

PATIO LUDENS AND EXTINCTION OF PLANTS

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ABSTRACT. The not infrequent occurrence of non-adaptive characters in plants (many of which are of taxonomic value), is discussed under the concept of 'patio ludens'. Several examples of patio ludens characters and structures, with particular reference to the tropics, are reviewed and their possible significance to a plant in a changed environment considered. Comparisons in the animal kingdom are drawn. The possibility that patio ludens characters, structural and ecological, might have played a role in the extinction of plants is considered but rejected.

In 1969 I discussed and have since then adhered to the idea that form-making and evolution in plants naturally evolved within the bounds of survival, including fitness to the animate and inanimate environment. All such characters, structural, physiological, ecological, karyological, etc. are compulsory for the survival of plants under their environment.

For the complex of these compulsory characters, which are sometimes called adaptive characters, I have introduced the term *survival level*, which caps this complex.

In testing those characters by which we judge affinity and deduce phylogenetic derivation on their compulsory presence for survival value, I have come to the conclusion that many of them, often of highly important systematic value, fall beyond this survival level and are *non-adaptive*.

This induced me to stress that the origin of the non-adaptive characters has not evolved through the action of selection and adaptation as the all-mighty forces in bringing about evolution in the (neo-)Darwinian sense.

I then tried to show that, especially in tropical and para-tropical zones (which through the ages have had the most tolerant and persistently undisturbed environmental conditions and through this been the scene of the big evolutionary form-development of the Angiosperms and possibly other phyla as well), plants have produced many non-adaptive structures. That is, structures in the free space—*patio ludens*—above the strict survival level (see van Steenis, 1977).

These characters involve many structures which the systematist uses for phylogenetic derivation, such as habit, number of flower parts, stipules, ovary and embryo structures, and even anatomical features (see Baas, 1976).

In 1977 I further elaborated this theory and came to the conclusion that in animals survival level lies at a much higher level than in plants. The more specializations are embodied (or incorporated) in the required survival character-complex the narrower or smaller becomes patio ludens. The raising of the survival level could even lead to the disappearance of patio ludens, in other words to a situation without possibility for admitting non-adaptive characters, and, hence, loss of potentiality for further variability (diversity), at which stage there would be no 'reserve' of potential patio ludens characters.

Before going further, I should insert here, for elucidation, a few words on

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adaptive and non-adaptive characters. I should begin to say that judgement should start (as in all scientific interpretation) from an objective point of view, and not from a sort of unfounded, almost superstitious pre-assumption that all structures in animate matter are *per se* adaptive. This does not mean, as Carlquist obviously says (at least *in litt.*), the acceptance of a 'null-hypothesis', by which he tries to create a sort of proof-load on the un-biased approach; absence of prejudice can, I feel, not be equated with a hypothesis. Naturally, the proof-load lies on those who accept a positive hypothetical adaptation value.

The situation is, as Bateson long ago (1894, p. 11) critically remarked, that we have no right to consider the utility of a structure *demonstrated* and must never use the utility of a structure as departure in considering the manner of its origin. And, furthermore, that (*l.c.* p. 79): "in examining cases of variation, I have not thought it necessary to speculate on their usefulness or harmfulness; such speculation is (usually) barren and profitless. If anyone is curious on these questions, he may easily exercise his imagination . . . In this class of speculation the only limitations are those of the ingenuity of the author."

From the earliest stages of mankind onward, man is used to judging his environment, both inanimate and still more so animate, in terms of usefulness and competition. This has become innate in the mind of man, but in strict science the approach should not be of this kind. It reminds me of the answer which Davy gave when demonstrating the primordium of the miner's safety lamp when a lady visitor asked him what would be the use of it, to which he is said to have replied: what is the use of a baby?

As Bateson stated, an ecologist wants to explain any structure, and such hypotheses, depending on his ingenuity, can always be given. Just one example of how light-heartedly such assumptions are sometimes proposed without checking facts. Venation patterns have been subject to eco-physiological assumptions: free venation would be adapted to humid conditions, whilst anastomosing (reticulate) venation was assumed to give better water distribution in leaf tissues and, hence, better resistance against water-stress. One would then suppose that the first type would prevail under ever-wet conditions and the latter to a better stand against water-stress in more arid conditions. However, I am told by Dr K. U. Kramer that the predominantly epiphytic polypodioid ferns, which are common in ever-wet tropical rain-forests, have generally anastomosing nerves and the davalloid ones in the same humid environment possess open venation; furthermore, the largely xerophytic gymnogrammoid ferns have mostly free venation; in *Adiantum* the reticulate-veined species are nearly all inhabitants of the rain-forest floor. Fortunately, in this case, the water-stress utility assumption can be shown to be the whim of a pre-occupied mind.

Another instance is the occurrence of a xeromorphic leaf structure which is generally assumed to be characteristic of plants of arid countries. This is truly admitted to occur in a general way (though there are marked exceptions), but I may stress that xeromorphic leaves are also very common among trees of the rain-forest under ever-wet conditions.

Patio ludens characters are of several kinds, structural and ecological. Probably they originated more commonly in more simple organisms and comparatively less frequently in more highly organized ones.

They have no absolute patio ludens nature, as such characters have that nature only under the environment where they emerged.

With changing environmental conditions they may come 'handy' under new conditions, which means that they may be then submerged under the survival level and become secondarily incorporated as an integral part of the character complex compulsory for the necessary equipment to survive.

Such change of environmental conditions may happen in their own range or, what can happen equally likely and frequently, they are confronted with new ecological conditions through extending their area by dispersal, whether forced or not to migrate.

An example in question may be the family Casuarinaceae, on which Dr Barlow (1959) has made intensive studies. The most primitive of the two sections (or subgenera or genera) is *Gymnostoma* which ranges in an east-west direction through Malesia, and is represented by some 15 species, from the Malay Peninsula eastwards through the archipelago (Java and the Lesser Sunda Islands excepted) to the Solomon Islands and New Caledonia. Though its morphology is similar to that of *Casuarina* (assimilation by the twigs, stomata in grooves, leaves reduced to scales), it forms part of the tropical mixed primary rain-forest on various kinds of soils (clay, peat, sand, depending on the species) under ever-wet conditions; certain species may tend to act as pioneers on landslips. Ecologically, the assimilation system and extreme leaf reduction is a patio ludens character without relation to selection pressure or survival.

However, if natural dispersal afforded *Gymnostoma* the opportunity to invade arid country, the patio ludens structure might facilitate this by becoming part of the compulsory adaptive complex below survival value. Presumably, this would be infinitely more easy by its pre-existing patio ludens structure which could be used under the new arid environmental conditions as a now useful, originally purposeless, aspect facilitating the extension of the range into the new environment. For genera without such pre-existing patio ludens structure as, for example, herbaceous-leaved genera as *Saurauia*, *Medinilla*, etc., invasion of arid environments would be infinitely more difficult.

I also want to call attention to the phyllodinous *Acacia confusa* Merr. which is a (smallish) tree confined to the ever-wet rain-forests of Formosa and Luzon. Though this has no relation to the Australian phyllodinous *Acacias*, and its possession of phyllodes must be regarded as a token of parallel development, it is in the genus *Acacia* in the tropical rain-forest a patio ludens character to be phyllodinous. It could not have been induced by the environment as an adaptive character, such as (possibly) is the case, as argued by ecologists, in arid countries of Australia and elsewhere.

I would like to add that plants living in certain biocoenoses may have concealed potentialities which remain unobserved. In the Malesian rain-forest *Schima* and *Gordonia* (Theaceae)—which are normal constituents of the canopy of the big trees in the high forest in which they regenerate perfectly well—show under disturbed conditions that they can perfectly well flower and fruit in two years from the seedling stage and could easily form part of other types of biocoenoses.

We could then conclude that patio ludens characters might be profitable for plants to live longer by providing them with escape possibilities. The

higher the survival level, the less *patio ludens* characters there can be, leading to more exacting, that is more vulnerable, organisms.

This would then also be reflected in geological time: simple organisms with low survival level and with more potentialities for *patio ludens* characters, hence higher diversity, would maintain themselves longer than more specialized ones with high survival levels and higher degrees of specialization.

In general, this would mean that plant taxa, with their less complicated structure as compared with animals, would have the longer life span. As far as we can trust palaeontological data this seems indeed to be the case.

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After this introduction to my ideas I come to the proper theme of this essay: can the application of the *patio ludens* principle lead to a better understanding of extinction, of species, genera, families, etc.?

For this matter, the test obviously lies with palaeontology. Here we come onto dangerous ground and must be very careful indeed, as there is often not sufficient evidence to judge to what degree fossil groups were specialized against anorganic factors of the environment (climate, substrate), against internal factors (resistance against disease, reproduction quality), and external organic factors (predation, competition).

Apart from this is the inadequacy of the fossil record, probably more so in botany than in zoology; a serious obstacle in measuring the ages of groups. To give a wholly fictitious example: if it would appear that there was an unrecognized missing link showing that Cordaitales and Angiosperms were two parts of a single lineage, our present estimate of both groups would have to be seriously revised. It would make, though, no essential difference, because it would not add information on the origin of Cordaitales, nor to the reason for the complete extinction of the many dead-ends of the Cordaitalian branch, which in fact holds true for all dead-ends of the ancestral tree.

The most appropriate approach is, of course, to make the test in a fairly 'permanent' environment, e.g. shallow coastal seas. I call this a 'permanent environment' because it cannot be expected that there has ever been an agency which could have affected this environment in any geological epoch on a world-wide scale. There have been transgressions and regressions which may have caused fluctuations in the dimension of its surface. Pollution of coastal waters by silting or poisonous minerals freed by erosion (copper, zinc, oil, etc.) or disturbances of a geological nature can only have had a local influence. Climatic changes too, even world-wide, cannot have caused a dramatic extermination of this habitat. A glacial epoch has made, of course, an enormous change in the habitat at higher latitudes, and more or less telescoped the lower latitudinal zones, but it should be borne in mind that such climatic changes develop very gradually in a secular way which gives the organisms plenty of time for migration towards ameliorated habitats comparable with their usual environment.

In the coastal habitat we find still Protozoa, Sponges, Coelenterata, Radiolaria, Sea-cucumbers, etc. existing from the Palaeozoic. Both Prokaryotes (bacteria, blue-greens) and Eukaryotes (algae, diatoms, fungi) have also persisted from the Palaeozoic (and some of them are still older) to the present.

But there are also whole phyla which become extinct very early, e.g. Graptolites and Trilobites. And even if these had developed into other phyla with unknown missing links, the same problem would arise as with the Cordaitales: how they arose and why have some representatives of these groups not continued to exist.

Desiccation of continents, which has taken place a few times on a cosmic scale, has sometimes been advanced as a reason for the extinction of large groups of organisms and even of phyla. The geologically rather recent desiccation of Australia has indeed had a most destructive effect. A genus like *Nothofagus* which had a dominant role in the mixed forest of the greater part of Australia since the Cretaceous, has now almost disappeared from that continent. A similar, but not completely destructive, effect is observed in the earlier desiccation of the drought area from Asia Minor to Mongolia, and even the recent one of the Sahara.

Though certain taxa with very restricted ranges fell victim and became extinct, the higher taxa had generally such large ranges that during the very slow, secular deterioration of the climate they could adapt by producing drought-resistant forms. In addition, it should be remembered that even in such large areas, desiccation was never universal and this allowed the persistence of local refugia.

For world-wide changes in the distribution of land, under the current theory of continental displacement, a similar argument can be given, as this has been an extremely slow, secular process giving ample opportunity for migration to organisms to keep up with their environment.

I conclude that, in spite of regional shifts of climatic conditions, the tropics and para-tropics were a persistent environment for vegetation and plants, probably more permanent than any other.

Nevertheless, extinction, partial or complete, has been the order of the day, as appears in making world distribution maps of plant taxa in the tropics. The *Nypa* palm, a tropical coastal brackish water genus, consisting of one species (and scarcely more in the past) was present in the Upper Cretaceous in tropical America (as proved by pollen), and west tropical Africa where it is now extinct. It now only survives in the Indian Ocean area and Malesia where it is widely distributed and occurs mostly gregariously. An inland, lowland tropical genus of trees, such as *Ctenolophon* (Linaceae), had a similar distribution, but survived in West Africa. There are many examples of Old World genera showing a disjunction between Indo-Malesia and tropical Africa, such as *Taeniophyllum* (Orchidaceae), *Argostemma* (Rubiaceae), *Rinorea* (Violaceae), and *Ctenolophon* (Linaceae) as mentioned above, etc. This disjunction can easily be ascribed to the development of aridity in the intervening area. However, why *Nypa* and *Ctenolophon* are extinct in the Neotropics remains an essential problem.

One factor is left unconsidered, viz. the origin of contagious aggressive bacteria or viruses which other organisms are not capable of withstanding because of an inability to produce antibodies and thus can be exterminated. However, experience with living plants shows, in general, that in matters of predation, competition and parasitism, organisms generally have an escape 'clause' in that there are always individuals which escape destruction in possessing qualities of resistance—as is the case against poisonous chemical substances. The only result normally is that the population survives, be it in

fragmented form and/or at a very much lower population-density in a devastated range. I know of no instance where an organism has completely vanished through such agencies.

After having thus scanned a number of possible reasons for extinction, it appears unfortunately that the *patio ludens* view likewise cannot contribute towards the solving of the problem of extinction, which appears to be a far more 'abominable problem' than that of the origin of Angiosperms, which may in future be solved with progress of palaeontological knowledge.

Among zoologists there is a similar uncertainty about the interpretation of both evolutionary processes and extinction. To quote Simpson speaking about the opportunism of evolution: (1951, p. 25, 51): "There is little suggestion that what occurs *must* occur. There is an odd randomness in the record, a suggestion that it involves a sort of insensate opportunism.' On the other hand he mentions "the 'immortals' like *Lingula* which is amazingly alike its Ordovician ancestor, some 400 million years ago, while an oyster of 200 million years ago would look perfectly familiar if served in a restaurant today, and *Radiolaria* which existed since the pre-Cambrian without one type ever becoming extinct." For these cases he assumed that "these animals were well adapted to a particular way of life which has ever since continued to be possible and the requirements for which have never changed. Most of them live in conditions which are not extreme or unusual as to climate. These environments are, as a rule, those of longest, most continuous existence." But this view is again not easy to reconcile with the fate of Trilobites, Graptolites, and the "mysterious decimation of the Cretaceous reptiles, while the extinct pelecypod genera had an average life span of nearly 80 million years and some lasted more than 200 million years before becoming extinct. The ammonite group, as a whole, consisting of marine invertebrate animals persisted from early Devonian to late Cretaceous, a span of c. 250 million years." Palaeontologists who hypothesized that with age they would have developed characters indicating 'senility' are victims of a pathetic fallacy, according to Simpson (*l.c.* p. 82).

These facts then cannot be ascribed to environmental factors which must have fluctuated in all sorts of ways during these colossal periods of time. Simpson did not reject over-specialization as a cause of extinction of certain groups, but correctly added that all living beings are specialized to some extent. He sees that, in general, the "true cause of extinction seems to be a change in the life-situation, the organism-environment integration, requiring in the organisms an adaptive change which they are unable to make." He also touches, of course, on competition as a usual process, but replacement often occurs after, not concurrently with, extinction.

Comparing these considerations with plants it is scarcely conceivable that changes of environment, competition or over-specialization are responsible; there seems at least no evidence for such explanation.

It is not seldom envisaged that the first step towards extinction is a fragmentation of the range, and further to deduct that the range fragments are then more vulnerable than the original range. The subsequent steps would then be the gradual extinction of the range fragments, one followed by another, and so on. I do not object to the view that this may have occurred in some instances, especially in island areas, but it gives no satisfactory solution in a general way. Extinction remains a most miserable mystery to me.

REFERENCES

- BAAS, P. (1976). Some functional and adaptive aspects of vessel member morphology. *Leiden Botanical Series* 3:157-181.
- BARLOW, B. A. (1959). Chromosome numbers in the Casuarinaceae. *Austr. J. Bot.* 7:230-237.
- BATESON, W. (1894). *Materials for the study of variation, treated with especial regard to discontinuity in the origin of species*. 598 pp. London.
- SIMPSON, G. G. (1951). *The meaning of evolution*. A special revised and abridged edition. 192 pp. Yale University Press. [Especially pp. 25, 51, 73-83.]
- STEENIS, C. G. G. J. VAN (1969). Plant speciation in Malesia with special reference to the theory of non-adaptive saltatory evolution. *Biol. J. Linn. Soc.* 1:97-133.
- (1977). Autonomous evolution in plants. Differences in plant and animal evolution. *Gard. Bull. Sing.* 29:103-126.