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LATITUDINAL GRADIENTS IN SPECIES DIVERSITY: A REVIEW OF CONCEPTS

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INTRODUCTION: DIVERSITY INDICES

The simplest index of diversity is the total number of species, usually of a specific taxon under investigation, inhabiting a particular area. Since this index does not take into account differing abundances of species, divergent communities may show similar "diversities." Because of this, more sophisticated measures have been proposed which weight the contributions of species according to their relative abundances. As early as 1922 Gleason described and discussed the now well known "species-area" curve (Gleason, 1922, 1925). Later, Fisher, Corbet, and Williams (1943) proposed an index, alpha, discussed in detail by C. B. Williams (1964), which can be shown to approximate Gleason's "exponential ratio" (H. S. Horn, personal communication). Margalef (1958) has also used a modification of this index "d," in phytoplankton diversity studies, as well as several other indices (Margalef, 1957). The most recent, and currently widely used diversity index, is the information theory measure, H , derived by Shannon (1948). This index, $-\sum p_i \log p_i$, in which p_i represents the proportion of the total in the i -th category, has been used to quantify the "dispersion" of the distribution of entities with no ordered sequence, such as species in a community, alphabetic letters on a page, etc. Unfortunately, there has as yet been little discussion of the application of statistical procedures to this quantity. However, even without statistical embellishments, H has been a useful and productive tool (Crowell, 1961, 1962; MacArthur, 1955, 1964; MacArthur and MacArthur, 1961; Margalef, 1957, 1958; Paine, 1963; and Patten, 1962).

The choice of the index used in any particular investigation depends on several factors, especially the difficulty of appraisal of species abundances, but also on the degree to which relative abundances shift during the period of study, and for many purposes the simplest index, the number of species present, may be the most useful measure of local or regional diversity. This index weights rare and common species equally, and is the logical measure of diversity in situations with many rare, but regular, species (such as desert lizard faunas, Pianka, in preparation).

THE PROBLEM: SPECIES DIVERSITY GRADIENTS

Latitudinal gradients in species diversity have been recognized for nearly a century, but only recently have some of these polar-equatorial

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trends been discussed in any detail (Darlington, 1959; Fischer, 1960; Simpson, 1964; Terent'ev, 1963). A few groups, such as the marine infauna (Thorson, 1957), and some fresh water invertebrates and phytoplankton appear not to follow this pattern, but many plant and animal taxa display latitudinal gradients. A phenomenon as widespread as this may have a general explanation, knowledge of which would be of considerable utility in making predictions about the operation of natural selection upon community organization. Because of the global scope of the problem, however, it has usually been impossible for a single worker to study a complete species diversity gradient.

Approaches to the study of diversity gradients have so far been mainly of two types, the method of gross geographic lumping with comparison of total species lists for a group (Simpson, 1964; Terent'ev, 1963), and the approach by synecological studies on a smaller scale, comparing the diversity of a taxon through many different habitats (MacArthur and MacArthur, 1961; MacArthur, 1964, and in press). Terent'ev and Simpson used the number of species as indices of diversity, and MacArthur and MacArthur used Shannon's information theory formula to calculate indices of faunal and environmental diversity. Simpson (1964) points out that diversity gradients indicated by the method of gross geographic lumping have two components, one due to the number of habitats sampled by a given quadrat (and thus to the topographic relief) and another component due to ecological changes of some kind. Low latitude regions have more kinds of habitats, (i.e., Costa Rica has a whole range of habitats from low altitude tropical to middle altitude temperate to high altitude boreal habitats; whereas regions of higher latitude progressively lose some of these habitats) and therefore the presence of more species there is neither surprising nor theoretically very interesting. The question of basic ecological interest is that of the second component of diversity—namely, what are the factors that allow ecological co-existence of more species at low latitudes? Ecological data relating to species diversity gradients are scant, and no one has yet attempted the logical step of merging the synecological with an autecological approach.

Despite the handicap of insufficient ecological data, or perhaps because of it, theorization and speculation as to the possible causes of diversity gradients has been frequent and varied (Connell and Orias, 1964; Darlington, 1957, 1959; Dobzhansky, 1950; Dunbar, 1960; Fischer, 1960; Hutchinson, 1959; Klopfer, 1959, 1962; Klopfer and MacArthur, 1960, 1961; MacArthur, 1964, and in press; Paine, in press; and C. B. Williams, 1964). These efforts have produced six more or less distinct hypotheses: (a) the time theory, (b) the theory of spatial heterogeneity, (c) the competition hypothesis, (d) the predation hypothesis, (e) the theory of climatic stability, and (f) the productivity hypothesis. It is instructive to consider each of these hypotheses separately, attempting to suggest possible tests and observations for each, even though only one pair represent mutually exclusive alternatives, and thus several of the proposed mechanisms of control of diversity could be operating simultaneously in a given situation.

In the following discussion, ecological and evolutionary saturation are defined as the ecological and evolutionary upper limits to the number of

species supported by a given habitat. The assumption of ecological saturation is implicit in ecological studies of species diversity gradients, an assumption without which the study of such gradients must be made in terms of the history of the area. There is reasonable evidence that the majority of habitats are ecologically saturated (Elton, 1958; MacArthur, in press).

The time theory

Proposed chiefly by zoogeographers and paleontologists, the theory of the "history of geological disturbances" assumes that all communities tend to diversify in time, and that older communities therefore have more species than younger ones. (The evidence behind this assumption is scanty, and the assumption may or may not be valid.) Temperate regions are considered to be impoverished due to recent glaciations and other disturbances (Fischer, 1960). It is useful to distinguish between ecological and evolutionary processes as subcategories of the theory. Ecological processes would be applicable to those circumstances where a species exists which can fill a particular position in the environment; but this species has not yet had time enough to disperse into the relatively newly opened habitat space. Evolutionary processes apply to longer time spans, to those cases where a newly opened habitat is not yet utilized, but will be occupied given time enough for speciation and the evolution of an appropriate organism.

Tests of the ecological and evolutionary time theories are by necessity indirect, but several authors have suggested possibilities for assessing the importance of evolutionary time as a control of species diversity. Simpson (1964) has argued that the warm temperate regions have had a long undisturbed history (from the Eocene to the present), long enough to become both ecologically and evolutionarily saturated, and that since there are fewer species in this zone than there are in the tropics, other factors must be invoked to explain the difference between tropical and temperate diversities. Beyond this, he reasons that if the time theory were correct, the steepest gradient in species diversities should occur in the recently glaciated temperate zone. Since, for North American mammals, at least, this zone shows a fairly flat diversity profile, there is some evidence against the evolutionary time theory. Simpson (1964) emphasizes that temperate zones have probably been in existence as long as have tropical ones. Newell (1962) stresses that temperate areas at intermediate latitudes were probably not eliminated during the glacial periods, but were simply shifted laterally along with their floras and faunas, and that, if this is the case, they have had as long a time to adapt as have the non-glaciated areas. R. H. MacArthur (personal communication) has suggested that possibilities exist for a test of the effects of glaciation, by comparisons of areas in the glaciated north temperate with their non-glaciated southern temperate counterparts. However, the evolutionary time theory is not readily amenable to conclusive tests, and will probably remain more or less unevaluated for some time.

The evidence relating to the ecological time theory, summarized in detail by Elton (1958), and discussed by Deevey (1949), indicates that most con-

tinental habitats are ecologically saturated. Only in those cases where barriers to dispersal are pronounced can the ecological time theory be of importance in determining species diversity. Islands have sometimes been considered cases of historical accident in which maximal utilization of the biotope is often achieved by pronounced behavioral modifications of those species which have managed to inhabit them (Crowell, 1961, 1962; Lack, 1947). More recently, several theories for equilibrium in insular zoogeography have been proposed, and data given which shows strong dependence of species composition on island size, distance from "source" areas, and time available for colonization (Hamilton, Barth, and Rubinoff, 1964; MacArthur and Wilson, 1963; Preston, 1962). These papers indicate that predictable patterns of species diversity occur even on islands, and further lessen the probable importance of the ecological time theory.

The theory of spatial heterogeneity

Proponents of this hypothesis claim that there might be a general increase in environmental complexity as one proceeds towards the tropics. The more heterogeneous and complex the physical environment becomes, the more complex and diverse the plant and animal communities supported by that environment. Again it is useful to distinguish two subcategories of this theory, one on a macro-, the other on a micro- scale. The first is the factor Simpson (1964) calls topographic relief, discussed in more detail by Miller (1958). The factor of topographic relief is especially interesting in the study of speciation, and has been much discussed in books and symposia on that subject (Blair, 1961; Mayr, 1942, 1957, 1963). The component of total diversity due to topographic relief has been mentioned earlier in this paper.

In contrast to topographic relief, micro-spatial heterogeneity is on a local scale, with the size of the environmental elements corresponding roughly to the size of the organisms populating the region. Elements of the environmental complex in this class might be soil particle size, rocks and boulders, karst topography, or if one is considering the animals in a habitat, the pattern and complexity of the vegetation. Environmental heterogeneity of the micro-spatial type has been little studied by zoologists, and is more interesting to the ecologist than to the student of speciation (considerations of sympatric speciation processes will, however, involve micro-spatial attributes of the environment). It should be noted here that in the only study which relates species diversity of a taxon to environmental diversity in a quantitative way, the environmental diversity is of the micro-spatial type (MacArthur and MacArthur, 1961; MacArthur, 1964). These authors demonstrate that foliage height diversity is a good predictor of bird species diversity, and that knowledge of plant species diversity does not improve the estimate. Further tests of the theory of environmental complexity will probably follow similar lines, although it would be useful to consider alternative ways of examining this hypothesis.

Spatial heterogeneity has several shortcomings when applied to the explanation of global diversity patterns. The component of total diversity due to topographic relief and number of habitats (macro-spatial heterogeneity) certainly increases towards the tropics, but does not offer an explanation for diversity gradients within a given habitat-type. Vegetative spatial heterogeneity is clearly dependent on other factors and explanation of animal species diversity in terms of vegetative complexity at best puts the question of the control of diversity back to the control of vegetative diversity. Since there is no reason to suppose that micro-spatial heterogeneity of the physical environment changes with latitude, the theory of micro-spatial heterogeneity seems to explain only local diversity. Ultimately, resolution into independent variables will require consideration of non-biotic factors such as climate which change more or less continuously from pole to pole (see section on the climatic stability hypothesis).

The competition hypothesis

Advocated by Dobzhansky (1950) and C. B. Williams (1964), this idea is that natural selection in the temperate zones is controlled mainly by the exigencies of the physical environment, whereas biological competition becomes a more important component of evolution in the tropics. Because of this there is 'greater restriction to food types and habitat requirements in the tropics, and more species can co-exist in the unit habitat space. Competition for resources is *keener* and niches 'smaller' in more diverse communities. Dobzhansky emphasizes that natural selection takes a different course in the tropics, because catastrophic indiscriminant mortality factors (density-independent), such as drought and cold, seldom occur there. He notes that catastrophic mortality usually causes selection for increased fecundity and/or accelerated development and reproduction, rather than selection for competitive ability and interactions with other species. Dobzhansky predicts that tropical species will be more highly evolved and possess finer adaptations than will temperate species, due to their more directed mortality and the increased importance of competitive interactions. No statement has been given as to exactly why competition might be more important in the tropics, but the hypothesis is testable in its present form.

Because the predation hypothesis predicts very nearly the opposite mechanisms of control of diversity than does the competition hypothesis, I will briefly outline the predation hypothesis before proceeding with discussion. These two hypotheses are almost mutually exclusive alternatives, and the same tests, by and large, apply to both.

The predation hypothesis

It has been claimed that there are more predators (and/or parasites) in the tropics, and that these hold down individual prey populations enough to lower the level of competition between and among them (Paine, in press). This lowered level of competition then allows the addition and co-existence of new intermediate prey types, which in turn support new predators in the

system, etc. The mechanism can apply to both evolutionary and dispersal additions of new species into the community. Paine (1966) argues that the upper limits on the process are set by productivity factors, which will here be considered separately.

According to this hypothesis, competition among prey organisms is *less* intense in the tropics than in temperate areas. Thus, a test between these two hypotheses is possible, provided that the intensity of competition can be measured. Several approaches to the quantification of competition might find application here (Connell, 1961a, 1961b; Elton, 1946; Kohn, 1959; MacArthur, 1958; Moreau, 1948). Also, if the predation hypothesis holds, community structure should shift along a diversity gradient, with an increase in the proportion of predatory species as the communities become more diverse. Evidence for such a shift in trophic structure along a diversity gradient is given by Grice and Hart (1962). These authors present data showing that the proportion of predatory species in the marine zooplankton increases along a latitudinal diversity gradient. A similar shift in community structure accompanies a terrestrial species diversity gradient in the deserts of western North America (Pianka, in preparation). Fryer (1959, 1965) has argued that predation enhances migration and speciation, thereby resulting in increased species diversity, in some African lake fishes. As will be pointed out in a later section, demonstration that species have either finer or more overlapping habitat requirements in the tropics could be used to support three of the six hypotheses, and is therefore not a powerful distinguishing tool.

The theory of climatic stability

According to this hypothesis, restated by Klopfer (1959), regions with stable climates allow the evolution of finer specializations and adaptations than do areas with more erratic climatic regimes, because of the relative constancy of resources. This also results in "smaller niches" and more species occupying the unit habitat space. Another way of stating this principle in terms of the organism, rather than the environment, is that, in order to persist and successfully exploit an environment, a species must have behavioral flexibility which is roughly inversely proportional to the predictability of the environment (J. Verner, personal communication). In recent years the theory of climatic stability has become a favorite for explaining the generality of latitudinal gradients in species diversity, but has as yet remained untested. Rainfall and temperature can be shown to vary less in the tropics than in temperate zones, but rigorous correlation with faunal diversity, let alone demonstration of causal connection, has not yet been possible. It should be realized that climatic factors could well determine directly floral and/or vegetative complexity, while being only indirectly related to the faunal diversity of the area.

Evidence that tropical species have more restricted habitat requirements than temperate species would support the competition hypothesis, the predation hypothesis, and the theory of climatic stability. Klopfer and Mac-

Arthur (1960) have attempted to test the hypothesis that "niches" are "smaller" in the tropics by comparing the proportion of passerine birds to non-passerines along a latitudinal gradient. Their thesis is that the non-passerines, possessing a more stereotyped behavior, are better adapted to exploit the more constant tropical environment than are the passerines, whose more plastic behavior allows them to inhabit less predictable habitats. Klopfer (in press, in preparation) has compared the degree of behavioral stereotypy in temperate and tropical birds, and tentatively concludes that "while tropical species are in fact 'stereotyped,' this is more likely an effect rather than a cause of their greater diversity."

An interesting variation on this theme is that of increased "niche overlap" in more diverse communities (Klopfer and MacArthur, 1961). Klopfer and MacArthur attempted to test this idea by comparing the ratios of bill lengths in congeners among several sympatric bird species in Panama and Costa Rica. Simpson (1964) notes that this ratio may come as close to 1.00 in temperate birds as it did in Klopfer and MacArthur's tropical species, but fails to realize that morphological character displacement is expected only in species occupying the same space (Brown and Wilson, 1956; Hutchinson, 1959; Klopfer and MacArthur, 1961; MacArthur, in press). Ratios of culmen lengths may often approach unity in species such as *Dendroica* which clearly divide up the biotope space (MacArthur, 1958), and thus demonstrate behavioral, rather than morphological character displacement. However, it is apparent that even if the comparison were valid, the test would not distinguish between "smaller niches" and increased "niche overlap" (C. C. Smith, personal communication). It is difficult to devise tests which will distinguish between these alternatives, and perhaps none can be suggested until "niche" has been operationally defined. Use of some of the dimensions of Hutchinson's (1957) multidimensional niche may allow partial testing between these alternatives, as in the work of Kohn (1959) on *Conus* in Hawaii.

Increased overlap in selected dimensions of the niche can imply either increased, decreased, or constant competition; the first if the overlapping resources are in short supply, the second if the overlapping resources are so abundant that sharing of them is only slightly detrimental to each species, and the third if independent environmental factors (such as more predictable production) allow increased sharing of the same amount of resource. Hence, because data supporting the niche overlap idea has ambiguous competitive interpretations, it does not distinguish between three (or four) hypotheses either.

Tests distinguishing between the theory of climatic stability and the competition hypothesis are especially difficult to devise, as there is considerable overlap between the two, and indeed, they are usually mixed when either is suggested. This similarity makes it all the more important to evaluate the importance of each, and in keeping with the rest of this paper they will be considered separately and at least two possible distinguishing tests suggested.

According to the theory of climatic stability, a unit of habitat will support the same number of individuals in the tropics and temperate regions, but since each of the species may be rarer (without becoming extinct) in the tropics, there can be more of them. The competition hypothesis implies that more individuals occupy the same habitat space, or else competition would not be increased. Considering a fixed areal dimension as a unit of habitat, abundance data from the tropics generally suggest that the number of individuals is relatively similar from temperate to tropics and therefore support the theory of climatic stability (Klopfer and MacArthur, 1960; Skutch, 1954). Another way in which these two theories might be separated is by examining the intensity of competition occurring along an increasing diversity gradient; if the level of competition remained constant, or decreased along the gradient, the prediction of an increased proportion of predatory species could be used to separate the predation hypothesis from the theory of climatic stability.

The productivity hypothesis

The most recent and most complete statement of this hypothesis is that of Connell and Orias (1964). They blend this hypothesis with the theory of climatic stability, distinguishing between the energetic cost of maintenance and the energy left for growth and reproduction. Their synthesis also includes aspects of the theory of spatial heterogeneity, and reasonably explains latitudinal trends in diversity, but the productivity hypothesis will be considered here in its "pure" form.

The productivity hypothesis states that greater production results in greater diversity, everything else being equal. Since it is patently impossible to hold everything else equal, the hypothesis can only be tested in crude or indirect ways. Experimental manipulation of nutrient levels in freshwater lakes, for instance, might provide a possible test. Such enrichments have often been made, both intentionally and accidentally (sewage), and quantitative data have been taken on the response of the biota. The data needed for calculating diversities probably exist, and it would be interesting to see such calculations performed. Qualitative indications are that enrichment usually causes an impoverished fauna (Patrick, 1949; L. G. Williams, 1964).

If productivity were of overwhelming importance in the regulation of species diversity, one would expect a correlation despite uncontrolled extraneous variables. Only one such correlation is known to me (Patten, Mulford, and Warinner, 1963), and in fact there may often be an inverse relation between species diversity and abundance or standing crop (which should usually be positively correlated with production) (Hohn, 1961; Hulburt, 1963; Yount, 1956; L. G. Williams, 1964; and my own observations on desert lizards). Those who would claim that the above studies are on non-equilibrium populations and thus not applicable to the problem at hand, would do well to search for data from "equilibrium" conditions which are relevant to the productivity hypothesis.

A common modification of the productivity hypothesis which has been claimed to be of importance in regulating species diversity is the notion of increased temporal heterogeneity in the tropics. The main argument is that the longer season of tropical regions allows the component species to partition the environment temporally as well as spatially, thereby permitting the coexistence of more species (MacArthur, in press). This notion has been rephrased by Paine (in press) who argues that the "stability of primary production" is a major determinant of the species diversity of a community. Paine integrates the predation hypothesis with this idea to form a sort of synergistic system controlling diversity. This hypothesis is also a blend of the stability and productivity theories, but in this case, the mixing suggests new observations, and a new mechanism of control of diversity than does either hypothesis alone. The mechanism for the regulation of species diversity by stability of primary production may be similar to the mechanism suggested for climatic stability, except that in this case, plants may buffer climatic variability by utilizing their own homeostatic adaptations and storage capacities to increase the stability of primary production.

These notions can be tested by analyses, such as that of MacArthur (1964), of the length of breeding seasons, but there are other ways of examining them as well. Thus, comparisons of the division of the day (or night) and season into discrete activity periods by different animal species might elucidate latitudinal trends. Another possible angle of approach is by means of the "stability of primary production," which can be measured directly and examined for latitudinal trends. Unfortunately, there are all too few reliable measures of primary production, let alone the variability in this quantity, and at this point it is difficult to assess the stability of primary production along a latitudinal gradient. The necessary data are simple enough in theory, but in practice a single determination of primary productivity is tedious (especially in terrestrial habitats). An indirect possibility for testing the hypothesis exists, however, for arid regions, where primary productivity is strongly positively correlated with precipitation (Pearson, 1965; Walter, 1939, 1955, 1962). In this environment, the amount and variability of precipitation can be used to estimate the amount and variability of primary production. Preliminary analysis of weather and lizard data for the deserts of western North America shows no correlation with either the average amount or the variability of rainfall and the number of lizard species (Pianka, in preparation).

Since clutch size is closely related to these ideas of increased temporal heterogeneity and stability of primary production, it may be profitably considered here. The fact of reduced clutch size in tropical birds (Skutch, 1954) has been discussed as a possible factor allowing the coexistence of more species in the tropics (MacArthur, in press). MacArthur argues that by lowering its clutch size, a species reduces its total energy requirements and is therefore able to survive in less productive areas which were formerly marginal habitats. He reasons that such reductions in total energy requirements will also allow the existence of more species, when the total

amount of energy available is held constant. Apart from the problems of population replacement raised by these theoretical arguments, there are other reasons for doubting the importance of reduced clutch size as a determinant of increased tropical diversity. For instance, it is highly possible that tropical habitats never achieve food densities as high as those usual further north, because of their greater species diversity and the fact that most of the breeding birds do not migrate. In contrast, great blooms of production characterize the temperate regions, and most of the breeding birds are migrants. Thus it may be energetically impossible for tropical birds to raise as many young as can be supported in the more productive northern areas (that is, more productive on a short term basis, during the short growing season) (Orians, personal communication). Support of this notion comes from the large territory sizes of many tropical bird species (Skutch, 1954), which suggests that food may be scarce. If this is indeed the case, the smaller clutches of tropical birds would be a result, rather than a cause of, the greater diversity in the tropics. These criticisms of the reduced clutch size hypothesis are, however, in themselves largely theoretical, and it will be worthwhile to examine clutch sizes of other taxa along various diversity gradients. Clutch sizes of desert lizards vary latitudinally, but whether or not the largest clutches are from the south depends on the species concerned (Pianka, in preparation).

CONCLUSIONS

Obviously, there is room for considerable overlap between these different hypotheses, and several may be acting in concert or in series in any particular situation. Because of the preliminary state of knowledge on the subject of species diversity, for the sake of clarity, and in order to suggest tests of the various hypotheses, it is useful first to consider and assess each of the components of control of diversity in isolation, before attempting various mixtures. Once the relative importance of each factor has been assessed for many different diversity gradients, an attempt may be made to merge them. In general, the compounding of hypotheses is to be avoided, unless such blending suggests new tests not applicable to the isolated theories. As more and more parameters are included, the more complex hypothesis tends to "answer" all cases and becomes less and less testable and useful.

A fact often overlooked is that most of the hypotheses can be either supported or rejected by appropriate observations on a limited scale; any species diversity gradient might be a suitable study system. If the broader geographical gradients are found to be qualitatively different from local diversity patterns, this in itself would be interesting, and understanding the difference would ultimately require thorough knowledge of the control of local species diversity.

Finally, since ecologists can seldom structure their experiments except by their choice of observations and measurements, the natural system usually sets the bounds within which they must work. The basic technique of de-

scriptive science is correlation, and it is well to keep in mind that correlation does not necessarily mean causation. This is especially true in the study of latitudinal gradients in species diversity, where many different factors vary along the gradient in a fashion similar to the taxon studied, and spurious correlations may be frequent. For these reasons all significant correlations must be carefully examined and attempts made to understand the mechanisms and causal connections (if any) between variates. Unambiguous demonstration of causality can only be attained by experimental manipulation of the independent variables in the system.

SUMMARY

The six major hypotheses of the control of species diversity are restated, examined, and some possible tests suggested. Although several of these mechanisms could be operating simultaneously, it is instructive to consider them separately, as this can serve to clarify our thinking, as well as assist in the choice of the best test situations for future examination.

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