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FACTORS CONTROLLING SPECIES DIVERSITY: OVERVIEW AND SYNTHESIS

Jared Diamond¹

ABSTRACT

Factors controlling species diversity are usually presented as a laundry list without organization—for instance, “The tropics have more species than the temperate zones because of greater stability and reduced seasonality and higher productivity and more diverse resources and . . .” This paper instead proposes a fourfold grouping of factors, termed the QQID approach. Q = resource quality, consisting of the habitat and resource factors that determine the “number of niches.” Q = resource and consumer quantity, consisting of factors determining the quantity of resources (i.e., area and productivity), and factors determining the number of consuming individuals (especially body size) that divide those resources. I = species interactions, which may boost or lower species diversity through effects on individual numbers or individual fitnesses. D = dynamic processes (e.g., extinction, immigration, and speciation), which affect species diversity in both equilibrium and nonequilibrium situations. I illustrate this approach by applying it to understand the famous gradients of species diversity over altitudinal and latitudinal gradients. A major problem for the future involves seeking generalizations as to which factors are likely to be most important under which circumstances. Another problem is to convert this empirical fourfold grouping into a natural hierarchy of factors, possibly based on a hierarchy of processes in space and time.

INTRODUCTION: THE QQID APPROACH

This article aims to provide an overview of the many factors controlling species diversity. My minimum goal is to construct a simple, four-step checklist for analyzing the determinants of species diversity in any given case (Table 1). I shall also briefly suggest an approach by which this checklist, designed for practical purposes, might be converted into a natural hierarchy of the determinants of species diversity. My examples will be drawn mostly from the other papers of this symposium.

At the outset, let us be clear why the problem of understanding species diversity is complicated. In the first place, species diversity is surely not determined in all cases by the same single factor but is the outcome of many contributing factors. Secondly, while one can formulate “rules” about species diversity, each rule has many exceptions. For example, island species diversity usually increases with island area, but there are more frogs on little Barro Colorado Island than on the much larger Cuba (Duellman, this volume). Island species diversity generally decreases with distance from

the mainland, but one of the world’s most remote archipelagoes, Hawaii, has more species of *Drosophila* than do continents. Species diversity as one ascends a mountain generally decreases with altitude, but along the western slopes of the Andes above Chile’s Atacama Desert it increases from middle to high elevations (Arroyo et al., this volume). Small-bodied species are generally more diverse than large-bodied species, but whale diversity exceeds insect diversity in the open ocean. These exceptions to rules based on single factors arise in part for the obvious reason that species diversity is the outcome of many factors, so that the effect of one factor may be overridden by others. Partly, too, the reason is that some of the determinants of species diversity, such as predation, herbivory, disturbance, seasonality, and environmental predictability, control diversity in a nonmonotonic way, so that an increase in those factors may yield either an increase or a decrease in diversity.

Do the factors controlling species diversity just constitute a laundry list, a catalog without organization? Discussions of the latitudinal

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TABLE 1. *The QQID formulation of factors controlling species diversity.*

Q = Quality

1. Diversity of niches or resources

E.g., habitat structural complexity, habitat diversity, resource species diversity, temporal variability, and diversity of consumer strategies.

Q = Quantity

2. Number of consumer individuals, N

$$N = R/R_0 = AP/R_0$$

where R = available quantity of resources

R_0 = resource requirements per individual (increases with body size)

A = area

P = productivity per unit area

I = Interactions

3. Species interactions

Effects on N

Increase of N

· Predation or herbivory on competing species

Decrease of N

· Resource competition

· Predation or herbivory on the consumer itself

Effects on individual fitness

Increase of fitness

· Mutualism

Decrease of fitness

· Interference competition

· Parasitism

· Disease

D = Dynamics

4. Species dynamics

Effects of dynamics at equilibrium

· Effects of extinction rates (decrease with N, etc.)

· Effects of immigration rates (increase with proximity, vagility, larval settling rates, etc.)

· Effects of speciation rates (decrease with vagility, etc.)

Nonequilibrium situations

· Pulse disturbance

· Transiently depressed species diversity

· Recent pulse decrease in area

· Transiently elevated species diversity

gradient in species diversity often read that way: "The tropics have more species than the temperate zones because of greater stability *and* reduced seasonality *and* higher productivity *and* more diverse resources *and*" In fact, life is full of multi-determined phenomena (e.g., whether to declare war, whom to marry, how many children to bear) that at first appear to be influenced by innumerable factors, but for which the factors actually prove to fall into just a few groupings. In some cases, the groupings may even define a natural hierarchy or decision path of factors.

For example, suppose you want to know what determines the number of children in any given candy store. The number obviously depends on the quality or variety of candy to be seen in the window. It is also heavily influenced by the quantity of candy or the size of the store. A little reflection also shows that the number of children in the store depends on interactions, such as those with attractive fairy godmothers beckoning at the door, or with bullies or hungry lions inside. Finally, there is also some role of dynamic or non-equilibrium factors, such as how long ago the doors opened, or how large is the pool of

children available for colonizing the store, and where the store is (particularly relative to a school). Thus, the numerous determinants of the number of children in the store sort out into four sets of considerations: quality of resources, quantity of resources, interactions, and dynamics.

It seems to me that species diversity as well is determined by the same four sets of factors—quality, quantity, interactions, and dynamics (Table 1). As a simple mnemonic, I shall abbreviate this accounting as “QQID.”

Q. Discussions of species diversity usually start out with an analog of the quality or variety of candy: namely, the diversity of niches or of resources. Hence my first, simplest approach will consider just the diversity of niches without taking into account the quantity of resources or the number of consumer individuals or species interactions. We shall pretend that the environment is constant and without temporal variation, that the world is at equilibrium, and that species dynamics are nonexistent or irrelevant.

Q. Next, I shall take account of the quantity of resources, which partly determines the number of consumer individuals.

I. Thirdly, I shall add consideration of species interactions.

D. Finally, I shall incorporate consideration of dynamics and shall allow for the possibility of nonequilibrium.

Q: RESOURCE QUALITY

The ecological equivalent of the variety of candy is the number of niches or of resources. One of the basic findings of ecology is that species diversity increases with niche or resource diversity, as expressed in the statement that each species must occupy a distinct niche. This ubiquitous generalization is the outcome of two facts. First, any given genotype can do certain things (e.g., harvest certain resources by a certain method) better than other things. Second, a single gene pool (i.e., one species) can comprise only a certain diversity of genotypes because of the constraint that the individuals carrying those genotypes must be reproductively inter-com-

patible in order to remain members of the same gene pool. The combination of those two facts has the consequence that each species occupies a certain “niche,” however defined, and that species diversity increases with niche or resource diversity.

Many familiar predictors of species diversity fall under this heading of niche diversity. Among the many examples of predictors that could be cited, I shall discuss five that are well illustrated by the papers of this symposium.

Habitat structure.

It is commonly found that habitats with a more complex or variegated structure contain more species than do simpler habitats. Thus, within any given group of taxa there are generally fewer species in a rock desert than in an adjacent grassland, fewer in the grassland than in an adjacent savanna, and fewer in the savanna than in an adjacent tropical rainforest. The symposium papers by Gentry, Erwin, and Duellman emphasized that peak diversities of plants, beetles, and frogs are achieved in tropical rainforest. For birds a rough quantitative measure of habitat structural complexity that serves to predict species diversity is the habitat’s foliage height diversity: that is, a diversity measure of how foliage is distributed among different vertical layers of the habitat (MacArthur et al., 1966).

Habitat diversity.

Another expression of niche specialization is that a particular species tends to occur only in certain habitats and not others. Thus, as one proceeds along a habitat gradient, one accumulates more and more species, and the accumulated number of species increases with the diversity of habitats encountered. Familiar examples are that species accumulate as one goes along an elevational gradient on a mountain, a depth gradient in the sea, or a horizontal sequence of habitats on land or in the intertidal zone. One example from this symposium is that most neotropical wet forest tree species are confined to a single forest

type or soil type (Gentry, this volume). Another example is that 83% of the beetle species at Manaus, Brazil, are similarly confined to a single forest type (Erwin, this symposium).

Species themselves as niches or resources.

Species may constitute niches or resources for exploitation by other species. Thus, diversity of consumer species tends to increase with diversity of resource species. For instance, there are more stenophagous herbivorous beetle species in tropical rainforest than in a temperate woodland because the rainforest has many more tree species. An example is that many neotropical rainforest beetle species are confined to a single tree species; some may even be confined to the interface of a particular pair of tree species (Erwin, this symposium).

Temporal variability.

Time also serves as a niche dimension that can be partitioned, so that temporal variability provides opportunities for differentiation absent in an environment that is constant with time. For example, the 24-hour solar cycle permits differentiation between nocturnal, crepuscular, and diurnal species exploiting similar resources in the same habitat. The annual cycle permits species to specialize by adopting various seasonal strategies, as exemplified by the coexisting insect species with different overwintering strategies, or by bird species that coexist in the breeding season but segregate in winter as a result of some being migratory, others resident. Still longer cycles in a variable environment permit the differentiation of K strategists from r strategists. A striking example from this symposium is the 97% turnover of beetle species in a single tree species of Barro Colorado Island between the wet season and dry season (Erwin, this symposium).

Consumer strategies.

Species that harvest similar resources in the same habitat may coexist by employing different foraging techniques, or by adopting differing life-history strategies. Here, too, this

symposium has provided a striking example: the 28 alternative reproductive modes by which frogs solve the common problem of producing offspring while protecting them from desiccation (Duellman, this volume).

These five sets of examples do not exhaust the axes along which coexisting species may segregate. Readers will undoubtedly be able to think of further biologically significant ways in which differences in resources or in other niche parameters are exploited by different species.

QQ: QUANTITY OF CONSUMER
INDIVIDUALS OR OF RESOURCES

In the preceding discussion we have ignored consideration of the quantity of resources. We have pretended that a resource is either present in sufficient quantity to support a species, or else the resource is absent. However, resource quantity is obviously important because species are packaged in discrete units (i.e., individuals), and a population consisting of too few individuals cannot survive. There is no hard rule as to how many constitutes "too few," but a population consisting of one individual of a species practicing sexual reproduction is clearly doomed to extinction within one generation, a population size of two (one male, one female) is extremely precarious, and only populations with an effective size above 500 are considered reasonably safe even in the short run (Frankel & Soulé, 1981; Soulé, 1986). Thus, the species diversity of any given group of taxa generally increases with the group's total population size.

However, population size, the number of consumer individuals, does not depend only on quantity of resources. More generally, population size equals the total quantity of resources available, divided by the quantity of resources required to sustain one individual. Resource quantity in turn equals the product of area times productivity per unit area, while quantity of resources required per individual increases with body size. Thus, the second "Q" in our "QQID" formulation

groups three factors: the increase in species diversity with area, productivity, and decreasing body size.

Area.

The most familiar generalization of island biogeography is that species diversity on islands, mainland habitat patches, or arbitrarily defined mainland census plots increases with area. This species/area relation arises partly from the increase in habitat diversity with increasing area sampled, but also from the direct proportion between area on the one hand and resource quantity and thus consumer population size on the other hand. An example from this symposium is Janzen's (this volume) comment that conservation areas in Costa Rican dry forest should be at least 500–1,000 km² in extent, because smaller areas would contain too few individuals of important species to sustain their populations.

Productivity.

Productivity increases with increasing rainfall or temperature, hence with decreasing latitude or altitude. Since number of consumer individuals increases with productivity, species diversity also increases with productivity. This symposium has provided three clear examples. First, plant species diversity on the western slope of the Andes rising out of the Atacama Desert of Chile increases with rainfall (Arroyo et al., this volume). Second, neotropical plant species diversity, collectively or else of each life form considered individually, increases with rainfall up to an asymptotic value (Gentry, this volume). Finally, neotropical rainforest beetle species diversity is much higher in the forest canopy than in lower vertical strata, because the canopy intercepts most of the solar energy and is the most productive stratum (Erwin, this symposium). (Note that these arguments implicitly assume a more or less uniform increase in productivity across the resource spectrum. If production of only certain resources is increased, as in a eutrophic pond, the outcome may be reduction rather than increase in species diversity, because those

consumer species specializing on the increased resource type will thrive and may eliminate other species by preempting their resources.)

Body size.

The product of area times productivity equals the total quantity of available resources, but the body sizes of the consumers determine among how many individuals those resources may be apportioned. Thus, for a given resource quantity and hence given consumer biomass (ignoring second-order effects from the variation in metabolic rate per gram of tissue with body size), consumer population size decreases with body size. Hence, all other things being equal (which they often are not), there tend to be more species of small-bodied animals than of large-bodied animals. In the canopy, Erwin (this symposium) encountered thousands of species of beetles but not of elephants. The whole neotropical region contains only 1,545 species of frogs (Duellman, this volume), a number exceeded by the beetle species in a single tree canopy (Erwin, this symposium). Even among beetles, species diversity is highest in Erwin's smallest size class of beetles.

All these examples illustrate that species diversity increases with the quantity of resources and, more generally, with consumer population size.

QQI: SPECIES INTERACTIONS

In our discussion of resource quality and quantity so far, we have ignored species interactions and have implicitly lumped all resource species together simply as "food." However, species interactions may boost or lower species diversity in comparison with the value that one would predict by ignoring species interactions. Some of these effects of species interactions on species diversity are mediated by effects of species interactions on population numbers (the second "Q" of "QQID"), while other effects require instead consideration of individual fitnesses.

Effects on number of individuals.

A familiar example of how species interactions may lower species diversity is that certain consumer species may competitively lower diversity of other consumer species at the same trophic level by preempting resources and hence lowering the population sizes of their competitors. An example of resource competition on a gigantic temporal and spatial scale is that the evolutionary history of vascular plants has involved a parade of successive dominants, starting with the rhyniophytes and proceeding through pteridophytes and gymnosperms to the angiosperms. The rhyniophytes disappeared completely, but the pteridophytes and gymnosperms continue to survive today, albeit represented by many fewer species than formerly. The most likely explanation is that each new evolving group of vascular plants preempted resources that would otherwise have been utilized by previously evolved groups, thereby reducing their numbers of individuals and consequently of species, or even driving them to extinction (Knoll, 1986; Niklas, this volume).

Species interactions may have the opposite effect—boosting species diversity by boosting the quantity of available resources, these supporting greater numbers of consumer individuals. This situation arises when predators or herbivores reduce the numbers of individuals of their prey or plant species, thereby making more resources available for other consumer species at the same trophic level and thus increasing the numbers of individuals and hence species diversity of those other consumers (Paine, 1966). However, predators or herbivores can also reduce species diversity of consumer species by greatly reducing numbers of individuals. Thus, predation and herbivory can either increase or decrease species diversity, depending on circumstances such as the intensity of predation or herbivory. By analogy with the intermediate disturbance hypothesis, one might speculate that a community's species diversity initially increases with increased community-wide intensity of predation or herbivory, then decreases with further increase in intensity. (The intermediate disturbance hypothesis pro-

poses that low levels of physical disturbance also increase species diversity by removing some consumer individuals, thus reducing competition for resources, while an increase in disturbance that more severely reduces consumer population sizes decreases species diversity. (See Yodzis (1986) for further discussion.)

Effects on individual fitness.

The species interactions of interference competition (e.g., physical aggression), parasitism, and disease tend to decrease species diversity by decreasing individual fitness. Conversely, the species interaction of mutualism tends to increase species diversity by increasing individual fitness. Effects on fitness merge into effects on population size as the effects on fitness become strong enough to kill individuals or else to permit them to survive where they otherwise could not.

QQID: DYNAMICS

Our discussion so far has ignored dynamic considerations. The final step in our QQID analysis takes species dynamics into account. We first retain the implicit assumption of equilibrium that we have made up to this point. Even at equilibrium, consideration of dynamics predicts trends in species diversity that one could not interpret without considering dynamics. We shall then relax our assumption of equilibrium and thereby encounter still further trends in species diversity. There are three dynamic processes underlying species diversity: extinction, which tends to decrease species diversity; immigration, which tends to increase it; and speciation, which also tends to increase it.

Effects of dynamics at equilibrium.

Effects of extinction dynamics. All else being equal, the probability (per unit time) of extinction increases with decreasing population size, hence with decreasing area. That inverse dependence of extinction rates on area provides the major reason why species number on islands increases with area. In this instance, dynamic considerations do not pre-

dict a new trend in species diversity that we have not already considered; instead, they provide the basis of a trend that we had already noted.

Effects of immigration dynamics. The second rule of island biogeography, after the species/area relation, is that species diversity tends to be higher on islands close to a colonization source than on distant islands, even if the close and distant islands are identical in area and in resources. In this case the phenomenon cannot be discussed at all without reference to dynamic considerations: immigration rates from the mainland source to a nearby island are higher than to a distant island, with the result that equilibrium species diversity is higher on the nearby island. Another consequence of immigration dynamics is that species groups with high immigration rates (high dispersal ability) are represented on islands by a higher fraction of the mainland species pool than are species groups with low immigration rates. Thus, compared with mainlands, oceanic islands have more species of birds and bats than of flightless mammals. As a final example of the effects of immigration dynamics on species diversity, high larval settling rates increase the diversity of barnacles, coral reef fish, and other marine organisms with planktonic dispersal (Roughgarden, 1986).

Effects of speciation dynamics. Anything that increases speciation rates will tend to increase species diversity. Speciation rates depend on numerous factors, such as frequency of chromosomal rearrangements, ease of developing reproductive isolation, and dispersal rates. I shall provide a few examples involving dispersal, which is important in speciation since reproductive isolation is more likely, even over shorter distances, for taxa with poor dispersal ability than for others with great dispersal ability. In part for that reason, there are many more species of flightless beetles and land snails than of tardigrades, which are readily wafted in the aerial plankton and are virtually panmictic and cosmopolitan. Because tropical species of birds and possibly of other taxa tend to be more sedentary than temperate species, considerations of dispersal

and speciation rates also contribute to the higher species diversities in the tropics. Note that dispersal has opposing effects on species diversity: with increasing dispersal, the fraction of the regional species pool that reaches a given site increases (increasing the species diversity at that site), but the frequency of speciation and thus the size of the regional species pool itself decreases.

This symposium provided several examples of the sensitivity of species diversity to dispersal through its effects on immigration and speciation rates. As an example of the effect on immigration rates, the plant diversity and composition of Costa Rican dry forests depend on the relative opportunities for seed dispersal by wind and by animals (Janzen, this volume). As an example of the effect of dispersal on speciation rates, the roles of biotic vectors both for pollination and for seed dispersal were a decisive factor in the diversification of angiosperms (Niklas, this volume). Biotic vectors can carry out pollination between conspecific individuals separated by a much greater distance than can be effectively bridged by wind, thus permitting angiosperms to live at much lower population densities than other plants and hence to evolve high diversities of relatively rare species. Biotic seed dispersal permits angiosperms to reach sites accessible only with greater difficulty to other plants.

Nonequilibrium situations.

All our discussions so far have referred to species diversity at equilibrium. However, it is a debated question whether it is frequent or exceptional for species communities to be at equilibrium. There is no doubt that many communities have species diversities below equilibrium values, while other communities have species diversities above equilibrium values (Janzen, this volume). Subequilibrium diversities are a transient result of pulse disturbances, while supraequilibrium species diversities are a transient result of pulse decreases in area.

Pulse disturbances leading to subequilibrium species diversity. If populations or resources are decreased or wiped out by dis-

turbance at a site, species diversity at the site will transiently be below the equilibrium value until the resources are restored, or until the consumer populations are restored by immigration or by speciation. The time constants or relaxation times for species communities to recover from disturbance vary enormously. It may be a few months or years after a storm batters a coastline until resources have been replenished and consumer species have returned. When a volcanic explosion destroys the biota of an island, as happened on Krakatau, it may be decades or centuries before immigration has restored the original species diversity. As a result of Pleistocene glaciations that backed populations of many northern European tree species against the Alps and exterminated them, tree species diversity in Europe today, 10,000 years after the end of the Pleistocene, is still below North American levels. It will presumably take much longer than 10,000 years for European tree species diversity to be restored by a combination of immigration and speciation. Finally, for many millions of years after an asteroid collision caused mass extinctions at the Cretaceous/Tertiary boundary—if indeed there was such a mass extinction, and if it was caused by an asteroid—species diversity of large terrestrial vertebrates remained low until it was eventually restored and surpassed by speciation of mammals.

Pulse decrease in area, leading to supra-equilibrial species diversity. Because equilibrial species diversity tends to increase with area, a decrease in area eventually leads to a decrease in species diversity. However, the greater the area after the pulse decrease, the slower the “relaxation time” required for species diversity to decay to the new lower equilibrial value (because “relaxation time” depends on extinction rates which are inversely proportional to area according to Diamond, 1972). Immediately after the pulse decrease in area, species diversity equals that prevailing at the site immediately before the pulse decrease in area. If one looked at the site immediately after the pulse area decrease and did not know that there had been such

an area decrease, one would be puzzled to find species diversity higher than the site would support if it had not just suffered such a pulse area decrease. This “supersaturation effect” lasts only for a century or so in the case of birds in a forest fragment of one km², but lasts for many millenia for birds or mammals on large land-bridge islands such as Java and Borneo, or on a large mountaintop with Pleistocene habitat connections to other mountaintops, such as the mountains rising out of the Great Basin (Brown, 1971; Diamond, 1984). Islands that lie today in shallow water near continents were connected to those continents at Pleistocene times of lower sea level by land bridges and were finally severed from those continents 10,000 years ago by rising sea levels. The larger land-bridge islands, which include Trinidad, Sri Lanka, Fernando Po, and Formosa, as well as Java and Borneo, are still supersaturated with bird and mammal species (Terborgh, 1974). It will presumably require many tens of thousands of years before their species diversities have declined back to the equilibrial values appropriate to their modern areas.

These considerations of how relaxation times of supersaturated habitat fragments increase with area have interesting implications for understanding continental biotas. Relaxation times for birds and mammals on islands of a few thousand square kilometers, and for insects, lizards, plants, and other species living at higher population densities than birds and mammals on still smaller islands, are in excess of 10,000 years. We must therefore expect that relaxation times for the world's continents are far longer, perhaps hundreds of thousands of years. As the continental tropical rainforests expanded in concert with Pleistocene climatic fluctuations, rainforest species diversity must also have tended to expand and contract. However, the expanses of rainforest in South America, Africa, or Asia are so large that species relaxation times for the rainforest biota may be longer than the interval between Pleistocene climatic optima. Thus, when the continental rainforests contracted during dry periods of the Pleistocene,

the rainforest biotas may still have been supersaturated at the time when the next wet phase arrived. Species diversity on the major continents may never have a chance to decline to "equilibrium values" and may be chronically supersaturated.

The decreases in species number after habitat fragmentation, and their relaxation times, are of great significance in the worldwide extinction spasm that is now under way. This accelerating extinction wave is due partly to the habitat fragmentation and reduction in habitat area that humans are producing by destroying natural habitats. The habitat fragments thus created start off with their pre-fragmentation species diversity and are gradually losing populations at rates that depend on their area. We have already launched a process that, if it is not miraculously reversed, must result inevitably in a massive extinction wave, even though the wave itself has not yet reached massive proportions. Some economists ignorant of biology question those extinctions that have already occurred, note that massive extinction has not yet occurred, and on this basis belittle predictions of an impending extinction spasm. This reasoning reminds me of the story of the man who fell off the top of the Empire State Building and who had a friend working on the 20th floor. The worker on the 20th floor looked out the window, saw his friend plunging past, and shouted out in concern, "My God, what is happening?" to which the falling man shouted back as he plunged past, "Nothing much is happening, everything is okay so far." As stewards of the world's biota, we have already pushed most of the world's species off the top of the Empire State Building. Those who deny the impending extinction crisis demand to see bodies smeared on the pavement before they will discuss erecting a safety net.

SPECIES DIVERSITY GRADIENTS ALONG ENVIRONMENTAL GRADIENTS

Discussions of species diversity often focus on the famous changes of diversity over environmental gradients, such as habitat gra-

dients, altitudinal gradients, and especially latitudinal gradients. All too often, ecologists seek to identify "the cause" of such a gradient. We should be suspicious of any such attempt. Since species diversity depends on many factors, diversity changes over such gradients are also likely to arise from gradients in multiple controlling variables. What we should seek instead is to provide a quantitative *partitioning* or *accounting* to tell us how the various factors that control species diversity vary along the environmental gradient and to tell how much each of the factors contributes to the species diversity gradient. Even along a given environmental gradient, the accounting will surely differ for different groups of species. For example, the form of the latitudinal gradient for birds is very different from that for salamanders, and these two gradients must be explained by different mixes of contributing factors.

To illustrate how the "QQID" approach provides a checklist of factors that may contribute to species diversity gradients, let us consider two of these famous gradients: the altitudinal gradient and the latitudinal gradient.

Altitudinal gradients in species diversity.

As one ascends from sea level towards the summit of a high mountain, species diversity tends to decrease with elevation, as exemplified in this symposium by the decrease in Andean tree species diversity (Gentry, this volume) and frog species diversity (Duellman, this volume) with altitude. However, this pattern is by no means universal. For example, the diversity of plant species along the western Andean slopes of northern Chile is extremely low at sea level, increases from middle to high elevations, and decreases only from high elevations onwards (Arroyo et al., this volume). In the Mediterranean zone of California the species diversity of birds reaches a maximum at middle elevations (Cody, 1975). How can we account for any one of these gradients, and why does the form of the gradient differ from case to case? Consideration of the QQID checklist suggests at least three important

contributing factors that vary along the altitudinal gradient, one of them involving resource quality, the other two involving resource quantity.

Changes in habitat structural diversity. Habitat physiognomy varies dramatically along an altitudinal gradient. For example, in the moist tropics habitat structural complexity decreases monotonically along the altitudinal gradient, from tropical rainforest at the base through montane forest and then alpine elfin scrub at higher elevations, to alpine grassland and eventually rocky slopes and glaciers at the highest elevations. This continuous decrease in habitat structural complexity and consequently in "number of niches" contributes to the continuous decrease in plant and frog species diversity with elevation in the wet tropics. In the Mediterranean zone, however, scrub formations such as chaparral at sea level yield to forest at higher elevations before finally yielding to alpine habitats on the highest summits, and this intermediate maximum in habitat structural complexity contributes to the intermediate maximum in species diversity.

Productivity gradient. Temperature generally decreases with increasing altitude, while the altitudinal gradient of rainfall (and hence of productivity, which depends both on rainfall and temperature) varies from site to site. In the moist tropics, productivity decreases with elevation, or there may be a slight increase in productivity from sea level up to a gentle maximum at medium-low elevations, followed by a decrease in productivity thereafter. This productivity gradient reinforces the effect of the gradient in habitat structural complexity and also contributes to the decrease in species diversity with altitude in the moist tropics. However, in the Mediterranean zone of California and in the Atacama Desert there is a marked maximum in productivity at middle elevations (owing to the marked maximum in rainfall there), and this contributes to the species diversity maximum at middle elevations.

Area gradient. The distribution of available area with altitude depends on the form

of the mountain. On conical mountains, area decreases continuously with altitude, tending to cause a monotonic decrease in species diversity with altitude. However, Tibet and the Peruvian/Ecuadorean Andes have a more trapezoidal shape, with a broad plateau at high elevations, so that the maximum area may actually be at high elevations rather than at sea level. These area considerations may contribute to the fact that species diversity at high elevations on the Tibetan Plateau and on the Andean Altiplano is much higher than in structurally similar habitats of New Guinea, whose mountains more nearly approximate steep narrow ridges with only tiny areas at high elevations. Quantitative analysis of the altitudinal distribution of area contributes to understanding the relative numbers of montane and lowland bird species on various islands of the Solomon Archipelago (Mayr & Diamond, 1976).

Thus, to account for the altitudinal gradient of species diversity in any particular case, one should at minimum consider that site's altitudinal gradient of habitat structural complexity, productivity, and area. Terborgh (1977) has shown that the quantitative accounting falls out differently for different trophic groups of birds (insectivores, frugivores, and nectarivores) along the altitudinal gradient of the Peruvian Andes. The same three variables—habitat structural complexity, productivity, and area—are also likely to be major contributors to species diversity gradients along horizontal habitat gradients such as the gradients of desert, grassland, scrub, and woodland in the Mediterranean zone, as illustrated by Cody's (1975) analysis.

Latitudinal gradients in species diversity.

No discussion of species diversity would be complete without consideration of the latitudinal gradient. Species diversity of most broadly defined groups of plants and animals is maximal in the tropics and decreases towards the poles. Examples considered in this symposium are the high tropical diversity of plants (Gentry, this volume), beetles (Erwin, this symposium), and frogs (Duellman, this

volume). In the analysis of plant species diversity in northern Chile by Arroyo et al. (this volume), a steep species diversity gradient arising from the rainfall gradient is superimposed on a gentler species diversity gradient associated with latitude itself. However, some plant and animal groups, such as sandpipers and Old World salamanders, do not exhibit a diversity peak in the tropics. Again using the QQID checklist, we can identify at least five factors with major contributions to the latitudinal gradient. Two of these factors involve resource quality, one involves resource quantity, and two involve dynamics.

Habitat structural diversity. Habitat structural diversity tends to decrease from the equator to the poles, the extreme ends of the gradient being equatorial tropical rainforest as contrasted with the polar ice caps. This environmental gradient contributes to the polewards decline in species diversity.

Gradient of resource types. The variety of resources, or of resources available year-round, tends to decrease with latitude. For example, the proportion of insect species with very large bodies decreases polewards, with the result that bird species (e.g., coucals) specializing on very large insects are mainly tropical. Nectar and fruit are available year-round in the tropics but not in the Arctic, contributing to the decrease in diversity of obligately frugivorous and nectarivorous bird species with latitude.

Productivity gradient. Productivity on land tends to decrease with latitude, reinforcing the polewards decline in species diversity. This latitudinal gradient in productivity is less regular in marine environments, because latitudinal effects of temperature changes in productivity are overridden by effects of nutrient upwelling in some high-latitude marine areas.

Disturbance gradient. One reason often proposed for the latitudinal gradient in species diversity is that disturbances on a geological time scale are supposedly more violent and produce more extinctions at high latitudes than at low latitudes. In particular, glaciations have periodically wiped out species diversity

at high latitudes. This argument, if valid, would involve a contribution of species dynamics to the latitudinal gradient of species diversity. In recent years there has been increased appreciation of the historical importance of environmental disturbances in the supposedly stable tropics. The Pleistocene involved alternate wet and dry periods that caused large-scale habitat changes in the tropics. It is nevertheless probably still true that environmental changes over geological times have been more devastating of habitats and more destructive of species diversity at high than at low latitudes.

Gradient in dispersal and speciation rates. Tropical species of birds, and possibly of some other taxa, tend to be much more sedentary than temperate species. Practically all bird species of North America and Europe are known to have crossed water gaps of at least several miles in modern times, while most species of the continental tropics apparently do not cross water gaps (Diamond, 1976; Diamond & Gilpin, 1983). These low dispersal rates in the tropics may have contributed to tropical species diversity by making it possible for formerly conspecific populations to achieve reproductive isolation over shorter distances, and thus by enhancing speciation rates.

Thus, the latitudinal gradient in species diversity involves multiple factors, but these factors are not infinite in number. What is now required is to attempt to partition the contributions of these various factors to latitudinal gradients of species diversity in particular cases.

SUMMARY AND OUTLOOK

We have seen that determinants of species diversity can be grouped into four sets of factors that may be remembered by the mnemonic "QQID": (resource) quality, (resource) quantity, (species) interactions, and dynamics. This is not to say that all four sets of factors are equally important in explaining species diversity of different taxa, or at different sites. For example, an interesting in-

terpretation of neotropical tree diversity within tree guilds dispenses almost entirely with considerations of niche differentiation and segregation by resource utilization, and instead stresses the dynamics of speciation, immigration, and extinction (Hubbell & Foster, 1986). A general explanatory theory of species diversity must ultimately tell us under what sorts of circumstances each factor is likely to be important and what factors contribute to species diversity gradients along various environmental gradients. At present, I doubt there is a single case where we have an adequate accounting that considers all four possible sets of factors for a given group of taxa at a given site. Thus, we shall have to obtain such analyses for many individual cases before we can begin to compare those cases and arrive at generalizations about species diversity. I view the gathering of such accountings as one of the two major tasks for future studies of species diversity.

The other major task is to attempt to convert empirical groupings of factors controlling species diversity, such as the one that I have proposed, to natural hierarchical groups. The QQID grouping is offered just as a convenient empirical checklist; it does not necessarily correspond to any scheme in nature. Must we always content ourselves with such an arbitrary laundry list, or is there any natural organization to the laundry list? I suggest that it may be possible eventually to account for species diversity by a hierarchy of processes in space and in time. The spatial hierarchy would begin or end with an understanding of species diversity at a single point in space, then within a single type of habitat (so-called alpha diversity), then diversity from end to end of a habitat gradient (species turnover along this gradient being termed beta diversity), and finally species diversity over areas large enough to permit geographic replacement (gamma diversity), or over whole biogeographic regions, or over the whole world. A hierarchy in time might begin with the rapid increase in species diversity during recovery

from a storm, then the much slower increase following a glacial period with its attendant fluctuations in sea level, and finally the slow generation of species over geological/evolutionary time scales. In this way, it may eventually be possible to obtain not just a convenient checklist, but a natural explanation for the number of biological children in the world's candy store.

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