Competition Is Important in Plant Extinctions

Plants, need it be said, are different from animals. Not so obvious, however, is the fact that some of the differences in metabolism and interaction with other organisms might be reflected in the pattern of plant evolution and specifically the pattern of extinction.

There is a growing realization that the shape of the history of animal life has been influenced in great measure by occasional mass extinctions. Following such extinctions there typically are rapid radiations of certain surviving groups that often alter dramatically the predominant fauna: the replacement of "the age of reptiles" by "the age of mammals" is of course a striking example.

"The pattern with plants is different," says Andrew Knoll of Harvard. "There is good evidence to suggest that the evolution and subsequent rapid radiation of new plant groups has been the cause of the extinction of other groups, not a consequence of it. Competition, which is often thought of as the classic extinction mechanism, apparently is much more important in plants than in animals." This phenomenon is most evident in the sequence of rhyniophyte, trimerophyte, and progymnosperm radiations early in plant evolutionary history and in the striking domination and almost total replacement of gymnosperms by angiosperms through the late Cretaceous and Early Tertiary periods.

The reason that plants might be particularly susceptible to extinction through competition, suggests Knoll, is that plants, in contrast with animals, are all rather similar in their metabolic and physical needs. They are not particularly differentiated into substantially separate trophic guilds, for instance: there is no equivalent to the hierarchy of primary herbivore through top-level carnivore. Although plants are able to evolve different light tolerances, they have less flexibility to switch food resources in the face of competition.

With all the data-scrutinizing that has gone on over the impact hypothesis for the Cretaceous/Tertiary extinction, it is perhaps surprising that the fate of plants through that period remains in some doubt. It seems likely, however, that the plant world came through the event relatively unscathed, a survival that might be attributed to the persistence of spores, seeds, and underground runners. "Many plants would be able to bounce back after an impact event," says Knoll. Ironically, then, the plant record might prove to be a particularly sensitive indicator of bolide impacts. "In sedimentary sequences with sufficiently detailed time resolution, a sharp extinction spike followed by recovery of plant species might be taken as possible evidence of an impact." Alvarez cites such evidence in association with the Cretaceous extinction.

The sixth annual Spring Systematics Symposium at the Field Museum of Natural History, Chicago, discussed extinctions, 13–14 May 1983.

K/T Asteroid Subducted to Oblivion?

No discussion about extinctions these days is complete without reference to the possibility of meteor impact. In fact, the impact hypothesis has often dominated people's attention, especially relating to the Cretaceous/Tertiary extinction that saw the demise of the dinosaurs. On this occasion Walter Alvarez, one of the principal authors of the modern version of the impact hypothesis, gave a low-key review of current evidence, stressed that meteorite impact does not necessarily imply instant extinction, and bemoaned the way in which "believers" and "nonbelievers" have become so polarized.

It would be extremely convenient if impact craters could be located, dated, and correlated with major extinctions; but life is not so simple. For one thing, there is a two-thirds chance that such an impact would be oceanic and therefore more than troublesome to discover. The basaltic nature of minute spherules associated with the Cretaceous boundary might be taken as evidence for oceanic impact in this case, says Alvarez, who is at the University of California, Berkeley. And there is reason to believe that the impact might have been in a part of the northern Pacific that through seafloor spreading and subduction no longer exists. In spite of the possible inconvenient disappearance of the smoking gun, the Chicago conference was generally warmly receptive to the once heretical notion of rocks falling out of the sky.

Mountain Refuges in United States Southwest

The mountains of the southwestern United States—through Utah, Colorado, Arizona, and New Mexico—share many features of plant and animal life, and yet are isolated from each other by lowlands that are much warmer and drier. This pattern of isolated montane life scattered through a desert and grassland sea is, however, the relatively recent product of the withdrawal of the last glacial period, about 10,000 years ago. The fauna and flora of the mountains today are therefore relicts of a biota that formerly was widespread throughout the southern United States. Bruce Patterson, of the Department of Zoology at the Field Museum in Chicago, has been studying the relictual montane populations of the Southwest in search of patterns of extinction.

As climates warm after glaciation, fauna and flora migrate both latitudinally and altitudinally. Those populations on mountain refuges eventually become vulnerable to extinction as the available habitat shrinks in area. "Montane biotas suffered extinctions of component species in accordance with island biogeographic theory," says Patterson. "Mountain ranges limited in area and habitat diversity support a correspondingly lower diversity of montane species."

Patterson's survey includes data from 28 locations, which vary in area from a few square kilometers to many thousands of square kilometers. As island biogeographic theory predicts, the greater the area available, the more species are accommodated, a relation that among other things reflects higher potential habitat diversity in larger areas. For the mammals that Patterson is particularly interested in, some of the smallest ranges had no species populations, while the largest had more than 20.

The pattern of extinction from the smaller ranges is also a nonrandom process: species with small populations are the most vulnerable to extinction. As population size—or density as it translates to in this instance—is determined by factors such as body size, trophic level, and habitat specialization, there is a selective loss of species during this process. Animals that have large bodies, are high in the food web, and have specialized habitat requirements are most susceptible to extinction as available territory shrinks. This selective aspect of the process is clearly an important element of extinction patterns.

Patterson points out that as many—perhaps most—populations of species are isolated from each other, even if incompletely, the lessons learned from montane populations are widely applicable. It is not yet clear, however, how much the degree of variability in population size might contribute to vulnerability to extinction. A small but stable population might fare better than a larger one that undergoes wide fluctuations.

Studying Humans as Animals

"Species centrism" is often so strong that paleoanthropologists tend to scrutinize events in human prehistory in isolation from changes in the rest of the living world. Alan Walker of Johns Hopkins University suggests that speciation and extinction in hominid evolution might better be viewed in parallel with shifts among contemporary herbivores and carnivores. A useful pattern emerges, he says.

Although there are many variants of interpretation, the basic course of human evolution is seen as follows. Before 2 million years ago the ancestor to the hominid lineage was some form of herbivorous *Australopithecus*. About that time a larger hominid species arose, *Homo habilis*, which was a scavenging, part-time carnivore. This short-lived species was replaced 1.6 million years ago by a larger hominid, *Homo erectus*, that appears to have been an active predator.

In addition to these events, Walker notes that a small *Australopithecus* became extinct about 1.6 million years ago while a larger form, *Australopithecus robustus*, persisted until 1 million years ago. Walker's approach was to look in the major herbivore and carnivore guilds for evolutionary changes that might shed some light on human prehistory.

Before 2 million years ago there were four species of stalking hunters (three saber-toothed tigers and one lionlike felid), one cursorial hunter (the running hyena), and one scavenger (*Hyaena hyaena*) in East Africa. Between 2 million and 1.6 million years ago, which was the time at which *Homo habilis* (a scavenger) arose, three more carnivores appeared. These were the leopard (a stalking hunter), the cheetah (a running hunter), and the spotted hyena (a scavenger). "Just the increase in scavenging species alone suggests there were more carcasses available," says Walker. Paleoecological data indicate a wetter climate that is consistent with a doubling of today's large herbivore biomass.

About 1.6 million years ago climates became drier again, which reduced the large herbivore biomass. The loss of the small *Australopithecus* at this time might be correlated with this climatic change, as too might the disappearance of *Homo habilis*, a scavenger. *Homo erectus*, a stalking hunter, appeared at this point and was part of a changeover in the hunting carnivore guild, which continued with seven species. The modern carnivore guild became established about 1 million years ago, which coincides with the extinction of the large *Australopithecus*. "It is unwise to speculate exactly what caused this extinction."

In addition to placing in a more general context the major changes in human evolution up to a million years ago, Walker also notes that the shift into the stalking hunter guild of *Homo erectus* might explain an important event in human prehistory: the migration of the first hominids from Africa into the rest of the Old World. For energetic reasons, large carnivores constitute only about 1 percent of the available large herbivore biomass. "In moving from the herbivorous trophic level to the higher carnivorous one, the population of the species must be reduced. . . . At the same time, the newly carnivorous species would now be able to extend its total range for, whereas a herbivore is limited to the plants (and water) to which its physiology is adapted, a carnivorous species is not so limited."

This argument explains the very large ranges in historic times of the lion and the cheetah, says Walker. "It is also my explanation of why *Homo erectus* was the first hominid species to migrate from Africa."

Old and New Extinctions Seen in Bird Data

Birds, particularly island populations, are popular subjects of ecological inquiry and have provided data on extinction in both the short and long term. Jared Diamond of the University of California at Los Angeles sees common threads throughout.

Studies on year-by-year species turnover on islands, for instance, highlight population size as the main predictor of extinction: the smaller the population, the more likely it is to become extinct. Additional factors play their part, however. Small songbirds, which tend to be short-lived, are particularly prone to extinction. And species whose populations fluctuate widely are also more than usually vulnerable. Certain birds, such as wrens, stonechats, and song thrushes, which are susceptible to harsh winters, might suffer a population crash no matter how large the population is. A fourth factor that enhances extinction proneness is loose breeding groups: small populations of birds with this type of breeding pattern are particularly susceptible. Carnivorous birds are twice as extinction-prone as the average bird species.

These inferences translate to the longer term instances of habitat fragmentation: in the postglacial isolation of islands such as Tasmania and New Guinea, for instance. And by teasing out predictions based on island size and isolation, it is possible to look at patterns in the much longer term.

The development of endemic species through evolutionary time would depend on low extinction rates, notes Diamond. And where low extinction would be predicted, such as on large isolated island archipelagoes, the percentage of endemism should be highest. Hawaii, the Galápagos Islands, and New Zealand fall into this grouping, whereas the New Hebrides, the Bismarcks, and Papau, all of which cling close to continental mainland, have low endemism.

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