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Island biogeography theory predicts that the equilibrium number of species on an island, the net number of species resulting from immigration less extinction, is related to the area of the island and its distance from a source region (MacArthur and Wilson 1963, 1967). In numerous studies the relationship between species number, S, and island area, A, has been well described by the power function $S = cA^z$, where c and z are fitted constants. May (1975) has shown that such species-area curves are to be expected if the relative abundance of species assumes a lognormal distribution. In such cases z values should lie within the range 0.15–0.39. As often noted, the species-area relation is an empirical description. Causal mechanisms include the correlation of island area with habitat diversity, and sampling artifact if the number of samples is correlated with island size, as well as the immigration-extinction equilibrium theory (see Connor and McCoy 1979 for review of these hypotheses). All three hypotheses are subsumed by the island paradigm. This body of theory has been used as a powerful tool for the analysis of species richness on real islands and for isolated habitats considered as islands (reviewed in Simberloff 1974; Connor and McCoy 1979).

Following Janzen's (1968) suggestion, a number of researchers have attempted to apply island biogeography theory, especially the species-area curve, $S = cA^z$, to situations involving animal hosts as islands for parasites (Dritschilo et al. 1975), symbionts of unspecified trophic relationships (Abele 1976; Abele and Patton 1976; Uebelacker 1977), and plant hosts as islands for herbivorous insects (see Strong 1979 for review) and mites (Tepedino and Stanton 1976). Hosts may be regarded as islands at three levels of organization: (1) individuals; (2) populations; (3) species. The studies of Abele (1976), Abele and Patton (1976), Tepedino and Stanton (1976), and Uebelacker (1977) treat individual host organisms or colonies as islands. Seifert (1975), Ward and Lakhani (1977), Lawton (1978), Freeland (1979), and Raupp and Denno (1979) study species richness using host populations as islands. Strong (1974c) and Strong et al. (1977) use the acreage of crops (cacao and sugar cane, respectively) planted in various political units (countries, states, and colonies) as islands. The remaining studies treat the geographic ranges of the host species as islands.

The establishment and maintenance of species diversity is one of the central

problems for modern ecological theory. Given the demonstrated value of island biogeography theory in the analysis of experimental and retrospective studies involving real islands and comparable isolated habitat units, we will examine how hosts may be regarded as islands and discuss the quality of data required to utilize island biogeography theory for host "islands". For hosts treated as islands from an individual, population, or species perspective we find that the assumptions of island biogeography theory require increasing degrees of modification. We believe that the data used to generate many of the published species-area curves for host species "population" or "geographic range islands" are substantially unsuitable for this intended purpose (e.g., Strong 1974a, 1974b, 1974c; Dritschilo et al. 1975; Strong and Levin 1975, 1979; Strong et al. 1977; Lawton and Schröder 1977).

HOST INDIVIDUALS AS ISLANDS

No man is an Iland entire of it selfe; every man is a peece of the Continent
[John Donne (1624)].

From a parasite's point of view, individual host organisms are unequivocal islands. Infection is equivalent to immigration of the parasite population. Extinction represents the loss of a parasite population either through natural death of parasites with short life spans (e.g., pinworms in humans), competition from other parasite populations (e.g., several larval echinostome trematode species eliminate preexisting larval schistosome populations from double infections in snail hosts [Lie 1967; Lim and Heyneman 1972; Kuris 1973]; see Kuris 1974 for other systems exhibiting similar competitive interactions), or host defensive responses. The host may simply eliminate the extant parasite population through processes such as immune expulsion of nematodes in mice (Behnke 1975) or the melanization and encapsulation of nematodes by mosquitos (Poinar 1969) or of parasitic isopods by crabs (Kuris et al. 1980). Some host defensive responses result in acquired sterile immunity. In such cases reinfection (= immigration) may be permanently prevented even though the parasite is no longer present. *Trypanosoma lewisi* of the rat, and other rodent trypanosomes, exemplify such a system (D'Alesandro 1970; Molyneux 1976). In some systems immunity may be homologous, effective against only the specific parasite which induced the immune response, or heterologous, preventing infection of other related species (Cohen 1973a). Plant host defenses also influence herbivorous insect populations (Janzen 1973). Indeed, catalytic models (Muench 1959) employing exponential rate functions to describe the pattern of acquisition and loss of parasite populations provide good fits to age-specific prevalence data for schistosomes (Hairston 1965; Sturrock and Webbe 1971; Cohen 1973b; Sturrock et al. 1975), filarial worms (Hairston and Jachowski 1968), and liver flukes (Manning et al. 1971).

Numerous studies (e.g., Mohr and Stumpf 1964; Chappell 1969; Cone and Anderson 1977; Kuris 1978; Gilbert and Smiley 1978) indicate that older and larger hosts (size and age are often correlated for fishes and many invertebrates) generally are likely to have more kinds of parasites and greater densities of particular parasite species than younger, often smaller, hosts. However, if parasite presence (as with parasitoids, Kuris 1974) or high parasite density (as with

typical parasites, Kuris 1974) is associated with host mortality, a decrease in the frequency of parasitization in the oldest age (largest size) classes may occur as a result of differential mortality of the heavily infected individuals. Unlike real islands, the very existence of host islands may be adversely affected by parasite presence. Comparison of parasite faunas of closely related taxa suggests that host species of large body size have more species of ectoparasitic lice than do smaller species (Dogiel 1964; Mohr and Stumpf 1964). This trend is also evident for herbivorous insects on plants (Price 1977; Gilbert and Smiley 1978; Lawton and Price 1979).

For certain parasite taxa having little pathological effect on host viability, parasite species richness may rapidly approach an asymptote. Hair and Holmes (1975) describe a species flock of intestinal helminths in Lesser Scaup from Alberta. As many as 25 species may simultaneously be present. A sample of 10 adult ducks had 13–25 intestinal parasite species ($\bar{x}$ = 16 species per bird). Hair (1975) found that six 3-day-old ducklings were already parasitized by six helminth species ($\bar{x}$ = 2 species per bird). Five 4–5-day-old ducklings had 14 helminth species ($\bar{x}$ = 9 species per bird). By the age of 1 mo a sample of six ducklings included 18 helminth species ($\bar{x}$ = 12 species per bird). Thus a full complement of intestinal parasites is rapidly approached. Competition for suitable sites in the intestine may put this limit well below the maximum possible (33). A study of the distribution of 10 or more pinworm species in the colon of tortoises (Schad 1963) suggests that similar factors may be operating in this parasite guild.

On long-lived hosts potential sites remain available for long periods of time. Assuming similar parasite transmission rates, these individuals are likely to be parasitized by more species of relatively avirulent parasites and have higher parasite densities at these sites than similar short-lived hosts.

Host size per se may also influence parasite species richness. Although hosts were not aged, host size was reported to be a significant factor determining species richness for the infauna of a tropical sponge (Uebelacker 1977), for decapod crustaceans associated with coral heads (Abele 1976; Abele and Patton 1976) and for hispid beetles on plants of the families Heliconiaceae and Marantaceae (Strong 1977). Since certain preferred anatomical sites are larger or more numerous (e.g., sponges, coral heads) on large hosts they may be able to hold more parasite individuals or species. Certain sites that are too small to harbor parasites on small hosts may become available to parasites only on large hosts. Such a host size factor was demonstrated in an analysis of ectocommensal populations of juvenile *Carcinonemertes* (a nemertean) site utilization on shore crabs (Kuris 1978). Sites on large hosts may facilitate niche differentiation and habitat segregation by competing parasite species more so than corresponding sites on small hosts.

For individual hosts as islands, the parameters of importance to island biogeography theory (MacArthur and Wilson 1967) all appear to operate to determine parasite species richness: (a) size and age of host, (b) habitat complexity (often highly correlated with [a]), and (c) distance to potential sources of infection (as estimated by host population density). To treat hosts as islands, modifications of the theory are needed to accommodate certain aspects of host biology. (1) "Interisland" distance through time may fluctuate (short time-scale for vagile hosts

and longer time scale for sedentary or sessile hosts) as host density fluctuates. (2) Seasonal differences in host behavior or physiological condition may affect the presence of parasites (Beaudoin et al. 1971; Lee et al. 1977). (3) The quality of the host island over ecological time changes as a result of growth and aging processes. (4) The presence of certain parasites themselves may affect characteristics of the host island, including survival. (5) The individual as an island is relatively ephemeral and the parasite species assemblages may never reach an equilibrium at least on the time scale of the host life span (Tepedino and Stanton 1976). Thus, many parasite communities are similar to the dipteran carrion assemblage that feeds upon snail carcasses (Beaver 1977).

HOST POPULATIONS AS ISLANDS

Something there is that doesn't love a wall [Robert Frost (1914)].

In the analysis of parasite species richness, host populations show certain characteristics of biogeographic islands. However, island biogeography theory requires significant modification before an analogue of the species-area curve may be applied to these host "islands". Host population density, habitat area occupied, and host dispersion patterns are likely to influence rates of parasitization and loss of parasites from the host population.

A parasite fauna having but a single host represents the simplest case. Where there are disjunct local populations of this host, island biogeography theory may be directly applied. Species richness of parasites would be related to local population size and interpopulation distance especially where these populations are small or short lived. For example, Seifert's (1975) study of the insect fauna associated with small dense clumps of *Heliconia* inflorescences was such a case. The species richness of associated insects exhibited a species-area curve of the form $S = cA^z$ but a distance effect between clumps was not demonstrated. Tepedino and Stanton (1976) suggest that *Heliconia* inflorescences do not survive long enough for the insect populations to equilibrate. Host populations that may be described as distinct islands are probably rare. Many populations do not have sharply defined boundaries or interdigitate with related host populations. Even Seifert's *Heliconia* populations required an operational definition of individuality (i.e., interclump distance had to exceed 1.2 m).

For parasites able to utilize several host species "interisland" distance and "island" area are not simple measurements at the host population level. Here "distance" must be expressed by area of overlap where overlap of populations of different host species occurs. If overlap does not occur, linear distance between interspecific host populations may be used. Populations of different host species may overlap spatially. Studies of the parasite fauna of freshwater fish communities indicate that the parasite fauna of a particular host species is influenced by the presence of other host species (Wootten 1973; Kennedy 1975). An alternative to treatment of each host population as an island in a community of related hosts is to regard all potential host species in a community as a single multispecies island. For freshwater fish communities the composition of the parasite fauna and parasite species richness are determined by physical characteristics of the habitat

(Wisniewski 1958; Chubb 1970), presence of nonpiscine definitive and intermediate hosts (Esch 1971; Kennedy 1978a, 1978b; Wootten 1973), and predator-prey relationships (Esch 1971). Transmission of parasites between vagile host populations also depends on the frequency of contact between individuals and the joint utilization of resources important to the epidemiology of the parasite (e.g., water holes for parasites with aquatic transmissive stages such as schistosomes). Frequency of multiple feeding by blood-sucking vectors may also affect the spread of parasites within and between host populations. Spatial relationships between populations of different host species are often complicated. These factors suggest that host-parasite species richness may not be adequately described by simple expressions such as $S = cA^z$.

Other factors influencing parasite species richness may be host species diversity and the degree of phylogenetic similarity of host species. The monogenetic trematode fauna of fishes on the Great Barrier Reef includes more parasite species per individual host than are reported from other well-studied habitats (Rohde 1977). These parasites on the Great Barrier Reef also infest higher proportions of host populations. However, density per host of these parasites is not higher on the reef. Host specificity is less restricted on the Great Barrier Reef than for the other locations studied, perhaps because the high host species diversity of the reef fishes includes many more closely related host species than co-occur in other less speciose fish faunas (Rohde 1977).

For insects on plants the taxonomic affinity of the hosts is a poor predictor of insect species richness (Futuyma and Gould 1979). In a review of several tropical plant-insect systems Gilbert and Smiley (1978) find plant biomass to be the single best predictor of insect species richness when plant species are compared within habitats. Further, host species richness and diversity are highly significant predictors of insect species richness when hosts are compared between habitats. Some studies suggest that insect species richness may not be a community attribute sensitive to changes in host patch size. Both Gilbert and Smiley (1978) and Raupp and Denno (1979) find that the density but not species richness of certain insect specialists is correlated with area of the host plant. Thus, insect species diversity rather than species richness is affected by differences in host population size.

In a pioneering study of animal parasites Freeland (1979) shows that the intestinal protozoan species richness of African mangabey monkeys is correlated with host social group size. In contrast, savannah baboon groups have identical protozoan faunas. Freeland proposes that parasite transmission is influenced by social factors. Control of parasite transmission may be an important selective determinant of social organization for primates.

The recent use of lists of insect pest species from political entities (nations, states, and colonies) to define "islands" of agricultural crop acreage (cacao and sugar cane; Strong 1974c; Strong et al. 1977) may be an inappropriate application of island biogeography theory in general and the species-area relationship in particular. We base this conclusion on the following general principles: (a) Political boundaries do not define "crop islands", (b) area under cultivation or harvested often has dramatic annual fluctuations, (c) pest species lists generally
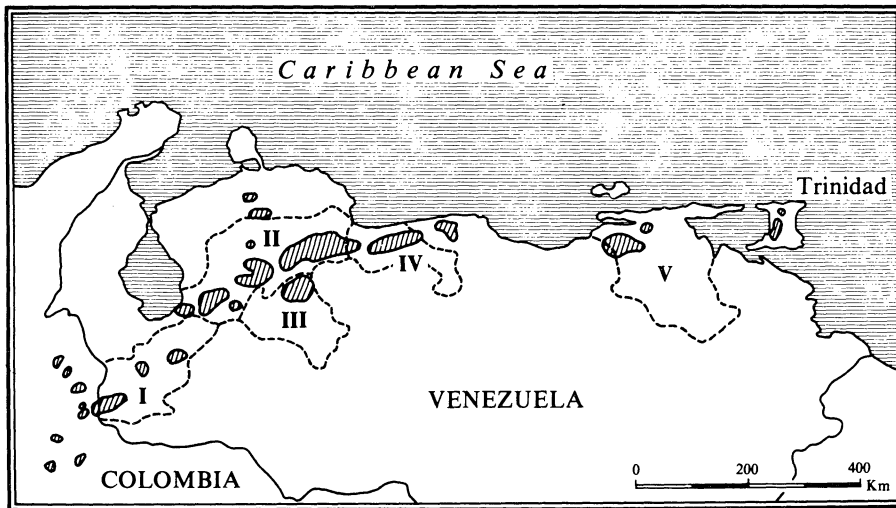
FIG. 1.—The major sugar cane growing regions of Venezuela, Trinidad and northeastern Colombia. Diagonally shaded areas depict regions which comprise at least 1% of total sugar cane acreage (World Atlas of Agriculture 1969). Zones I-V are distinctive regions based on economic factors and type of cultivar grown (Venezuela-CVF 1977).

accrue but seldom if ever delete species, and (d) economic factors may seriously affect pest species list compilations.

"Crop islands" used by Strong and coworkers include the New Hebrides, Solomon Islands, Fiji Islands, Philippines (1974b), Indonesia, Japan, Philippines, and Hawaii (1977). Each of these archipelagos include numerous real islands often separated by long distances. For instance, in 1952–1953 (the year Strong et al. [1977] report 44×10^3 ha of sugar cane on the Hawaiian Islands) cane was cultivated on four islands (Hawaii, Kauai, Maui, Oahu). These islands are separated from the nearest cane-growing island by 40–110 km of oceanic conditions, presumably a real barrier to sugar cane pest dispersal.

In most of the reported political entities (especially the large ones) crops are not grown in a single monoculture patch, but are scattered about to varying degrees in different geographic regions. To illustrate the inappropriate use of political units as "islands" we analyze sugar cane distribution in Venezuela, which reported 20×10^3 ha under cultivation in 1952 (the year used in Strong et al. 1977). Venezuela is a typical cane-growing nation, ranking thirtieth among the 75 nations listed in Strong et al. (1977). Figure 1 shows that sugar cane is intensely cultivated in several widely separated areas. Gaps up to 260 km wide separate some of these regions of cane cultivation. Areas near the Colombian border are closer to several regions of cane cultivation in that neighboring country than to any other area within Venezuela. Similarly, the cane-growing regions in eastern Venezuela are closer to the cane-growing island of Trinidad than they are to other Venezuelan cane-growing regions.

Within Venezuela cane cultivation is concentrated in five regions (fig. 1). These

TABLE 1

HECTARES OF SUGAR CANE CULTIVATED IN FOUR WIDELY SEPARATED
DISTRICTS ALONG THE COAST OF QUEENSLAND, AUSTRALIA.
(Districts listed north to south.)

District	ha × 10³	Distance to Nearest Cane Culti-vation District to the South (km)
Mareeba	50	125
Townsville	15	140
Mackay	65	470
Maryborough	25	...

SOURCE.—World Atlas of Agriculture 1969.

regions differ markedly in predominant cultivar planted, economic development, agricultural practices and intensity of cane cultivation (Guagliumi 1962). Venezuelan internal agricultural statistics treat these regions as separate distinctive entities (Venezuela-FUSAGRI 1976). Susceptibility to sugar cane pests varies with agricultural techniques and cane cultivar. Thus the five main sugar cane regions have different incidences of pest problems (Venezuela-FUSAGRI 1976) and a distinctive pest fauna (Guagliami 1962). A further demonstration of the inappropriate use of "political islands" is provided by Australia (table 1) where cane cultivation is concentrated in four areas of Queensland. These areas are separated from each other by as much as 470 km.

Unlike geographic islands, the area under cultivation of a given crop in a political unit often fluctuates sharply on an annual basis. Figure 2 (based on data in Guagliumi 1962; Venezuela-MAC 1962, 1974; Venezuela-CVF 1977) shows that over a 36-yr period the area devoted to cane in Venezuela has increased from 3.5 × 10³ to 73 × 10³ ha, a 20-fold increase in "island size." Examination of annual changes in area devoted to cane cultivation in major cane-producing political units (FAO 1966; Anon. 1947) from 1920–1964 (the length of the record varies with political unit) shows that cane acreage increases up to the dates of the most recent available data. Many of these cane "crop islands" do not appear to have reached an areal symptote. Thus, if pest species richness is increasing in response to area under cultivation the number of insects would not be expected to be at equilibrium as argued by Strong and coworkers unless pest species equilibrate with "crop island" size within a year or so.

Annual statistics for cane acreage (or production) and knowledge of economic history also show that date of introduction of cane to a political unit as an indicator of "crop island" age (Strong et al. 1977) can be misleading. Sugar cane was introduced in Puerto Rico in 1515 (Strong et al. 1977). The large "crop island" represented by Puerto Rican cane acreage was established much more recently as a consequence of a political event (Anon. 1947, p. 108):

As a result of the Spanish-American War of 1898, Puerto Rico was ceded by Spain to the United States. Since 1901, sugar produced in the Island has been imported free of duty into the United States. This has made sugar production a much better business enterprise than it had ever been in Puerto Rico,
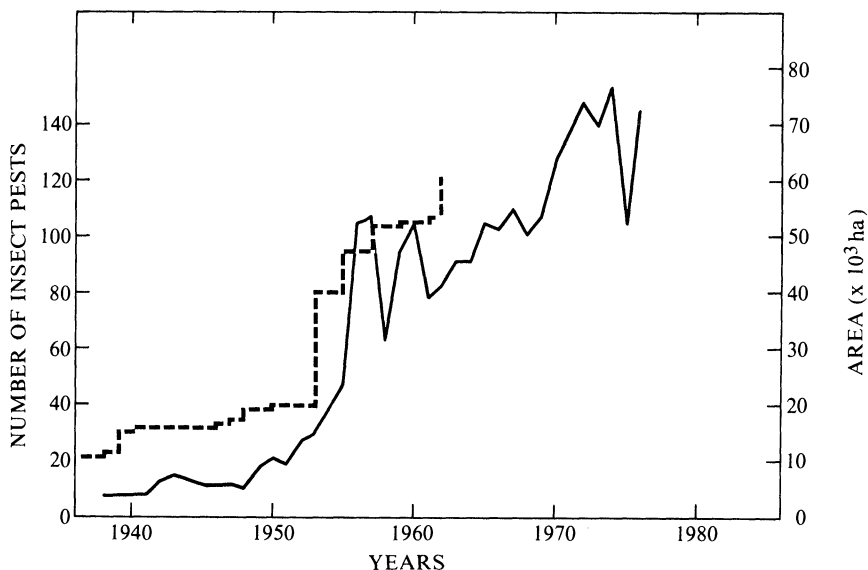
F<small>IG</small>. 2.—Number of insect pests reported (broken line) and area of sugar cane harvested per yr (solid line) in Venezuela.

and, consequently, production expanded enormously. The old time *ingenios* were replaced by large *centrals*, more efficient equipment was installed, railroad lines were laid down for sugar cane hauling, and methods of cultivation were improved. By 1920, the total production of the Island has risen to 485,077 tons, that is, about 600 per cent as large as the 1899–1900 production of 81,526 tons.

Although area under cane cultivation has tended to increase in most political units, this tendency has not been monotonic. Sharp decreases occurred in Venezuela, for instance, from 1956 to 1957 and 1960 to 1961 (fig. 2). Since the number of pests in species lists tends only to increase (see below), the pest species-area relationship for a given political unit will vary widely depending on the year selected for analysis. Again, unless one argues that pest species equilibrate rapidly with "crop island" size (i.e., annually), such sources of error may lead to unjustifiable conclusions.

Compilations of species lists generally only increase in length because species are irregularly added to such lists but rarely if ever deleted. This is partially due to disappearances of species which are usually difficult to document. Also, few if any species lists are evaluated on (let us say) an annual basis; species are added or removed as information accrues. The species lists used by Strong et al. (1977) are, in one case (Box 1953), a compilation from numerous regional species lists of varying ages. Forty-four percent of the references antedate 1930, while the list is used (Strong et al. 1977) to estimate pest species richness at the date of publication of the compilation. The other species list (Cantelo 1965, referred to as Anon. 1965 in Strong et al. 1977) is simply a record of collections, made by Thailand Department of Agriculture personnel. The stated aim of Cantelo (1965) is "primarily . . . to assist . . . in identifying the insects found on different crops and to describe the

host range of these insects." As such Cantelo properly does not delete, but only accumulates, species.

The insect species list for sugar cane in Venezuela has increased with time (fig. 2). Pest species reported from cane doubled in 1953 as the result of a major increase in research effort. H. E. Box was hired by the Venezuelan Ministry of Agriculture in 1947 to lead research on sugar cane borers (Guagliumi 1962). His several publications of 1953 (listed in Guagliumi 1962) are largely responsible for the sharp increases in pest numbers. The 69 species listed in Box (1953) exclude 11 previously described species as shown by Guagliumi (1962). Figure 2 shows that the 1953 increase in pest numbers precedes by 3 yr the abrupt rise in acreage of sugar cane harvested. Although acreage and pests are correlated, the causal mechanism for the increase in pest numbers cannot be a response to increases in crop area if the pests "arrive" on the list before acreage increases.

The recent controversy over turnover rates of bird species on real islands (Lynch and Johnson 1974; Jones and Diamond 1976) demonstrates the critical importance of careful sampling and accurate census data in applying island biogeography theory to species distributions. Appropriate data are also a requisite for the application of species-area curves to host-parasite (pest) systems.

HOST SPECIES AS ISLANDS

We previously (Kuris and Blaustein 1977) suggested that intensity of research effort in the compilation of host species lists provides as likely an explanation for the number of mites reported from rodent hosts as does host geographic range. Problems relating to the construction of pest or parasite species lists detailed in Kuris and Blaustein (1977) and above for "crop islands" may also apply to the recent use of host geographic ranges as "islands" by Strong (1974a, 1974b), Strong and Levin (1975, 1979), and Lawton and Schröder (1977; see also Claridge and Wilson 1978). Host density, range overlap, and species diversity confound the relationship between pest or parasite numbers and host geographic range. Factors affecting parasite transmission may be different for large, often solitary species with extensive home ranges, such as bears, whales or certain oceanic fishes, than for sedentary or gregarious animals with comparable geographic ranges.

The recent history of the gray whale and its highly host-specific ectoparasites (all but one species are found only on gray whales; Grüner 1975) demonstrates that geographic range may be an irrelevant factor in determining species richness. This parasite fauna includes three species of whale lice (cyamid amphipods) and a coronulid barnacle. Cyamids on cetaceans are a well known group, 21 species are considered valid, all but five having been described at least 90 yr ago (Grüner 1975).

Prior to its depletion, the gray whale occupied the most restricted geographic range of the large whales (blue, fin, sei, Bryde's, minke, humpback, bowhead, right, sperm; Slijper 1962), being confined to the Bering and adjacent seas in the summer and migrating close inshore to winter breeding grounds along the coasts of Korea, California, and Baja California. Its restricted breeding grounds and predictable migration routes made it easy prey for late nineteenth century whalers. The western Pacific stock was virtually exterminated and the eastern Pacific

decimated to an estimated few hundred individuals by the early 1900's (McVay 1974). Despite the restriction of its breeding geographic range (loss of the entire western Pacific stock and many of the breeding harbors of the eastern stock) and the great reduction in population size and density, the gray whale did not lose any of its four species-specific ectoparasites. The apparent reason for the retention of all ectoparasites (the gray whale also has a rich endoparasite fauna compared with other large whales; Rice and Wolman 1971) is that parasite life cycles are well synchronized with the host life cycles. Parasite reproduction (the barnacle) and transmission (the whale lice) occur when the whales are calving in the remaining breeding lagoons of Baja California. Hence, northbound young of the year have the full complement of parasites found on nearly all adult gray whales (Rice and Wolman 1971; Kuris and Simmons, personal observation). Thus, determination of the effective population size and geographic range necessary for parasite transmission requires detailed knowledge of coevolutionary aspects of host and parasite life histories.

Ward (1973, 1977) has studied the insect fauna of declining populations of juniper in Great Britain. She documented only one insect extinction for this species. We suggest that coevolutionary studies will disclose why insect species richness was not decreased by a decline in host geographic range.

The species-area curve of Opler (1974) for a guild of leaf-miner insects on California oak trees is a curve based on a valid sampling procedure. Each oak species is represented by a series of pest samples taken by a single researcher using standardized techniques in a census attempt (rather than a checklist comparison). Since Opler noted that the curve relating pest discovery to sampling effort approached an asymptote for most host species, censuses virtually have been attained. Opler also reports both the number of days spent searching each host for leaf-miners and the number of localities visited (providing some information on how thoroughly leaf-miners were sampled over the actual geographic range of the host species). Our analysis shows that all three variables are highly correlated ($P < .01$) with log numbers of leaf-miner species reported (log geographic range $r = .948$, log days search effort $r = .859$, log number of localities visited $r = .876$). An index of ecological range of each host species was also significantly correlated ($r = .692$) with number of leaf-miner species. A partial correlation analysis shows that host geographic range has an independent significant effect (partial correlation coefficient $= .815$, $P < .01$) when the search effort and ecological range variables are held constant. When log geographic range is partialled out, partial correlation of log days versus log species drops to .496 (.01 $< P < .05$), of log localities versus log species to .455 ($P \cong 0.05$), of log ecological range versus log species to .253 (NS). Thus, these variables have a marginally significant effect independent of log geographic range.

Other recent studies (Cornell and Washburn 1979; Lawton and Price 1979) have similarly examined critical variables and demonstrate species-area relationships for selected insect taxa on host plants. Lawton and Price indicate that plant architecture, size, and habitat significantly influence insect species richness. Since leaf shape and plant size are correlated with plant geographic range the interactions between these factors remain to be unravelled.

All three of these studies (Opler 1974; Cornell and Washburn 1979; Lawton and

Price 1979) involve trophically specialized groups of insects. The large majority attack only one or a few closely related hosts. Thus overlap of host range islands plays a negligible role in the distribution of specialized insects since foreign hosts are unsuitable habitat.

Some studies (Claridge and Wilson 1978; Gilbert and Smiley 1978; Futuyma and Gould 1979) found geographic range to be a poor predictor of insect species richness, particularly within a given locality. These observations suggest that determinants of insect species richness may be sought in studies of interactions with other consumers, predators and parasites, host plant characteristics (structure, phenological events, chemistry), and other resources (Schultz et al. 1977; Gilbert 1977; Gilbert and Smiley 1978; Futuyma and Gould 1979). Lawton and Price (1979) provide a thoughtful analysis of some of these factors for agromyzid flies on umbellifers. They suggest that the number of fly species has not saturated the number of suitable resources and guilds of leaf-miners are not equilibrium assemblages.

Insect-plant coevolution may explain the density and diversity of insect species. Crude counts of insect species richness poorly describe the structure of insect communities. With Lawton (1978) we suggest that insect guild structure and the effect of insects on host plants may reveal the patterns of insect community organization.

From the perspective of animal parasites we also suspect that coevolution may be an important determinant of species richness. In addition to feeding adaptations of insects and structural and biochemical adaptations of host plants, parasite life cycle synchrony, host behavior, and other epidemiological aspects are likely to have an important influence on the number of parasites or pests found on host individuals, populations, and species.

CONCLUSIONS

At each level of organization, attempts to apply island biogeography theory to hosts have been beset with two kinds of difficulties: (1) technical problems with potential solutions and (2) fundamental theoretical difficulties that may render the host as island analogy invalid in principle. For host individuals as islands, separating the interrelated effect of host size and age is a significant but rectifiable problem. Difficulties in principle are more numerous. (1) Hosts with defensive responses, unlike islands, may defend against immigrants or extant populations. (2) Age-specific host defensive responses associated with growth, metamorphoses, maturation and senescence contrast with the relative constancy of islands. (3) Parasite-induced host mortality is not paralleled by islands which are never eliminated by colonists. (4) The short-lived nature of individual hosts relative to transmission rates of some parasites is unlike the long-term existence of islands relative to host immigration rates. (5) Vagility of many animal hosts causes inter-host distances to fluctuate whereas interisland distances are essentially constant.

Host populations as islands are technically difficult to study because operational definitions of populations may be arbitrary and unrealistic, and interpopulation distance is hard to measure. Political units do not define host islands. Agricultural

crop acreage is generally unsuitable as an island analog because area under cultivation may fluctuate dramatically. Species checklists are generally unsuitable representations of crop "island" faunas. If accurate census data are not available, parasite (or pest) sampling procedures must be carefully designed.

Several theoretical difficulties are associated with the analogy of populations as islands. (1) Population size may fluctuate over short time intervals relative to parasite transmission rates. (2) Measures of host island size are confounded by the interrelationship between host density and host area occupied. (3) Interspecific population overlap has not been evaluated as an influence on parasite species diversity. (4) Host community diversity may affect parasite transmission. (5) The role of intermediate host behavior in the transmission of some parasites to their definitive hosts presents factors never associated with dispersal to real islands.

Host species as islands present formidable sampling difficulties because parasite census is rarely possible. There are fundamental theoretical problems associated with the concept of a host species as an island. (1) Differences in host social behavior may make otherwise similar species very different in terms of parasite transmission within the species. (2) Overlap of interspecific host geographic ranges may influence transmission between their respective parasite faunas. (3) Host species diversity may influence the species richness of the parasite assemblage. (4) Both geographic area and density of host populations may interact with a resultant effect on the parasite fauna. (5) Coevolutionary considerations are poorly understood and may greatly influence parasite population equilibria, competition, and speciation rates.

We have put forth our criticisms of the application of island biogeography theory to parasites and plant pests. We wish it were possible to indicate the appropriate modifications of the theory or propose a replacement hypothesis to predict species richness of parasites or pests on hosts. However, we know of no host taxa where species richness of parasites on the three interacting levels of organization, individuals, population, and species, has been sufficiently characterized to permit an inductive search for theoretical modifications or alternative models. Important aspects of parasite-host relations such as host defensive responses, the operation of natural selection on both the host and the parasite, and complex life cycles are poorly understood from a coevolutionary perspective. Available deductive analytical models can probably be modified to incorporate some theoretical difficulties. Examples include incorporating both area and density into a concept of island size, the short-lived nature of hosts relative to parasite transmission, and host vagility as it affects interhost differences. But since coevolution is probably important, the coevolutionary models are too poorly developed to contend with the complexities suggested for host-parasite relations, the search for deductive models presently may be an exercise in futility. In short, we cannot yet see the patterns nor understand the operating principles. Fortunately, fruitful avenues to enhance our understanding of parasite species richness are available including careful description of pattern at the three levels or host organization, experimental tests of hypotheses generated from these observations, and analyses of the coevolutionary nature of the host-parasite associations involved.

SUMMARY

Hosts may be regarded as islands at three levels or organization: (1) individuals, (2) populations, and (3) species.

For individual hosts as islands, parameters which are important to island biogeography theory may determine species richness: (a) size and age of host, (b) habitat complexity, and (c) distance to potential source of infection. Modifications of the theory are needed to account for fluctuations of interisland distance through time, the seasonal differences in host physiology and behavior, and the change in quality of the host island as the result of growth and aging. The presence of certain species of parasites may affect the ability of other parasites to inhabit a host island. Since the individual is a temporary island, parasite species assemblages sometimes cannot reach equilibrium within the hosts' life span.

Most of the following problems concerning individuals as islands apply in varying degrees to host populations as islands. (1) Difficulties occur in measuring interisland distance, particularly since populations of potential host species may overlap. (2) Population size often fluctuates so rapidly that it is hard to envision parasite assemblages reaching an equilibrium level of species richness. (3) Lack of a source area impedes the analysis of island biogeography theory. Futhermore, political boundaries cannot serve to define populations as islands and species lists compiled for other purposes often do not provide appropriate data to construct a species-area curve.

The use of geographic range of a host taxon as an estimate of "island" size may be an unacceptable oversimplification. Differences in host density, range overlap, and species diversity, as well as most of the other problems discussed with reference to host individuals or populations as islands complicate the assessment of "host species" island size. Large, often solitary, animals having vast home ranges present a very different aspect from the point of view of parasite transmission than do sedentary or gregarious animals having a comparable geographic range. Coevolutionary factors between parasite and host may be important determinants of species richness as well.

A positive correlation between parasite or pest species with host geographic range can be obtained with suitable data. However, demonstration of a species area curve of the form $S = cA^z$ is supportive but not sufficient evidence for the applicability of the equilibrial theory of island biogeography. Microhabitat diversity, physiological and morphological variability of hosts, and coevolution of parasite and host are probably important factors influencing the number of pest or parasite species infesting a host taxon.

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