

Species change in coastal heathland in the Netherlands.

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Coastal heathland is found in the Netherlands in the dunes with low calcium content. North of Bergen the dune sand is poor in calcium, in contrast to the dunes south of Bergen which are rich in calcium.

This difference in substrate is the cause of the boundary between two phytogeographic districts: the Waddendistrict and the Duindistrict. Heathland is rare on the calcium rich dune sands of the Duindistrict. Only on small localities on the most inland and oldest parts of the dunes, decalcification has gone far enough to permit heathland development.

These small heathlands are poor in species, which makes it difficult to decide whether they belong to the alliance *Empetrium* as do the coastal heaths of the Waddendistrict, or to the *Calluno-Genistion*, the inland heath. *Calluna vulgaris* is the dominant dwarfshrub, *Hypnum jutlandicum* is a species with high constancy in the moss layer. This makes at least one thing clear: the community belongs to the heathland order of *Vaccinio-Genistetalia*. The absence of *Genista* and *Lycopodium* species makes it difficult to place it in the *Calluno-Genistion*. But the lack of *Empetrum* causes the same problem toward the *Empetrium*. The only species that can help is *Carex arenaria*, pointing into the direction of *Empetrium*. But the *Empetrium* itself is poorly characterised. This alliance has no charactic species, only a ken-combination of *Empetrum nigrum* and *Carex arenaria*. As the most important of these two, the ericoid dwarfshrub, is absent it must be concluded that the small heathlands of the Duindistrict are fragmental communities of *Empetrium*.

The explanation could be that shrub development is not yet far enough to carry fully developed *Calluno-Genistion* communities. Decalcification and subsequent podzolisation might be still too superficial. In South-England fully developed heathland communities are found on the chalk hills of the Downs. But these are much older and the precipitation surplus is higher, thus the soil is much deeper leached out.

Another point which has to be explained is that most of the differential species are absent too. Coastal heath differs from inland heath mainly by species of relatively nutrient rich soils, e.g.: *Genista tinctoria*, *Lotus corniculatus*, *Calamagrostis epigejos*. This could bring us to the hypothesis that leaching has gone so far that coastal species are absent, but soil development is not far enough for inland species. The absence of *Empetrum* however, is a climatic question. These small heathlands have no north slopes because the old dune ridges have hardly any relief, and they are outside the distribution area of the species.

The two dominants

The presence or rather the dominance of *Empetrum nigrum* is very characteristic of the heathlands of the Waddendistrict. In the inland heath *Empetrum* can also dominate, but very local. This raises the question why this boreal and montane species is so much more successful in coastal heath than in the inland heath. If it is a climatic factor that makes *Empetrum* more successful than *Calluna*, it must be the cool summer, as the mild atlantic winters will certainly not much help a boreal species.

The cool summers are particularly important to *Empetrum* in the juvenile phase. There is evidence that to germinate and establish, *Empetrum* needs bare soil that stays wet during the growing season. Such permanent wet bare situations do occur in dune valleys where windblown dune sand has been deposited on wet places. This demonstrates the importance of the dynamic of the dunes as an ecological factor.

This explains also why *Empetrum* on its inland localities prefers also sand dunes above stable localities that can be recognized by their well developed soil profile. It is not the podzol profile that hampers *Empetrum*, the profile is a result of long stability and this stability offers little chance to *Empetrum*. *Empetrum* can easily grow when it is partly buried by a sand blow. It produces new roots on the branches that can be several meters long. *Calluna* however has great difficulty to survive in moving sand.

Calluna requires for germination the opposite of fresh blown sand, namely fixed sand with a high humus content. Also in their response to fire the two dwarf shrubs behave as opponents. Fire kills *Empetrum* and does not stimulate regeneration in any sense. *Calluna* however is a real pyrophyte. It has deep lying buds at the stem base. Nicely protected against the heat of the fire, ready to sprout and produce flowers and seeds within a year. Only stems older than eight years have difficulty to make new sprouts because the buds are buried too deep in the xyleme. But then the huge numbers of *Calluna* seeds begin to germinate. Ten to thirty thousand per square meter, strongly stimulated to germinate by the short exposure to heat. (DE SMIDT, 1995)

What does this explain in the balance between *Empetrum* and *Calluna*? Fire is a traditional part of human use of inland heath. To produce fresh food for the sheep it was regularly burnt. This expelled *Empetrum* from the inland heaths. This effect is clearly demonstrated in the Dwingelose heide. This heath burned in the dry summer of 1959. Just a few years before a herd of Drenthian heathland sheep was established. After the fire the sheep found hardly anything to eat and trampled the bare soil every day in search of some green leaves. The area turned into a dust bowl. But then came the extreme wet years 1961-1968. There was plenty of bare soil, staying wet all over the summer and there was a mass germination of *Empetrum* seeds. Thanks to no more burning since 32 years the heath has now a strong dominance of *Empetrum* on podzol soil.

Change in management and effect on species composition

In the coastal dunes, farmers and villagers did not burn the plant cover. They stripped it off the dunes and carried it to the village as fuel and fodder. This kept the dynamics of the dunes at a high level. *Empetrum* was able to maintain itself, at least on some places. For *Calluna* the environment was hostile. Only at the land inward border of the dunes *Calluna* had a refuge. The villagers protected their crop fields and vegetable gardens against moving dunesand with a buffer zone. In this zone, the vegetation was kept intact. There *Calluna* could become the co-dominant together with *Empetrum*. WESTHOFF (1991) described this situation as the starting point of the development of dune heath. This starting point, at the beginning of this century, was due to the decision of the government to forbid the stripping of dune vegetation. From that moment onward both *Empetrum* and *Calluna* spread over the dunes. Also *Erica tetralix* heath developed, in the wet dune slacks.

WESTHOFF started the study of these communities in 1936. By that time existed already more or less closed patches of heathland. Physiognomically they were heathland, but as a community they were still unsaturated.

The floristic development of these communities can be studied by comparing vegetation tables from different periods since. WESTHOFF calls this analysis of community development synepiontology. This branche of vegetation science differs from synchronology which uses palynological methods and is therefore also called paleo-ecology. It differs also from syndynamic studies as these are based on permanent plot studies.

Synepiontology studies the changes in time by means of vegetation tables as complete as possible from different moments. The question to be answered is not to reconstruct the plant cover in ancient times (paleo-ecology, synchronology), nor the changes in a community (syndynamic). Synepiontology seeks to answer the question how a certain community came into statu nascendi and subsequently in saturated species composition. In his recent paper (1991) WESTHOFF took the development of dune heath as an example of synepiontology. He demonstrated this in changes in the syntaxonomy. WESTHOFFS research of the nineteen thirties resulted in the description of four associations of dune heath.

Two associations of *Empetrium*.

1. *Polypodio-Empetretum* with *Polypodium vulgare* and *Empetrum nigrum* on north slopes.
2. *Pyrolo-Salicetum* in humid dune slacks, developed from *Junco baltici-Schoenetum nigrican-tis* by acidification and drainage of the soil.

One association of *Calluno-Genistion*.

3. *Empetro-Genistetum tinctoriae* with two subassociations:
 - a) *caricetosum arenariae* with *Carex arenaria*
Lotus corniculatus
 - b) *molinetosum* with *Potentilla erecta*
Molinia caerulea
Lotus uliginosus

Finally one association of the class *Oxycocco-Sphagneteta* in the alliance *Ericion tetralicis*.

4. *Empetro-Ericetum* of wet dune slacks.

Syneptionology is best demonstrated on the association *Empetro-Genistetum tinctoriae*.

The extensive tables from BARENDREGT (1982) made it clear that the two subassociations of *Empetro-Genistetum tinctoriae* had become two separate associations: *Carici-Empetretum* of dry heath and *Salici-Empetretum* of humid heath, both belonging to *Empetrium*.

To understand the mechanisms of this change, it is of interest to compare the species composition of the early phase with that of the later phases. The change in species composition is documented for the humid dune heath (table 1 and 2) and for the wet dune heath (table 3).

To make sure that data are actually comparable, the original relevés were used instead of synoptic relevés. This explains the difference between WESTHOFFS and our lists of decreased and increased species. The main conclusion, however, remains the same.

Three sets of relevés are compared all from the Frisian Islands. The earliest set, from the nineteen thirties, derives from an unpublished manuscript from WESTHOFF (1947). The most recent set is from the seventies, published by BARENDREGT (1982). From the intermediate sixties, a number of relevés are selected of *Salici-Empetretum typicum*, published by DE SMIDT (1977). For the selection of relevés were used the characteristic species combination of *Salici-Empetretum typicum*, *Salici-Empetretum orchidietosum* and *Salici-Empetretum gymnocoleto-sum* (BARENDREGT, 1982).

The syneptionological study indicates the same direction of change in the three syntypes. The decreased species are mainly meso-productive herbs graminoids and cryptogams from species rich gradients in near neutral soil conditions. The increased species are mainly low productive cryptogams and graminoids from more acid and oligotrophic soil conditions. The overall change in these almost 50 years is the conversion of coastal heath toward inland heath. This is the effect of the loss of mainly *Empetrior*s and *Calluno-Genistrior*s species.

This change can be explained as the effect of three different processes. A natural process is the leaching of calcium and subsequent lowering of pH by rain water which is enhanced by the heath vegetations itself through the acids of the raw humus. The two other processes are part of the affection of the environmental quality by acid rain and dessication through dropping of the water table. Leaching is speeded up by the acid rain and can affect the root layer to a greater depth because of the lower water tables. Indicators of this acidification are in particular the monocotyledons *Carex arenaria*, *Calamagrostis epigejos*, *Luzula campestris* and *Eriophorum angustifolium* and the mosses *Hypnum jutlandicum*, *Dicranum scoparium* and *Pleurozium schreberi*.

As nearly allways in nature, other processes complicate the situation. The ban on stripping of the dunes also means ageing of the vegetation and consequently less space for species of younger succession phases. This could explain the disappearance of species such as *Drosera rotundifolia*, *Peltigera canina*, *Drepanocladus uncinatus* and *Zygogonium ericetorum*.

Confirmation of the relation between neutral conditions and the presence of species in coastal heath that are absent or rare in inland heath, can be obtained from heath on cliff coasts in Southwest Europe. OUDHOF and BARENDREGT (1987) found dry heath on rocky coasts

Table 1: SALICI-EMPETRETUM subass. typicum

Author	Westhoff	de Smidt	Barendregt
Data from	1937-1940	1960-1967	1976-1978
number of relevés	19	34	19
<u>decreased resence</u>			
<i>Calluna vulgaris</i>	100	44	63
<i>Genista tinctoria</i>	63	41	32
<i>Luzula multiflora</i>	26	35	5
<i>Anthoxanthum odoratum</i>	37	32	5
<i>Eurhynchium praelongum</i>	21	24	5
<i>Agrostis tenuis</i>	11	15	0
<i>Lotus uliginosus villosus</i>	26	21	0
<i>Agrostis canina</i>	16	6	0
<i>Rhytidiadelphus triquetrus</i>	11	0	0
<i>Juncus conglomeratus</i>	11	0	0
<u>increased resence</u>			
<i>Carex arenaria</i>	26	65	95
<i>Hypnum jutlandicum</i>	53	79	100
<i>Dicranum scoparium</i>	47	62	89
<i>Pleurozium schreberi</i>	16	35	63
<i>Lotus corniculatus</i>	16	18	32
<i>Hypogymnia physodes</i>	16	18	32
<i>Lophocolea bidentata</i>	0	59	68
<i>Cladonia chlorophaea</i>	0	21	53
<i>Cladonia portentosa</i>	0	12	53
<i>Luzula campestris</i>	0	18	32
<i>Cladonia furcata</i>	0	6	32
<i>Poa pratensis</i>	0	9	16
<u>almost stable resence</u>			
<i>Empetrum nigrum</i>	89	94	95
<i>Salix repens</i>	95	97	100
<i>Erica tetralix</i>	95	85	79
<i>Potentilla erecta</i>	68	71	53
<i>Festuca ovina tenuifolia</i>	47	68	58
<i>Carex trinervis</i>	74	44	84
<i>Genista anglica</i>	68	29	58
<i>Calamagrostis epigejos</i>	53	74	68
<i>Pseudoscleropodium purum</i>	21	44	26
<i>Hieracium umbellatum</i>	32	6	26
<i>Molinia coerulea</i>	26	3	16
<i>Rosa pimpinellifolia</i>	21	3	11
<i>Holcus lanatus</i>	16	26	11
<i>Hypnum lacunosum</i>	1	6	11
<i>Betula pubescens</i> juv.	21	0	11
<i>Agrostis stolonifera</i>	16	41	11
<i>Danthonia decumbens</i>	16	29	11

Table 2: SALICI-EMPETRETUM subass. orchidietosum

Author	Westhoff	Barendregt
Data from	1937-1940	1976-1978
number of releves	5	9
<u>decreased resence</u>		
Pedicularis sylvatica	100	0
Eurhynchium praelongum	80	0
Cladonia gracilis	60	0
Brachythecium rutabulum	60	0
Luzula multiflora	100	33
Drepanocladus uncinatus	60	11
Peltigera canina+polydactyla	80	33
<u>increased eresence</u>		
Dicranum scoparium	0	89
Lophocolea bidentata	0	89
Carex arenaria	0	78
Pleurozium schreberi	0	78
Cladonia portentosa	0	56
Cladonia chlorophaea	0	56
Cladonia glauca	0	33
Luzula campestris	0	44
Danthonia decumbens	0	33
Calamagrostis epigejos	20	56
Hypnum jutlandicum	60	100
<u>almost stable resence</u>		
Dactylorhiza maculata	100	100
Empetrum nigrum	100	100
Carex trinervis	100	100
Salix repens	100	100
Erica tetralix	100	100
Pseudoscleropodium purum	40	33
Potentilla erecta	40	44
Platanthera bifolia	40	44
Calluna vulgaris	40	44
Lotus corniculatus	40	33
Juncus arcticus balticus	40	22
Oxycoccus macrocarpos	80	78

Table 3: SALICI-ERICETUM* subass. gymnocoletosum

Author	Westhoff	Barendregt
Data from	1937-1940	1976-1978
number of relevés	6	21
decreased resence		
<i>Juncus arcticus balticus</i>	67	10
<i>Drosera rotundifolia</i>	83	14
<i>Zygogonium ericetorum</i>	67	24
<i>Pedicularis sylvatica</i>	83	14
<i>Dactylorhiza maculata</i>	17	5
<i>Sphagnum compactum</i>	33	0
<i>Peltigera canina</i>	50	0
increased resence		
<i>Gymnocolea inflata</i>	0	57
<i>Eriophorum angustifolium</i>	0	52
<i>Agrostis canina</i>	0	43
<i>Polytrichum commune</i>	0	43
<i>Festuca ovina tenuifolia</i>	0	38
<i>Juncus conglomeratus</i>	0	33
<i>Sphagnum fimbriatum</i>	0	29
<i>Danthonia decumbens</i>	0	24
<i>Dicranum scoparium</i>	0	24
<i>Cephalozia bicuspidata</i>	0	14
<i>Hypnum jutlandicum</i>	17	43
almost stable resence		
<i>Erica tetralix</i>	100	100
<i>Carex trinervis</i>	100	100
<i>Salix repens</i>	100	100
<i>Empetrum nigrum</i>	67	52
<i>Potentilla erecta</i>	83	71
<i>Oxycoccus macrocarpos</i>	67	76
<i>Hydrocotyle vulgaris</i>	67	57
<i>Molinia coerulea</i>	50	57
<i>Calamagrostis epigejos</i>	50	43
<i>Calluna vulgaris</i>	67	38
<i>Platanthera bifolia</i>	17	10
<i>Anthoxanthum odoratum</i>	17	14
<i>Aulacomnium palustre</i>	17	33
<i>Cephaloziella divaricata</i>	50	30
<i>Juncus alpino-articulatus</i>	33	24
<i>Drepanocladus uncinatus</i>	33	29
<i>Agrostis stolonifera</i>	33	33
<i>Carex panicea</i>	50	24

* Synonym of Empetro-Ericetum

to be differentiated by the species group: *Holcus lanatus*, *Festuca rubra*, *Lotus corniculatus* and *Daucus carota*. Again a mesotrophent species group of near neutral conditions separates the coastal heath from the inland heath. These species are restricted to the zone with marine spray, which compensates acidifying processes.

Conclusion

Coastal heath is separated from inland heath by mesotrophent species that find their optimum in natural or semi-natural species rich grasslands on relatively poor soil, e.g. *Violion caninae*.

These species find suitable conditions in dunes as long as acidifying processes have not yet strongly reduced the acid buffer of the soil. On cliffs this process is compensated by marine spray. Dunes receiving marine spray are too mobile to carry heath vegetations. The leaching in humid and wet dune heath is hampered by periodically high water tables.

New habitats not only need time to come in the right abiotic conditions for heath vegetation, they also need time until the full set of species has reached the location. This process can occur on a regional scale as was the case on the Frisian Isles and then lead to the formations of new syntypes.

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