are likely before individual invasion occurs, the more important ought group selection to be. In the limit, of course, complete cessation of inter-population dispersal establishes the pre-condition for allopatric speciation (22).

Even if individual invasion occurs relatively frequently, group selection could still be an important determinant of changes in gene frequency (23). All that is required is a distinct dispersal stage and a nondispersal stage in which mating, feeding, and other ecological acts are performed in "trait-groups" that are smaller than the deme of which they are components. Certainly many mangrove island arthropods conform at least to this model if not to that discussed in the previous paragraph. Lepidopteran caterpillars, for example, are restricted to one island while adults of at least some species (*Phocides pygmalion*, *Automeris io*) can be observed moving from island to island and presumably mixing with individuals that matured on other islands.

To falsify the hypothesis of equilibrium turnover, one would simply have to demonstrate that, on an island of unchanging ecology, short-term local extinction and immigration were not occurring. With local extinction defined by either of the above definitions, it would be sufficient to have periodic, accurate census lists which showed that species composition remained approximately constant. Such data are difficult enough to gather, but to determine whether the turnover was of evolutionary interest in the sense given above, much more elusive data would be required—namely, an estimate of the extent to which recruitment to breeding populations is by intra-island breeding rather than inter-island invasion. Recruitment primarily by invasion would correspond to Smith's model of robins in apple trees. Presence or absence data alone could demonstrate a dynamic equilibrium even if most local population recruitment were by invasion. In this event, one would simply be sampling from a large number of species which are constantly and rapidly changing "population" sizes on the island in question as individuals invade or leave. A certain number of species, and not the same ones, would by chance be absent any time a census was performed. If the total number of species in the species pool and the size of the island were large enough, the number of species absent (or present) would remain approximately constant, which could be

interpreted as demonstrating equilibrium. But data on actual amount of inter-island dispersal would, except in very special circumstances, require observation of movement of individuals. Even allowing for sophisticated vertebrate

marking techniques, one would be hard-pressed to do more than demonstrate that some inter-island movement had occurred. For insects and spiders even this much information would be difficult to gather.

Mangrove Island Evidence

In the summer of 1970 the previously defaunated (by tent-fumigation) mangrove islands E1, E2, E3, and ST2, all near Sugarloaf Key, one of the Florida

Table 1. Colonists on the Sugarloaf islands (E1, E2, E3, and ST2) during years 0, 1, 2, and 3. In the tabulated results, o signifies inferred presence, x signifies observed, and the space signifies not observed and inferred not present.

Order	Family	Genus and species	E1 0123	E2 0123	E3 0123	ST2 0123
Collembola	Entomobryidae	<i>Seira bipunctata</i>			x	
	Poduridae	Genus sp.			x	
Thysanura	Lepismatidae	<i>Lepisma</i> sp.	x			
Embioptera	Teratembiiidae	<i>Diradius caribbeana</i>		x	x	x x
Orthoptera	Blattidae	<i>Latiblattella</i> n.sp.	x	x xx	xxxx	xxxx
		<i>Latiblattella rehni</i>		xxxx		
	Gryllidae	<i>Cycloptilum spectabile</i>	x	x x	xxxx	x x
		<i>Cyrtoxipha confusa</i>		xxx		
		<i>Orocharis gryllodes</i>		x x		
		<i>Tafalisca lurida</i>	x	xxxx	xxxx	xxxx
	Tettigoniidae	<i>Turpilia rostrata</i>		x		
Isoptera	Kalotermitidae	<i>Neotermes castaneus</i>		x		
		<i>Neotermes jouteli</i>		x x	x x	x
Coleoptera	Anobiidae	<i>Tricorynus inflatus</i>	xx	xxx	xxx	xox
	Anthicidae	<i>Sapintus fulvipes</i>	xxx			
	Anthocoridae	Genus sp.		x		
	Buprestidae	<i>Actenodes auronotata</i>			x	
		<i>Chrysobothris tranquebarica</i>		xxx		
		<i>Mastogenius</i> sp.		x		
	Cerambycidae	<i>Elaphidion irroratum</i>		x		
		<i>Styloleptus biustus</i>		xxx	x	xxx
	Curculionidae	<i>Cryptorhynchus minutissimus</i>	ox	x	x	
		<i>Pentarthrinus atrolucens</i>		x		
		<i>Pseudoacalles sablensis</i>	xxxx	xxxx	xxxx	xxxx
	Lampyridae	<i>Micronaspis floridana</i>		x		
	Lathridiidae	<i>Melanophthalma floridana</i>			x	
	Scolytidae	<i>Trischidias minutissima</i>		x		
Hemiptera	Miridae	<i>Campylomma</i> sp.		x		
		<i>Psallus conspurcatus</i>		x		
		Genus sp.		x		xx
	Nabidae	<i>Carthasis decoratus</i>			xox	
Homoptera	Aleyrodidae	<i>Aleurothrixus</i> sp.		x		
		<i>Paraleyrodes</i> sp.1		xxx		
		<i>Paraleyrodes</i> sp.2		x		
		<i>Tetraleyrodes</i> sp.		xox	x	
	Cicadellidae	<i>Coelidia melanota</i>		x	x	
		<i>Scaphytopius nigrinotus</i>		xox	x	
	Coccidae	<i>Ceroplastes rubens</i>	x			
		<i>Dysmicoccus brevipes</i>		x	x	x
		<i>Pseudococcus</i> sp.		x		
Psocoptera	Caeciliidae	<i>Caecilius incoloratus</i>	x	xxx		xx
	Lepidopsocidae	<i>Echmepteryx youngi</i>		x		
	Liposcelidae	<i>Belaphotroctes ghesquierei</i>		xox	x	
		<i>Liposcelis bostrychophilus</i>			xxx	xxx
	Peripsocidae	<i>Ectopsocus</i> sp.C	x			
		<i>Peripsocus pauliani</i>	x			
		<i>Peripsocus stagnivagus</i>	x			
	Psocidae	<i>Indipsocus texanus</i>	x xx	oxx	ox	xox
Thysanoptera	Phlaeothripidae	<i>Barythrips sculpticauda</i>		xx		
		<i>Haplothrips flavipes</i>				xx
		<i>Liothrips islandica</i>			x	
	Thripidae	<i>Pseudothrips inequalis</i>	xox	x	xxx	oxx
Neuroptera	Chrysopidae	<i>Chrysopa collaris</i>	x	x x	x	x
Lepidoptera	Eucleidae	<i>Alarodia slossoniae</i>	x xx	x	x	xoxx
	Hesperiidae	<i>Phocides pygmalion</i>	xxx	xxx	xxx	x
	Olethreutidae	<i>Ecdytolopha</i> sp.	xxxx	x	xx	xxx
	Phycitidae	<i>Bema ydda</i>	xxx	xxx	xox	xxox
	Saturniidae	<i>Automeris io</i>	x	x		
	Tineidae	<i>Nemapogon</i> sp.	x	xoxx	x x	x x
Diptera	Hippoboscidae	<i>Lynchia albipennis</i>	xx			
	Unknown family 2	Genus sp.				x

Keys, were exhaustively censused for arboreal arthropods. These data extend to 3 years after defaunation the observations on these islands. Data from before

defaunation (year 0) and censuses of years 1, 2, and 3 are presented in Table 1 (24). A few changes in the published censuses for year 0 to year 2 are the

result of ongoing systematic work on these collections; in no instance do these changes alter the conclusions drawn from the data. The censuses of year 0 to

Order	Family	Genus and species	E1	E2	E3	ST2
			0123	0123	0123	0123
Hymenoptera	Bethyidae	<i>Scleroderma macrogaster</i>	x	x		x xx
		<i>Apanteles hemileuca</i>		x		
	Braconidae	<i>Callihormius bifasciatus</i>		x	x	
		<i>Macrocentrus</i> sp.			x	x
	Chalcidae	Genus sp.			x	
		<i>Cheiloneurus</i> sp.			x	
	Encyrtidae	<i>Encyrtus</i> sp.			x	
		<i>Ooencyrtus submetallicus</i>		x		
	Eumenidae	<i>Pachodynerus nasidens</i>	x		x	
		<i>Camponotus abdominalis</i>		xxx		xxx
	Formicidae	<i>Camponotus tortuganus</i>		x		
		<i>Camponotus (Colobopsis)</i>	x		x	x
		<i>Crematogaster ashmeadi</i>	xox	xxx	xxxx	xxxx
		<i>Monomorium floricola</i>		x	xx	
		<i>Paracryptocerus varians</i>		x xx	xxox	xxxx
		<i>Paratrechina bourbonica</i>		xx	xxx	
		<i>Pseudomyrmex elongatus</i>	x xx	xxxx	xxxx	xxxx
		<i>Tapinoma littorale</i>		x	x	xxx
		<i>Xenomyrmex floridanus</i>		xxxx	xx	xx
	Ichneumonidae	<i>Calliephialtes ferrugineus</i>		ox	x	x
		<i>Casinaria texana</i>	x	x		x
	Scelionidae	<i>Probaryconus striatus</i>		x	x	
	Sphecidae	<i>Trypargilum johannis</i>			x	x
Araneida	Anyphaenidae	<i>Anyphaena</i> sp.				x
		<i>Aysha velox</i>	xx	xxxx	xxx	xxx
	Araneidae	<i>Eustala</i> sp. 1		x x		
		<i>Nephila clavipes</i>		x x		x
	Clubionidae	Genus sp. A		x		
		<i>Gnaphosa</i> sp.		x		
	Gnaphosidae	<i>Sergiolus</i> sp.		x	x	
		<i>Admetina</i> sp.		x		
	Salticidae	<i>Hentzia grenada</i>	x	xxx	xxxx	xxxx
		<i>Metacyrba undata</i>		x		
		Genus sp.		x		
	Segestriidae	<i>Ariadna arthuri</i>		x x	x	xox
	Tetragnathidae	<i>Tetragnatha antillana</i>		x		
	Unknown family	Genus sp.	x			
Acarina	Acaridae	<i>Suidasia medamensis</i>		x		
	Argasidae	<i>Argas radiatus</i>	xox			
	Ascidae	<i>Arctoseius</i> sp.				x
	Bdellidae	<i>Bdella</i> sp.			x	
		Genus sp.		x		
	Dermanyssidae	Genus sp.		x		
	Eupodidae	<i>Eupodes</i> sp. nr. <i>fusifer</i>			xxx	
	Galumnidae	<i>Galumna</i> sp.	x	xxox	x	x
	Oribatulidae	<i>Scheloribates</i> sp.	xxx	x	xxx	x
	Phytoseiidae	<i>Amblyseius</i> sp.		x		xxox
	Unknown family 1	Genus sp.	xx			
	Unknown family 2	Genus sp.		x		
	Unknown family 3	Genus sp.		x		
	Unknown family 4	Genus sp.			x	
	Unknown family 5	Genus sp.				xx
Chelonethida	Cheliferidae	<i>Tyrannochelifer</i> n. sp.				x
	Chernetidae	<i>Lamprochernes</i> sp.			x	
Diplopoda	Polyxenidae	<i>Lophoproctinus bartschi</i>	x	x	x xx	x xx
Isopoda	Oniscidae	<i>Rhyscotus</i> sp.	x x	x x	xox	x
Pauropoda	Unknown family	Genus sp.				x

Summary of statistics

Year	Number of species (days after defaunation)			
	E1	E2	E3	ST2
0	20 (0)	35 (0)	22 (0)	25 (0)
1	13 (360)	32 (371)	28 (379)	28 (322)
2	17 (726)	37 (730)	27 (725)	28 (691)
3	19 (1235)	48 (1256)	33 (1239)	30 (1167)

year 2 include certain species inferred present while not actually seen. The general rules for such inference (13) are conservative with respect to turnover, since they do not allow the recording of local extinction if there is a reasonable probability of failing to observe a small population of the species in question. I believe that the censuses of year 0 to year 2 may be underestimates by one to five species because of unobserved colonists; in general, we tried to avoid damage to the islands and this lessened collecting efficiency slightly (14). Evidence for completeness of the censuses is given by Wilson and Simberloff (12). The censuses of year 3 were more destructive and were conducted for approximately one and one-half times as many man-hours as the earlier censuses; I feel that they must be very nearly complete.

A similar but untampered with *Rhizophora mangle* island (IN1) was censused in 1969, 1970, and 1971 as a control for continuing experiments in the Keys and was found to have virtually the same number of species each time (25). This suggests that there is no monotonic change in the physical environment of the Keys or its species pool acting to change the experimental communities. Actual environmental data, or even an assessment of which environmental variables would be critical to colonizing success of the hundreds of species in the pool, are lacking; for each species such information would require a massive research effort. Species number equilibrium was reached within a year on all islands but E1; by year 2 E1 was within 15 percent of its species number before defaunation. Table 2 presents the fraction of species held in common between the biota before defaunation and the biotas of year 1 to year 3, respectively, on each island. The figures, including six increases and two decreases, are consistent with our earlier suggestion (14) that, even after species number equilibrium is reached, an "assortative" equilibration process (26) occurs as more highly co-adapted species sets find themselves by chance on an island and persist longer as sets. Further demonstration of the assortative equilibration would require measurement of actual turnover rates, a forbidding task under any circumstances and an impossible one without nearly continuous monitoring. In any event, the similarity of the last two columns in Table 2 suggests that at least by year 2, if not earlier, the effects of the drastic change wrought by defaunation no longer affected the island communities. In sum, we can look for equilibrium turnover rates on these islands in reasonably

Table 2. Species held in common between the time before defaunation and subsequent censuses, as a fraction of composite list.

Island	Years 0 to 1	Years 0 to 2	Years 0 to 3
E1	0.100	0.194	0.219
E2	.196	.263	.239
E3	.190	.225	.250
ST2	.395	.514	.341

secure knowledge that the islands are, in fact, in biotic and abiotic equilibrium.

In the first place, observed turnover rates obtained from Table 1 by looking for extinction between years 1 and 2 or between years 2 and 3 must be a great underestimation of the actual rates because of unobserved immigration between successive monitoring periods (Lynch and Johnson's "cryptoturnover"). For the recolonization period with approximately 18-day intervals between census periods, Simberloff (20) suggested that perhaps half of all turnover is unobserved from this source alone. Gilroy (27), likening the mangrove island system to one of molecular adsorption, showed that the colonization data as a whole are consistent with the hypothesis that 90 percent of actual turnover was observed. In either event, with a year between censuses the number of missed turnovers must be greatly increased, and almost certainly exceeds the number of observed ones.

If this inaccuracy and the conservatism imposed by inferring presence are borne in mind, the observed numbers of local extinctions from Table 1 are 3, 8, 5, and 7, respectively, for the first interval and 2, 13, 7, and 6, respectively, for the second. The number of immigrations is slightly larger in all but one instance. It is clear, then, that on these islands much turnover is occurring in ecological time, a scale of years rather than millennia.

How much of this turnover represents local extinction of relatively isolated breeding populations, rather than the vagaries of short-term transient movement between islands, is not as easily assessed. Direct evidence, consisting of observations of inter-island dispersal, is minimal and anecdotal. In a few instances here, as in the original colonization experiment, we can be almost certain that a given local extinction is the "uninteresting" event of death or emigration of a chance individual or pair which probably never bred on the island. The termite *Neotermes castaneus* recorded as disappearing on E2 between years 1 and 2 constitutes such an extinction. The original observation was of a

single founding pair which had not established a colony, and mortality of such pairs must be high.

Two more general classes of indirect evidence may be used to assess the nature of a given local extinction. First, many species are capable of ready inter-island movement. This leads to a conservative estimate of nontransient turnover, since some species that are capable of moving between islands apparently do not do so. Island E2 gives the clearest proof of this, for although it is only 2 meters from the enormous, mangrove-fringed Snipe Keys, most of the arthropods of the Snipe Keys have never been observed on E2.

Second, from the unusual initial circumstances of the six defaunated mangrove islands of the original experiment it is possible to estimate the amount of individual movement between islands in the following way. For each species and each island there is an observed number of monitoring periods before the species was first tallied. In some instances a species never reached an island over the approximate 1-year duration of the experiment. We may take the mean number of monitoring periods before appearance times 18 as a lower limit to the average number of days between invasion recruitment episodes for a species. This is a conservative estimate since the monitoring intervals on island E7 often exceeded 18 days. In calculating this statistic we may restrict our attention to only those islands on which immigration actually occurred, but this surely yields too low an estimate (henceforth called i_1) of intervals between invasion, since failure to invade at all in 1 year suggests that the mean interval between invasions is long. For those islands on which invasion never did occur, one cannot average in infinity; and, although 270 days is a lower limit to the time of invasion on these islands, it is used in calculating a less conservative estimate (i_2) of the mean inter-invasion interval.

On the whole, one using this procedure is likely to overestimate the amount of inter-island movement by individuals for the reasons just stated. This tendency is countered in two ways. (i) An individual, such as a single male, that would not itself constitute a propagule (20) could nevertheless participate in gene flow upon invasion of an island already containing a conspecific population. Approximately ten times during the year after defaunation, males alone were observed on islands before females had been recorded; at these times, immigration was assumed not to have taken place yet. (ii)

There must have occurred invasions that quickly failed and would therefore have constituted a form of "cryptoturnover" as defined above; in effect, the observed immigration represented invasions that were successful at least to the extent that they persisted until the next monitoring period. They may also have been disproportionately successful in reproducing, as it would be easier to overlook a single individual than a small group; I believe, however, that we recorded even most single-individual populations on these tiny islands (13). In any event, invasions that would likely fail to establish breeding populations might well contribute genes to an extant breeding population.

For all 116 species of Table 1, presumably a fair representation of the equilibrium fauna of small Florida Keys mangrove islands, the mean i_1 is 177 days and the mean i_2 is 215 days. A few species, of course, typically invade more frequently, with i_1 and i_2 in the range of 90 days. But the distribution is strongly skewed in the other direction; first quartile, median, and third quartile for i_2 are 174, 240, and 270 days, respectively. I have observed that almost all colonists appear to breed year-round in the Keys; and, although precise generation times are not known for these species, i_1 and i_2 must greatly exceed generation times for most or all colonists. Indeed, for many colonists in the Hemiptera, Homoptera, Psocoptera, Hymenoptera, and Acarina the generation time must be closer to 1 month. Thus, it is clear that inter-island movement is not so frequent in this system as to preclude local extinction of populations isolated for several generations. Unfortunately I lack data on the mean length of colonization episodes since equilibrium was achieved. But during the first year of colonization, when persistence should have been greater, if anything, than after reequilibration because of less predation and competition, mean persistence for the four Sugarloaf islands varied from 41 days on E3 to 55 days on E1—shorter than the mean inter-invasion intervals estimated above.

Of the 51 extinctions recorded between years 1 and 3, are there any which could unequivocally be described as elimination (i) after reproduction had occurred, and (ii) where inter-invasion intervals are likely to be sufficiently long so that I have not simply recorded the chance presence or absence of transients? More than half (that is, 28 of the 51) were observed in only one census before extinction was recorded, and hence *might* have been transient non-

Table 3. Unequivocal extinctions of resident populations. In all instances flightless immatures were recorded, and several individuals had usually been observed in each prior period.

Organism	Island	Year	Consecutive periods previously resident (No.)	i_2 (days)
<i>Peripsocus stagnivagus</i>	E1	1 to 2	6	192
<i>Ecdytolopha</i> sp.	E2	1 to 2	10	111
<i>Amblyseius</i> sp.	E2	1 to 2	12	111
<i>Tricorynus inflatus</i>	E2	2 to 3	17	132
<i>Tetraleurodes</i> sp.	E3	1 to 2	11	204
<i>Chrysopa collaris</i>	E3	1 to 2	13	39
<i>Monomorium floricola</i>	E3	2 to 3	9	249
<i>Xenomyrmex floridanus</i>	E3	2 to 3	9	162
<i>Xenomyrmex floridanus</i>	ST2	1 to 2	6	162
<i>Scheloribates</i> sp.	ST2	1 to 2	7	240
<i>Indiopsocus texanus</i>	ST2	2 to 3	8	165
<i>Tapinoma littorale</i>	ST2	2 to 3	8	249

breeders on this ground alone. (Some of these certainly bred, however; for example, *Nephila clavipes* at year 2 on E2 was represented by about 100 small spiderlings.) Three other recorded extinctions are of wasp species (*Pachodynerus nasidens* and *Calliephialtes ferrugineus*) which appear to disperse well enough between islands so that they could conceivably represent just chance presence, then absence, of transients. These species colonized all islands; $i_1 = i_2 = 72$ days for *Pachodynerus* and 87 days for *Calliephialtes*. One recorded extinction, of *Psallus conspurcatus*, could conceivably be a taxonomic artifact, as nymphs of this true bug are very difficult to distinguish in vivo from the subsequently recorded species *Campylomma* sp. Finally, to be ultraconservative I discount seven species recorded as extinguished between years 2 and 3 after two or more consecutive census observations. Although the censuses of year 3 were exhaustive, all these species when present are usually not numerous and are often secretive; since I have no subsequent check on the year 3 census, I disallow these seven local extinctions even though I would guess that most of them are "valid."

This leaves 12 observed local extinctions (Table 3) for which I can be virtually certain that a long-standing, breeding population which received few or no recruits from other islands was extinguished. To this lot, one may add data from three yearly censuses of island IN1. A standing biota of 63 to 68 species (flies and mites not included) showed extinctions in two successive years of 19 and 20 species, respectively (25). Of these, perhaps three each year (including two of ants) would satisfy the stringent requirements set out above.

For island IN1 as well as the experimental islands, the other premise of the equilibrium theory of island biogeog-

raphy, that unidirectional environmental change is not the cause of observed turnover, has not been proved. Animals respond to their physical environments so subtly that such proof is probably precluded in any natural system. The best we can do is to avoid an equilibrium interpretation where gross environmental change is apparent, such as that on Barro Colorado Island. The equilibrium theory does not, of course, postulate a constant environment; local extinctions may be due to environmental events such as storms or droughts, as long as the probabilities of such events are constant, and as long as they are relatively frequent with respect to the time scale of the observations.

Despite extreme, consistent conservatism in all matters of judgment or estimation, 12 local extinctions (about 1.5 extinctions per island per year) can be described as elimination of breeding, nontransient colonists. Probably the greatest source of underestimation is the "cryptoturnover" necessitated by long intervals between censuses, and actual turnover of breeding nontransients must be several times the above figure when this and other inaccuracies are considered. This granted, it is still clear that, even though such valid turnover occurs, its rate is far less than the estimated 0.5 extinction per island per day recorded during an earlier colonization experiment (part of which clearly occurred during nonequilibrium conditions). In other words, most observed turnover on these small mangrove islands involves transients; that is, it is "pseudoturnover." If they breed there, such transients can still contribute to group selection, but less strongly than if there were little inter-island movement.

These conclusions rest on the special circumstance of a closely monitored set of empty islands, permitting inferences of inter-island movement without actual

observation of moving individuals. In most other examples given as evidence for the validity of equilibrium biogeography, such inference is impossible and direct observation of dispersal rates will be required. Until such observations have been made on a number of systems, the equilibrium theory of island biogeography must be considered a hypothesis, and one which is difficult to test. To the extent that it can be accorded provisional acceptance because of work done to date, all we can say is that there often appears to be approximate short-term constancy of species numbers and a fair amount of turnover. Much of the latter may prove to involve transient movement, with or without breeding. Finally, for the equilibrium theory of island biogeography as for any other empirical statement about how nature is structured, we must be aware of the possibility that, when the field observations are made, they will show that certain taxa (or ecosystems) conform more closely than others to the theory.

References and Notes

1. R. H. MacArthur and E. O. Wilson, *Evolution* **17**, 373 (1963); F. W. Preston, *Ecology* **43**, 185 (1962).
2. R. H. MacArthur and E. O. Wilson, *The Theory of Island Biogeography* (Princeton Univ. Press, Princeton, N.J., 1967).
3. D. S. Simberloff, *Annu. Rev. Ecol. Syst.* **5**, 161 (1974).
4. J. Brown, *Am. Nat.* **105**, 467 (1971).
5. R. E. Cook, *Syst. Zool.* **23**, 257 (1974).
6. J. F. Lynch and N. K. Johnson, *Condor* **76**, 370 (1974).
7. T. S. Kuhn, *The Structure of Scientific Revolutions* (Univ. of Chicago Press, Chicago, ed. 2, 1970).
8. J. M. Diamond, *Science* **179**, 759 (1973); D. S. Simberloff and L. G. Abele, *ibid.* **191**, 285 (1976).
9. A. L. Sullivan and M. L. Shaffer, *ibid.* **189**, 13 (1975).
10. K. R. Popper, *Conjecture and Refutation: The Growth of Scientific Knowledge* (Harper & Row, New York, 1963); *Objective Knowledge, An Evolutionary Approach* (Clarendon, Oxford, 1972).
11. A. MacFadyen, *J. Anim. Ecol.* **44**, 351 (1975).
12. E. O. Wilson and D. S. Simberloff, *Ecology* **50**, 267 (1969).
13. D. S. Simberloff and E. O. Wilson, *ibid.*, p. 278.
14. ———, *ibid.* **51**, 934 (1970).
15. F. E. Smith, *Bull. Ecol. Soc. Am.* **56**, 2 (1975).
16. N. Richter-Dyn and N. S. Goel, *Theor. Pop. Biol.* **3**, 406 (1972); M. E. Gilpin, cited in G. L. Hunt and M. W. Hunt, *Condor* **76**, 363 (1974).
17. J. M. Diamond, *Proc. Natl. Acad. Sci. U.S.A.* **64**, 57 (1967).
18. J. Terborgh, in *Tropical Ecological Systems*, F. Golley and E. Medina, Eds. (Springer-Verlag, New York, 1975).
19. E. O. Willis, *Ecol. Monogr.* **44**, 153 (1974).
20. D. S. Simberloff, *Ecology* **50**, 296 (1969).
21. R. Levins, in *Some Mathematical Questions in Biology. Lectures on Mathematics in the Life Sciences*, M. Gerstenhaber, Ed. (American Mathematical Society, Providence, R.I., 1970), vol. 2; S. A. Boorman and P. R. Levitt, *Theor. Pop. Biol.* **4**, 85 (1973); B. R. Levin and W. L. Kilmer, *Evolution* **28**, 527 (1974); E. O. Wilson, *Sociobiology* (Harvard Univ. Press, Cambridge, Mass., 1975); M. E. Gilpin, *Group Selection in Predator-Prey Communities* (Princeton Univ. Press, Princeton, N.J., 1975).
22. P. J. Darlington, *Proc. Natl. Acad. Sci. U.S.A.* **68**, 1254 (1971).
23. D. S. Wilson, *ibid.* **72**, 143 (1975).
24. Year 0 and year 1 data from Simberloff and Wilson (13); year 2 data from Simberloff and Wilson (14).
25. D. S. Simberloff, *Ecology* **57**, 629 (1976).
26. E. O. Wilson, in *Diversity and Stability in Ecological Systems*, G. M. Woodwell and H. H. Smith, Eds. (Brookhaven National Laboratory, Brookhaven, N.Y., 1969).
27. D. Gilroy, *Ecology* **56**, 915 (1975).
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A Western Perspective on Energy: A Plea for Rational Energy Planning

Federal energy programs, possible effects of energy development activities, and suggested actions.

Bill Christiansen and Theodore H. Clack, Jr.

Dwindling supplies of energy and materials resources pose what may be the most significant problem for the United States in the last quarter of the 20th century. The nation's response to these shortages could prove to be the measure of its ability to respond to crises in an equitable and farsighted manner. Our absolute dependence on energy and raw materials demands the most stringent exercise of reason in coping with shortages. Errors in allocating resources and poor judgment in the pursuit of alternative means of using our remaining natural resources will have international repercussions that will persist for generations.

In its search for solutions to the energy

crisis, the nation has turned to the Rocky Mountain region. Immense reserves of accessible fossil fuel are perceived as the short- and mid-term answers to the energy crisis. National leaders believe these resources will allow the nation to develop strategies to avoid recurrences of the energy crisis. As a consequence, the federal government and the energy industry have prepared plans to develop western energy resources. These plans have been proposed despite evidence that they are *not* the answer to the energy crisis; they also ignore the possibility that western coal and oil shale reserves may have far greater value as future sources of hydrocarbons than as simple fuels for the present.

Limitations of Current Plans

Many of the federal and industrial plans to resolve the energy crisis are objectionable in several respects. Beneath the bureaucratic and technical jargon, these plans propose maintenance of the status quo—continued annual growth in the consumption of resources. None of the plans seriously addresses the concept of limits to growth. All are based on the assumption that increasing economic growth is feasible and necessary to national survival. No major policy statement portrays resource conservation as a central part of a successful solution to shortages, although the importance of energy conservation is given more emphasis in a publication of the Energy Research and Development Administration—*ERDA 76-1 (1)*. Concern with the expenditure of irreplaceable energy resources is conspicuous by its absence. The public is not aware, nor has it been informed, that severe energy, food, and materials shortages are likely to be with us for the foreseeable future.

Two major federal plans exhibit these shortcomings. If implemented, these plans will have significant political, social, and environmental effects, and they

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