Blurry Catastrophes

D. H. Janzen

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Extinction events range from those that remove a single population from a local habitat to those megacatastrophes that obliterate tens of thousands of species over continents or oceans. When considering megacatastrophes, and especially whether a particular fossil chronology documents one of the latter, catastrophes are generally viewed as short-term events with short-term direct consequences: the catastrophe occurs, species go extinct, and ambient conditions rapidly return to "normal" (after which the survivors spread, multiply, re-radiate, etc.). However, the pre-catastrophe presence of widespread species may blur our perception of a catastrophic event, since their resultant extinctions may occur hundreds to thousands of years after the event. Such a paleoscenario is relevant to the contemporary scene in tropical conservation biology; we are currently being deceived by the same blurry perception.

The world contains many local species that occupy small habitats and many widespread species that occupy both these small habitats and large (and often many) habitats. When an abrupt perturbation occurs over a large geographic area (e.g., meteorological changes following a major meteor impact), a substantially greater proportion of the local species than the widespread species will be extinguished. This is because the widespread species occupy many habitat areas and types; there is a chance that at least a few of these habitats will have conditions that ameliorate or even avoid the direct influence of the catastrophic event. The greater the proportion of the species that are widespread within the area of influence of a megacatastrophe, the more blurry will be the overall outcome.

However, the presence of widespread species blurs the outcome of a megacatastrophe in another and less obvious way. When ambient conditions have returned to normal, the surviving fragments of the formerly widespread species do not necessarily rapidly spread and coalesce to reoccupy their former distribution. There are at least two reasons. First, a widespread species may well have taken thousands of years or generations to come to occupy its widespread distribution, often by opportunistic crossing of barriers during rare events. The catastrophe abruptly reduces it to fragments that are again separated by barriers that again will take a very long time to cross. Second, through the catastrophic elimination or allospecific replacement of biotic interactants in the habitats to reoccupy, novel biotic barriers will be erected in the path of range re-expansion by the once widespread species. The intensity of effect of both of these processes depends on the detailed biology of the species. There will be some life-forms that will be more subject to one process than to the other; immunity to both processes may well be one of the important traits for professional survivors of catastrophes.

While a megacatastrophe may not immediately extinguish a widespread species, it may reduce it to, and hold it in, a fragmented geographic status whereby it is more prone to extinction through lesser catastrophes (operating asynchronously on its fragments) and through the process of speciation (through rapid evolution, founder effects, drift, etc. in the small fragments). For example, species that are slow to reoccupy former wide ranges following semi-obliteration and fragmentation may be especially likely to generate new species over time and therefore appear to be particularly susceptible to catastrophes and evolutionarily labile.

The consequences of longterm fragmentation of widespread species for the record of extinctions per unit time in a geological record is that all the extinctions attributable to a catastrophe do not occur at the moment of the catastrophe. There is a lag period that may be substantial in years or generations, with its length depending on the biology of the species and on the thoroughness with which the biotic interactants between species' fragments have been obliterated.

Megacatastrophes range in duration of direct ambient change from a meteor impact to longterm climatic changes. The longer the duration of the change, the longer the fragments of the once widespread species are held in their fragmented state by the inhospitable matrix. That is to say, the longer the duration of the change, the greater the chance that the fragments of a once widespread species will be extinguished by subsequent smaller and more local catastrophes, catastrophes of a magnitude that would hardly have been noticed in

the ecological and evolutionary history of the species in its widespread state. And the longer the duration of the catastrophe, the longer will continue the extinctions of once widespread species that were made extinction-prone by the catastrophe.

A glance at the modern tropical world with the above paleoscenario in mind does not lead to optimism about the future of tropical wildlands. With respect to the local species mentioned earlier, the catastrophic effects of contemporary agriculturization of tropical habitats are so obvious as to hardly need mention. When a local wildland habitat is converted to a sugarcane field, *Eucalyptus* plantation or polyculture vegetable garden, its occupants are extinguished. Some consequences of agriculturization are more gradual and simulate a catastrophe of longer duration. Regional weather changes. These changes appear to simulate natural weather changes but their effects is very different from the natural case. Local species often survive a natural catastrophe of long duration by virtue of their habitat being pushed into a neighboring area, or by having their habitat expand as conditions change. Neither event occurs if the original local habitat is surrounded by agricultural lands, habitats that are maximally hostile biological deserts and oceans. A mountain-top species cannot drift down the mountain as upper elevations cool, since the lower mountain slopes are covered with pastures, fields and orchards. An increase in rainfall does not result in biologically meaningful stream capture if all streams but a few are conduits for agrochemicals or rich in introduced predaceous fish such as trout. That is to say, tropical agricultural habitats are much more hostile (and remain that way as crop types change with gradual climate change) than is almost any kind of natural adjacent habitat.

Tropical agriculturization is also setting up widespread species for extinction, but by a somewhat different process. It has been argued that many (widespread) tropical species are not endangered because they still do in fact grow (live) in many different geographic areas and habitats over many degrees of latitude. For example, the lowland Neotropics from Mexico to Colombia and Venezuela is rich in such species. However, while their distribution maps may be large, almost all of such species have been converted to isolated fragments in hostile agroecosystem matrices. They are now extremely prone to a widespread catastrophic event. Like a nuclear winter. Like a meteor impact. Like El Niño. It is well understood that the small fragments (of once widespread species) in national parks and other kinds of preserves are highly susceptible to local extinction; what seems to be forgotten is that with their cumulative local extinctions arrives the extinction of the species as a whole. Just as each tropical country seems bound to reinvent its neighbors' wheels, it is also extinguishing its own fragments of what were once widespread species. Local or endemic species status is a tragically incomplete criterion for inclusion on an endangered species list. We are constructing a blurry catastrophe, with the blur being 1–3 human generations in length.

When a species breaks, the fragments are often smaller than are breeding populations. Agriculturization is a major perpetuator of such microfragmentation. In addition to the breeding fragments of widespread species that are scattered through the Neotropics in preserves (and preserves-to-be), there are also a large number of individuals of many species (especially perennial plants) that have long ago ceased being ecologically (and evolutionarily) reproductive; they flower but set no seed, or if they set seed, the seedlings never lead to recruitment of adults. These are the living dead. They are just as dead as if they were rotting in the litter. They are extremely important in blurring our perception of modern catastrophes. Such individuals give the illusion of persistent species in habitats where in fact the species is already extinct. The animal breeding populations that survive by feeding on the living dead plants are also living dead species, waiting briefly for their certain contemporary demise; their gradual extinction likewise increases the blur of the catastrophe.

In much of the Neotropics, what we call endangered is for the most part already extinct. What we call secure, in a preserve or elsewhere unthreatened by direct chainsaws, is what is endangered. Our gift to our grandchildren will be a coterie of professional survivors of catastrophes, and this coterie will not be species-rich. As presently conducted, the biology of agriculturization is largely hostile to tropical wildland habitats and their species. Intense social compensation is mandatory if that hostility is to be countered.

D. H. Janzen, Dept of Biology, Univ. of Pennsylvania, Philadelphia, PA 19104, USA.