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Biological determinants of species diversity

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ABSTRACT. We consider four categories of biological mechanisms of determinants which cause and maintain species diversity: niche relations, habitat diversity, mass effects and ecological equivalency. Two of these determinants are original to this paper: mass effect, the establishment of species in sites where they cannot be self-maintaining; and ecological equivalency, the coexistence of species with effectively identical niche and habitat requirements. The mode of action and ecological implications of each biological determinant are discussed using a schematic method for measuring alpha (community), beta (differentiation), and gamma (regional) diversities. The importance of mass effects and ecological equivalency to species richness is documented with several types of field data from Israel and California, U.S.A.

Floristic richness and, in particular, the richness of floristic transitions, are discussed and interpreted by use of the biological determinants of diversity. Contact transitions between distinct floras are rich predominantly because of mass effects. Transitions induced by marked environmental changes are rich because of the combined influences of habitat diversity and mass effects.

The rate at which species richness increases with sample area is related to the combined effects of all four biological determinants. This complexity explains the failures of simple species–area models. The relative intensity of each determinant is related to area: niche relations are most important at within-community scales, habitat diversity most important at both within-community and landscape scales, and ecological equivalency most important at regional scales. We suggest that understanding patterns of species diversity will be enhanced by the partitioning of total species richness into the richness caused by each of the four ecologically distinct determinants of diversity.

Introduction

Numerous hypotheses have been proposed to explain patterns of species diversity (see reviews by Fischer, 1960; MacArthur, 1965; and Whittaker, 1972, 1977). No hypothesis has been found to apply well to all bodies of data. Instead, the hypothesized mechanisms may function together, with their relative importance dependent on particular circumstances (Pianka, 1966; Slobodkin & Sanders, 1969). In studies of species diversity most attention has been placed on processes within the community, that is, on niche relations among species. However, no community is a closed system, isolated from all other sites.

This work is dedicated to the memory of R. H. Whittaker, who taught us the importance of understanding natural diversity.

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When communities are viewed as interacting locations within an integrated, continuous system several other processes can be examined. We consider three categories: habitat heterogeneity, mass effect (the establishment of species in sites where they cannot be self-maintaining), and ecological equivalency (coexistence of species with effectively identical niche and habitat requirements). For each of these, plus the category of niche relations, we examine the mode of influence on diversity and the scale of action. Each mechanism is shown schematically by use of diversity displays. Examples are presented documenting the importance of the mechanisms.

At least three aspects of diversity problems have been emphasized by various workers: phenomena, measurements and mechanisms. The *phenomenon* of diversity is a characteristic of species distributions in communities, and, as such, cannot be entirely perceived without a complete knowledge of community composition. Most ecological studies have been concerned with the phenomenon of alpha-diversity, the species richness of samples representing communities (generally 10^2-10^4 m^2) (Whittaker, 1977). MacArthur (1965) and others use the term within-habitat diversity as a synonym of alpha-diversity. The diversity of landscapes (10^6-10^8 m^2) is gamma-diversity. Each level or scale of inventory diversity (*sensu* Whittaker, 1977) is nested within the higher level diversity. The manner in which inventory diversities at one scale combine to produce the inventory diversity at the next larger scale is a differentiation diversity, the amount of biotic change among units. The differentiation of units on the alpha-diversity scale is beta-diversity (Whittaker, 1960), or between-habitat diversity (MacArthur, 1965). The *measurement* of diversity is the manner in which field observations of diversity phenomena are summarized.

Partly separate from relationships and measurement is a third aspect, the *mechanisms* or determinants of diversity. The ecological interpretation of diversity and its measurement has historically been simple and clearcut: alpha-diversity results from niche differentiation among species and beta-diversity from species responses to a range of habitats (Whittaker, 1960, 1967, 1972; MacArthur, 1965, 1972; Sanders, 1969; Terborgh, 1973; Cody, 1975; Diamond, 1975; Routledge, 1977). We demonstrate that there are additional biological determinants – mass effect and ecological equivalency – that combine with niche differentiation and habitat response to produce patterns of diversity.

In order to keep distinct the three aspects of diversity we follow this convention: The word diversity alone, or with a prefix of scale (e.g. alpha-diversity) refers to the phenomenon of diversity; a greek symbol (e.g. α) refers to the corresponding measure of diversity; and a determinant of diversity is represented by the symbol D, with a subscript denoting the type of determinant (e.g. D_{ME} for mass effect).

The three fields of classical biogeography, quantitative phytosociology (community analysis), and theoretical population ecology are all concerned, in part, with comparative species diversity. Each of these approaches has its own viewpoint and manner of interpretation of the phenomena of diversity. Classical biogeographers are concerned with the relative richnesses of regional faunas or floras (e.g. Grisebach, 1884; Schimper, 1903; Cain, 1944; Darlington, 1957; Udvardy, 1969). Richness is sometimes calculated as number of species per unit area (Wulf, 1950; Good, 1964), leading to the construction and interpretation of species–area curves. The similarity between regions is calculated by measures of Jaccard (1912), Sorensen (1948) and others (see Simpson, 1949). Classical biogeography stressed historical factors (migration, isolation, speciation) in the interpretation of diversity (Udvardy, 1969).

Quantitative phytosociologists have developed techniques for assessing diversity as dissimilarity or 'ecological distance' between community samples (Goodall, 1952, 1973; Whittaker, 1952, 1960, 1977; Williams, 1971; Gauch, 1973; Mueller-Dombois & Ellenberg, 1974). The phytosociological concept of beta-diversity or species turnover along environmental gradients has been applied also to animal communities (MacArthur, 1965; Cody, 1975; Tramer, 1974). Interpretation of patterns of diversity in quantitative phytosociology generally consists of the direct correlation of ecological distance with differences in environmental conditions, the unexplained variance in field data often being labelled 'noise' (Whittaker, 1975a). Irregular spatial patterns (Greig-Smith, 1964; Kershaw, 1973), non-uniform dispersal (see Harper, 1977), and historical effects (Heinselman, 1973; Loucks, 1970) and sampling error or bias (Bormann, 1953; Kershaw, 1973) can contribute to the incomplete correlation of vegetation with the physical environment.

Theoretical population ecology has concentrated on the role of species interactions, especially competition and predation, in the explanation of species diversity patterns. Niche theory (Hutchinson, 1957; MacArthur, 1968; Whittaker, 1969), models of coexistence (MacArthur & Levins, 1967; May & MacArthur, 1972; Vandermeer, 1972), and theories of resource partitioning (Shoener, 1974) all focus on competition of species within communities. Because of the concentration by theoretical population ecologists on small-scale species interactions, until recently the notion of noise mostly has not been entertained. Conversely, because classical biogeographers deal with complete lists of the biota of large regions, the effects of noise are decreased and become unimportant. A summary of the differences among these three approaches to diversity is presented in Table 1.

Although workers in diversity are aware of the accomplishments in each of the three approaches, the interpretation of diversity is usually limited to a small set of the possible determinants. For example, observations of latitudinal trends in diversity have spawned numerous explanations (see reviews by Fischer, 1960; MacArthur, 1965, 1969; Pianka, 1966; Terborgh, 1973; Rosenzweig, 1975; Osman & Whitlach, 1978) with population ecologists emphasizing species interactions within communities, quantitative phytosociologists emphasizing environmental trends, and biogeographers concentrating on historical factors.

Several attempts have been made to merge the concepts and terminologies of the different approaches. Many island biogeography studies have involved relationships between species richness and area in terms of population-level processes (see MacArthur & Wilson, 1967; Simberloff, 1974). Other attempts at the synthesis of different approaches to diversity include Williams' (1964) monumental summarization of the relationships between species richness and area, and the long-term work of Whittaker (1960, 1969, 1972, 1977) on the measurement and evolution of diversity.

By discussing biological mechanisms, and by using a single terminology, we attempt to combine insights from these traditional fields into a more complete understanding of the phenomena of species diversity.

The diversity display

Certain simplifying assumptions are necessary to facilitate examination of the determinants of diversity. First, we assume that a true, single community gradient or coenocline of monotonically changing environmental conditions can be identified for a given set of field data. As natural systems typically show the combined effects of several environmental factors the structure of the landscape usually must be summarized by stratification or composite samples. Second, we assume that all species in the system (or a high percentage) are actually observed in the samples. In practice, this assumption is not overly restrictive if the field data are from exhaustive field studies, typical of large-scale vegetation analysis or from range records, museum specimens and floristic manuals that indicate the extremes of species distributions.

The discussion of diversity relationships is aided by a pictorial representation or diversity display (Fig. 1) of species distributions within an ecosystem. The abscissa of the diversity display is a transect along an environmental gradient (or complex-gradient, *sensu*

TABLE 1. Characteristics of three approaches to the study of diversity

	Classic biogeography	Phytosociology	Theoretical population biology
Scale of observation	Regional	Among-communities	Within-communities
Type of diversity	Gamma	Beta	Alpha
Primary proposed determinants	Historical	Environmental	Species interactive
Role of noise	Irrelevant	Important	Unobserved

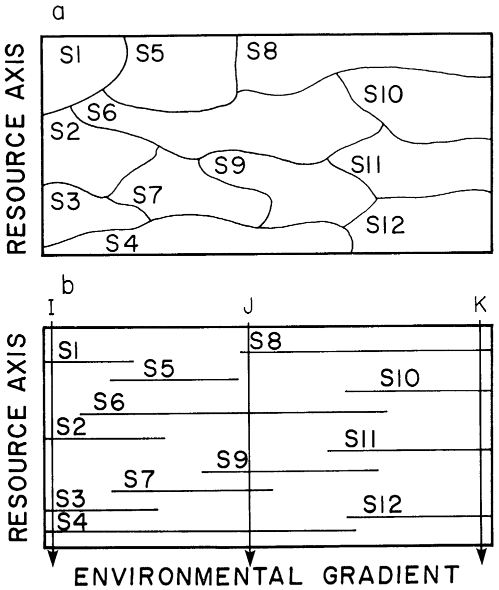

FIG. 1. Diversity displays showing species occurrences (S1–S12) in a hypothetical landscape. (a) Species are distributed with respect to interacting resource axis and environmental gradient. (b) Simplified diversity display. I, J and K are the sampling points. (See text for details.)

Whittaker, 1967) and the ordinate is a major resource axis. Many studies use, as least implicitly, the framework of the diversity display (e.g. MacArthur & Wilson, 1967: 103). Species' overall occurrences are the enclosed areas in the field of environmental and resource conditions. In the terminology of Whittaker, Levin & Root (1973) the niche of a species includes that range of resources used at a single point along the environmental gradient, whereas the habitat of a species is the range of environmental conditions in which the species is found. The species' ecotope is the intersection of its niche and habitat, or the enclosed area in the diversity diplay of Fig. 1. Fig. 1(a) is an over-simplified pattern of the species distribution within a given community in nature: we assume no overlapping of ecotopes between coexisting species (for a different approach see Shmida & Ellner, 1984). However, it is important to assume for our idealistic diversity display a monotonic changing environmental gradient which corresponds with non-disjunct species ranges.

A more realistic diversity display should reflect, at the least, more than single niche and habitat axes, a larger number of species, and the abundances of these species. The complexity prohibits adequate representation in a figure. We choose instead to use a still simpler version of the diversity display (Fig. 1b). Because we are primarily concerned with meso-scale (among-community) aspects of diversity and not the details of species interactions within communities, the form of species distributions along the niche axis may be reduced to mean values without much loss of important information. Also, because we deal with single habitat gradients at any one time and are concerned with the presence or absence of species only, the two dimensions of niche and habitat suffice. For the remainder of this paper we use only this simple form of the diversity display shown in Fig. 1(b). Note that species distributions along the habitat gradient are in effect summaries of species ranges in communities in the field.

The measurement of diversity

Diversities of a system shown in a diversity display are easily measured. Samples are represented as vertical segments at points along the environmental gradient. In Fig. 1(b), segment J is such a community sample. The index of the alpha-diversity of J is simply the number of species intercepted by the sample ($\alpha = 5$). The measure of landscape, or gamma-diversity, is the total number of species in the diversity display ($\alpha = 12$).

Measures of beta-diversity with qualitative (presence/absence) data have been proposed by Whittaker (1960), Cody (1975) and Routledge (1977). We have compared the performance of these measures and have proposed a new and superior one (Wilson & Shmida, 1984) that mirrors directly the aspect of beta-diversity in which we are most interested here: the increase and decrease in species richness along gradients. We will use this new measure, β_T, throughout the present paper. β_T ('beta-turnover') is calculated as:

$$\frac{g(H) + l(H)}{2\bar{\alpha}}$$

where H is the given range of a habitat gradient, $g(H)$ is the number of new species encountered or gained along H, $l(H)$ is the number of species that drop out or are lost along H, and $\bar{\alpha}$ is the average number of species found in samples along H. β_T can be easily calculated from species range data. In the diversity display of Fig. 1(b), β_T between samples I and K is:

$$\beta_T = \frac{8+8}{2 \times 4.4} = 1.8$$

β_T can be interpreted as the value that would be obtained in a system of exactly β_T complete changes in community composition. Thus, in Fig 1(b), an equivalent of $1.8+1=2.8$ communities are depicted. That is to say there are 1.8 changes and the equivalent of 2.8 communities. Whenever we mention beta diversities, these are calculated by the β_T index.

Determinants of diversity: evidence and effects

In this section we discuss the contribution of each of four biological determinants to species diversity. For the well-known determinants niche relations and habitat diversity we examine only their influence on alpha-, beta- and gamma-diversities. For the determinants we introduce here, mass effects and ecological equivalency, we also document their importance to overall species diversity with field data and observations.

Niche relations

The interactions among species and between species and environment within a community describe the niches of species. Field observations and theoretical developments on niche relations have been ably reviewed elsewhere (e.g. Levins, 1968; MacArthur, 1972; Whittaker *et al.,* 1973; Schoener, 1974; Colwell & Fuentes, 1975; Pianka, 1975). In general, the niche and resource characteristics of a community have been related to species diversity in three broad modes: more species can be accommodated in communities with larger niche hyperspaces, in communities in which average niche breadth is reduced, and perhaps in communities with high average niche overlap. Aspects of the size of the niche hyperspace include the range of food sizes available (Cody, 1968; Pianka, 1975; Whittaker, 1977), the small-scale structural diversity of the environment (MacArthur & MacArthur, 1961; Harper, Williams & Sagar, 1965; Cody, 1968; Bratton, 1976), and the temporal heterogeneity of resource availability (Whittaker & Niering, 1965; Whittaker, 1972).

Niche relations influence species diversity at the within-community scale (Whittaker *et al.*, 1973). In a restricted region of more or less homogeneous environment, niche relations should not vary systematically through space. That is, niche relations as a determinant of diversity (denoted D_{NR}) will usually not show spatial trends, although fluctuations must be expected. Niche characteristics determined by microsite heterogeneity (Whittaker & Levin, 1977) are possible exceptions to this rule of independence of niche and space if new kinds of microsites are added along a gradient.

The influence on species diversity of altering D_{NR} is shown in the diversity display of Fig. 2. Fig. 2 represents a landscape system with $\alpha = 2.2$, $\beta = 2.05$, and $\gamma = 7$. If the combined effects of D_{NR} are doubled, with all other determinants of diversity held constant, the number of species within a community will approximately double. (Species richness will not double exactly because of possible interaction with other determinants of diversity, as explained below.) Fig. 2(b) shows this doubling

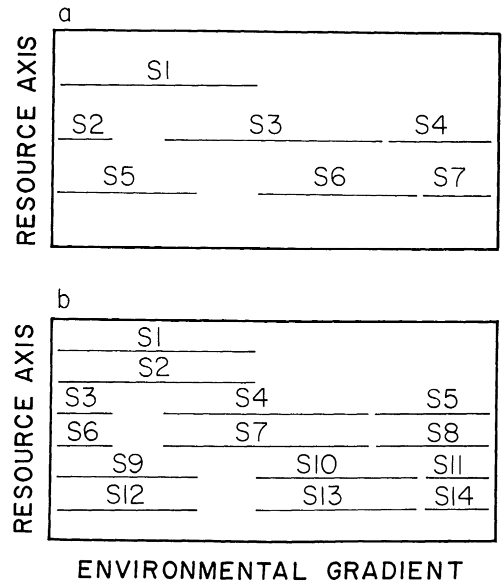

FIG. 2. The influence of niche differentiation (D_{NR}) on diversity. Each species occurrence in the system shown in (a) is duplicated in the system in (b), causing α and γ to double but leaving β unchanged.

of D_{NR} by the simple replication of each species by a new species of identical range. In the new system $\alpha = 4.4$, and $\gamma = 14$, twice those of Fig. 2(a), while $\beta = 2.05$, unchanged. Thus D_{NR} affects alpha- and gamma-diversity but does not alter beta-diversity.

Habitat diversity

Differences in habitat conditions are widely known to influence the distribution and coexistence of species in the landscape (Grisebach, 1884; Schimper, 1903; MacArthur, 1965; Whittaker, 1975a). Three scales of habitat heterogeneity (and corresponding differentiation diversities) can be recognized: the heterogeneity of microsites (pattern), the heterogeneity among community samples (beta), and the heteogeneity among regions (delta diversity; Whittaker, 1977). As the scale approaches the size of individual organisms, spatial (microsite) heterogeneity is more profitably viewed as a niche factor (MacArthur & MacArthur, 1961; Cody, 1968; Whittaker *et al.*, 1973). Because differences in species composition owing to differences in habitat are reflected in measurements of beta-diversity, the term 'between-habitat diversity' (MacArthur, 1965) is often used as a synonym for beta diversity. Since, as we demonstrate below, phenomena other than habitat heterogeneity can cause changes in species compositions among sites, we prefer to alter MacArthur's term to 'between-site diversity' with no implication of which determinants cause the observed diversity. We denote the role of habitat diversity as a determinant of species diversity as D_{HD}. Systems with low and high D_{HD} are shown in Fig. 3. All other determinants remain constant. In Fig. 3(a), $\alpha = 5$, $\beta = 0$, and $\gamma = 5$. Fig. 3(b) shows a second system, identical to the first except for a larger D_{HD}. For this new system $\alpha = 5$ (unchanged) while $\beta = 3$ and $\gamma = 20$. Thus D_{HD} affects beta- and gamma-diversity but does not alter alpha-diversity.

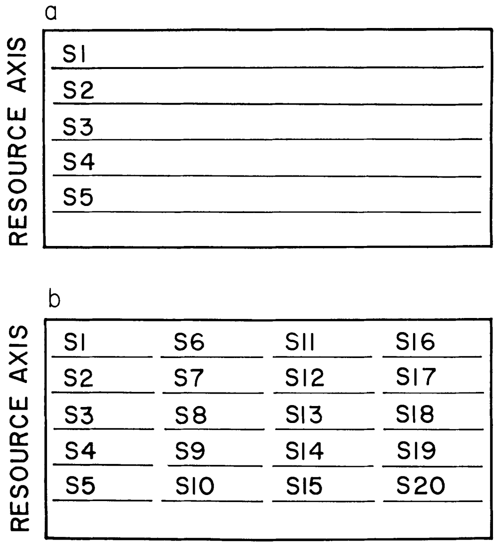

FIG. 3. The influence of habitat diversity (D_{HD}) on diversity. The five communities shown in (b) each have the same structure as the single community in (a). D_{HD} does not change α, but increases β and γ.

The effects of habitat differences on species diversity can be mediated through competitive interactions. Colwell & Fuentes (1975) show that displacement by competition (niche truncation) can be different for different sites along a habitat gradient. Tansley (1917) and Byer (1969) have demonstrated that, though plant species may be equal in their ability to survive a broad portion of the habitat gradient when grown in competition-free plots, their natural distributions are limited to dissimilar ranges of habitat conditions. In such cases, the resulting increase in beta-diversity from competitive exclusion is properly ascribed to the ultimate determinant, habitat diversity (D_{HD}).

Mass effect

In nature, communities are never closed systems, exempt from the influences of adjacent areas. One type of influence is dispersal. With a high rate of propagule influx, some individuals of a species will become established in sites in which they cannot maintain viable populations. This flow of individuals from areas of high success (core areas) to unfavourable areas we call the mass effect (Shmida & Whittaker, 1981; Shmida & Ellner, 1984).

Mass effect always functions to increase alpha-diversity. Note that the species found in a community can be divided into two groups: those that are self-maintaining, coexisting with other species, and those whose presence

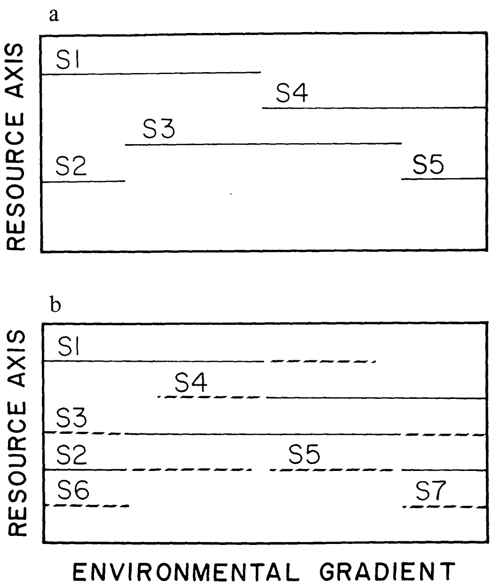

FIG. 4. The influence of mass effect (D_{ME}), in the form of range extensions only, on diversity. Each species in the sytem shown in (a) has an exactly doubled range in (b). Included are species that encroach from outside the original system.

depends entirely on high reproductive success in adjacent areas. Thus the species richness of a community is determined by the processes of niche differentiation (D_{ND}) and mass effect (D_{ME}).

Fig. 4 is the diversity display for a simple hypothetical system in which the spatial distribution of species is primarily determined by a single widespread gradient. Here mass effects result only in range extensions of the species along the gradient. The proportional increase in α (2.0 – 4.0) is in fact equal to the average range extension. The influence of mass effect on beta-diversity depends on the properties of the system. In the hypothetical case of Fig. 4, beta-diversity is decreased (β = 1.15 to β = 0.75) because of the homogenizing effects of expanded species ranges. Beta-diversity can only decrease when mass effects cause the expansion of species ranges within the system (Wilson & Shmida, 1984). Gamma-diversity increases ($\gamma = 5$ to $\gamma = 7$) to the extent that species from beyond the extremes of the gradient encroach into the system.

An opposite effect on beta-diversity can obtain if the transect is adjacent to areas of high heterogeneity. Consider another hypothetical example of a flat valley and its projection into surrounding steeply sloping foothills (Fig. 5a). Diversity displays are presented in Fig. 5(b–d) for transects through the valley but uninfluenced by the hills (transect 1), along the slope of the hills (transect 2), and through the projection of the valley that is influenced by the hills (transect 3). A, B, C, D and E represent intergrading habitat types. Transect 1 has low beta-diversity (β = 0.6) and transect 2 has high beta-diversity (β = 2.2) Because of the chance establishment of species from the hills along adjacent portions of the beach, transect 3 takes an intermediate value of beta-diversity (β = 1.7), but one higher than would occur without mass effects.

One goal of phytosociology is relating species distributions to environmental factors. Mass effects, the occurrence of species outside their core habitats, will dilute this relationship between species and environment. In fact it might be that much of the noise, that is unexplained patterns of species distributions in phytosociology, can be explained in terms of mass effects.

Field data from a study area in the Judean Desert, Israel, have been collected to test our assertion that mass effects can increase overall species richness. Species were recorded along three sample transects in a homogeneous valley floor (T1) in foothills through five habitat types (chalk, small-rock, limestone, stone terra-rosa and bare terra-rosa) (T2), and in the same homogenous valley but adjacent to the foothills (T3). Thus these transects duplicate the conditions shown in Fig. 5(a). Fig. 6 shows the cumulative number of species recorded in each of the three Judean desert transects. Relatively few species (44) were found in transect 1. In contrast, transect 2 had many more species (107); intervals of rapid accumulation of species correspond to the transitions between habitat-types. Transect 3, although in the same habitat as is transect 1, contains consistently more species (80) than does transect 1. Moreover, thirty-one of the eighty species of transect 3 are common in the foothill transect (T2), and twenty-nine of these were not found at all in transect 1. We conclude from these results that mass effects (D_{ME}) from the foothills to the adjacent valley are responsible for the presence of at least twenty-

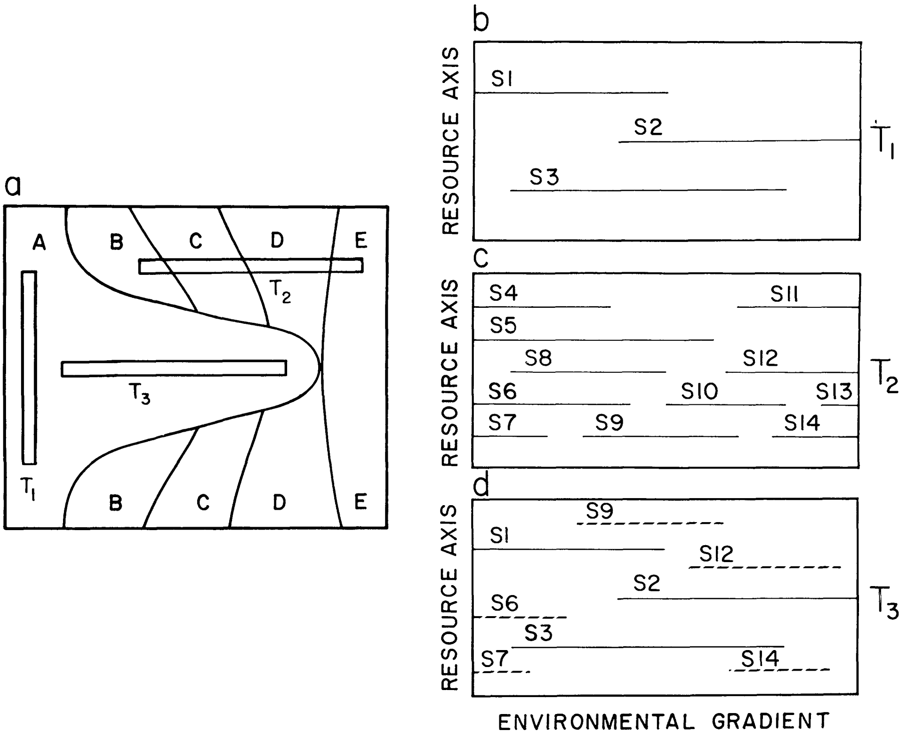

FIG. 5. The influence of mass effect (D_{ME}), in the form of neighbourhood effects, on diversity. In the map in (a), transect 1 (T_1) passes through a single habitat type (A). Transect 2 (T_2) passes through several habitat types (B, C, D, E). Transect 3 (T_3), like T_1, is in a single habitat type but is adjacent to B, C, D and E. The diversity displays for the three transects are shown at right (transect 1, b; transect 2, c; transect 3, d). Species present in transect 3 only because of mass effect are shown with dotted lines.

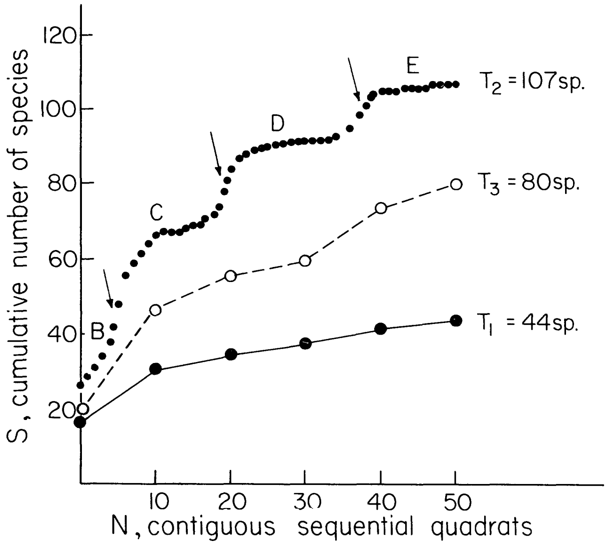

FIG. 6. Cumulative number of species recorded in transects in three habitats in the Judean Desert study area. Transect 1 (T_1) is in a homogeneous valley habitat, transect 2 (T_2) is in heterogeneous foothill habitats, and transect 3 (T_3) is in a homogeneous valley habitat adjacent to the foothills. Transect 3 has more species than transect 1 because of mass effects (D_{ME}) from the foothills to the adjacent valley. Quadrats are 1 m^2 in area.

nine species or 36% of the total species of the habitat represented by transect 3.

The desert washes of the Middle East provide another example of the strong influence of mass effect on vegetation. Some washes have apparently identical environmental characteristics but often contain different sets of plant species. Although the washes may provide similar environments, the upslope localities can be quite different from site to site. Data from washes in the Judean Desert support these ideas. Table 2 summarizes the species diversity of three contiguous but different slope habitats, which are dissected by a wash. The species compositions of the chalk, rock-outcrop and hard-limestone slope habitats are quite different (average floristic similarity [Sorensen, 1948] = 24%). Although this stretch of the wash is a uniform environment, many slope species, when found in the wash, are restricted to that segment of the wash directly downslope. The differences in slope-species composition of the three segments of the wash indicate that these species are present because of mass effects from the slope to the wash. We feel that it is the creation of open microsites in the wash, by frequent disturbance by flooding, that makes the wash susceptible to repeated slope-species invasion.

Ecological equivalency

Consider three examples of unexpectedly high levels of species richness. The first example is the species–area curve for vascular plants on the Yizreel valley (Esdraelon plain) in the Mediterranean region of Israel and the Sharm-E-Sheikh, an extreme desert region of South Sinai. The Yizreel Valley is a large, flat, alluvial valley. The Sharm-E-Sheikh plain is a vast, alluvial aridisol hammada. Because of their uniform topography, soils and climate it is reasonable to consider that the Yizreel Valley and the Sharm-E-Sheikh have very low habitat diversity (D_{HD}), and any pattern of differences between microsites that exists is certainly repeated on the meso-scale, from sample to sample. Moreover, mass effects (D_{ME}) are absent, because of the great distances to other landscapes. Nonetheless, nested samples of increasing area always show an increase in the number of species encountered (Fig. 7).

The second example is the large number of shrub species in the transition between chaparral and semidesert in southern California (Shmida & Whittaker, ms.). Although any single sample (area 0.1 ha) contains approximately thirty shrub individuals of about seven species, the total number of shrub species encountered in six samples of the same transition habitat is twenty-one. The composition of the particular subset of shrub species present in any single sample appears to be determined largely by chance. Similar irregular, apparently chance assortments of some shrub species have been observed in local, north-slope stands of Sonoran semidesert in the Santa

TABLE 2. Species richness values for six sampled habitats in the Judean Desert. Three contiguous slope habitats (chalk, rock-outcrop and hard limestone) contribute species through mass effects (D_{ME}) to the wash directly downslope.

Slope habitat	Chalk	Rock-outcrop	Hard limestone
(a) Species per 10^3 m^2 in slope habitats	22	67	34
(b) Species per 10^3 m^2 in segment of wash adjacent to each slope habitat	48	61	58
(c) Species found in both slope habitat and its adjacent segment of wash	20	28	21
(d) Number of species in row (c) found exclusively in that segment of wash directly below each slope habitat	11	18	13

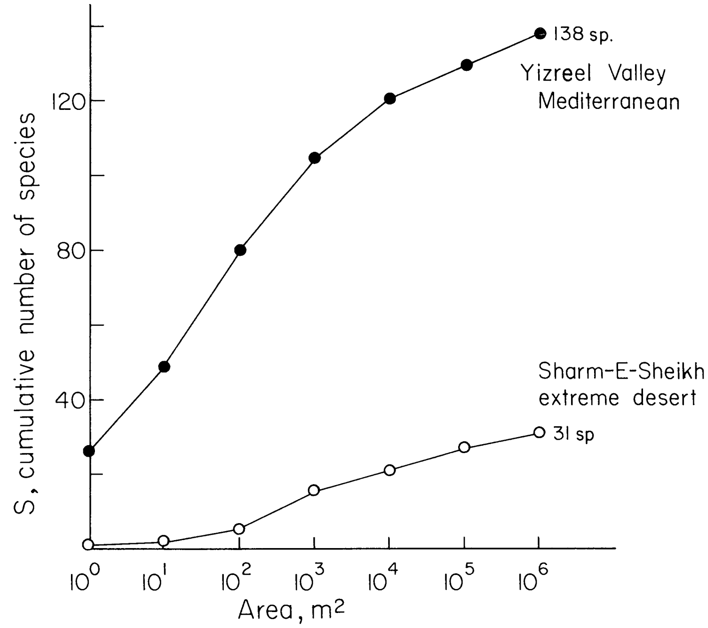

FIG. 7. Species–area curves for the Yizreel Valley and Sharm-E-Sheikh regions of Israel. Each region is a nearly homogeneous environment. New species are steadily encountered with increasing area because of the occurrence of ecologically equivalent species.

Catalina Mountains, Arizona (Whittaker & Niering, 1965).

The third example is the semidesert of Death Valley, strongly dominated by *Larrea tridentata* (Shmida & Whittaker, 1981). *Larrea* shrubs cover about 10% of the ground surface and are closely similar habitat-islands in a matrix of open conditions. A group of annual plant species dominates the openings and a second group is restricted to shrub patches. Fifty 1 m^2 quadrats were sampled both under shrubs and in openings. Quadrats were randomly ordered. The cumulative number of species encountered in each microhabitat-type is shown in Fig. 8. The average number of species per m^2 is nearly the same under *Larrea* (11.0 species) as in openings (8.7 species) yet a much greater number of species are found in all 50 m^2 under *Larrea* (52 species) than in openings (30 species). Moreover, the curve for openings indicates a saturation in species richness whereas the *Larrea* curve shows a steady increase in new species encountered. In short, more species are associated with *Larrea* than are found in openings, although the species richness per m^2 is roughly equal.

These three sets of observations seem to conflict with the competitive exclusion principle (Gause, 1934; Hutchinson, 1957; Hardin, 1960): more coexisting species occur than can be accounted for by processes of niche and habitat differentiation. Such species we call ecological equivalents.

At least four explanations are available for the reconciliation of observation with theory. (1) It can be claimed that our assertion of no differences in environmental conditions among sites is false. Such differences cannot be disproved but are not supported by our field observation. (2) The apparently equivalent species may have undetected differences in niche. Trivial differences among species can always be found but these do not necessarily form the basis for successful coexistence. In our second and third examples above it is to be expected that any significant niche differences among the apparently equivalent species would manifest themselves in spatial segregation of species in consistent subunits or assemblages or in correlations of species with microenvironmental conditions. Instead equivalent species co-occur more or less randomly (Shmida & Ellner, 1984). (3) Continual disturbance may reduce the number of

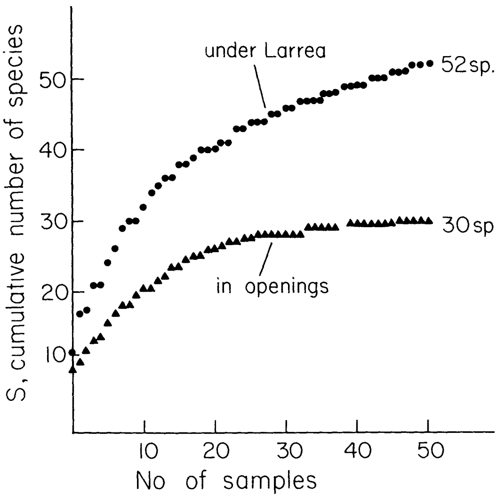

FIG. 8. Cumulative number of species recorded in 1 m^2 samples under *Larrea* and in openings at Death Valley, California. The island-like *Larrea* shrub are surrounded by a matrix of open conditions. The spatial separation of the shrubs allows the coexistence of ecologically equivalent species, which produce the more rapid accumulation of species under *Larrea*.

individuals in the system, thus preventing the completion of competitive exclusion of otherwise equivalent species (Connell, 1978). Disturbance that permits coexistence can include predation (Paine, 1966;Connell,1971; Janzen, 1970), fire and wind, but must be severe enough to reduce competition while not severe enough to cause local extinctions (cf. Sanders, 1969). (4) Random dispersal of individuals in mosaics can allow coexistence (Whittaker, 1975b; Whittaker & Levin, 1977; Levin, Cohen & Hasting, 1984; Shmida & Ellner, 1984). If individuals must vacate their locations, for example at death, an equilibrium situation can obtain wherein species even with closely similar characteristics coexist, with their populations turning over through available microsites. Possible field examples of such equilibria are the vegetation of rock outcrops and cliffs (Runemark, 1969) and shrubs found at the bases of cypress trees in Okefenokee Swamp (Schlesinger, 1977). In rocks and in swamps microsites favourable for plant growth are discrete and often large enough only for a few plants. Although the microenvironmental conditions of the microsites can be quite similar, rock outcrops and swamps often maintain high species richness.

The first explanation presented above maintains that the observed diversity results from undetected habitat diversity (D_{HD}). The second explanation allocates the observed diversity to niche differentiation (D_{ND}). The diversity resulting from the third and fourth explanations can be considered a product of ecological equivalency (D_{EE}). The higher than expected richness shown in the Yizreel Valley and the Sharm-E-Sheikh, the high diversity of shrubs in the transition habitat of southern California, and the numerous annual herbs associated with *Larrea* can best be explained, we feel, by the coexistence of ecological equivalents in equivalent habitat patches. The patches can be on any scale from microsites or individual *Larrea* shrubs to the meso-scale of equivalent stands and a macro-scale of geographical replacement. The magnitude of influence of ecological equivalency on overall richness should be highest in systems in which habitats are discrete and patchily distributed and/or in which competitive interactions are reduced. Systems comprising sedentary organisms with limited dispersal are also more likely to contain ecological equivalents (Sale, 1977, 1979; Itzkowitz, 1977; Menge, 1979; Shmida & Ellner, 1984) because the potential of competitive interaction is much reduced.

The effects of ecological equivalency on species diversity are shown in the diversity display of Fig. 9 depicting two systems in areas with identical habitat and resource conditions. The only difference between Figs. 9(a) and 9(b) is the effects of D_{EE}: species 1 (Fig. 9a) and species 7 (Fig. 9b) are identical in niche position and range of habitat, as are species 5 and 8. The two systems have the same diversity values of $\alpha = 2.5$, $\beta = 1.4$ and $\gamma = 6$. However, the total number of species in the two systems combined is eight, two more than can be accounted for by the determinants of niche relations, habitat diversity, or mass effect. Thus, the effects of ecological equivalency are apparent only in comparisons among systems, or in nested samples of expanding area.

The concept of ecological equivalency of single sets of species can be broadened to equivalent communities. Alternative community composition can exist under several circumstances. In the case of large-scale disturbance, community development (succession)

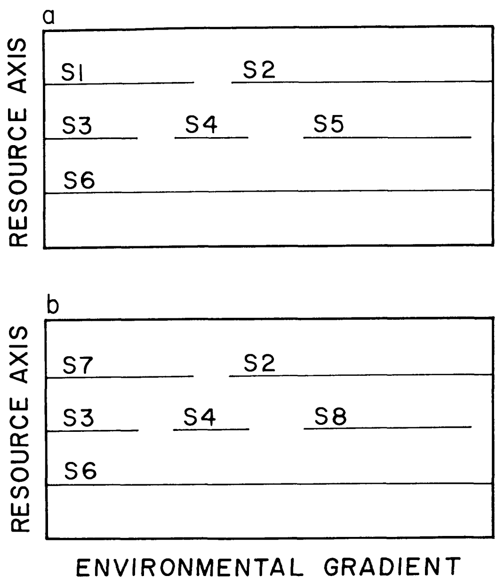

FIG. 9. The influence of ecological equivalency (D_{EE}) on diversity. The systems shown in (a) and (b) are identical in α, β and γ. Species 7 and 8 in (b) are the ecological equivalents of species 1 and 5 in (a). The total number of species for the two systems combined is greater than for either of the single systems.

may take several forms in different locations because of differences in seed or spore banks (Egler, 1954; Marks, 1974) or from differences in propagule inflow (colonization) (Sutherland, 1974; Simberloff & Wilson, 1969). Initial differences in composition during community development may develop into stable equilibria (Sutherland, 1974). Also, repeated localized disturbances can lead to a mosaic of communities representing different successional stages (Loucks, 1970; Heinselman, 1973; Levin & Paine, 1974; Whittaker & Levin, 1977; Bormann & Likens, 1979). There is evidence (Simberloff, 1974; Holland, 1978; Paine & Levin, 1981) that many mature (climax) communities undergo continual changes in species composition not induced by changes in environmental conditions.

The occurrence of alternative community compositions influences diversity patterns (MacArthur, 1972). The alpha-diversities of alternative communities are not predictable except that the expected or average difference in richness between alternatives should be zero ($E(\alpha_i - \alpha_j) = 0$). Because species composition changes, local beta-diversity is increased by the occurrence of alternative communities. However, overall beta-diversity increases only to the extent that the alternatives contain species not previously present in the system. The main consequence of the phenomenon of ecological equivalency is the increase of gamma-diversity from the addition of species from alternative communities.

The relationship between ecological diversity and floristic richness

In this section we examine the role of mass effect and ecological equivalency on macroscales. Classical biogeographers observed that some regions are richer in species than others (Wulf, 1950; Darlington, 1957; Polunin, 1960; Good, 1964; Takhtajan, 1969; Udvardy, 1969; Zohary, 1973).

Classical biogeographers accepted that several factors contribute to biotic richness (*sensu lato*):

(1) The total number of species (inventory diversity on the gamma scale; Whittaker, 1977);

(2) The number of different higher taxonomic categories such as families and orders;

(3) The number of endemic taxa, at different levels of the taxonomic hierarchy, and the number of these that are relicts;

(4) Community-level diversity: the number of community-types within an area;

(5) The number of guilds found within community-types. That is, for plants, the number of growth-forms present.

These several aspects of biotic richness have been related to two determinants or causal mechanisms. The total number of species in a landscape (factor 1) is explained by classical biogeographers as owing to the richness of individual communities from niche relations or the heterogeneity of the landscape (habitat diversity) (Turrill, 1929; Walter, 1973; Zohary, 1973; Daubenmire, 1974; Raven, 1977). High alpha-diversity has often been ascribed by classical biogeographers to high precipitation, temperatures or productivity (Cain, 1950; Walter, 1962; Good, 1964).

Factors 2, 3 and 4 of biotic richness have been correlated with the refugial role of the region (Zohary, 1973, for the Caspian Sea;

Whittaker, 1961, for the Klamath region, U.S.A.; Stebbins & Major, 1965, for California). In a modern diversity context, this corresponds to long-term stability of the environment without major catastrophe or climatic change (Sanders, 1969; Whittaker, 1977). Given such stability, the rate of species extinction is thought to be low. This stability enables old genera and families to survive as relict and palaeoendemic elements (Graham, 1972; Zohary, 1973; Stebbins, 1974; Raven & Axelrod, 1978). Climatic fluctuation, short of catastrophic changes, may lead to increases in species number because of the establishment of habitat islands surrounded by unfavourable environments leading to rapid divergence and speciation (Vuilleumier, 1971). If time and stability give opportunity for niche-differentiated species to evolve and accumulate in biotas, gamma-diversity should increase through time (Hutchinson, 1957; Whittaker, 1969, 1977). Time and stability may especially influence factor 5 – the number of different guilds (growth forms in plants) and the structural diversity of vegetation (Shmida & Whittaker, ms.).

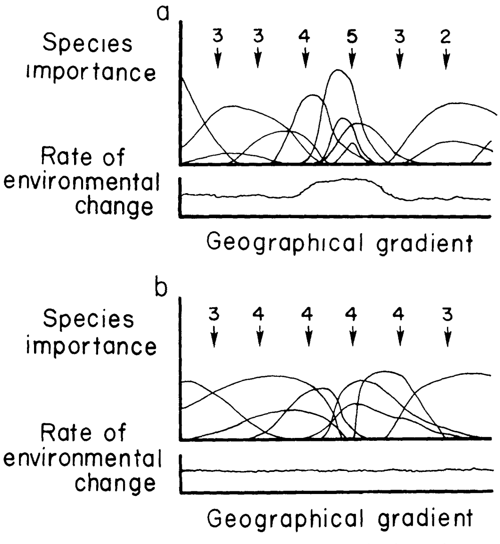

FIG. 10. Species distributions through floristic transitions. In an environmentally induced transition (a) species ranges are narrow in the zone of rapid environmental change, with some species centred in the transition zone, causing higher species richness. In a contact transition (b) there is no zone of relatively rapid environmental change. Although no species are centred in the transition zone, species richness is higher because of the mingling of species from the two floras in contact. Digits above arrows indicate the number of species found at single points along the geographical gradient.

Results of studies of biotic richness in biogeography cannot always be explained by the customary determinants of niche relations (D_{NR}) and habitat diversity (D_{HD}). The biotic richness of regions we interpret as a summation of diversity effects on lower levels, including stand richness and community pattern, but also as results of mass effects and ecological equivalencies. The concept of ecological equivalence in historically distinct biotas has been recognized by several authors (polytopic evolution of Stebbins, 1950; evolutionary duplication of Udvardy, 1969; convergent evolution of Cody & Mooney, 1978). The French phytosociological school discusses the similar concept of ecological vicariants (Quezel & Pamukcuoglu, 1973), limited to allopatric situations. Ecological equivalents are also found sympatric in regions of strong habitat patchiness, such as within cliffs and among mountain tops isolated from each other (Runemark, 1969; Quezel & Pamukcuoglu, 1973; Zohary, 1973).

The richness of floristic transitions

Biogeographers recognize floristic transition areas between different regions as zones in which many species distributional borders occur (Good, 1964; Darlington, 1957). To date some of these regions of high species richness are not completely explained by the principles of classical biogeography. The high species richness of floristic transition areas may, in many cases, be explained by mass effects and ecological equivalency.

Two types of floristic transitions are *contact transitions,* where historically distinct floras have migrated into contact, and *induced transitions,* where the coincidence of many species boundaries has been set by sharp environmental changes. Both transition-types have high floristic richness, with high rates of species turnover relative to the turnover of species outside the transition area. The high biotic richness of induced transitions is due primarily to habitat diversity (D_{HD}). Induced transitions (Fig. 10a) would be more likely than contact transitions (Fig. 10b) to have species centred in the transition zone. In contrast, the high biotic richness of contact transitions is due primarily to macro-scale mass effects (D_{ME}) from the two floras, as well as to overlapping species ranges. In addition, a high percentage of ecological equivalents is expected in contact transitions maintained by continual invasion of species from the two floras (mass effect), habitat shifts, and patch occurrences. In contact transitions, unlike induced transitions, if the distinct floristic regions did not exist as core areas influencing the transition, the species composition of the latter would change and its gamma-diversity decrease considerably.

Mt Hermon

An example of a floristically rich contact transition is the mid-elevation zone of Mt Hermon, in the Middle East (Shmida, 1977; Wilson & Shmida, 1984). The richness of each belt of 100 m in elevation is shown in Fig. 11. The altitudinal interval between 1200 and 1300m does not show greater habitat diversity than other elevation belts: temperature and precipitation gradients are smooth, and substrate-type is not discontinuous in this belt (Shmida, 1977). The analysis of species' ranges (Fig. 11) reveals that the high gamma-diversity of the mid-elevation zone is not due to species centred in it. Instead, the high richness is derived primarily from the overlapping ranges, caused by large-scale mass effects, of species from the Mediterranean flora (lower elevation) and the montane-alpine flora (higher elevation). Other examples of contact transitions are widespread in the biogeographical literature (Eig, 1931; Rikli,

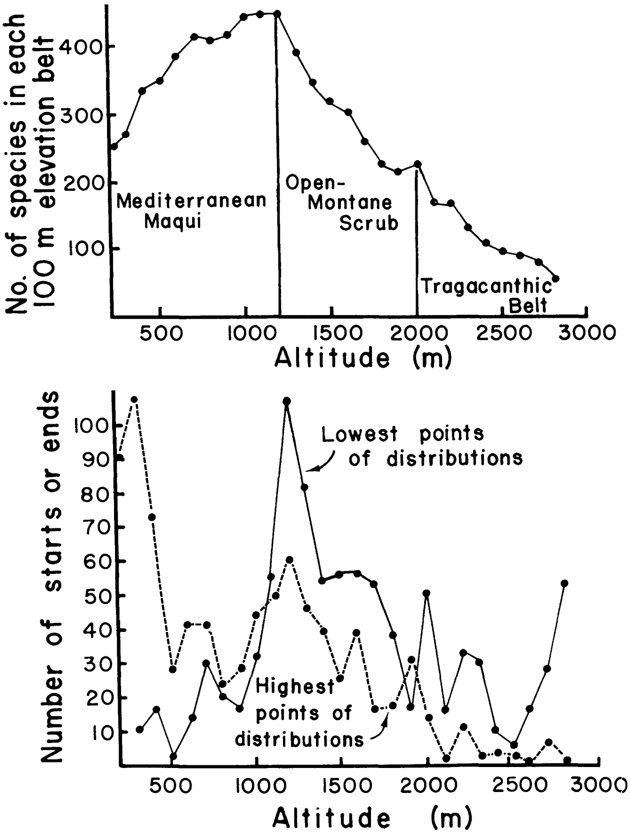

FIG. 11. Species distributions along the elevation gradient of Mt Hermon, Israel. (a) The number of species found in 100 m elevation belts. The peak in richness occurs between 950 and 1250 m. (b) The number of endpoints of species ranges by 100 m elevation belts. Both start (lower endpoints) and end (upper endpoints) are more frequent at 1200 m.

1943–48; Darlington, 1957; Good, 1964; Zohary, 1973). Also, transitions may occur because of a combination of explanations 1 and 2 wherein contact transitions are superimposed on rapid environmental change (e.g. the Anatolian Plateau and the coastal Mediterranean zone in southern Turkey: Zohary, 1973; Walter, 1956).

The Judean Desert

A 35 km west-to-east macrogradient from the Judean ridge to the Judean Desert in Israel illustrates some similarities and differences in contact and induced floristic transitions. Along the macrogradient (Fig. 12) elevation decreases from 900 to 399 m below sea level; precipitation decreases with elevation and with increasing distance east from the Judean ridge. The greatest topographic relief is at 750–900 m elevation, and precipitation, we presume, also changes abruptly at that point. Vegetation changes along the macrogradient from mattoral (chaparral) west of and along the ridge, through a semidesert steppe (100–750 m elevation), to typical desert vegetation.

Species richness values, compiled from thirty-three 0.1 ha diversity samples are shown in Fig. 12. Also plotted are the number of species, by each elevation belt, that are found exclusively within that elevation belt along the transect. Two peaks in species richness occur. Peak A, at the transition between chaparral and semidesert, is associated with a large number of exclusive species (33%), whereas peak B, at the transition between semidesert and desert, is not associated with many exclusive species. Because of the large number of exclusive species at A and the rapid environmental change that occurs there, we consider peak A to be within an induced floristic transition. These results agree with phytosociological and floristic observations of many restricted and endemic plants in this transition belt (Zohary, 1973). In contrast, the lack of abrupt environmental change and the low number of exclusive species show the peak in species richness at B to result from a contact floristic transition alone.

Along the macrogradient of Fig. 12, all four determinants – niche relations, habitat diversity, mass effects and ecological equiva-

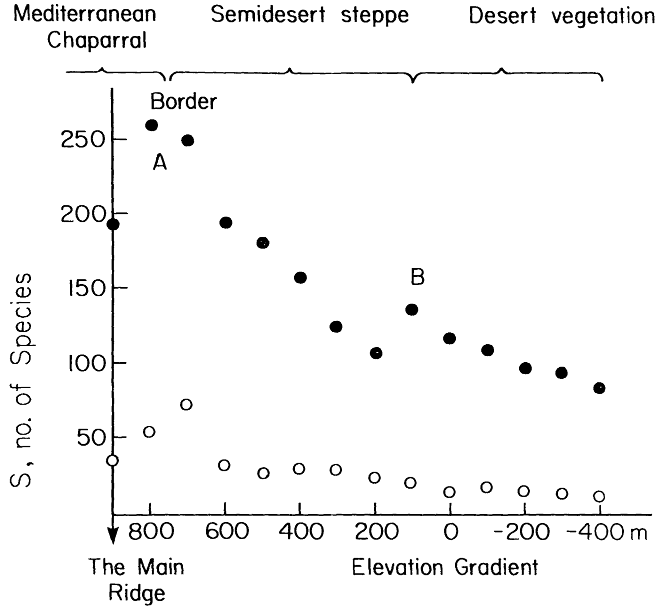

FIG. 12. Species richness (●) of 100 m elevation belts from 900 m near Jerusalem to −400 m in the Judean Desert. Also shown are the numbers of species (○) found exclusively in each elevation belt. The peak in richness at A corresponds to rapid environmental change and shows a peak in number of exclusive species, so is an *induced floristic transition.* The peak at B shows no peak of exclusive species and it corresponds to a *contact floristic transition.*

lence – contribute to species richness. The peak in species richness at area A in Fig. 12 occurs because of the locally high habitat diversity (D_{HD}) in that section of marked topographic relief, and because of the strong mass effects (D_{ME}), from the adjoining but environmentally different habitats. The peak at area B in Fig. 12, however, follows only from the relatively great influence of mass effects (D_{ME}), from the different floras in contact. This pattern of induced and contact transitions is also typical of the Mediterranean border in California, where many relictual and endemic species are found (Stebbins & Major, 1965; Raven, 1977).

Species richness and area

The relationship between species richness and area has long been of interest to phytosociologists (e.g. Gleason, 1922; Braun-Blanquet, 1932; Cain, 1938) and biogeographers (e.g. Williams, 1964; Good, 1964). Effects of area on diversity are commonly represented by species–area curves in which a curve traces the accumulation of species with increasing sample area. The traditional form for phytosociologists of the species–area curve is with nested samples, which retains information about the similarity in species composition of different samples. In contrast, most species–area curves in island biogeography are not nested (MacArthur & Wilson, 1967).

The influence of sample area complicates the intepretation of species richness patterns. In reaction, many mathematical models for species–area curves have been prepared (see Williams, 1964; May, 1975; Pielou, 1975; Connor & McCoy, 1979) that attempt to reduce species–area effects to one or two understandable parameters. Good (1964) uses a linear model, $S = mA + n$, where S is the number of species in area A, and m and n are model parameters. Gleason (1922), Dahl (1960) and Whittaker (1972) favour a logarithmic model, $S = b + d \log A$, where the model parameter d, in particular, has been used as an index of diversity (see also Fisher, Corbet & Williams, 1943; Whittaker, Niering & Crisp, 1979; Shmida & Whittaker, 1981). Preston (1948, 1962) and MacArthur & Wilson (1967) propose a power-relationship model, $S = cA^z$, where z has commanded most attempts at interpretation. The parameters m, d and z each summarize the rate at which species richness increases with sample area. Williams (1964) observes that most data fit either the logarithmic of power-relationship models although neither model is consistently successful (Connor & McCoy, 1979). Lacking a basis for choosing among models, Pielou (1975) recommends the use of an empirical function. However, for none of these models has a link been established between mathematical expression and biological mechanism.

We assert that the characteristics of species–area curves from nature are due to the combined effects of four distinct biological determinants of diversity–niche relations, habitat diversity, mass effects, and ecological equivalency. In our terminology:

$$S_{\text{area}} = f(D_{NR}, D_{HD}, D_{ME}, D_{EE})_{\text{area}}$$

For the remainder of this section we discuss how we expect the relative intensity of each determinant to vary with spatial scale.

Niche relations consist of small-scale, intensive interactions, such as nutrition, competition and predation; relations that, on average, do not vary greatly with expanding area. Therefore, the relative intensity of D_{NR}, that is, the contribution of niche relations to overall species richness, should be highest at small spatial scales and decrease as more species occur because of other causes. The relationship of habitat diversity (D_{HD}) to area depends on gradients of environmental change through the sampled area, as well as on spatial patterning. The intensity of D_{HD} should be proportional to differences in environmental conditions with expanding area but with a reduction in effect due to repeating spatial patterns. Therefore, the contribution to overall species diversity by habitat diversity at first increases with area, then gradually decreases.

Mass effects (D_{ME}) should be most intensive at meso-scales. The number of species that are found in a sample outside the region of self-maintenance should be a complex function of the dispersal abilities of the species and the heterogeneity of the biota (together determining the potential number of encroaching species), the area of the sample itself (the target area), and the range of environmental conditions represented in the sample. At scales that exceed the majority of dispersal

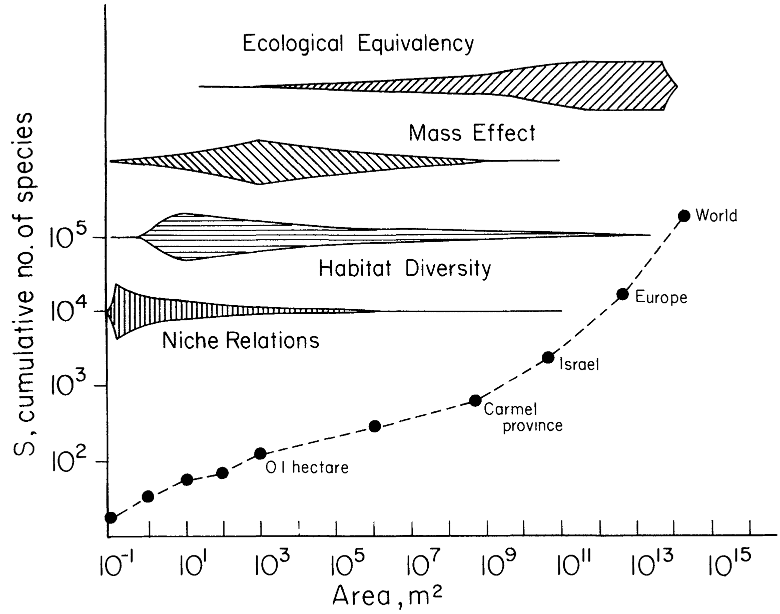

FIG. 13. Species–area curve extending from samples in the mattoral (chaparral) in Israel to the entire world. The thickness of each hatched area shows the hypothesized relative contribution of each biological determinant to species richness at different spatial scales. Niche relations are most important at the smallest scales (<1 m^2), habitat diversity is most important at scales $<10^2$ m^2, mass effects are most important at meso-scales (10–10^6 m^2) and ecological equivalency is most important as macro-scales (10^7 m^2).

distances of species the significance of mass effect to overall species diversity will decline. At very small scales, the decreased target area will limit the number of species present from mass effect. Therefore, the scale at which mass effects should be most important is the median dispersal distance of the species present in the landscape.

The effects of ecological equivalency (D_{EE}) occur at all spatial scales, as noted in our examples, but should be most intense at large spatial scales, where geographical and topographic barriers to mingling are most predominant. The contribution by D_{EE} to overall species richness should be particularly high in regions with long historical barriers. Such historical isolation can result in ecological convergence (Cody & Mooney, 1978) and the existence of alternative community equilibria (MacArthur, 1972) containing many sets of ecological equivalents. The effects of ecological equivalency on global biotic richness has been well demonstrated by classical and modern biogeographers (Darlington, 1957; Udvardy, 1969; Valentine, 1972).

In Fig. 13 we present a simplified and generalized summary of our ideas on the relative intensities of the four determinants of diversity at different spatial scales, from m^2 quadrats to the globe. Against a nested species–area curve centred on samples in Israel we depict the relative intensity of each determinant at each spatial scale. At smaller scales ($10\,m^2$) niche relations (D_{NR}) and habitat diversity (D_{HD}) are the major contributors to overall species richness. Their relative influence decreases with area, largely because of the increasing importance of mass effects (D_{ME}) and ecological equivalency (D_{EE}). Mass effects peak next, at meso-scales corresponding to typical dispersal distances, and decrease as area increases. Ecological equivalency (D_{EE}) alone continues to increase in importance with increasing area. In a sense, global species richness is mostly a product of ecological equivalency.

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