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Animal Life in Relation to Vegetation and Soil.

By
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Wherever vegetation spreads on the earth, animal life will follow, into high mountain regions and arctic tracts, out into the plankton of the sea, and down into the soil with the roots of the plants. Animal life is an integral part of the organic life, dependent on plants, since its existence is based on the solar energy absorbed by them, but, on the other hand, it sets its mark on the vegetation in many different ways, entering as an element, which leaves its imprint on the whole, not only into the plankton of the sea, as is well known, but also into the organic life of the dry land.

At first sight the influence of animal life on the vegetation is not very conspicuous, apart from the vast ravages of insects, which in a short time may destroy hundreds of hectares of forest. After such destructions, without the interference of man, a change in the vegetation of the same character as after a forest fire might take place, the dark spruce wood being replaced for instance by light birch and pine woods, which would only in the course of a century or more again give way to spruce wood; or the consequences may be far more catastrophic, in the form of sand drift, wild brooks, and mountain slides. But the daily influences of animal life are of at least equal importance, for they may cause

the vegetation to be different from that which would be present if animal life were excluded.

However, in those places in Denmark in which we have the opportunity of studying this phenomenon, we shall always meet with a combination of these influences and that of man. The results are more or less a consequence of the influence of man, even though these results were not directly aimed at.

A well-known striking example of this is to be seen in the plains of the Jægersborg deerpark with their umbrella-shaped hawthorns. The normal picture of the vegetation here would be the closed wood. Under natural conditions the possibilities for the growth of trees are so good that the wild animal life would be unable to prevent the growth of the forest trees and preserve the plains; but artificial protection of a large number of red-deer and fallow-deer has produced a savannah-like vegetation picture. If the wild animals were removed from the plains of the deerpark, the latter would be covered with trees in the course of a few decades. A similar picture of the vegetation may be met with in several other parts of the country, the state of affairs there being maintained by grazing cattle.

In other parts of the globe, for instance in the savannahs of Africa, where the growth of trees is more handicapped by a dry climate, the tremendous numbers of wild ruminants tend to limit the growth, so that trees only occur scattered and in groups, and if lions and other carnivores did not keep down the number of the ruminants, the trees would possibly perish. As it is, there is a state of equilibrium between trees, ruminants, and animals of prey, of such an early date that a species like the giraffe, so specialised for the savannah, can exist.

However, to return now to Denmark, we have here a different and to us far more important type of vege-

tation than that of the deerpark, namely the heath; the basis of its existence is just as composite, as I shall try to show by the following example.

In 1913 Nørholm Heath, an area of 350 hectares belonging to the Estate of Nørholm situated 10 km north-east of Varde, according to the desire of the late owner, Miss Kristiane Rosenørn Teilmann, was declared a preserve by duly registered royal resolution. Previously the heath had been used as a pasture for both sheep and cattle, but this had almost ceased at the time, and I have been told that after the old heath sheep had been replaced by more up-to-date breeds, the sheep preferred the meadows to the heath. At the time when it was used as a pasture, the heath was almost entirely devoid of trees. A few junipers occurred, some few birches were found in a large tufted boggy area, and on a steep slope towards Varde Aa on the northern margin of the heath there grew some rowans, alders, and bushes.

As soon as the heath was freed from the ruminants, the trees began to spread. They were partly ancient Danish deciduous species, such as birch, rowan, black alder, and oak, and of bushes notably hawthorn, rose, and willow, and partly the introduced conifers, mountain pine, Scotch pine, and Canadian white spruce. Already in 1921, when I made the first calculation of the stock of trees, numerous small trees were found in the area, but on each investigation which has taken place since at five years' intervals, the number had increased and the plants had naturally grown larger. By now they are so large that notably birch, rowan, hawthorn, mountain pine, and white spruce produce seed in abundance, and while the first trees developed from seeds derived from areas outside the heath, a propagation of the trees of the heath itself is now taking place. Of special interest is the distribution of the oak, for which the lively jays are probably responsible. The beech, too, is dispersed,

but it very soon disappears again. The heavy-fruited trees, oak and beech, would not naturally have become the dominant trees in the Danish woods, if their fruits had not been transported by birds up through Europe into Jutland and the Danish islands.

The first count made on Nørholm Heath in 1921 showed the number of trees to be 1036, of which 49 were junipers, 561 deciduous trees, and 426 different conifers. In addition about one hundred bushes occurred. Since then the number has been increasing, the total number in 1942 being found to be about 6700 trees and 1800 bushes, a total of 8500, that is to say that the number has been multiplied by eight in twenty years. Equally distributed, this would mean twenty-four trees and bushes per hectare, but they occur to some extent in groups. Two birch scrubs, in particular, will be noted, one of which has not come into existence till after 1921. These scrubs are responsible for the recent immigration of roedeer on the heath, and this interferes strongly with the immigration of the trees. The rowan, which from 1921 to 1927 had increased from 85 to 403 individuals, had in 1942 decreased to 200, and numerous trees were so badly gnawed that sooner or later they will perish, if the roedeer continue to browze on them. Next to the rowan, the birch had been most badly gnawed. The number of scattered birch trees had increased from 283 in 1921 to 1132 in 1937, but in 1942 the number was only 1127. For the time being the roedeer prevent the birch from spreading to fresh areas, while the number of birches in the groups was still somewhat on the increase. The oak, which had increased from eleven specimens in 1921 to 300 in 1927, had in 1942 increased to 394 individuals.

All the conifers had increased in number, Scotch pine from 127 in 1921 (with a decrease to 57 in 1926 owing to a rather extensive heath fire) to 217 in 1937 and 284 in 1942, mountain pine from 94 in 1921 to 1947 in 1937 and 2911 in 1942, white spruce from 205 in 1921 to about 800 at present. Thus the chance for the deciduous trees, rowan and birch, to cover the heath is being checked by the immigrated roedeer, notably as regards the rowan, while the conifers are constantly increasing in number and are thus assisted by the roedeer in their competition with the deciduous trees.

The bushes also have increased in number, the hawthorns from c. 50 to c. 150 and the willow, which was favoured by the appearance, for a short space of years, of some lakes that have now disappeared again, has increased from a very few to 1600.

The aspen has likewise increased considerably in number, but it is very low, rarely more than knee-high, and has, as well as *Salix repens*, *Vaccinium uliginosum,* and *Myrica,* not been included in the counts.

Thus, according to the above, the trees on the heath are influenced by animal life. The removal of the cattle rendered the immigration of trees possible, birds undertake the dispersion of rowan and oak, while the wind disperses most of the other species, the roedeer oust the rowan and hamper the birch, so the percentage number of the conifers increases more than would otherwise be the case. A similar influence of roedeer is known from the forests, where their predilection for biting the tops off ash plants makes this species of tree far less numerous than it would otherwise be.

Forest is the natural vegetation of this area, but an abnormally large number of ruminants on the ground prevents its natural maintenance and leads to the development of a heath. After the Ice Age the vegetation that first immigrated to the heath areas consisted of deciduous trees and bushes, probably especially willow and birch. At that time the soil was virgin soil rich in lime and other bases. The presence of lime is borne out by the numerous soft, rounded lumps of silica found in the gravelly layers of the heaths. At the time when they were transported by the ice, they were hard lumps of lime; in their present soft, non-calcareous state they would not have tolerated the transport, but would have been crushed. It was not till a layer of decaying plant remains had been formed and produced soluble acid humus substances, which were carried down with the soil water, that the lime was dissolved. Thus at the outset such conditions were present as give rise to the development of earthworm mull, and the present soil section of the heath can only be conceived to have been formed by the original presence of an earthworm fauna.

In the mull of the Danish deciduous woods we find a fine-grained layer of soil generally at a depth of 30—60 cm, and below this a layer which is richer in stones than the underlying soil. The upper layer, the mull, has passed through the alimentary canal of earthworms, and there is therefore a maximum limit to the diameter of the grains. While the earthworms carried the fine-grained soil to the surface, the stones, which originally occurred scattered in the uppermost layers of the soil, have sunk down till they reached the unbelaboured part of the soil, where they form a frequently very conspicuous layer.

On considering a section of the soil of the heath, we shall find precisely the same distribution of the grain sizes of the mineral soil if the layers have not been disturbed by sand drift. The leached sand is fine-grained throughout, and thus corresponds entirely to the layer of mull-soil. In the lower part of the layer we most frequently find a relatively soft, black humus layer, which is called peat-like pan and is a layer of washed down humus deposited on the dense precipitation horizon, in which the mineral grains are surrounded by a colloid membrane, at the top black or blackish-brown, farther downwards brown, the humus content decreasing downwards and the rusty colour of the iron setting its mark on it. In the upper part of this precipitation horizon, the hard pan, a more or less marked stony layer occurs, corresponding to that of the mull-soil. Thus the sorting of the grains is entirely analogous, and this speaks strongly in favour of the supposition that the heaths, too, while still calcareous and covered with deciduous plants, had a layer of mull with an earthworm fauna. This is, in fact, the only satisfactory explanation of the distribution of the different sizes of grain.

In the wet climate the calcareous state could not be maintained. The large surplus of percolating rain

water which characterises the humid climate, washed out the bases of the sandy soil by the aid of the humus acids, and subsequent conditions have favoured the pine wood and its acidophilous calciphobous associates, bilberries, cowberries, heather, mosses, and lichens. The latter still occur on the heath, while the pines should be sought in a fossiliferous state in the peat bogs, where they are easily observable, thus also on the aforementioned Nørholm Heath.

The pine wood grew unchecked as long as Denmark was inhabited only by hunters and animals of prey, which kept down the number of ruminants; but when tribes with herds of cattle and goats immigrated, the forest was faced by an enemy which in conjunction with fire was bound to destroy it on the meagre soil, where it was composed of plants that easily caught fire. Fire and felling destroyed the old trees, and the animals prevented new ones from growing up. The deciduous wood on the rich soil, where the ground was covered by herbs, was much more resistant, and fresh plants soon grew up on the fertile soil. Without exactly intending it, man, with the assistance of fire and cattle, caused the development of the heath. The pollen analyses show that the actual heath with *Calluna* as the dominant plant arose comparatively late.

A stock of ruminants without its natural enemies: bear and wolf, as found under the protection of man, is capable of preventing the forest from maintaining itself. The vegetation picture marked by domestic animals is extensively distributed over vast areas of the globe, for instance in Scandinavia, especially in western Norway, in the Alps above the present tree-limit, in China, and in North America, and these areas now require an artificial reforestation and protection against the animals in order to meet the demand for timber of these countries.

To the vegetation belts of the globe correspond certain characteristic types of soil. Here, too, the climate is the main factor, temperature and precipitation being decisive, but still the vegetation may exert a great influence on the results. Oak and spruce growing side by side on the same geological formation may produce diametrically opposite soil types, mull and raw humus. On level terrain in Oldenburg I have observed old oak woods with a fine mull and a luxuriant anemone flora, but in between the oaks there occurred large old beeches, and as far as they spread their branches, there was a thick layer of raw humus and no anemones.

In the forests of the cold temperate regions a single species of tree is frequently the only one present, excluding competitive species often over vast areas and thus setting its mark on the organic life of the whole tract. This is true of the Danish beech woods on higher ground, but to an even greater extent of the Scandinavian spruce woods and, on meagre soil, of pine woods. Outside the woods it applies especially to the heaths. It is obvious that such a one-sidedness affects the soil and animal life, not least the insect fauna, which thus in a peculiar way depend on a single species of plant. If, for instance, we imagine that the species Norway spruce did not exist, the condition of the soil, the ground flora, and the animal life would be entirely different over vast stretches.

Thus the vegetation sets its imprint on the soil, and as animal life influences the vegetation, it is to some extent determining. Even grazing may have a catastrophic effect, for instance in the Alps it may cause landslips and exposure of the unweathered rock. But still more interesting and of far greater influence is the fauna living in the soil, for through its mechanical work, by its preparation of the soil, it takes a direct part in the formation of the soil. The most important

animal group in this respect is that of the earthworms. It may be said with perfect justice that a number of the most important soil types would not exist at all without the cooperation of these animals, but other types of soil vividly reveal the presence of an arthropod fauna consisting chiefly of insects and their larvæ and of mites.

The type of mull formed by the earthworms has been so frequently mentioned in the literature that it will not be dealt with in detail here; it should merely be stated that the more or less abundant occurrence of the earthworms depends on the type of vegetation. The type is characteristic of all deciduous woods, where the condition of the mull is normal, while the raw humus is a morbid condition, a phenomenon of degeneration which especially prevents the natural regeneration of the beech, so that without the assistance of man the beech wood would in such places be replaced by heath, as has happened to a great extent in central Jutland; or by other trees such as birch, oak, pine, and spruce, which are better able to grow in the raw humus soil. Destruction of the earthworm fauna, as it may take place for instance in the open outskirts of woods, goes hand in hand with a degeneration of the soil type in which the absence of the earthworms plays a decisive part. One of the consequences of this is a change in the vegetation of the place, the anemones, wood-ruff, larkspur, etc., being replaced by wood meadow-grass, woodrush, and mosses of the impoverished soil "bare of mull", and if the development proceeds and raw humus is formed, these plants are again replaced by the plants of this type of soil, viz. waved meadow-grass, cow-wheat, smilacina, and trientale, later on possibly bilberry, cowberry, and heather.

In the raw humus the action of earthworms is lacking. The consequence is that the lumpy structure produced

by a mixture of mineral soil and plant waste (humus) passing through the alimentary canal of the earthworms, disappears. The structure of the soil now becomes single-grained, and the division of the soil by chemical action into a leaching horizon and a precipitation horizon is allowed to proceed, whereas previously it was constantly obliterated again by the earthworms carrying the deeper-lying layers to the surface.

The washing effect of the humid climate which is actually present to some extent, though not visible in good mull, may, when the work of the earthworms ceases, develop the characteristic podsol type with a layer of superficial humus (raw humus), a washing horizon (leached soil), and a precipitation horizon (rusty soil or pan).

Although the raw humus lacks the diligent work of the earthworm, it is by no means without the influence of a soil fauna. Animal life in the raw humus layer is exceedingly rich. Of earthworms, as a rule merely the small moss worm, *Dendrobaena octoedra*, occurs, which only carries little mineral soil up to the humus layer. It is chiefly insects and mites which characterise the fauna of the raw humus; the microscopic mites, in particular, may be numerous, up to several hundred thousands in a square metre. Second in frequency are the Collemboles, and, of larger insects, a number of dipterous larvæ, of which the large larvæ of the crane-flies are most readily observed. Millipedes and centipedes are likewise conspicuous.

Now, what is the effect of all these animals? A close inspection of the waste layer of the forest will reveal that it does not simply consist of decaying plant remains, but that the latter have been bitten into small fragments and mixed with the excrements of the small animals. This is especially easily ascertained where the waste layer is formed of spruce needles. The deeper-lying part of the raw humus is a coprogenous mass of

an amorphic nature. But for the prolific animal life, the raw humus would be a swampy compressed mass without porosity and probably an exceedingly poor soil for the plants.

Precisely the same picture is presented by the raw humus in the heath, and here, too, there is a rich animal life, which belabours the mass of humus, but in addition several animals work their way down into the mineral soil, though they can by no means compete with the large earthworm species of the mull, but probably with the only earthworm species of the heaths, *Dendrobaena octoedra*. Ant-hills of small black ants are very numerous (the large red forest ant, *Formica rufa*, too, is not rarely found), and these ant-hills are to a great extent built up of sand grains, which the ants have fetched from the leached sand below. In this way a mixing of sand and raw humus will take place in the course of time, but fossorial wasps, dung-beetles, mice, foxes, lizards, toads, salamanders, and other animals that burrow in the ground also take part in such work, which will no doubt exert a fertilising influence on the raw humus and increase the possibilities of a more varied flora, most likely of the sprouting of the seeds of trees also.

The Crysomelid beetle *Lochmaea suturalis*, which lives on the heather tops and in some years is present in such large numbers that the heather is entirely defoliated and partly dies away, may no doubt affect the vegetation picture of the heath, since the withering of the heather will make room for crowberries and other plant species, and thus also indirectly influence the insect fauna.

Some few aspects of the part played by animal life in the organic life of the dry land have been fairly thoroughly dealt with, notably, however, the damage done to culture plants; and the part played by the ani-

mal world in the construction of the formations of earlier earth periods has long attracted attention. On the whole our knowledge is only scattered and casual in this field, and perhaps still too fragmentary for us to form any general impression of the whole.

Detailed investigations will be necessary, if we are to come to a closer understanding of the conditions. Investigators of the biological communities of dry land have no doubt much to learn from marine investigators and fresh water biologists, who largely combine the various factors. The study of plankton, where the investigators gather all in one net, points the way to a consideration of the whole and its correlation to a few easily determinable factors such as the water's content of salt, lime, and oxygen, its temperature and p_H value. Investigators of the dry land have been much more inclined to regard the individual conditions, such as the type of soil and the type of flora, as isolated and static phenomena, while actually they form part of a dynamic biological system.

A statistical determination of the land fauna presents far greater difficulties than that of the plankton, which can simply be separated from the medium by a sieve, while the individual factors of the land fauna involve greater technical difficulties, and for various reasons. Only by repeated observations over a long period can an approximate count be made of fairly large animals such as mammals and birds, which move rapidly from place to place, and it requires intimate knowledge of the locality. Of small animals which live in the vegetation, for instance in the tops of trees and shrubs, a fairly accurate count may indeed be made per areal unit, if they can be beaten down; insects are therefore often more easily counted in the larval stage. In this connection mention may be made of Trägårdh's quantitative determinations of bark-beetles. The small

animals living in the low vegetation and in the soil may be counted by investigating the samples taken, and, as regards the very small and numerous fauna, this can be fairly satisfactorily done, though several technical difficulties present themselves and different methods must be used if all the different forms are to be included in the investigations. An investigation of the land forms will, at any rate, be more troublesome than investigations of the plankton of the sea; however, the greatest difficulty is that while the organisms of the plankton owing to the water currents are constantly mixed, the fauna of the dry land will vary within very small areas. The individual species often occur in societies, possibly attracted by a nutrient substance, for instance animal excrements, a carcase, or a special plant species. Certain essential elements of a fauna will be fairly evenly distributed in a certain type of vegetation, so that by means of a number of random samples we may form a reasonable quantitative idea of the main elements of the fauna in it, but the work is considerably increased by the fact that the investigations must be repeated so frequently that the change of seasons and weather and fluctuations from one year to the other are taken into account. To this must be added the importance of the age of the biological system, most easily recognised by the age of the plant community. If, for instance, we are dealing with a forest stand, we should have to know the age of the vegetation, the history of its origin, the influence of cultivation, and the previous condition of the area, as we should here be concerned with a succession of living organisms, which is especially readily observable in the flora of the forest ground; but in addition we must know how the vegetation thrives, as expressed, for instance, in the height attained at a certain age, and we must likewise know the quantitative value of the essential processes of production and

destruction. All these difficulties speak strongly in favour of laying the main stress on the study of a limited number of specially prominent and characteristic types.

In the dynamic biological system a constant interaction takes place between plants and animals, soil and climate and the activities of man. Each species exerts its influence on the whole, greater or smaller according to the quantitative importance of the species. All this must be studied as a whole, so that the total aspect is not forgotten for the individual factors, and the conditions must be considered dynamically, while the factor of time must constantly be taken into consideration.

Dansk Oversigt.

Overalt hvor der findes planteliv paa jorden vil dyrelivet følge med til dettes yderste grænser, op i højfjældene og i de arktiske egne, ud i havets svæv og ned i jorden med planternes rødder. Dyrelivet er en integrerende del af det organiske liv, afhængigt af planterne paa basis af hvis optagne solenergi det eksisterer, men til gengæld prægende plantelivet paa mangfoldige maader.

I ekstreme tilfælde kan dyrelivet helt omstille vegetationen (insekthærgninger, drøvtyggere i overtal), men ogsaa den mindre iøjnefaldende stadige paavirkning af dyrelivet ændrer vegetationen. Som vegetationstyper, der er iøjnefaldende præget af dyrelivet, kan nævnes dyrehavesletter, overdrev, savanner og heder, f. eks. den jydske hede, hvor der, naar den fredes mod drøvtyggere, indvandrer træer og buske.

Særlig stor indflydelse har jordbundsfaunaen af orme, insekter og mider, der gennemgribende præger jordbundstyperne og derved faar betydning for vegetationen. Paa heden spiller antagelig myrerne en rolle ved at transportere sand op paa mortørven.

Der foregaar i naturen en stadig vekselvirkning mellem jordbund, klima, planteliv og dyreliv, hvortil de fleste steder kommer direkte eller indirekte menneskelige paavirkninger, hvilket resulterer i dynamiske, biologiske systemer, hvori hver enkelt art paavirker helheden, mere eller mindre efter dens kvantitative betydning.

Skal man forstaa et saadant biologisk system, maa dets forskellige faktorer gennemforskes nøje og bestemmes kvantitativt. Dette er relativt let tilgængeligt ved havenes og ferskvandenes svæv, hvor alle de enkelte organismer let lader sig skille fra mediet og begivenhederne sættes i relation til let bestemmelige faktorer som vandets indhold af salt, kalk, ilt, dets temperatur og pH. Studiet af landsfaunaen byder langt større tekniske vanskeligheder, og arbejdet forøges overordentlig, ved at undersøgelserne maa gentages til forskellige aarstider og under forskellige vejrlig, hvortil kommer at landjordens organismer ikke er saa ensartet fordelt som svævets. Det dynamiske biologiske system er aldrig i ligevægt, der sker dels periodiske svingninger om en middeltilstand, dels en forskydning af denne sidste eftersom systemet ældes, og faktoren tid maa derfor altid tages med i betragtning.