

NOTES ON
CONVERGENCE AND IDENTITY IN RELATION
TO ENVIRONMENT.

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Any community of plants is characterized in four main ways — by a definite floristic composition, by definite life-forms, by a definite structure and by a definite habitat or environment.

Of these four characters, floristic composition is the most important in defining a plant community in any particular locality. It is a commonplace fact that many parts of the world may show communities of higher plants identical in life-form, structure and habitat but differing widely in their floristic composition. By utilising the three last named characters of a plant community we can group our unit biocoenoses into larger groups.

Life-form alone is sufficient to define the general types of vegetation which form great zones in different latitudes. Examples are the evergreen needle-leaved coniferous forest, the broad leaved deciduous forests, the hard-leaved sclerophyll scrubs, rain forests, grassland and steppe.

If we take structure and habitat into consideration as well as the life-form, it is possible to define smaller units of vegetation as for example sclerophyll forests and scrubs, savannah forests and so on. Although the floristic composition of these communities is different in different parts of the world, their physiognomy, their general make up and environment are similar. Examples for the sclerophyll scrubs are the maquis or macchia of the Mediterranean coasts, the chapparal of California, the espiñol of Chile and the scrubs of Southern Australia and South Africa. Similar savannah woodlands or forests occur in these same areas. Savannah woodlands dominated by *Quercus* and *Eucalyptus* in California and South Australia respectively, show this convergence in facies of communities in a similar environment, but with entirely different floristic compositions.

Even within a large continent such as Australia, the same vegetation type may show different floristic compositions in different localities.

An example is seen in the high sclerophyll forests of *Eucalyptus* in the Mount Lofty Ranges in South Australia and in the Blue Mountains in New South Wales. In both cases the soil is a podsol poor in mineral nutrients and both are characterized by well-marked alternating wet and dry periods. The facies is similar and the total number of species in the communities is approximately the same. The character plants of the areas belong to the same genera but to different, but closely allied, species. The following list gives the „abundant” plants in the two areas, but could also be extended to include the „occasional” and „rare” plants where a similar replacement of a species by one closely allied to it will be found.

Characteristic plants of Sclerophyll forests in New South Wales
and South Australia.

New South Wales.

Eucalyptus piperita
Persoonia salicina
Leptospermum flavescens
Banksia spinulosa
Hakea dactyloides
Isopogon anemonifolius
Dillwynia ericifolia
Acacia discolor
Pultenaea scabra
Phyllota phyllicoides
Lissanthe sapida
Tetralthea ericifolia
Epacris grandiflora

South Australia.

Eucalyptus obliqua
Persoonia juniperina
Leptospermum scoparium
Banksia marginata
Hakea ulicina
Isopogon ceratophyllus
Dillwynia ericifolia
Acacia myrtifolia
Pultenaea daphnoides
Phyllota pleurandroides
Lissanthe strigosa
Tetralthea pilosa
Epacris impressa

The same replacement of one species by another closely allied to it can be seen in scrubs on shallow soils or on laterite soils in the two areas and dominated by *Eucalyptus stricta* and *Casuarina distyla* respectively in New South Wales and by *Eucalyptus fasciculosa* and *Casuarina stricta* respectively in South Australia.

The difference in floristic make-up, but convergence in affinities is accounted for by the evolutionary history of the Australian flora. The genera of Eastern Australia are also found in Western Australia. Statistical analysis of the flora shows that the native Australian genera probably arose in the South Western portion of the continent and from this centrum a dispersal of species occurred to the east. In late Creta-

ceous times the eastern and western portions of Australia were virtually separated by a vast sea so that two centres were present in which endemic species could arise. When the Gulf Regions of South Australia were uplifted in Pleistocene times migration occurred from both these centres to give the present flora of South Australia. This isolation of the two parts of the continent accounts for the different floristic composition of similar vegetation types in similar environments in different parts of the continent and there is little doubt that were the flora of Australia more evenly distributed the floristic composition of the sclerophyll forests in different regions would show little variation.

Changes in floristic composition of a vegetation community, occur with changes in the habitat. The factors of the habitat can be grouped under three headings — climatic, soil and biotic factors. The first two are the more important and are not completely independent. With the higher plants, climate especially exerts a sifting effect upon the vegetation. In general, the more extreme the climatic environment becomes, the more specific becomes the plant community in equilibrium with the environment: from a community containing plants belonging to numerous families there is a change to one containing only a few species belonging to a few circumscribed families.

The mechanism of this sifting effect is clear. Owing to deep-seated metabolic changes or owing to structural changes brought about by changed metabolism, certain species in a migrating population of plants will have a better chance of surviving when entering a new environment than other species with less specialised mechanisms. Such plants are often said to be better „adapted” to their environment which does not mean that any change in the Lamarckian sense has occurred but simply that they have a greater survival value, a value which is probably intrinsic in its genetical make-up. They have been selected by the external milieu.

The sifting effect of climate may be seen in the mallee regions of South Australia. The mallee is really a vast ecotone connecting the sclerophyll communities of the south with the arid communities of the north. The terrain is even, the soil type constant throughout and the climate slowly changes from north to south, the chief difference being a range of mean annual rainfall from 20 inches to 8 inches. The only constant species are the mallee eucalypts, *Eucalyptus oleosa* and *E. dumosa*: the associated species slowly change as one progresses northwards until the numerous sclerophyll species of the south are replaced by the few Chenopodiaceae of the north. Finally the mallee eucalypts

themselves disappear and a chenopodiaceous shrub-steppe composed of *Atriplex*, *Kochia* and *Bassia* species forms the only vegetation of the plains. These genera, or others closely allied to them, are components of arid shrub-steppe in Northern Africa, in Central Asia and in Western America.

In the mallee the concentration of the soil solution increases with decreasing rainfall. The selective effect of climate is seen more clearly perhaps in the case of mangroves where the composition of the soil solution remains approximately constant but the aerial environment changes. In Northern Australia, mangroves belonging to various genera, but especially *Rhizophora*, *Ceriops*, *Bruguiera*, *Aegiceras*, *Avicennia* and *Sonneratia*, form extensive rain forests along the swampy coasts. As one progresses southwards and the humidity decreases various species drop out from the forest until near Sydney *Avicennia officinalis* and *Aegiceras majus* alone form a forest; whilst in South Australia *Avicennia officinalis* is the only member of the mangrove communities.

When the edaphic milieu becomes more extreme, and especially when the aerial milieu remains approximately constant, the selective effect becomes even more marked; and in a given milieu the same families and frequently the same genera are to be found as components of the biocoenose in all parts of the world. Two examples will serve to illustrate this convergence of floristic units, when the milieu becomes extreme; one is the halophytic vegetation of salt lakes and marshes and the other that of peat bogs and moors.

In South and Central Australia precisely the same species of plants are found in definite zones corresponding to the salt concentration in both coastal swamps and far inland salt lakes. To illustrate the convergence of species we give lists of the character plants in three zones around salt lakes in three regions, one from South Australia, one from the Great Salt Lake at Utah and one from the Caspian Sea. The prominent plants are restricted to a few genera of the Chenopodiaceae.

| <i>South Australia</i> (13) | <i>Utah</i> (5) | <i>Caspian Sea</i> (10) |
|--|--|---|
| 1. <i>Arthrocnemum</i> <i>arbuscula</i> <i>Salicornia australis</i> | 1. <i>Salicornia rubra</i> <i>Salicornia utahensis</i> | 1. <i>Haloenemum strobilaceum</i> <i>Salicornia herbacea</i> |
| 2. <i>Arthrocnemum</i> <i>haloenemoides</i> <i>Suaeda australis</i> <i>Kochia oppositifolia</i> | 2. <i>Allenrolfia occiden-</i> <i>talis</i> <i>Suaeda erecta</i> <i>Suaeda Moquinii</i> | 2. <i>Petrosimonia crassifolia</i> <i>Suaeda maritima</i> |

| <i>South Australia</i> (13) | <i>Utah</i> (5) | <i>Caspian Sea</i> (10) |
|------------------------------|------------------------------|---------------------------------|
| 3. <i>Distichlis spicata</i> | 3. <i>Distichlis spicata</i> | 3. <i>Atriplex verruciferum</i> |
| <i>Atriplex paludosum</i> | <i>Atriplex hastata</i> | <i>Atriplex canum</i> |
| <i>Sporobolus virginicus</i> | | <i>Anábasis salsa</i> |

In high moor bogs the convergence of the flora is equally striking. The most characteristic feature of these bogs is their oligotrophic character, that is, their dearth in mineral substances and their high hydrogen-ion concentration (pH usually about 4.0 to 4.5). We give examples of the typical flora of two such bogs which agree in the above characteristics; but in one the peat is a sphagnum-peat, in the other a sedge-peat. The former is in Drenthe, Holland, the latter at Mt. Compass in South Australia. The flora of the peaty heaths in Drenthe is similar in all respects to that of oligotrophic heaths, described by KOPPE (11) for Northern Europe and by KATZ (9) for Western Siberia.

| <i>Drenthe.</i> | <i>Mt. Compass.</i> |
|----------------------------------|---|
| 1. <i>Rhynchosporium albae</i> | 1. <i>Chorizandretum enodis.</i> |
| <i>Rhynchospora alba</i> | <i>Chorizandra enodis</i> (peat former) |
| <i>Batrachospermum vagum</i> | <i>Batrachospermum moniliforme</i> |
| <i>Drosera intermedia</i> | <i>Drosera pygmaea</i> |
| <i>Lycopodium inundatum</i> | <i>Lycopodium carolinianum</i> |
| <i>Utricularia minor</i> | <i>Utricularia lateriflora</i> |
| <i>Eriophorum angustifolium</i> | <i>Selaginella Preissiana</i> |
| <i>Sphagnum recurvum</i> } peat- | <i>Microtis atrata</i> |
| <i>S. cuspidatum</i> } formers | <i>Levenhookia dubia</i> |
| 2. <i>Sphagnetum medii.</i> | 2. <i>Cladietum juncii.</i> |
| <i>Vaccinium oxycoccus</i> | <i>Sprengelia incarnata</i> |
| <i>Andromeda polifolia</i> | <i>Drosera binata</i> |
| <i>Drosera rotundifolia</i> | |
| <i>Empetrum nigrum</i> | |
| <i>Eriophorum vaginatum</i> | |
| <i>Euphrasia nemorosa</i> | |
| <i>Orchis maculata</i> | |
| | <i>Euphrasia Brownii</i> |
| <i>Lycopodium clavatum</i> | <i>Diuris palustris</i> |
| <i>Pilularia globifera</i> | <i>Microtis porrifolia</i> |
| | <i>Lycopodium laterale</i> |
| | <i>Schizaea fistulosa</i> |
| | <i>Lindsaya linearis</i> |

| Drenthe. | | Mt. Compass. |
|---------------------------------|----------------------|-----------------------------------|
| Blechnum Spicant | | Blechnum discolor |
| Sphagnum medium | } peat- formers } | Cladium junceum |
| S. rubellum | | Schoenus brevifolius |
| S. acutifolium | | Hypolaena laterifolia |
| S. molluscum | | H. fastigiata |
| S. recurvum | | Leptocarpus tenax |
| Polytrichum commune | | Lepidobolus drapetocoleus |
| P. strictum | | Polytrichum juniperinum |
| Hypnum sp. | | Hypnum sp. |
| 3. <i>Ericetum Tetralicis</i> . | | 3. <i>Epacridetum impressae</i> . |
| Erica Tetralix | | Epacris impressa |
| Calluna vulgaris | | Leptospermum scoparium |
| Molinia coerulea | | |
| Juncus squarrosus | | Lepidosperma exaltatum |
| Scirpus caespitosus | | Cladium glomeratum |
| Carex panicea | | Cladium tetragonum |
| Sphagnum compactum | | |

In these peats the convergence of the flora owing to the selectivity of the milieu is more striking than that of the salt lakes for the flora is richer. Neglecting the peat-forming elements, the same genera in approximating equal numbers are common to both these widely separated localities.

Aqueous milieu is, in many respects, more homogeneous. The transpiration factor and its deep consequences upon metabolism is excluded. Even if the aqueous milieu changes in „climate” as well as in composition, its homogeneity allows us to characterize it with greater certainty than a subaerial milieu. Peatwater, freshwater and seawater show a number of biocoenoses which would allow of very interesting parallels in the sense given in the „terrestrial” examples. However, this would prove a veritable „mer à boire” and we shall, therefore, pass to slightly more selective environments. Evaporating seawater or inland-water might reach a certain concentration at which the fresh-water or the marine components markedly decrease in importance, because either the limits of their physical and chemical milieu or the limits of their biotic milieu are reached (e.g. competition). The most striking instance of this biocoenosis we find in the so-called „condensor” stage of solar evaporation of seawater, where the concentration increases from 3.5—

$\pm 12\%$ total salts, concomittant with the deposition of calcium carbonate. Apart from local (chiefly faunistic) elements this community proves to be similar all over the world. The leading form is here *Ruppia maritima* L.. Although the cosmopolitan nature of this form was recognized by ENGLER (3) as early as 1874, BRAUN BLANQUET mentions its occurrence „in the northern hemisphere” (2). SETCHELL (15) remarks that it occurs „to some extent, at least, even in the southern hemisphere”. ASCHERSON (1) discusses its cosmopolitan nature in relation to a possible common origin of the present land masses!

Without embarking upon a discussion of the origin of this distribution, and without considering the modes of dispersal (GRAEBNER, 6), we have to accept the fact that the „*Ruppion maritimae*” is a cosmopolitan association. In view of the apparent differences of opinion it may be well to illustrate this by mentioning a few localities represented in the beautiful collection of *Ruppia* in the Rijksherbarium, Leiden, which were kindly put at our disposal by its Director. If we add to these a few localities cited from the literature we obtain the following picture. The plant occurs throughout Europe, North America, the West Indies, the Caribbean coasts, the Northern and Eastern coasts of Africa, British India, Java, Madoera, the Philippines, China, Japan, Korea, Australia and Tasmania.

From the preliminary experiments of SETCHELL (15) it seems to follow that *Ruppia* is unable to withstand extreme conditions of temperature and salinity: SETCHELL gives 15—20° C. for germination and seedling-development, 20—25° C. for vegetative growth and reproductive activity; salinity 0.68—4.59%. It is obvious, however, that the range of salinity and of temperature for *Ruppia* is greater than these limits. One of us was able to observe the Ruppion near Setubal, Portugal; near Dadar, Bombay Presidency; on the island of Madoera, Dutch East Indies; and in the Bay of St. Vincent, Port Price, South Australia. In Portugal a large form (var. *longipes* HAGSTRÖM?) was observed early in September in water containing 7% solids at a temperature of 28° C. A small variety corresponding to var. *rostellata* KOCH, was observed in fruit in the condensor ditches at Dadar (Bombay Presidency) during February 1936. Here the salinity varied between 7 and 11%! In Madoera, the plants, corresponding to the var. *spiralis* KOCH were in apparently healthy condition, covering vast stretches of subaquatic meadow at a salinity of 6% and at a temperature around 30° C. At the Ruppion of Pt. Price, South Australia, the salinity varied between 6—7%!

The gypsum lakes of Yorke Peninsula when visited by one of us in March 1936, only contained saturated brine and salt-crusts. Still, LOCKHART JACK (8) mentions the occurrence of „salt-weed” in the wet season which disappears at higher concentration. The dried and salt-incrusted stalks, found by us at e.g. Fowler and Black-Hill lakes undoubtedly belonged to *Ruppia*!

From the above it appears that *Ruppia* is cosmopolitan, that its temperature-range extends well beyond 25° C. (where SETCHELL found, for the races studied by him, a deficient anthesis) and that, furthermore, the salinity tolerated might be higher than 10 % total salts. In these respects *Ruppia* appears to be unique; competition with other Phanerogams (even *Zostera*) is excluded and therefore it appears wherever this particular environmental „niche” is given on this planet. The faunistic elements of the *Ruppion* vary e.g. Molluscs: in S. Australia and Tasmania we find *Coxiella badgerensis* and *Hydrobia* spec.; from Ehrenberg's *Ruppia* material collected near El Tor, Red Sea in 1825 we extracted a shell of *Potamides* sp. while in Holland the Molluscs of the *Ruppion* are species of *Hydrobia* — *H. stagnolis* and *H. ulvae*; but the floristic elements seem to be more specific. These are *Enteromorpha* and *Chaetomorpha* from the greens, from the Diatoms e.g. *Amphora coffaeiformis* and *Navicula haliphila*, from the bluegreens two or three species of *Spirulina* and especially the mat-forming cosmopolitan *Microcoleus chthonoplastes* THUR. From our own collections as well as from the material of the Rijksherbarium, Leiden we obtained the following list of localities for the latter: Europe, North America, North and East coast of Africa, British India, Samoa, Dutch East Indies, Australia. As other elements we may mention the curious *Eutreptia viridis* PERTY, var. *Schizochlora* ENTZ, found in Siebenburgen by ENTZ, and appearing again in California and Setubal!

The „*Ruppion maritimae*”, while cosmopolitan and, as far as its floristic elements are concerned, rigidly specific still shows, in its faunistic components certain regional (i. e. non-cosmopolitan) traits. Apparently even at salinities of 10 % the milieu is not yet sufficiently specific to determine all components unambiguously.

A milieu both sufficiently extreme (exceeding the general potentialities of most organisms) and specific (exceeding the specific potentialities of most organisms) may be found in hot springs, in excessively alkaline or acid lakes and also in saturated brines. The second author has been carrying out a comprehensive study of these brines from various localities all over the world and from this study it

appears that this biocoenosis is identical whether the brines are studied in North America, South America, Australia, Asia or Europe. The characteristic organism here appears to be a green polyblepharid flagellate, *Dunaliella viridis* TEODORESCO and the community may be designated as a „Dunaliellon”. Drawing only from personal experience, the occurrence of this community was observed in Argentine, Brazil, Venezuela, West Indies, California, Nevada, Utah, Portugal, Italy, Roumania, Hungary, Crimea, Palestine, Egypt, Tunis, Algiers, Djibouti, South Africa, Java, Madoera, Gobi-desert, Hawaii, South Australia, Victoria.

This Dunaliellon is further characterized by the occurrence of another polyblepharid flagellate, *Asteromonas gracilis* ARTARI (Crimea, Portugal, California, Brazil), by a bluegreen, *Aphanocapsa salina* FRÉMY and by a group of colourless flagellates, originally described by NAMYSŁOWSKY (12) and ENTZ (4). Curious salt-loving bacteria (e. g. *Micrococcus morrhuae* KLEBAHN) and Fungi (*Oospora halophila* v. BEYMA THOE KINGMA) occur also. The selective factor is, in this case, the salt-concentration.

When, for a certain organism other factors (alkalinity, ionic proportions, temperature) may be limiting but not NaCl-concentration as such, we observe, even in concentrated brines, a group of real „die-hards”, the most eurytopic organisms but which, like Achilles, have their vulnerable spot — namely in the rare cases where the terrestrial milieu exceeds their potentialities. Having progressed, in the course of this discussion from the general to the specific we are faced, at this point with the most „general” organisms! *Polytoma uvella*, a colourless biflagellate occurs in freshwater and in salt, in cold water and in hot springs at 42° C. Species of *Amoeba* occur in concentrated brine, in freshwater and in saline hot springs. Bluegreens of the genus *Phormidium* perform the same feat, and also *purple* and *thiobacteria*. Special mention should be made here of the bacteria capable of decomposing cellulose and sulphate anaerobically, for there is no natural solution without them. A large number of *Ciliates* and *Flagellates* and even *Nematodes* and *Flies* are apparently equally unlimited in their potentialities and, therefore, in their distribution. Possibility of universal dispersal is a reality for the majority of living things.

In this case the selective milieu, picking out from the mass of latent life those that show „resonance”, those that are awakened to active development, is all-important. From organisms with a more limited capacity for dispersal the milieu selects as well. The available mass of

organisms is herded into the various biocoenoses. Any new evolutionary unit, whether a mutation or a true-breeding hybrid is weighed by the environmental complex and is found fit or may be found wanting.

It has been most refreshing to us to consider convergence and identity in its relation to dispersal and external environment in this simple Darwinian way. While aware of many partly conflicting theories on this subject, we feel that in the main our trail has been that of the man who sailed in the „Beagle” more than a century ago.

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