Recovery as a function of community structure

VALENTIN A. KRASSILOV

Palaeontological Institute, 123 Profsojusnaya, Moscow 117647, Russia

Abstract: According to the climax cut-off model, ecological succession can be truncated at an early stage by environmental factors thus causing elimination of climax species and their replacement by new dominants derived from successional species. Such profound restructurings are caused by prolonged stresses rather than by episodic impacts. Recovery of a dominant group is due to its representatives in the early stages of 'mixed' successions. In the 'graded' successions with the serial and climax species belonging to different evolutionary grades (e.g. dinosaurs and mammals in the terminal Cretaceous communities) such recoveries are less probable.

Recovery as an integral concept means a regaining of numbers, ranges, dominance and/or diversity after a temporal reduction of some or all of these parameters and applies to populations, species, higher taxa and communities. On the other hand, recovery as an analytical concept treats them differentially as separate kinds of recovery with their own causality.

Incidentally, population recovery is a part and parcel of the crash–founder–flush cycle (Carson 1975). The founder effect is in fact a recovery with change leading to punctuated speciation (Eldredge & Gould 1972), though recent genetic studies cast some doubt on the validity of the founder–flush speciation model (Galiama *et al.* 1993).

Recovery is likewise a normal issue of perpetually ongoing successional processes in biotic communities. Not only natural disasters such as hurricane or fire but also the fall of a large tree can set out ecological succession starting with population growth in pioneer species – their recovery after a reduction in the period of relative ecological stability – and leading, through a sequence of several species, to the recovery of dominant climax species.

Yet the question is to what extent these short-term events can be used as a model of the geological scale processes deduceable from the fossil record, such as near extinction and reappearance of species and higher taxa.

Climax cut-off model

The evolutionary significance of ecological succession is underscored in the climax cut-off model (Krassilov 1992a, b) which maintains that under environmental stresses a succession can be halted at an early stage, never reaching the potential climax. In effect, recovery of the climax species is postponed and, in the long sustained disclimax situations, would never occur. Major ecological crises truncate successions over a wide range of terrestrial and marine habitats, thus leading the climax species to extinction (this would explain mass extinctions of the fossil record which are simultaneous disappearances of apparently unrelated dominant species and higher taxa in a number of different environments). With stabilization a new climax phase is formed by derivatives of polymorphic successional species which experience speciation bursts in the process.

For instance, rudist bivalves evolved as the climax stage dominants of Cretaceous reefal communities starting with bryozoans (Kauffman 1974). The end-Cretaceous extinction of rudists and the simultaneous rise of bryozoans may evidence a climax cut-off event.

The climax cut-off model predicts that even mild long-duration impacts would produce larger and less recoverable changes than occasional short-term catastrophes. Moreover, their effects would be qualitatively different: episodic stresses endanger rare species while prolonged stresses induce replacement of dominant species. Incidentally, glaciations in Europe caused periodic reduction of beech forests followed by their rapid range recoveries while some exotic elements, such as *Cathaya*, presently a far-eastern conifer, were shed in the process. In contrast, the non-glaciated areas, such as southern Primorye in the Russian Far East, have preserved a number of Arcto-Tertiary relics, yet the beech forests, a dominant plant formation in the Miocene, perished with the steady lowering of winter temperatures (Krassilov & Alexeyenko 1977).

An additional feature of the model is that,

insofar as phylogenetically ancient plants and animals may survive a˄ pioneers of biotic communities dominated by phylogenetically younger groups, cut-off of the latter would bring them to the fore. Their rapid increase would then appear as recovery. For example. *Selaginella*, phylogenetically the most ancient extant genus appearing in the Carboniferous as a common herbaceous plant, was rare through the Mesosoic and Tertiary, but then emerged as a dominant in the stunted Pleistocene tundra–steppe communities.

There was mass extinction in the dominant Mesozoic gymnosperm groups, cycadophytes, ginkgophytes and czekanowskialeans in the mid-Cretaceous. Some of them survived, however, as accessory components of riparian and delta plain marsh communities. Characteristically, they became more prominent again in the terminal Cretaceous just before the great floristic turnover at the K–T boundary. *Czekanowskia* was found, after a long period of non-occurrence, in the uppermost dinosaur bed of the Amur Basin. In the K–T boundary tuff assemblage of the Augustovka River Section in western Sakhalin there are two cycadophyte genera, *Pterophyllum* and *Cycadites*, giving it a definitely Mesozoic aspect (Krassilov 1979) while *Encephalartites* is common in the Maastrichtian dinosaur beds of Chukotsk Region in the northeast (Krassilov *et al.* 1990). Such recoveries of the long-surviving relics usually presage a major ecological crisis.

Recoveries in mixed and graded communities

As for the dominant taxa, their recoveries seem to depend on their ecological roles as the climax or successional components or both. Schematically, there are two kinds of successions: the 'mixed' and the 'graded', differing in the distribution of major taxa among the stages.

In the mixed successions, a dominant taxon participates in all or most stages. For instance, in broadleaf forests dicotyledonous angiosperms occur as both successional and climax trees, e.g. hazel and lime. In the heavily polluted environments lime recovery is hampered but dicotyledons as a taxon are not endangered.

It can be different in the plant communities where early successional species are predominantly monocots, as in the forest–steppe ecotonal zone, or even ferns, as in *Nothofagus* rain forests. Such successions are graded in the sense that successional and climax species belong in different evolutionary grades. Here the climax cut-off would endanger the dominant higher taxon as a whole.

The fossil examples are all interpretations, but they seem plausible at least in the cases of the mid-Cretaceous cycadophyte and the end-Cretaceous lowland redwood extinctions. The Mesozoic cycadophyte-dominated communities have their closest extant analogue in the *Encephalartos* shrub savanna where the upper storey is formed by a phylogenetically primitive cycad grade while advanced monocots prevail in the lower storey. The Early Cretaceous angiosperms were small shrubs or herbs of cycadophyte shrublands which turned into angiosperm shrublands following the cut-off of the dominant cycadophyte species.

The late Cretaceous lowland evergreen redwoods dominated by *Sequoia reichenbaechii*, *Cupressinocladus cretaceous* and related conifer species were likewise graded, with angiosperms, notably small-leaved *Trochodendroides*, as successional shrubs or low trees. After the K–T climax cut-off they disappeared as a major lowland plant formation surviving in the scattered upslope refugia alone. At the same time *Trochodendroides* emerged as a dominant tree of the newly formed flood plain deciduous hardwood forests. The Palaeocene *Trochodendroides* species show exceptionally high polymorphism of their leaf and fructification characters far exceeding the range of variation in the earlier Cretaceous and the later Eocene species. They were used as an example of cyclic speciation (Krassilov 1989, 1992*a, b*) in which marcropolymorphism results from a decrease of selection pressure and release of latent genetic potentials in disclimax ecosystems, the macropolymorphic populations serving then as a source of subsequent bursts of adaptive radiation.

Dinosaur recoveries after the Jurassic–Cretaceous and mid-Cretaceous extinctions and the K–T non-recovery extinction could also be related to the mixed v. graded community structures. Each of these events correlates with a certain vegetational change, i.e. (1) reduction of fern marshes at the Jurassic–Cretaceous boundary followed by their partial recovery; (2) replacement of the macrophyllous cycadophyte shrub communities by the microphyllous early angiosperm shrubs resulting in a considerable foliage mass reduction; and (3) spread of the low capacity deciduous forests at the expense of the more resilient plant communities (Krassilov 1981).

However, in the recovery cases, dinosaur communities might have been of mixed type with, for example, smaller protoceratopsians and related groups as putative pioneer forms, while in the terminal Cretaceous non-recovery case, graded types prevailed, with dinosaurs as

the climax dominants and mammals as the pioneer-successional forms (locally also as the climax codominants which perished with dinosaurs).

Giants recovery

Admittedly a much more detailed palaeoecological analysis is needed to overcome a plain schematism of the above reasoning. A further problem related to the dinosaur story is the recovery of gigantism among phytophagous vertebrates. It was repeatedly suggested that dinosaurs were poisoned with angiosperm metabolite chemicals. In that they survived in the angiosperm-dominated surroundings for at least 30 Ma, poisoning is not feasible as a cause of extinction.

There is, however, another little-explored aspect to herbivore intoxication. It was suggested (Bryant *et al.* 1991) that satiation marks a threshold beyond which further eating is dangerous because of excessive accumulation of unpalatable matter. Satiation is, thus, a meeting point of the plant–animal coevolution.

Since larger animals need more food, they have to be tolerant of a larger dose of intoxication. Their potential size would increase with tolerance to habitual plant secondary metabolites and decrease with new ones. It follows that any vegetational change in the succession of diplodocian–indricotherian–elephantid life forms relates to the mutual physiological adjustments of plants and plant-eaters.

References

BRYANT, J. P., PROVENZA, F. D., PASTOR, J., REICHARDT, P. B. & CLAUSEN, T. P. 1991. Interaction between woody plants and browsing mammals mediated by secondary metabolites. *Ann. Rev. Ecol. Syst.*, **22**, 431–446.

CARSON, H. L. 1975. The genetics of speciation at the diploid level. *American Naturalist*, **109**, 83–92.

ELDREDGE, N. & GOULD, S. I. 1972. Punctuated equilibria: an alternative to phyletic gradualism. *In:* SCHOPF, T. M. (ed.) *Models in Paleobiology.* San Francisco, 82–115.

GALIAMA, A., MOGA, A. & AYALA, F. J. 1993. Founder–flush speciation in *Drosophila pseudoobscura* – a large-scale experiment. *Evolution*, **47**, 432–444.

KAUFFMAN, E. G. 1974. Cretaceous assemblages, communities and associations, western interior United States and Caribbean Islands. *Sedimenta*, **4**, 1–27.

KRASSILOV, V. A. 1979. *Cretaceous flora of Sachalin.* Moscow [in Russian].

———— 1981. Changes of Mesozoic vegetation and the extinction of dinosaurs. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **34**, 207–224.

———— 1989. Vavilov's species concept and the evolution of variation. *Evolutionary Theory*, **9**, 37–44.

———— 1992a. Ecosystem theory of evolution. *Rivista Biologia*, **85**, 243–245.

———— 1992b. [*Nature protection: principles, problems and priorities.*] Institute for Natural Conservation, Moscow [in Russian].

———— & ALEXEYENKO, T. M. 1977. succession of plant assemblages in the Palaeogene and Neogene of southern Primorye. *In:* KRASSILOV, V. A. (ed.) *Palaeobotany in the Far East.* Far-Eastern Scientific Centre, Vladivostok, 7–17.

———— GOLOVENEVA, L. B. & NESSOV, L. A. 1990. Cycadophyte from the Late Cretaceous dinosaur locality in northern Koryakia. *In:* KRASSILOV, V. A. (ed.) [*Continental Cretaceous of USSR.*] Academy of Sciences, Far-East Branch, Vladivostok, 213–215 [in Russian].