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Pest Pressure, an Underestimated Factor in Evolution

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1. DEFINITION

BY 'pest' in this article is meant any sort of minor predator, parasite, or herbivore which preys upon an organism much bigger than itself. Fungi or bacteria attacking a higher plant, caterpillars eating its leaves, and gall insects infesting it are pests: a cow feeding on it, or a rival plant competing with it, are not pests in the present sense. Fleas, lice, ringworm fungi, pathogenic bacteria, spirochaetes, *Bilharzia* flukes, and blood-sucking flies are some of the pests of Man: lions are not.

2. THE PROBLEM TO BE SOLVED

Why are some regions extraordinarily rich in species as compared with others?

In the comparison shown in Table I between the flora of the Cape region of South Africa, here taken as the area south of the Orange river and west of longitude 24°E., and that of the British Isles an average species concept is used, such as that employed by Clapham, Tutin, and Warburg (1952). It will be seen that the Cape region is enormously richer, area for area, in species of higher plants than are the British Isles. Various attempts have been made to account for this greater richness of the Cape flora, but none of them can be considered really satisfactory. There is a greater range of habitat in the Cape region, but this cannot explain the wealth of species in quite small, rather uniform, areas such as the Stellenbosch flats. There

seems no evidence that mutagenic agents such as cosmic rays are more powerful in the Cape than in Britain. Veldt fires have been suggested as a possible cause, since mutations sometimes arise in wound tissue, but the wealth of species seems to be as great in areas not subject to fires as in those in which they occur. The most serious attempt to explain the matter is the ingenious theory of gaps developed by Weimarck (1941). Weimarck points out that in relatively humid periods the ranges of xerophytic Cape species were broken up

TABLE I

The Cape Region Compared to the British Isles in Wealth of Species

Whole Cape region	*c.* 300,000 sq. km.	*c.* 9,000 species
Cape Peninsula	*c.* 500 sq. km.	*c.* 2,100 species
Stellenbosch flats	*c.* 10 sq. km.	*c.* 744 species
Whitehill district	*c.* 100 sq. km.	Over 700 species
Whole British Isles	*c.* 300,000 sq. km.	*c.* 1,500 species
Isle of Wight	*c.* 400 sq. km.	*c.* 870 species
Trees and shrubs over 2 m. tall		
Forests of Cape Peninsula	*c.* 3 sq. km.	32 species in 22 families
Whole British Isles	*c.* 300,000 sq. km.	76 species in 20 families

Large genera, with over 50 species in each

British Isles: 1 genus (*Carex*) with 77 species.
Cape Region: 45 genera, including:
17 genera with 100–250 species each, *Oxalis* with *c.* 300 species, and *Erica* with *c.* 400 species.

Sources for Table I: Bolus (1903), Adamson (1950), Clapham, Tutin, and Warburg (1952), Phillips (1951), Duthie (1929) and Compton (1931).

into a number of disjunct rain-shadow areas in which speciation by isolation could take place. In drier periods these areas became continuous, allowing the formerly isolated incipient species to meet and hybridize. The converse was true for the mesophytic species, which had continuous ranges in humid, discontinuous ranges in drier, periods. This alternation of speciation by isolation and hybridization leading to increased variability is held to explain the great wealth of species.

Weimarck's hypothesis might be thought satisfactory, were it not possible to check it by comparison with regions not possessing the Cape type of topography in which mountain blocks are separated by gaps (see Table II). When this comparison is made it is seen that a surprising wealth of species is no monopoly of the Cape, nor of regions with the Cape type of topography. What then is the evolutionary process which has led to such a multiplicity of species in fairly uniform areas?

It will at once be pointed out that Britain is poor in species because it was devastated during the Ice Age, while the other regions discussed

have been for a long time relatively undisturbed. But this is merely to state that the process which is sought takes a long time to produce a multiplicity of species: it does not tell us what the process is. It may be conceded that part of the answer is to be found in the

TABLE II

Number of Species in Fairly Uniform Tropical Areas not possessing the 'Cape' Type of Topography

(*a*) Dandu area N. Kenya (*c.* 100 sq. km.), *Acacia-Commiphora* dry deciduous scrub.

Trees and shrubs over 2 m. tall
120 species in 36 families

(*b*) Moraballi creek area, British Guiana, equatorial rain forest.

		Trees over 10 cm. in diameter at breast height	
		No. of individuals	*No. of species*
Plot A	1·5 hectares	310	60
Plot B	1·5 hectares	309	71
Plot C	1·5 hectares	432	91
Plot D	1·5 hectares	519	95
Plot E	1·5 hectares	617	74

Plots A–E were chosen as each representative of a particular type of forest; of these, that represented by plot C was most characteristic of the area as a whole.

(*c*) Amazonian rain forest, near Castanhall, Pará, Brazil.

	Trees over 10 cm. in diameter at breast height		
	No. of individuals	*No. of species*	*No. of families*
3·5 hectares	1482	179	48
of these Leguminosae	174	30	..
and Sapotaceae	266	25	..

Sources for Table II: (*a*) Gillett (unpublished), (*b*) Davies and Richards (1934), (*c*) Pires, Dobshansky, and Black (1953).

fact that not every ecological niche in Britain has yet got its own appropriate species; over a long period evolution might be expected to increase the number of species to provide one for each niche. But can it be seriously suggested that a rather uniform area of Amazonian rain forest provides, in 3·5 hectares of land, anything like 179 separate ecological niches for trees?

3. A SUGGESTED SOLUTION

At Dandu, North Kenya, in 1952 it was observed that the handsome shrub *Adenium somalense* (Apocynaceae), which has large

rose-coloured flowers, although apparently well adapted by its succulence and poisonous sap to prevailing conditions of aridity and heavy grazing, was nowhere abundant, though it occurred over large areas as widely scattered individuals, or in small groups. This seemed puzzling since if some undetected factor was making it scarce, why had this not led to its disappearance ? Eventually fruits of this plant were found, but when dried out to obtain the seeds almost all proved to be infested by the ovule-eating larvae of the fly *Dacus brevistylus*. Here was an answer to the puzzle: had the *Adenium* been numerous the flies would also have been more numerous and would have found the plant more easily, so that it would have been able to produce even fewer seeds than when it was scarce, and thus it would have again become scarce. *Dacus brevistylus* might proclaim the ancient Roman maxim 'Debellare superbos, et subjectis parcere'; spare the scarce, but beat down the dominant species.

Ovule-eating insects are not rare: plant collectors frequently note 'Seeds eaten by insects'. Greenway (1936), writing of a widespread Papilionaceous shrub in the Tanga province of Tanganyika, says, '*Mundulea* is nowhere frequent, it has everywhere to be searched for', and later, 'most of the seed pods which I have seen are infested with a boring insect and contain very few seeds'. But the principle applies to every kind of pest. It will always be easier for the pests to attack, and become adapted to, the common species, and, with their relatively short life-cycle, they will normally be able to evolve in this direction more rapidly than the attacked species, to escape their attentions. Thus the reproductive capacity of common species will be worn down by an ever-growing burden of pests, while scarcer species, especially if new to the area, will, relatively speaking, escape.

Here is the answer to the mystery. Pest pressure is the inevitable, ubiquitous factor in evolution which makes for an apparently pointless multiplicity of species in all areas in which it has time to operate.

Following the example of Darwin in *The Origin of Species*, we may appropriately illustrate this thesis by reference to human activities. Wherever Man covers an area with a single species of cultivated plant he is faced by the problem of pest pressure. He evades it by the rotation of crops, so that the pests face a different host, preferably belonging to a different family, each year; or he grows his plants, particularly if they are perennial and so ill-suited to rotation, far from their native homes and natural pests; we may think of Arabian coffee grown most successfully in Brazil, Amazonian rubber in Malaya, American cacao in Ghana, Mediterranean *Trifolium subterraneum* in Australia. Or, as happens with wheat, Man may artificially accelerate evolution, continually breeding new pest-resistant strains, which, each in its turn, become obsolete, as the pests, in this instance the rust fungi, become adapted to them. Or, lastly, Man may use all sorts of pesticides, on which he spends thousands of millions of pounds annually, to protect his crops.

The value of genetic diversity as a protection against pests is apparent in many agricultural practices. Rotation is merely diversity in time to replace diversity in space. Maize breeders in the U.S.A., while popularizing their famous pure lines, know well that they must maintain, and even increase, the genetic diversity of maize, preserving pools of it at plant-breeding stations from which they produce new pure lines to replace those which have become overburdened by pests. In Ceylon, where non-European cultivation of tropical tree crops has been developed to its highest extent, the pattern is for a large number of species to be grown, each in 'penny packets', so that there is nowhere a considerable concentration of any one species; this is an imitation of the natural forest with economically valuable species.

4. Applications of the Theory of Pest Pressure

The reason why ecologists so often fail to find in other regions the one or two dominant species in each plant association to which they are accustomed in temperate Europe or America needs no further explanation.

The answer to a problem which has been discussed by Haldane (1955), why each species does not come to consist of a single genetic type, that most suited to its environment, is also plain: the effect of pest pressure in producing genetic diversity applies at the intraspecific as well as at the specific, generic, or family level. That strain within a species which is commonest is the one to which the pests of that species will tend to become most adapted; therefore the viability of this strain will be reduced and other forms will be favoured.

As has already been suggested, further light may be thrown on the past history of the earth by the theory of pest pressure. Other things being equal, those regions where conditions have longest been stable will have the greatest density of species, genera, and families. Thus it can be assumed that arid conditions have been stable for a longer period in the Horn of Africa or in south-west Africa than in the belt of arid country running across West Africa since the density of species is greater in the first two regions than in the third.

The natural grassland areas of Africa, induced by fires caused by lightning, may be distinguished from those which have come into existence only since Man started to increase the number of fires, perhaps 40,000 years ago, by the greater number of species which they may be expected to contain. It will be noted, however, that pest pressure is not uniform in all areas; it will be less where there is a cold winter, or a long dry season, than in constantly warm and humid areas where the pests can live and breed all the year round. For this reason it should not necessarily be assumed that conditions have been stable longer in the Amazonian rain forest than in the dry bush lands of northern Kenya simply because the species density is greater in

the former area. The availability of species which may be drawn into the pest-ridden community must also be considered; an oceanic island may remain with comparatively few species for a very long time simply because there is nowhere from which additional species can readily come.

The problem of vicarious taxa not separated by an insuperable barrier is also illuminated by the theory of pest pressure. If species or genus 'A' supports a population of pests which can also attack the related taxon 'B', the latter will find it more difficult to spread into the area occupied by 'A' than into an area not occupied by any closely related taxon and therefore relatively free from its pests. It is a well-known practice in agriculture to eliminate from an area in which a crop is to be cultivated related wild plants which might harbour pests of the crop. Growers of cotton try to eliminate wild Malvaceae, growers of water melons wild Cucurbitaceae, from the neighbourhood of their crops. In Iraq it is well known that land where tobacco has been long cultivated may become useless for this crop because of infestation by the parasite *Phelipaea* (Orobanchaceae); this land is then also useless for the cultivation of other Solanaceaous crop plants such as the tomato and the egg-plant, *Solanum melongena*. The white race of *Homo sapiens* finds it easier to colonize an empty tropical island such as Mauritius, or areas such as America where Man has not lived for long, than areas where a negroid or Mongoloid population, which has been resident for hundreds of thousands of years, supports a large number of the pests of man.

Related to the last statement is the well-known fact that the original home of a species can often be suggested by counting the number of pests which it supports in each part of its range, and considering the complexity or otherwise of their adaptation to it: nowhere is there such an immense variety of the pests of Man as in Africa where, in all probability, he evolved.

Three aspects of the life-spans of taxa are illuminated by the theory of pest pressure. First, why they exist at all: it is not immediately apparent why species should seem to undergo old age, decline, and death when the factors making for senescence in the individual presumably do not apply to species. The ever-growing burden of pests adapted to each species and the difficulty which each species must experience in evolving away from the attacks of organisms which can evolve more rapidly than itself form a sufficient answer to this. Secondly, why do major taxa, such as the Angiosperms, so often begin their period of abundance by a sudden explosive burst of evolution followed by a much longer period of relative stagnation? The forerunners of the group achieve some great evolutionary advantage which makes them common; pest pressure then helps to bring about rapid diversification, but, once this is achieved, there is no such urgent reason for further rapid evolution, and relative quiescence follows. Thirdly, why do orders or classes which have been

very important in the past so often survive for many millions of years as a few, often rather rare, remnant genera? Surely if the wheel of fate long ago turned against the mighty Articulatae of the Carboniferous, the factors which ruined such large important forms as *Calamites* should wipe out even more effectively their petty relatives the Horsetails? The survival of such remnant groups is, however, explicable when it is seen that there was a great evolutionary advantage for pests which became adapted to attack the great dominant species of the past, but comparatively little in becoming adapted to the comparatively scarce and small survivors.

One plant-geographical problem which is solved by the theory of pest pressure is so familiar that it does not usually attract the attention which it deserves. This is the extraordinary power of invasion possessed by many taxa. Why, for example, has *Trifolium*, which seems to have evolved in the Mediterranean region, and is therefore adapted to the conditions there prevalent, been able to penetrate to the Cape on the one hand and through California to Chile on the other? It has twice crossed the Equator and spread, at every stage of its journeys, through regions to which it was not originally adapted, in competition with local floras which had been longer in those regions and were therefore, presumably, better adapted to their conditions than the invader. Why should *Quercus cerris*, native of, and presumably adapted to, the conditions of south-eastern Europe, be able to compete successfully in many parts of southern England with our native oaks, which have had thousands of years to become adapted to our conditions? One might have thought that the Cape flora, in all its diversity, would have filled every ecological niche in the Cape peninsula to the exclusion of new-comers. And yet *Pinus* from the Mediterranean and *Hakea* and *Acacia* from Australia are spreading rapidly over the peninsula, often destroying the native vegetation in large areas. And at the same time Cape species are spreading in Australia, often becoming a nuisance to Man in the process. The answer surely is that in each case the invader has got away from its pests while the native plants are still burdened down by theirs. One doubts, for instance, whether *Quercus cerris* in England is attacked by anything like as many insects as the 250 species which are said to attack the native *Q. robur*. *Opuntia* was disastrously successful in Australia until pests from its Mexican home reduced it to comparative scarcity. *Hevea* is grown successfully in Malaya, often in pure culture over thousands of square miles, without much difficulty. But when the Americans tried to grow it in its native home in the Amazon basin they had to resort to such elaborate devices as 'three-layer trees'; the rootstock chosen for resistance to fungi attacking the roots, the trunk selected for high rubber yield, and the crown selected for resistance to pests attacking the leaves. Then they dusted everything with pesticides from aeroplanes, and still they failed.

It will be seen that this invasiveness of taxa, due to pest pressure, applies as well to the spread of species from one plant association to another as to their spread from one country to another. It is a commonplace of African botany that genera very often have one or more species in the rain forest and other species in the savannah. Again this is so well known that we do not stop to think how odd it is: for, if the genus was evolved in the first place in the rain forest, it should be ill suited for success in the savannah, in competition with genera which have been evolved to meet savannah conditions. And if it evolved in the savannah it should be ill suited for success in the forest. When we see that by moving from one formation to the other it escapes to a great extent from its own pests, while entering into competition with plants which are still burdened down by theirs, the phenomenon is easy to understand.

Hitherto it has been shown that pest pressure may increase the number of species in a community by promoting the invasion of this community by species from outside. It will now be shown how pest pressure may increase the speed of evolution. In so doing we shall help to meet an objection, often raised by critics of the current Huxley–Haldane neo-Darwinian theory of evolution, that it is impossible for this type of evolution to have produced the observed development, specialization, and diversity of living organisms in the time which has elapsed since the origin of life on earth.

First, every time that pest pressure helps a species to spread out of the region in which it evolved and to whose conditions it is adapted, a new evolutionary process is started to adapt the species to the conditions of its new habitat.

Secondly, even though a species can never wholly escape the burden of pest pressure by evolutionary change, it may nevertheless achieve thereby some reduction in this burden. Two examples of this effect may be cited from our own species. It is true that these changes are not genetic but cultural, which makes them faster and easier to observe, but the two types of change must be stimulated in the same way by pest pressure and are in any case interconnected. The first of these human changes is from a pattern of reproductive behaviour similar to that of other semi-gregarious primates to patterns which involve chastity, at any rate among the females. Anyone even slightly acquainted with the way in which tribes that have not undergone this change may be decimated by venereal disease will understand the part played by the latter in promoting this change. The second change is that from the pre-industrial (or pre-scientific) to the industrial, or scientific, type of Man. Of course the latter has other advantages, besides a greater power of combating pests, to set against the fact that he is much more expensive to maintain, but anyone who has lived in areas where cholera, typhoid, malaria, &c., are still common will realize what enormous advantages his power to overcome such pests gives to the newest type of humanity.

Thirdly, a group of organisms which is already diverse because of pest pressure will be much better able to evolve in response to some change in inorganic conditions than a uniform group, since the liability to produce mutations of any particular sort varies greatly from species to species.

Fourthly, a species, at any rate one capable of self-fertilization, may well become divided into two or more daughter species in the process of evolving to escape pest pressure. For example, let us suppose, as is likely, that *Adenium somalense* is capable of self-fertilization, and let us further suppose that a mutant arises which flowers at an unusual season, when *Dacus brevistylus* is not on the wing. This mutant will not only be favoured, as compared to the parent type, by its escape from the pest but it will also be genetically isolated. It will therefore be a possible basis for a new species.

5. Conclusion

It is hoped that the foregoing discussion of what is, to the author at least, a new theory, may be useful in stimulating discussion and research. It will have been noticed that the theory has been produced primarily to explain phenomena observed among vascular plants. This is only partly because the author is a botanist; it is also clear that pest pressure will have less effect on animals than on plants (*a*) because animals so often carry their pests around with them, and (*b*) because animals, being mostly incapable of self-fertilization on other grounds, cannot employ in evolution mutants which are separated genetically from the parent stock. The author is grateful to members of the Systematics Association who criticized this theory at or after the meeting of the Association in April 1959. They will see that slight changes have been made in the way in which the theory is here presented, which, it is hoped, may have made it more acceptable. It is regretted that, in the heat of discussion, no record was kept of who said what, so that it is impossible for the author to record his gratitude to each colleague by name. Apologies may also be due to those biologists, unknown to the author, who have very likely previously published everything that is set out here. So great is the volume of published work, in so many different languages, in which this theory might have appeared, that more than one lifetime would probably be needed to make the search that, in theory, would be desirable.

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