plays an essential role in the toxic changes induced by TCDD. We favor this explanation, which is also consistent with reversal of the biochemical disturbance of PCT in man by venesection. In addition, reversal by repeated venesection of cirrhosis apparently caused by hepatocellular iron deposits has been reported (*16*).

These results have far-reaching significance. First, they demonstrate synergism between a normal concentration of dietary iron in laboratory animals and the specific toxin TCDD. Second, the toxic effects of TCDD are not unique to this molecule. Although TCDD may be the most potent of this class of MFO-inducing agents, the difference may only be quantitative; polychlorinated biphenyls demonstrate similar effects, and Poland and Glover have shown (*17*) that polychlorinated and polybrominated biphenyls with halogen atoms in the appropriate positions closely resemble TCDD as inducers of AHH and heme synthesis.

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6. Teklad mouse-rat diet (6 percent fat). The calculated iron content of this diet was 0.013 percent (Teklad Test Diets, Box 4220, Madison, Wis.). We measured the total iron after digestion in nitric acid and found 0.07 percent. The bioavailability of this iron is unknown.
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A Theory of Diversity Equilibrium and Morphological Evolution

Abstract. *If the world can only support a finite amount of biomass, species might be added over time, with a decrease in population size of an average species. Population sizes of species will decrease to the extent that stochastic events eliminate species as fast as others appear, yielding an equilibrium. A resource diversity control of niche subdivision is therefore not needed to generate an equilibrium number of species. Morphological evolution may decelerate over time for similar reasons.*

Several paleontologists have characterized evolutionary diversification as a balance between speciation and extinction rates (*1*). The establishment of an evolutionary equilibrium between speciation and extinction due to area effects has been suggested by some workers (*2*), and the control of resource limitation on the upper limit of species number has been suggested by others (*3*). Both approaches predict an equilibrium number of coexisting species, and Sepkoski (*4*) has developed the mechanics of a logistic model of species addition. Whatever the mechanism, some evidence suggests that taxon richness can remain constant over long periods of geologic history. Taxon equilibria have been suggested for the entire shallow water marine biota as well as for species richness within a single fossil sedimentary basin (*4*, *5*). I here provide a model with a minimal number of assumptions to account for an equilibrium.

Consider an unchanging world in which competitive interactions set no limit on the maximum number of coexisting species. Also assume that regardless of species richness, S, the total number of individuals is limited, simply because the world can hold only so much biomass. If both these assumptions are true, then the species present at any one time have a mean individual species population size, $\bar{P}$, with some undefined distribution about the mean. The more species present, the smaller is the mean population size per species. Under this scheme, resource utilization is mainly established by priority. We can imagine such a case for marine epibenthic invertebrates, where space limits the total number of individuals.

Next assume a rate of diversification for a given taxonomic group that is at first positive and constant. The value of this rate should depend on the adaptive mode, reproductive type, and degree of social organization (*6*). However, a species evolving into a biota that has many species will of necessity attain a probabilistically smaller population size than when few species are present. We cannot predict what population size a specific newly evolved species will attain. Given the above assumptions, there is a critical lower value of $\bar{P}$, $\bar{P}_c$, below which more species will become extinct than appear. With an upper limit to the total number of individuals, the addition of new species will bring $\bar{P}$ below the level that the rarest species are likely to survive random events causing population decline. These events might be disease, invasion of parasites, competitive displacement by neighboring species, or a short-term climatic change that disrupts reproduction. When $\bar{P} > \bar{P}_c$, the addition of species will not have this effect. If species richness is minimal, immigration from outside areas can depress local extinction. There is a corresponding species richness, S_c, which is the equilibrium point. The ratio S/S_c might indicate the factor by which speciation success can be gauged, as suggested by Sepkoski (*4*).

We can imagine an adaptive radiation in the context of this model. When a new taxonomic type appears and as S approaches S_c, the proportional survival of newly proliferated species will decrease as $\bar{P}$ approaches $\bar{P}_c$. Overshoots and oscillations could be imagined, but an evolutionary equilibrium can be attained

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strictly on the basis of every decreasing mean population size with increasing standing diversity. The number of resources need not be invoked as an upper limit to the number of coexisting species. Thus two biogeographically isolated habitats may have the same number of coexisting species. But this is not necessary evidence that the two respective habitats have imposed an upper limit due to resource heterogeneity (for example, foliage diversity of birds). Environmental predictability can be integrated into the model by noting that $\bar{P}_c$ increases with decreasing predictability. Therefore, the equilibrium species richness is less in unpredictable environments.

Morphological evolution in an adaptive radiation can also be explored with this model. As a biota evolves from a single taxonomic stem line, and if the environment is sufficiently predictable, we expect some if not most descendants to be more and more ecologically specialized. Such specialization would inevitably reduce population size or area covered as the required structural habitat or resource is more limited in abundance. Thus morphological proliferation may send a clade on a course toward reduced population size per species. At a certain critical upper bound of mean morphological specialization, $\bar{P}_c$ will be attained. More specialization will not be favored. This consideration predicts that morphological evolution will eventually decelerate, as has been found in previous empirical studies (*7*). In an unpredictable environment, daughter species are likely to be morphologically identical to their parent species, as any increase in specialization will bring $\bar{P}$ below $\bar{P}_c$. It is possible, however, that selection for increased efficiency without reducing niche breadth might permit some types of morphological evolution to proceed without limit.

In a predictable environment, the survival of a more specialized descendant would be more likely simply because $\bar{P}_c$ is less. This prediction conforms to the results of Stehli and colleagues (*8*) who show that the mean longevity of a genus of coral or foraminifera is greater in species-poor than in species-rich environments. What these data are telling us, I think, is that generic overturn, which is an estimate of morphological change, is dampened in unpredictable environments (high latitudes for the case of foraminifera, and cold and variable peripheries of the Pacific coral reef province). Thus, a new foraminiferan species may be generated in high latitudes. But, if it is to survive, the daughter must phenotypically resemble the parent species and not be more specialized.

The model favors stochastic forces as a regulatory mechanism for the upper limit to the number of species. This will be uncomfortable to those, such as myself, who have cherished the idea that interspecific competition and resource diversity alone determine the upper limit. Van Valen's (*9*) fascinating "Red Queen" hypothesis suggests that evolutionary advances by one taxon must cause a concomitant environmental deterioration for another taxon. But it is my contention that most "advances" increase specialization, reduce niche breadth, and thereby increase the probability of extinction during, say, an unfavorable climatic event. I have omitted the problem of habitat heterogeneity by assuming an unchanging world. This is clearly an unacceptable oversimplification as species richness itself generates habitat complexity. The effect of increased species richness is not easy to assess because it generates new habitat complexity (new prey species for example) that might change the taxon-specific rate of morphological evolution. But it also might simply result in increased evolution with an eventual decrease of $\bar{P}$ below $\bar{P}_c$. Some theoretical arguments suggest that the length of food chains may also be limited by population dynamical forces (*10*).

The problem with this model, and all others like it, is that it can be made so general as to be untestable. Boucot (*11*) presents an impressive amount of evidence that taxon longevity of brachiopods is related to geographic coverage. Similar results obtain for fossil Bivalvia (*12*). Sepkoski (*4*) demonstrated a remarkably logistic-type accumulation of orders in the early Paleozoic. But the problem here is whether the number of ordinal level taxa is representative of species richness or is an indicator of morphological diversification. Coexisting epibenthic invertebrates, all requiring the same resource of space, might be an adequate test group. We would expect the fossil record to show accumulation of species to a constant level, regardless of the apparent fact that species continue to coexist on homogeneous surfaces throughout the whole history of the biota, with no major niche subdivision. The value of epibenthic invertebrates is that a lack of structural habitat heterogeneity can at least be imagined within one surface. The work of Jackson and Buss (*13*) on coexistence of cryptic epibenthic organisms on coral reefs can be viewed in the light of this model. The generally recognized relation of number of pest species to area of planted crop may also be manifestation of this equilibrium.

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