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A RELATION THEORETICAL APPROACH TO PATTERN AND PROCESS IN VEGETATION

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ABSTRACT

A theoretical approach to the problems concerning the relations between plants and their environment, methodically allied with the discipline of cybernetics and based on researches made into plant succession.

Three fundamental relations of universal character have been distinguished, the third of which is showing the basic connection between *pattern* and *process*. The three basic relations also provide an approach to the effects of *concentration* and *dispersion* in space and time, which phenomena are considered as to be of dominant importance with regard to pattern and process.

The relations associated with concentration and dispersion on their turn have proved to be an useful expedient for getting a better understanding of the ecological relations in border areas, which have been divided in two main types of boundaries, respectively described as "*limes convergens*" (*ecotone*) and "*limes divergens*" (*ecocline*).

Many examples are given with regard to the application of the theory.

1. INTRODUCTION

During the last two decades the botanical section of our Institute has regularly investigated more than 500 permanent plots, distributed over the whole country, with a frequency of about 200 samples per annum. The results of this yearly repeated examination into a large number of vegetations types with regard to the alteration or non-alteration of their floristical composition and other spatial patterns are mainly used as directives for the control of nature reserves.

In connection to some ideas given by W. Ross Ashby (1956) and other pioneers in the field of cybernetics we were able to develop a new theory, founded on the investigations first mentioned and directed to ecology and nature conservation. In this "*Relation Theory*" much attention is paid to the environmental conditions in border areas.

1.1. *Cybernetics and ecology*

Cybernetics has been started by N. Wiener during World War II as a special scientific discipline with respect to the construction of machines for fire-control. Soon however he discovered that its principles could also successfully be applied to the problems concerning organisms and their internal and external vital functions. Since the cybernetical approach in biology and allied subjects, leaning on the hypothesis that "*life*" and "*regulation*" are closely allied, has steadily increased.

All questions suitable for research can be reduced to the basic problems of *equality* or *inequality* in space and time. The possibility of this reduction, by which complicated mutual relations are turned into the more simple ones between only four primary elements, constitutes the central idea in modern cybernetics. These four elements are: 1) equality in space; 2) inequality (difference, variety) in space; 3) stability (=equality in time); 4) change (=inequality in time).

When equality is seen as a special case of inequality (difference = zero) then we may agree with the assertion of Ross Ashby (1956) that "*difference*" is the most fundamental concept in cybernetics, either that two things are recognizably different or that one thing has changed with time.

Viewed in this light the study of pattern and process in vegetation has no other aim than tracing the mutual connections between "*variety-in-space*" (pattern) and "*variety-in-time*" (process) within plant communities. It even may be said that ecology on the whole is concerned with exactly the same questions as does cybernetics, studying problems such like regulation, selection and dynamic balance. In the work of Nature Conservancy we meet again with all these phenomena, the name itself (conservation) already expressing the element of non-alteration.

Within the scope of cybernetics the technical-mathematical Information Theory is considered as one of its best elaborated foundations. It has been developed by C. E. Shannon a.o., chiefly in order to get a better apprehension of the possibilities and difficulties linked up with communication (carrying messages).

Several ecologists, most of them working in U.S.A., have already tried to apply this quantitative theory on their study of ecosystems. But nearly all publications that have appeared up till now are quite in the strain of "*biomass and energy flow*", thus of "*matter and energy*" or "*production*", not of "*pattern and process*" (compare PATTEN, 1959; GALOUX, 1963).

So far as we know only MARGALEF (1957, 1961) has pointed out the difference between these two types of approach, showing the importance of spatial patterns or differentiation with regard to succession and degree of stability or regulation in an ecosystem. This author also gives fruitful ideas about some qualities of spatial patterns, particularly about "*granulation*" and the size of its "*grains*".

For the sake of ecology Ross Ashby's many-sided General System Theory provisionally seems to give a better starting-point than does highly specialized Information Theory. In the Relation Theory dealed with hereafter we suppose to have found an addition still more suited for this purpose.

It should be borne in mind that, applying a cybernetical approach to ecology, we are not so much interested in environmental factors simply, as for example lime content of the soil on a single place, as in the sharp or gradual contrasts in space and time "*lime available/lime not available*". Consequently we are taking the line that plants and other organisms primarily react on spatial and temporal patterns, build up by the various environmental factors.

1.2. *Elements of spatial patterns*

Ecology is possible and pregnant partly by the fact that life circumstances are *not* equal everywhere as well as by the fact that an organism can*not* live under all circumstances. This spatial limitation or restriction offers the base to their building up of distribution patterns, which we are able to trace.

Now, generally spoken, spatial patterns and limits are only present when "*inequality*", "*choice*", or "*no*" is available. For, within the two combinations "*yes–yes*" and "*no–no*" equality or non-pattern is found, either couple giving "*yes*". Using the alternative "*yes–no*" however, we shall find "*no*", expressing the difference or inequality between "*yes*" and "*no*". In the same way choice or selection is connected with the couple "*yes–no*", thus with using "*no*". One of the purposes of Shannon's theory is measuring the amount of information or selection as a statistically weighed quantity of such alternatives.

Every spatial pattern is showing three mutually related properties, viz. 1) *form*; 2) *size*; 3) *border type*. For example 1) the geographical distribution area of a plant species (a spatial pattern) may represent a roundish patch or look like a narrow ribbon; 2) its extensiveness may be large or small; 3) its external and internal limits may be sharp or gradual. The mutual relations between these three qualities can be expressed by using the alternative "*yes–no*".

A narrow ribbon means that in the longitudinal axis of the pattern a relatively large quantity of "*yes*" is available, so a small amount of inequality or selectivity. Following this axis we shall continually meet "*the same*" or "*equality*". In contrast herewith we shall find a relatively large quantity of "*no*", in the transversal direction of the ribbon, thus a high amount of inequality or selectivity. So a distribution pattern looking like a narrow ribbon will always contain more ecological significance than a pattern resembling a roundish patch. This greater significance however is mainly connected with the transversal direction of the ribbon. For example, the presence of a central european grassland species on several localities within the Dutch region more or less influenced by the river Rhine in the first place has to be explained in relation to the ecological contrast *wet river/dry surroundings*, not, what is usually done, in relation to the line of communication between southern Germany and the Netherlands formed by the stream. This principle is also clearly demonstrated in the line-shaped distribution pattern of a plant bound to tidal drift along sea coasts.

In the same way a small or scattered pattern, which we are calling "*fine grained*" comparatively will be of more ecological indication value than a large, continuous one ("*coarse grained*"), at least in spatial relations. The scientific importance of endemics and local rarities, one of the main objects for nature conservation, is founded here upon.

The qualities of patterns in respect of various border types will be dealed with later on. It will become evident that in this case granulation is playing a dominant part again (compare also VAN LEEUWEN, 1965).

1.3. *Elements of temporal patterns*

With regard to temporal patterns (process) we also may discern elements of equality and those of inequality. By equality is meant *non-alteration, permanence* or *stability*. On the contrary inequality-in-time is indicating *alteration, change* or *instability*.

Analogous to the case of spatial patterns we should suppose that a process is showing a temporal pattern only when change or instability can be established. Nevertheless now the element of equality or permanence appears to be of more importance, which means that the process is determined and the system studied is showing a more or less fixed "*line of behaviour*".

In the first part of our theory special attention will be given to the basic relation between spatial and temporal patterns.

2. THE THEORY OF BASIC RELATIONS

2.1. *Starting point*

We have started with the idea taken from the philosophical work of WHITEHEAD (1926), that every relation shows aspects of *connection* and aspects of *separation*. Further we call a relation *open* when there is connection, but *closed* when there is separation. Next we place in one line with "*open*" all that is spoken of as *equal* (in space and time) and with "*closed*" all that is concerned with *unequal* (in space and time).

2.2. *Basic relation of equality (1st basic relation)*

With the help of the position given under 2.1 we now are able to set up the first basic relation, which we will call the *basic relation of equality* and which can be written in the two following "*relation chains*":

1. Connection ≈ open ≈ equal
2. Separation ≈ closed ≈ unequal.

Both chains in the first place aim to express that significally there is hardly any difference between the three concepts linked together, no more than between all other terms which are closely related to each of them.

2.3. *Spatial relations and the first basic relation*

Moreover chain number 1 directly tells us that spatial connection and openness must lead to spatial equality and that, on the reverse, equality-in-space must lead to connection. The first conclusion agrees with a common well known fact, but the second result is a considerable less obvious one. In ecological relations it means among other things that a species living in one of two environments nearly showing the same life circumstances much easier will reach the other place than we should expect. This possibility of "*conduction by equality*" even holds in the case of small, rather scattered localities, as is demonstrated by the famous flora of zinciferous soils in Central Europe.

On the other hand chain number 2 indicates that spatial closure and separation will end in spatial inequality and that, on the reverse, spatial inequality must bring separation with it. Both conclusions fit very well the modern ideas about the relation between isolation and genetic difference as given by Dobzhansky (1951).

The following concepts are representing some aspects of spatial connection:
hole, gap, breach, known, public, joining, "on", contact, communication, touching, affirming, permission, "yes", positive, unlimited, similarity, homogeneity, continuity, monotony, evenness, general (common), everywhere.

Concepts expressing spatial separation are, for example: *wall, dam, barrier, unknown, secret, locking, "off", distance, isolation, protection, negation, veto, "no", negative, restraint, difference, heterogeneity, discontinuity, variety, unevenness, differentiation, particular (uncommon), unique.*

A large number of *relation chains of direct connection* can be compounded from aspects of spatial connection and separation. Thus for a chain of type number 1 we have chosen: *open ≈ plain ≈ herd ≈ aggregation.* We not only know the expressions "open plain" and "herd aggregation", but also these two phenomena belong to each other. For an example of type number 2 we can give: *island≈isolation≈unequal≈apart ≈unique.*

The significance of *isolation* as a factor in biogeography and ecology is often over-, respectively under-rated. In the absence of certain organisms from an island in the sea it is quite usual to ascribe this to the surrounding salt water operating as a geographical barrier. But why is it that such islands often accommodate precisely some organisms which elsewhere, or at least in the adjacent environment, are found wanting? The chain compounded above gives a direct explanation of this problem.

The aim of *nature-protection*, an aspect of spatial separation, is expressed by the chain: *isolation≈protection≈hands off≈veto≈differentiation≈particular.*

It is principally a question of *saying no*, an isolation mechanism (= regulation mechanism) like a modern analogue of our remote ancestors' *taboo* (noli me tangere). From this follows the great importance of islands (such as our Wadden and Delta islands) for nature conservation. And in the reverse, nature protection must lead to the development of island situations, viz. of reserves rich in species, surrounded by a landscape impoverished by modern culture.

The connection between the pairs of concepts "*Order and disorder*" (from Thermodynamics) and "*Information and noise*" (from Information Theory) and the first basic relation we show as follows:

1. Connection≈equal≈disorder≈noise≈known.
2. Separation≈unequal≈order≈information≈unknown.

One can isolate "*noise*" which signifies the preservation of information. On the other hand "*information*" can be communicated, which means growing equality between giver and receiver. The paradoxical looking relation between "*information*" and "*unknown*" is explained by the Information Theory which demonstrates that a quantity of "*information*" is identical to an amount of "*missing knowledge*" which will be the higher the more complex or isolated the system studied is.

For ecological relations it is very important to consider that *competition* belongs to the aspects of chain number 1 whereas *co-operation* falls under 2. Expressed in terms of MATHER (1961) we therefore can write:

like≈competition

unlike≈co-operation

Competition, based on various types of spatial equality, ultimately must always lead to the loss of spatial variety and increasing monotony, while co-operation, based on various types of spatial difference (division of tasks and interests), will result in growing variety-in-space.

The setting up of spatial isolation necessary for *observation* and *research* (both aspects of chain number 1) must automatically involve addition of disorder upon the eco- or bio-system which we want to study. Herein we run great risks of getting a distorted picture of reality by finding an excess of equality aspects, competition for example. Therefore the competition concept still plays a dominant part in the thought of most ecologists who do not realize that competition tends to be the result of their own activities. In the same way ecological research in nature reserves can result in serious disturbance of relation networks in the area concerned, leading to decreasing spatial variety.

Combinations of 1 and 2 are found in all types of natural and artificial regulators, such as *thresholds*, *canals*, *sieves*, *membranes*, *diaphragmas*, *punch cards* and *valves*. The phenomenon "*life*" is closely associated to these "*yes-no apparatuses*", thus on the application of "*no*", as already mentioned before in the case of nature protection. This fundamental connection finds its expression in cybernetical concepts such as *restraint*, *prohibition*, *vetoing*, *blocking* and *negative feed back*.

2.4. *Temporal relations and the first basic relation*

For relations in time we also can write:

3. Connection≈open≈equal (remaining the same).
4. Separation≈closed≈unequal (change).

Among the aspects of connection in time in the first place we consider concepts as *permanence*, *constancy*, *stability*, in short all that has to do with *remaining the same*.

In the second place we can have connection through time with on the one side the *past* and on the other the *future*. Connection with the past goes among other things through:

remembrance, *tombstone*, *experience*, *inscription*, *relic*, *fossil*, *historical continuity*.

Similarly, connection with the future for example can go through: *instruction*, *programme*, *design*, *blueprint*, *agenda*, *testament*, *warrant*, *prediction*.

The tying-up of the past with the future runs through:

maintaining the status-quo, *continuation*, *conservation*, *preservation*, *conservancy*, *archives*, *memory*, *storage*, *provision*, *saving*, *faith*.

In addition to these *logistical* aspects belonging to chain number 3 are likewise:

long duration, *durability*, *low speed*, *always* and *less uncertainty*.

Concepts expressing separation-in-time are, for example:

instability, *change*, *transformation*, *disturbance*, *interruption*, *strike*, *precariousness*, *new*, *news*, *start*, *find*, *invention*, *revolution*, *transmutation*, *mutation*, *loss*, *to forget*, *destruction*, *ending*, *production*, *improvisation*, *adventure*, *surprise*, *risk*, *unexpected*.

In addition to these *heuristical* aspects belonging to chain number 4 are likewise:

short duration, *shock*, *high speed*, *some times*, *once and more uncertainty*.

Here we can again link up chains of direct connection between the various aspects of 3 as well as between those of 4. So for an example of 4 we can write: *conservation≈fossil≈storage≈provision≈continuation≈less uncertainty*. Not only does this chain form a reassuring thought when we have started the winter with a satisfactory fuel supply, but also the continued existence of our technical society is dependent on this.

As an example of agricultural craft can be given: *ploughing ≈ manuring ≈ annual plants ≈ production.* The connection between high productivity and environmental instability and between a low degree of productivity and stability of an ecosystem which represents one of the most important scientific results within the scope of the study on "biomass-and-energy flow" (ODUM, 1963) fits very well the chains given above.

Combinations of 3 and 4 are found in all progressions where *change* joins with *remaining the same.* Belonging to this are among other things: *motion, inheritance, repetition, rhime, vibration, adaptation, restoration, renovation, dynamic balance, succession, evolution, line of behaviour, cyclic process.* Together they form the characteristic elements of "*life*" (compare also the combinations of 1 and 2 mentioned under § 2.3).

At the outset we have introduced our theorems under the name "*Open-and-closed*" *Theory,* but because many students have difficulties in using the terms "*open*" and "*closed*" for temporal relations, we have abolished it in consultation with VAN DER MAAREL (see elsewhere in this issue). Therefore we do not use here the abbreviations $o(s)$, $c(s)$, $o(t)$ and $c(t)$, but:

$$\bar{a}(s) \tag{1}$$

$$a(s) \tag{2}$$

$$\bar{a}(t) \tag{3}$$

$$a(t) \tag{4}$$

in which a stands for *variety*, $\bar{a}$ for *no variety*, s for *space* and t for *time.*

2.5. *Basic relation of inequality* (*2nd basic relation*)

The *basic relation of inequality* we see in the difference or division between connection and separation. When we introduce a connection ($\bar{a}$) in a definite direction, for example by means of a thread, then a relation of separation (a) develops transversely there at that point. In order to get from $\bar{a}$ to a, and vice versa, one has to turn through an angle of 90° (compare the working of doors, bridges and bars).

As a definition we give: *The basic relation of inequality is the complementary relation between equal and unequal, that which is found in the expression* $\sqrt{-1}$ (= to turn through an angle of 90°). One can say also that the second basic relation provides the key relation to all other relations of inequality. Expressed in symbols:

$$\bar{a} \# a.$$

Here $\bar{a}$ stands for: equal ≈ open ≈ connection, a for: unequal ≈ closed ≈ separation and # for: "in the direction 90° different from, but at the same time complementary to and indissolubly allied with".

2.6. *Basic relation between connection and separation in space and connection and separation in time (3rd basic relation)*

The most important question we can put in this chapter is: "Which relation may exist between $\bar{a}$ (s) and $a(s)$ on one hand and $\bar{a}(t)$ and $a(t)$ on the other?"

Given that the second basic relation, thus the connection between $\bar{a}$ and a, is just the same as the relation between space and time (also $\sqrt{-1}$), we should be able to lead from $\bar{a}(s)$ to $a(t)$ and from $a(s)$ to $\bar{a}(t)$. Thus expressing this in symbols we should get:

$$\bar{a}(s) \rightleftarrows a(t) \quad (5)$$

$$a(s) \rightleftarrows \bar{a}(t) \quad (6)$$

Now the connections of (5) and (6) are evidently in very good agreement with reality. This can be demonstrated by many different examples:

a) In the field of nature protection a discussion has ranged for a long time over the problem of what term should be used for preference: "*nature protection*" or "*nature conservation*"? In spite of the priority felt by many for the first name still more favour the second one. The argument against the first name is that "*protection*" has a *negative* sound, while, on the other hand, "*conservation*" has a *positive* connotation. Now the first term is standing under the negative $a(s)$, but "*conservation*" comes under the positive $\bar{a}(t)$. According to (6), therefore we can write:

nature protection ⇄ nature conservation.

b) The second law of thermodynamics states that with every change spatial equality has increased. According to (5):

equality ⇄ change.

c) Environments with precarious living conditions are poor in species, for example *Salicornia* communities. According to (5):

poor in species ⇄ precariousness.

d) Stable environments on the other hand accommodate communities rich in species, for example coral reefs. According to (6):

rich in species ⇄ stability.

e) The territorial singing of male grashoppers is very monotonous in time. By means of this other males are repelled. According to (6):

repulsion ⇄ permanence.

f) Their courtship song is strongly varied. Females become attracted to them by this variety-in-time. According to (5):

attraction ⇄ variation.

The most important conclusion that we can draw from the foregoing is that *equality-in-space* and *equality-in-time* cannot be treated alike, any more than *variety-in-space* and *variety-in-time*.

Ross Ashby (1956) assumes this in his "Law of requisite variety": – *Only variety can destroy variety.* – From our formulas (5) and (6) it follows that *variety-in-space* can be counteracted only by *change* and that, on the reverse, *variety-in-time* can be destroyed only by *spatial differentiation.*

The mutually allied phenomena *life* and *regulation* are obviously aimed at formula (6), thus at *variety-in-space* and *stability.* The work of nature conservation has no other purpose.

In accordance with what is said in § 1.2 and § 1.3 formula (6) is also expressing the connection between spatial and temporal patterns.

2.7. *Paradox of the second basic relation*

Paradoxical relations easily come out from the key relation. This confusion is due to the indissoluble bond ($= \bar{a}$) between $\bar{a}$ and a. There are numerous paradoxes of this type. To mention just one: "Close by" is an aspect of $\bar{a}$ although "to close" belongs to a.

A scientific very important paradox of this type is found in the relations between *noise* and *information* and between *communication* and *information*, which may bring us to the idea that *noise* and *information* (or *communication* and *information*) are equal in fact. Inkspots blurring out the letters of a written message as permanent spatial patterns indeed carry the information that someone has messed with his pen but they have disturbed the original context by *change.*

Within this scope it is also of importance to show on the difference between the ideas of an electric engineer dealing with "*information*" and a geneticist doing the same. The first one, from whom may be presumed to be especially interested in *communication* (the carrying of information) will award a great value to the heuristical aspect of *surprise*, according to formula (5):

$$\text{communication} \rightleftarrows \text{surprise.}$$

The geneticist however, more interested in *isolation* and the *permanence* of spatial structure within the ovum, will put in the forefront the logistical aspect of *blueprint*, according to formula (6):

$$\text{isolation} \rightleftarrows \text{blueprint.}$$

Connection in a certain direction is possible where in the complementary direction separation is present, and the same for the reverse. The possibility of being able to observe ($= \bar{a}$) always rests with the presence of separations or differentiations ($= a$) in our surroundings. These differences appear to us as spatial *patterns* and *structures.*

When, on the other hand, a connection across our line of sight is found, then it is difficult or even impossible to observe. The hiding action of *mimicry* and *camouflage* is tied up with the key relation. The object becomes invisible ($= a$) in our direction through connection ($= \bar{a}$) with the surroundings in the complementary one.

It is most important to take into account the "*basic paradox*" in the study of ecological relations. This is especially the case when horizontal and vertical situations are brought into relation with each other. So a high degree of vertical differentiation ($= a$), for example in a soil profile or in a strongly layered forest, is coupled with a high amount of horizontal uniformity ($= \bar{a}$) of the vegetation in question.

3. Concentration and dispersion in space and time

By means of the three basic relations it is possible to approach the very essential effects belonging to *concentration* and *dispersion* in space and time.

For concentration (compression, convergence, accumulation, condensation, etc.) and dispersion (expansion, divergence, dilution, evaporation, etc.) may be considered as the two fundamental antagonistic processes which are completely dominating the events in the world around us.

When spatial concentration is playing a part connection or equality will be introduced to the centre (internally), but separation or inequality will increase to the outside (externally). According to the third basic relation in this case the result will be more internal instability combined with more external stability.

On the contrary the internal spatial variety will be amplified in the case of dispersion and thus the internal stability, while, on the other hand, the spatial equality to the outside will increase together with the external instability.

The assertion of Pask (1961) that convergence is going together with stability and divergence with instability in our opinion is only true when the external relations are taken into account. With regard to the internal aspects the situation is quite the reverse.

Spatial concentration is attended by a coarse grained pattern, as shown in Fig. 1, spatial dispersion however by a fine granulation. We also can establish that spatial concentration is characterized by a lower quantity of border lines than has spatial dispersion.

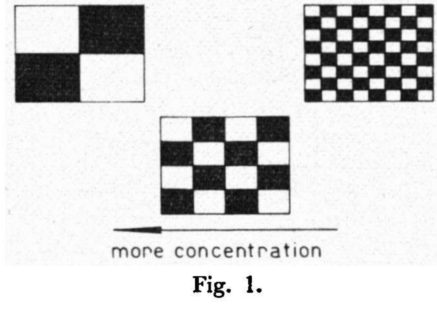

Fig. 1.

When a single plant species is dominating over a relative large territory, 100 m^2 for example, then this situation is rather improbable, taken into account that in the surroundings a thousand species are available. Spatial concentration in fact means a high content of external selectivity or information. To the inside however no more taxonomical selection is possible, only one species being present.

When, on the contrary, a hundred species are found on the same area, then the situation is more probable, considering the external relations. Thus in the case of dispersion less information is met with to the outside combined with a high degree of internal selection. Nearly every point on the inside of the territory in question is differing from each other. As MARGALEF (1961) has shown this distinction in pattern formation is very important when we are studying ecological relations.

Further we ought to consider that temporal concentration (*simultaneity*) has the same effects as caused by spatial concentration, just as the results of spatial dispersion can be amplified by spreading or distribution in time. Difficulties brought on by spatial concentration (for example: traffic flocking from all quarters on cross-roads) therefore are to be solved by spatial dispersion as well as by spreading in time. This type of internal regulation is well known in nature as is demonstrated by the seasonal differences in the floristical composition of many woodland communities.

4. SOME PROPERTIES OF BORDER AREAS

By means of the external and internal basic relations connected with concentration and dispersion two main types of boundaries can be discerned, as already has been demonstrated by us elsewhere (VAN LEEUWEN, 1965). The most important qualities of these two types, which are called "*limes convergens*" (allied to spatial concentration) and "*limes divergens*" (allied to dispersion) may be recapitulated here in short.

The first-named type, in its patterns characterized by coarse granulation and sharp, often straight border lines ("*all-or-nothing*"), is marked by unstable conditions on the inside, coupled to a low amount of internal variety-in-space. Life circumstances in border areas of the limes convergens show a high degree of instability ("*now-and-then*" or "*to-and-fro*") while the vegetation there is poor in species, most of them represented by many individuals (production of mass). We have suggested to confine the concept of "*ecotone*" to this border type, considering stress or tension as an aspect of instability.

A limes divergens, on the contrary, which shows a fine granulation in its patterns together with faint lines of demarcation ("*more-or-less*") is marked by stable conditions on the inside, coupled to a high amount of variety-in-space. The vegetation of such gradual transition zones between mutually differing environments is rich in species, many of them represented by only a few individuals. The concept of "*ecocline*", as it has been worked out by VAN DER MAAREL and WESTHOFF (1964), is quite appropriate to the limes divergens.

Both types accommodate their own organisms and communities. Characteristic plant species for the limes convergens are for example: *Rumex crispus*, *Ranunculus repens*, *R. flammula*, *R. sardous*, *Potentilla anserina*, *P. reptans*, *Trifolium repens*, *T. fragiferum*, *Hydrocotyle vulgaris*, *Plantago maior*, *Inula britannica*, *Juncus effusus*, *J. inflexus*, *J. maritimus*, *Carex hirta*, *C. otrubae*, *C. vulpina*, *Agropyron repens*, *Agrostis stolonifera*, *A. canina*, *Festuca arundinacea* and *Lolium perenne*, all bound to the synsystematical class of the *Plantaginetea maioris* Tx. et Prsg. 1950. The plant communities of this class are living in environments which, mutually compared seem to be very different but which show one important feature in common: strong and often irregular temporal variety in life circumstances as caused by alterations between wet and dry, salt and fresh and poor and rich (manuring) which heavy changes among other things result in soil compactioning.

This "*loss of spatial structure*" (increasing convergence) in the top soil is also due to "*off-the-road-locomotion*" in all types of heaviness from treading to the riding of tanks and tractors. On soils sensitive for this disturbance, as for example are found on reclaimed heaths in the eastern parts of the Netherlands, it is possible to induce a vegetation rather looking like a brackish salt-marsh, with species such as *Trifolium fragiferum*, *Ranunculus sardous*, *Triglochin palustris* and *Festuca arundinacea*, only by means of wrong agricultural measures.

The effects of grazing (treading, manuring and damaging of the vegetation), especially when it is done by large animals living in herds, are closely allied to what is found in the unstable situations of the limes convergens. This similarity is so great that a succession based on an artificially accelerated desalination of a former salt-marsh is accompanied by just those plants which are considered to be typical for pastures more or less overgrazed. This connection has clearly been demonstrated in a series of permanent plots on several localities along the North Sea Coast. So-called "*tread-plants*", like *Potentilla anserina* and *Plantago maior* often found along roadsides, proved to be important elements of the succession, there without any influence of grazing or treading being present.

Natural surroundings favourable to plant communities of the limes convergence in the first place are met with along sea coasts and river banks, on flat areas now-and-then inundated, on boundary lines between eutrophic and oligotrophic environments where "*rich*" dominates "*poor*" and on all other places where disturbance or "*environmental noise*", thus a high degree of $a(t)$, is found.

Secondly these plant communities grow on various soil types, the bad structure of which can induce quick or strong changes with regard to the water management from bone-dry to soaking wet, especially in extensive flat areas.

Next to these natural possibilities man-made landscapes are pre-eminently suited for the limes convergens and its vegetation types, above all in their present form. For the modern technical civilization more and more favours the limes convergens by making sharp lines of demarcation, monotonous vegetations, barrages, metalled roads, straight canals, by soil compactioning and by scale enlarging in re-allotments.

The anthropogeneous landscape represents a special sub-type of the limes convergens showing a "*seeming stability*" which is related to external regulation by man. The uncertainty of now-and-then however is always threatening here as is demonstrated in the case of barrages and dikes.

Environments of the limes divergens accommodate quite another set of plants among which we call for example: *Botrychium lunaria*, *Silene nutans*, *Dianthus superbus*, *D. armeria*, *Hypericum pulchrum*, *Pinguicula vulgaris*, *Genista tinctoria*, *Lathyrus montanus*, *L. nissolia*, *Trifolium medium*, *Agrimonia eupatoria*, *Polygonatum odoratum*, *Carex dioica*, *C. pulicaris*, *C. hosteana*, *C. buxbaumii*, *Eriophorum latifolium* and all species of orchids. In many cases the total number of individuals belonging to these species which is present in a certain area comes to no more than one or two, the circumstances required being limited to almost a single spatial point. The internal stability of the situation on the other hand can ensure the presence of such tiny populations for tens of years.

Typical environments of the natural limes divergens may be expected in the same localities where the limes convergens is found, but in this case nearly always confined to places where gradual differences in height or great distances are available as a fundament for other types of gradual transition zones. They are found on border areas between salt-marshes and fresh dune valleys, on slopes of dry and rather poor sand dunes never inundated shading off into wet and clayey soils often inundated and on boundaries between eutrophic and oligotrophic environments where "*poor*" dominates "*rich*", the last situation being quite opposed to what is mentioned in respect of the limes convergens. Instructive examples of this situation are shown in the lagg-zone of bogs on limestone, in swimming marshland situated in areas where oligotrophic water, coming down from a higher level, reaches an eutrophic environment and on the slopes of limestone hills covered by poor sandy soils.

The biological culminating-point of the limes divergens is found in the gradual transition-in-space between woodland and non-woodland which will be specially treated later on in this article.

Just as a "*stable*" sub-type of the limes convergens could already be distinguished, it is also possible to mark off an "*unstable*" form of the limes divergens. This sub-type is found on places where instability shows gradual differences in space, varying from a high to a low degree. It may be clear that several environments just mentioned are belonging to this sub-type which is characterized by a large quantity of species such as *Linum catharticum*, *Gentiana campestris* subsp. *baltica*, *G. amarella* subsp. *uliginosa*, *G. germanica*, *Parnassia palustris*, *Fritillaria meleagris*, *Scirpus planifolius*, *Carex flacca*, *Briza media*, *Juncus capitatus*, *J. tenageia*, *J. mutabilis* and orchids like *Spiranthes spiralis*, *Orchis morio*, *O. maculata*, *Epipactis palustris*, *Platanthera bifolia* and *Gymnadenia conopsea.* (We even can put the thesis here that our Relation Theory, started from the "*convergent*" framework of the three basic relations, has developed to the "*divergent*" idea that a gradual scale is conceivable, on the one side of which the limes convergens is standing and on the other side the limes divergens. This concept finds its expression in the "Law of requisite environmental instability" dealed with in the last chapter.)

Species of the unstable limes divergens also appear to prefer loamy soil types showing a structure which is intermediate between dry sand and water-logged clay, thus providing an auspicious micro-instability in the water management of the top layers.

In contrast with the modern situation the former agricultural and mining systems automatically lead to amplification of the spatial diversity in life circumstances. This internal regulation amplifying was mainly the result of three factors:

1. The methods did not change for centuries. By this stability the variety-in-space steadily increased.

2. Isolation by distance gave a gradual restriction to human influence on the landscape. This restraint was minimal near the dwelling-places in the centre of the action-radius and maximal at the outside with all possible degrees of influence between the extremes.

3. Our ancestors were operating gradually and on a small scale. By this dispersion-in-time, which, as we have already shown before, has the same effects as dispersion-in-space, the spatial variety increased still more.

Besides these three main factors (now used as basic rules for the control of our nature reserves) numerous smaller elements of divergence occurred in the landscape, such as the unevenness of the soil surface, the windings of ways and watercourses and the borders of old-fashioned footpaths and roads not or only primitively metalled by means of loam.

It may be obvious that the preservation and control of areas which still contain vegetation types belonging to the old man-made landscape constitutes one of the most important and at the same time most difficult tasks for the Dutch Nature Conservancy. The more so as our over extensive areas flat country is missing the shelter against spatial equalisation provided by the differences of level common to regions more accidented.

The relation theoretical approach to ecology makes it also clear that diking in and reclamation of the Wadden Sea, combined with straightening of the coastal line along the Wadden-islands should rob the Low Countries from their last area where spatial divergence based on nearly all types of contrasts reaches an almost mountainous height.

The continued research into the properties of border areas has to pay special attention to the ecological relations bound to the steepness of environmental gradients as well as to the spatial meeting zones between convergent and divergent environments, which, as we have observed on various places, are often characterized by screen shaped vegetation patterns looking like networks.

5. The theory of basic relations applied to ecology

In the preceding chapters the possible connection between the three basic relations and certain ecological phenomena has already been pointed out many times. It may however be useful to broaden this perspective to some other important facets of the relations between plants and their environment.

Approaching ecological problems from the basic relations we postulate, according to the cybernetical way of thinking, the complexity of pattern and process (or structure and organisation) in the ecosystem we want to study. Form, size and border type are considered leading elements in respect of spatial patterns, next to type and degree of stability for temporal ones. So we are of opinion that form, size and border type of a lake will have a determining influence on course and character of the local succession from open water to marshland.

To start from structure and organization means among other things that the famous "*Struggle for life*" is interpreted as a struggle for survival and regulation, thus for $\bar{a}(t)$. This fight, directed against change threatening from all sides, thus against $a(t)$, can be crowned with success only by means of the various aspects of $a(s)$, thus by spatial variety.

Therefore a plant which is able to form offshoots we do not consider a "*strangler*" tyrannizing its fellow-creatures in ruthless competition for light and water, but as an organ which can observe and wipe out temporal variety within the concerning ecosystem. Such a plant even can grow only on places *where* forming offshoots is allowed and, besides, local circumstances are determining *when* they will be formed, as we could experimentally demonstrate on a.o. *Mentha aquatica.*

Externally and internally resistance is offered to all types of "*noise*" or disturbance as caused by the abiotic environment, by virusses, genetic damage, uniform mass growth, quarrels within communities, etc. The most effective weapon forged for this many-sided battle is called "*homeostasis*" (Cannon, 1929) or "*the know-how of equalisation-in-time*".

During history of life the various organisms have developed a large quantity of regulation mechanisms for "*maintaining their status quo ante*" with the aim of numerous $a(s)$ aspects. One of these aspects is the enormous richness in species available, each of which can be understood as a regulator itself with respect to the stability of the ecosystem it is belonging to.

The function of a certain plant species as a regulator we suppose to be closely associated with a special trajectory and degree of environmental instability. In other words: *Every plant species would need an* *own trajectory and degree of instability for its germination, development and functioning as an efficient regulator.* A simplification of this "Law of requisite environmental instability" which we regard as a useful hypothesis for our further research is represented in Fig. 2.

In this hypothetical model only a graduated scale of all possible changes between extreme dry and extreme wet (a type of instability) has been drawn at the top but of course many other environmental factors which are showing change may be drawn into it, either single or in combination. Further, for the sake of simplicity, frequency and rapidity of the alteration regarded are left out of consideration.

In respect of six fictive plant species a–f the figure is showing:
Species a and b are lying within the same trajectory (a), but they are different in size.
Species c and d are equal in size but different in trajectory.
Species e requires a high degree of instability while species f needs a low one.

Next we can read that the combinations a–b, a–d, a–d–e, a–b–e–, a–e–f, c–e, d–e, and e–f are possible, but not so the combinations a–c, b–c, b–d, c–d, c–f and d–f. This, for example, may explain why the combinations *Epipactis palustris – Potentilla anserina* (c–e) and *Lolium perenne – Potentilla anserina* (d–e) are found, but not, so far as we know, the couple *Epipactis palustris – Lolium perenne* (c–d). When we finally assume that every species has its own trajectory and degree of requisite instability, then Fig. 2, demonstrates that as environmental instability

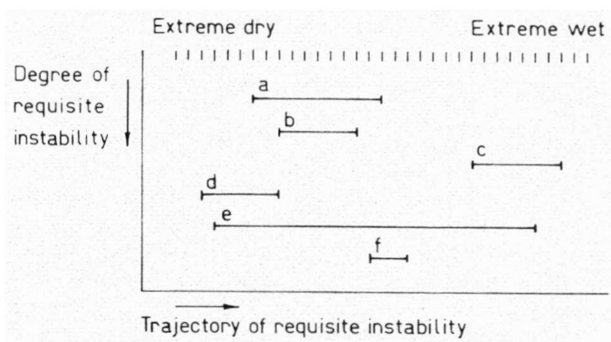

Fig. 2.

is diminishing, inaccordance with the third basic relation, the total amount of species will increase, the possible numbers of trajectories indicating a low degree of instability being much larger than of those marking a higher one. The Relation Theory may also be helpful when we try to explain the fundamental problems belonging to phenomena like *dissemination*, *accessibility* (HEIMANS, 1954), *accession* (term proposed by Dr. V. Westhoff meaning the integration of a plant with a new locality and for the first time mentioned in VAN LEEUWEN, 1962a) and *succession*.

For briefness sake we shall here confine ourselves to some problems around plant succession. As an orderly and regulate process every succession is showing a marked line of behaviour. In a complete series vegetation develops gradually from a convergent pioneer stage poor in species and characterized by a high degree of environmental instability to a divergent terminal community rich in species with a degree of stability as high as allowed by the local situation.

It is striking that many pioneer plants are able to settle as soon as a new environment has arisen, no matter how this newness, an aspect of $a(t)$ has come into being. A good example is formed by *Scirpus maritimus*, a plant not only found along brackish waters near the sea coast but also in the fresh water tidal delta of the Biesbosch and around young waterfilled sand- and claypits in the eastern parts of the Netherlands.

For such young environments the herd aggregation of $\bar{a}(s)$ is very characteristic, next to the fact that the possibility for a species to establish itself is marked by an extreme shortness and even may be confined to no more than one time. Just in the case of perennials which usually are growing in closed formations (for example *Juncus maritimus*) it is a bit of good luck when we come across the moment of their first appearing anywhere. It also means that the settling of such species can be prevented when intervention comes in the right time. After that its establishing has become impossible.

When an individual of a certain species has once established itself on a bare plain we can often observe that this species is gradually extending to its surroundings, starting from the first individual. Many ecologists are inclined to consider this "*conquest of the empty space*" as a matter of course, quite in accordance with the classic view in ecology that more individuals and more species coming into the area competition will begin.

From a relation-theoretical point-of-view however an expansion like this is only probable when the environment is still showing a type of change favourable for the species in question. This condition not being fulfilled a further expansion will be improbable. According to our experience so-called powerful and intolerant plants like *Phragmites communis* and *Cladium mariscus* then cannot win even a square centimetre of ground on their weaker brethren as for example *Plantago coronopus* or *Carex lasiocarpa*. On the other hand just one abnormal change in the water management of a divergent swimming marshland rich in species may give *Phragmites* complete dominance within one or two years.

The alteration which underlies a succession consists in a decrease of the environmental instability, thus in an augmentation of the local $\bar{a}$ (t) elements. This increase of stability is stimulated, as MARGALEF (1961) has pointed out, by storage of organic structure or "information".

This may happen by formation of humus and peat in the topsoil, by increasing divergence (refining of the spatial pattern grains) and by growing co-operation (division of tasks and interests). The stable state at the end of the series, often consisting in a cyclic change as clearliest is shown in heaths and bogs (OSWALD, 1923; WATT, 1947; STOUTJESDIJK, 1959; VAN LEEUWEN, 1962) is always remaining dependent for the greater part on the stability of the surroundings. In reverse the large quantity of $\bar{a}(t)$ common to a "climax community" may be helpful in destroying the environmental variety-in-time within the landscape it forms a part of, the community thus functioning as a regulator.

As our study on permanent plots has shown, course and direction of a succession are highly dominated by the rapidity of the basic alteration, the transition from $a(t)$ to $\bar{a}(t)$. This transition passing in a very short time, a "head over heels succession" develops soon leading to a convergent monotonous vegetation. When however the transition lasts for tens of years on the same spot a much more divergent situation will be the result. This divergence will become the larger the more environmental divergence is already available their working as a buffer.

Therefore we do not put our expectations too high with regard to the botanical richness of the future marshlands along the Zealand aestuarium, where, during the Delta-activities, the environmental circumstances will change, so to speak, at one blow. Those areas will get the highest value as a nature reserve which are showing a relatively accidented surface, next to the localities already being less saltish now and those which will remain salt for the longest time. The main task for the controller of such reserves will be to regulate in behalf of the slowing-down of the basic change. We have found that grazing by horses and cattle is the best and at the same time most practical method for this purpose.

Many other aut- and synecological questions can be approached by means of the Relation Theory among which we mention those concerning *ecotypes*, *adventives*, *pests*, *relics*, *rarity of species* and *endemics*. An interesting example with regard to the problem of endemics in a phytogeographical sense is given by BEEFTINK in his recent thesis (1965) about the salt-marshes of Western Europe. He could associate the occurring of numerous endemic plants along the western coast of Europe with four areas in each of which a gradual transition zone is found between a pair of mutual different climatic types (compare also STEBBINS & MAJOR, 1965).

At the end of this chapter some attention may be paid to our new ideas about the plant communities of forest borders (Mantle communities or *Prunetalia spinosae* Tx. 1952 and Outskirt communities or *Trifolio-Geranietea*, Th. Muller 1962). In central Europe botanical richness culminates in these communities forming the spatial transition zone between woodland and non-woodland and characterized by species like *Crataegus monogyna*, *Rosa canina*, *Prunus spinosa*, *Cornus sanguinea* and *Rhamnus cathartica* (*Prunetalia spinosae*) or like *Trifolium medium*, *Polygonatum odoratum*, *Geranium sanguineum*, *Origanum vulgare* and *Agrimonia eupatoria* (*Trifolio-Geranietea*). This richness indicates that their environment spatially is the most variegated and at the same time the most stable one nature can produce here, even more than that of a pure woodland. In a mosaic composed by mantle and outskirt a maximum of divergence is realised, each vertically wedge shaped forest edge giving a botanical gradient "pur sang".

We must assume that this botanical gradient can only develop on an ecological gradient already present on the spot and formed by the contrasts wet/dry, salt/fresh, grazed/not grazed, etc. or a combination of them. The contrast woodland/non-woodland itself seems to be not necessary as these mantle- and outskirt-communities are also known from all kinds of localities in the landscape where this contrast is wanting, while, on the other hand, many artificial forest edges are found where the concerning communities are scarcely or not occurring.

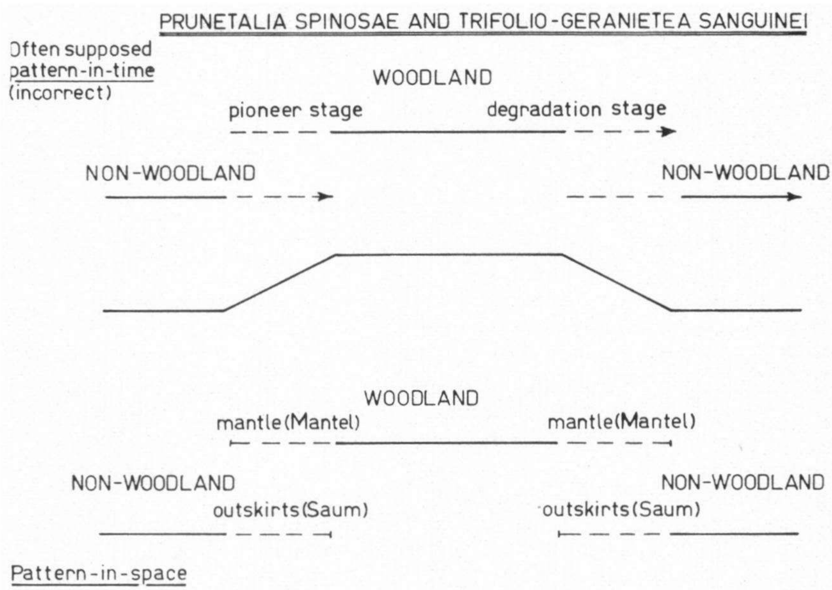

Fig. 3.

The contrast woodland/non-woodland may exist in time and space as illustrated in Fig. 3. In the first case (at the top of the figure) we are concerned with a succession from grassland or heath through a pioneer stage (first state of temporal transition) to woodland and, later on, from woodland through a degradation stage (second state of temporal transition) to grassland. A former idea, still often met with, that species like *Crataegus monogyna* and *Rosa canina* should indicate these two transition periods of radical change we now scorn in view of the supposition that hawthorns and wild roses are needing a high amount of spatial variety combined with a low degree of change as is found along gradual transition zones in space (at the foot of the figure). The two transition periods are characterized by quite another set of plants such as *Salix* spec., *Betula* spec., *Alnus glutinosa, Epilobium angustifolium,* etc.

Fig. 4.

The close relation between *Prunetalia* communities and spatial gradients is shown in Fig. 4. On this map of the Netherlands their most important gradients on a larger scale, mainly based on geomorfologically determined contrasts have been drawn as lines or as shadings. The greater part of the natural dutch specimina of the *Prunetalia* and *Trifolio-Geranietea* is bound to these lines which are indicating border areas between pleistocene and holocene, between fresh and saltish surface water as well as the slopes of the South Limburg table-land, the edges of rivervalleys, the whole dune landscape, etc. On a much smaller scale such gradients suitable for mantle – and outskirt – communities are occurring along the slopes of many dikes and ditches and on particular spots as for example the meeting area between basic lime stone and acid boulder clay east of Winterswijk near the German frontier.

By the lines drawn on the map at the same time those areas of the country are indicated where most of its rare plant species and communities have been found or are still occurring. Beyond the seacoast this has in particular been the case within the areas limited by a circle and characterized by a concentration of gradients.

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