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The separation of fluctuation and long-term change in vegetation dynamics of a rising seashore*

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Abstract

Field layer vegetation in four transects across a rising seashore of the island Skabbholmen (59°47′N, 19°12′E) in the Stockholm archipelago, eastern central Sweden, was sampled at the beginning and end of a six-year period. The data were analyzed by canonical correspondence analysis (CCA) with two external predictor variables, year of sampling and elevation (a proxy for the longer-term trend of change). During the sampling period, the vegetation changed in the direction of the longer-term trend at a rate consistent with the known rate of land uplift. However, a major part of the observed change was in a different direction, reflecting a shorter-term response to disturbance. The analysis effectively separated different types of floristic dynamics related to processes with different time-scales. A comparison with (unconstrained) correspondence analysis (DCA) illustrated the interpretive advantages of multivariate direct gradient analysis over conventional floristic ordination.

Introduction

There is a large amount of data on the general trend of long-term vegetation change on rising Baltic and Bothnian seashores (Ericson & Wallentinus, 1979). These data mainly come from repeated sampling of the shore vegetation zonation during long periods (11–30 years, e.g., Brunberg-Schwanck & Bärlund, 1948; Schwanck, 1974; Ericson, 1980), and repeated floristic inventories on rising islands (e.g., Valovirta, 1937; Luther, 1961; Vartiainen, 1980). On a time-scale of tens to hundreds of years, field layer species populations have been shown to 'migrate' downwards along the sea-land gradient at about the same speed as new land emerges from the sea (Ericson, 1981). Also establishment of more long-lived woody species tracks the downward trend in relative sea level (Cramer, 1985; Verwijst & Cramer, 1986).

On a shorter time-scale (< 10 years), the shoreline does not move smoothly, but is subject to fluctuations caused by different years' weather conditions. During short periods, sea level may be seen more as providing a disturbance regime with irregu-

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* Vascular plant nomenclature follows Tutin *et al.*, Flora Europaea, except for *Deschampsia cespitosa* (L.) Beauv. spp. *bottnica* (Wahlenb.) G. C. S. Clarke, which is named *D. bottnica* (Wahlenb.) Trin.

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larly recurring catastrophic destruction of the established vegetation (White, 1979) than as a continuous environmental change. Some data have been published on the short term responses of species populations to sea level changes (Ericson, 1980, 1981). We present here an application of a general technique to study such changes on a community level and to see whether the long-term trend of vegetation composition (as reflected in the spatial changes along the transect) can be separated from the short-term changes observable during six years.

Analysis of vegetational variation in space and time

Multivariate analyses of floristic data from more than one point in time have followed two principal lines:

1. The 'classification approach' clusters the samples and estimates transition frequencies between clusters, either based on the structure of the first analysis [e.g., Williams *et al.*, 1969; Londo, 1974; Persson, 1984], or on the structure of all samples at all sampling dates (e.g., Van Noordwijk-Puijk *et al.*, 1979; Persson, 1980; Austin & Belbin, 1981; Zhang, 1984). The two variants have been discussed by Williams *et al.* (1969). Transition diagrams often form comprehensible summaries of such studies, but it may be difficult to apply the approach to data with continuous floristic variation.
2. The 'ordination approach' locates all samples (from all sampling dates) in a multidimensional space on the basis of differences in species composition. The location of the samples from the same site but from different dates are compared graphically, e.g. by drawing time trajectories (Van der Maarel, 1969, 1975, 1980; Austin, 1977; Persson, 1980, 1984; Van Hecke *et al.*, 1981; Zhang, 1984; Gunnlaugsdottir, 1985). Such diagrams give an impression of the relative rate of change of species composition of the sites and of the increase or decrease of individual species' abundances. Information about the underlying processes can be gained by correlating the ordination axes with known environmental gradients ('indirect gradient analysis').

This approach is in fact a simplification of a three-dimensional (species × sites × times) matrix (c.f., Williams & Stephenson, 1973). Swaine & Greig-Smith (1980) noted the difficulty in separating temporal change from environmentally determined gradients in such ordinations and provided a mathematical method to overcome this.

An extension of the ordination approach is provided by a new technique for multivariate direct gradient analysis, namely canonical correspondence analysis (CCA – Ter Braak, 1985, 1986, 1987). CCA combines the analysis of floristic gradients with external (often environmental) data for the sites. The axes extracted by CCA represent those directions of variation in species composition that are related to supplied external variables. Like its parent method, correspondence analysis (Hill, 1979a; Hill & Gauch, 1980), CCA can be combined with a detrending to remove arch effects.

In our study, the continuous appearance of both the spatial floristic gradients and the long-term trend, suggested the application of a gradient analysis technique. We therefore applied (detrended) CCA (DCCA) with two external variables, standing for two scales of change: (1) elevation (in the first sampling season – 1978) as a proxy for each sample's location on the long-term trend, and (2) year with the states '0' for the first sampling 1978 and '6' for the second in 1984, as an index of the actual change during our six-year period of observation. Thus, we aimed for an ordination of the entire data which would explicitly indicate the extent of congruence between floristic variation related to elevation (and therefore to the long-term trend caused by land uplift) and to shorter-term changes in the environment.

Materials and methods

Study area

The island Skabbholmen is situated in the northern Stockholm Archipelago (59°47′N, 19°12′E). The region falls into the boreo-nemoral zone (Sjörs, 1963) and belongs to the inner archipelago ('the coniferous forest zone', cf. Du Rietz, 1925).

Vegetation sampling

In 1978 and 1984 we sampled the field layer vegetation of (in total) 135 1-m^2 plots (in the following called 'sites') along 4 transects, all running from slightly below mean water level into old-growth forest. The transects were chosen to represent different degrees of exposure and different vegetation gradients. Under the tree canopy, the vegetation was sampled in June, when the field layer of these spring – geophyte woodlands is maximally developed. The shore vegetation was sampled in early August. The sites were placed adjacent to each other in the open vegetation of the shore and the nearby woodland, and with 5 m-spaces in the forest. In each site, we noted vascular plants with cover degrees of the ordinal five-degree Hult – Sernander – Du Rietz scale. The total moss cover was estimated in %.

Geomorphic dynamics of the shore and fluctuations in water level

The eastern shore of Skabbholmen is exposed to 'Havssvalget', a several km wide strait where relatively high storm waves can develop. Most of this shore belongs to the type 'moderately exposed shore' (Cramer, 1980) and is characterized by a coarse, stony substrate indicating that erosion is more common than accumulation in the wave-wash zone. There are no conspicuous cliffs. In shallow bays, some sandy and organic material accumulates.

No tides with relevance to shore vegetation occur in the Baltic. Seasonal water level fluctuations usually result in a continuous lowering of water level during winter, with a minimum around May, then a rather rapid increase during summer, followed by an unstable period during autumn and the yearly maximum around the end of the year. Differences from year to year are great (Fig. 1). On a longer time-scale, post-glacial isostatic land uplift causes an apparent lowering of sea-level, at a rate of ca. 5.0 mm/yr in the study area (calculated from Åse (1964). Due to eustatic changes, this relative land uplift rate has changed during historical times, but the differences have been small during the last 200–300 years (Åse, 1980).

Sampling of environmental data

At both sampling dates (1978 and 1984), we estimated percentage of cover of stones (>2 cm) at the soil surface, of (allochthonic) drift material and of (autochthonic) plant litter. We measured elevation above present water level for each site in August 1984. For comparison of the habitat characteristics of seashore plants during the period of 1975–1984, we compared water levels of the period August 1975–July 1978 with those of the period August 1981–July 1984, i.e. for the three-year-periods prior to each of our samplings (Fig. 1). Data were obtained from the tide-gauge 'Forsmark', 85 km NNW of Skabbholmen. The data were transformed for the difference in relative land uplift between the tide gauge and the study area, by subtraction of (1.1 × 'No. of years since 1970') mm.

Data analysis

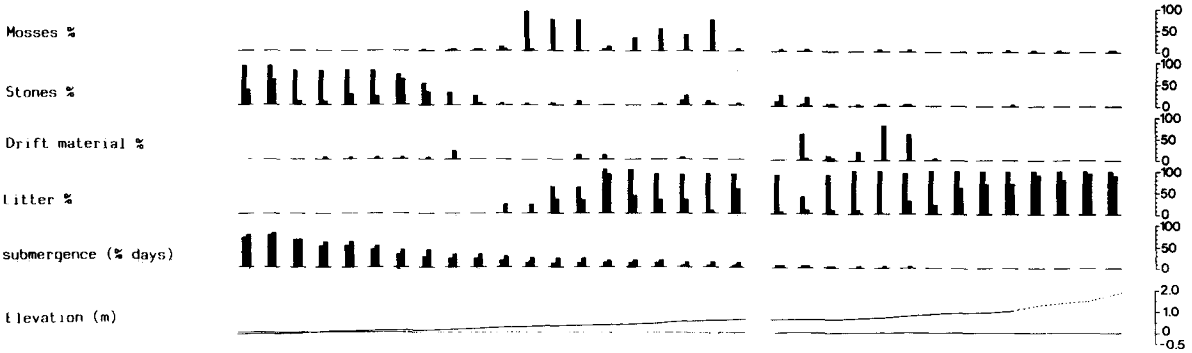
To remove the largest and most obvious part of floristic heterogeneity in the data set, we separated the main matrix into two subsets, 'shore' and 'forest'. All subsequent calculations were based on these two subsets, comprising (after removal of 3 sites that had no vegetation at either sampling date) 63 and 69 sites respectively. The borderline between these units was drawn on the basis of a TWINSPAN – analysis (Hill, 1979b) of the 1978 material.

Our application of CCA involved the same straightforward matrix simplification as was discussed above (each observation = one sample), but now combined with the treatment of elevation and year as external variables. We treated change along the elevation gradient as an estimate of the long-term average rate of vegetation change (evidence supporting this assumption for woody species populations in the same environment is given by Cramer (1985, 1986); Verwijst & Cramer, (1986). The introduction of elevation as an external variable in CCA required the ordination scores to be a linear combination of both elevation and year. Note that elevation had been measured only once – this implies that elevation and year were essentially uncorrelated in this treatment. Elevation and year can thus be seen as expressions of floristic change on different time-scales: elevation corresponding to the longterm trend caused by land uplift, and year referring to the actually observed change in species composition during a six year period. Slopes and approximate significances of the relations between these variables and the ordination scores are given in the standard output.

Investigation of the regression between species scores and the two external variables should then allow one to see to what extent the overall change in floristic composition during six years is due to the long-term trend or to other processes causing fluctuations on shorter time-scales. A more spatially detailed analysis can be made by comparing locations for sites in the two different years in the ordination diagram and relating these time trajectories to more local changes in environment.

Table 1. Transect 3, comparison table. In all columns the left entry is the 1978 value, the right one is from 1984. Species abundances according to the ordinal five-degree Hult – Sernander – Du Rietz scale. Plot numbers indicate distance from lowest plot in transect. Submergence calculated as percentage of all daily means during three years prior to each sampling.

Plot number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	35	40	45	50
Aster tripolium	11	11	11	11	11	11	11	1.	11	1.	1.	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Triglochin maritima	11	11	11	11	2.	11	31	11	11	11	11	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Agrostis stolonifera	11	11	11	11	11	11	21	21	11	11	.1	.1	11	..	.1	11	1.	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Deschampsia bottnica	..	11	.1	.1	11	11	31	31	1.	11	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Eleocharis uniglumis	..	11	11	21	31	21	21	41	11	1.	11	1.	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Glaux maritima	..	..	.1	11	11	11	11	12	12	12	11	11	11	11	1.	1.	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Juncus gerardi	..	..	..	.1	.1	.1	.1	11	11	31	31	31	11	11	11	11	1.	1.	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Plantago maritima	..	..	..	..	..	1.	1.	1.	11	1.	11	1.	11	1.	1.	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Scirpus lac.ssp.tabernaem.	..	..	..	..	..	.1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Juncus articulatus	..	..	..	..	..	.1	.1	.1	11	11	11	11	1.	11	11	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Agrostis gigantea	..	..	..	..	..	..	.1	..	.1	.1	11	11	11	11	31	31	21	11	12	11	12	12	.1	.1	..	..	..	..	..	..	..	..	..	..
Carex extensa	..	..	..	..	..	..	..	21	11	1.	1.	11	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Festuca rubra	..	..	..	..	..	..	..	.1	.1	.1	11	23	43	4.	34	13	11	11	11	1.	.1	..	..	..	..	..	..	..	..	..	..	..	..	..
Plantago major	..	..	..	..	..	..	..	.1	..	1.	1.	..	..	..	..	..	1.	.1	..	..	..	..	..	.1	..	..	..	..	..	..	..	..	..	..
Filipendula ulmaria	..	..	..	..	..	..	..	..	11	1.	11	.1	.2	.1	11	23	24	13	13	14	25	13	15	15	24	11	12	14	12	1.	..	1.	..	..
Centaurium littorale	..	..	..	..	..	..	..	..	.1	..	11	11	1.	1.	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
C. pulchellum	..	..	..	..	..	..	..	..	.1	..	11	1.	.1	.1	..	..	..	.1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Parnassia palustris	..	..	..	..	..	..	..	..	.1	.1	11	11	11	11	11	11	11	11	11	.1	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Odontites verna ssp.litor.	..	..	..	..	..	..	..	..	..	1.	1.	1.	1.	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Leontodon autumnalis	..	..	..	..	..	..	..	..	..	.1	11	11	11	11	1.	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Samolus valerandi	..	..	..	..	..	..	..	..	..	.1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Calamagrostis stricta	..	..	..	..	..	..	..	..	..	.1	.1	..	.1	.1	.1	.1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Lythrum salicaria	..	..	..	..	..	..	..	..	..	..	1.	11	11	11	.1	1.	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Alnus glutinosa seedlings	..	..	..	..	..	..	..	..	..	..	.1	.2	..	11	..	..	..	.1	.1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Sagina nodosa	..	..	..	..	..	..	..	..	..	..	..	1.	1.	1.	1.	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Carex serotina ssp.pulch.	..	..	..	..	..	..	..	..	..	..	..	1.	1.	1.	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Sagina procumbens	..	..	..	..	..	..	..	..	..	..	..	1.	..	1.	..	..	.1	11	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Valeriana salina	..	..	..	..	..	..	..	..	..	..	..	1.	..	..	..	.1	..	11	11	1.	1.	..	..	..	..	..	..	..	..	..	..	..	..	..
Fraxinus excelsior seedl.	..	..	..	..	..	..	..	..	..	..	..	1.	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.	11	..	..	..	..	..	..
Potentilla anserina	..	..	..	..	..	..	..	..	..	..	..	1.	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Galium palustre	..	..	..	..	..	..	..	..	..	..	..	.1	..	..	..	..	11	11	1.	1.	..	..	..	..	..	..	.1	..	..	..	..	..	..	..
Taraxacum vulgatum coll.	..	..	..	..	..	..	..	..	..	..	..	..	1.	..	..	..	..	..	..	.1	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Angelica sylvestris	..	..	..	..	..	..	..	..	..	..	..	..	11	.1	11	11	..	31	31	41	2.	11	11	21	.1	..	.1	..	..	..	..	..	..	..
Calamagrostis epigejos	..	..	..	..	..	..	..	..	..	..	..	..	.1	11	11	41	51	21	21	31	31	11	1.	31	1.	1.	..	..	..	..	..	..	..	..
Hierochloe odorata	..	..	..	..	..	..	..	..	..	..	..	..	.1	.1	.1	.1	.1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Ophioglossum vulgatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	.1	.1	.1	.1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Rubus caesius	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	.1	.1	12	13	12	11	.1	.1	..	..	..	..	..	..	..	..	..	..
Moehringia trinervia	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.	..	..	..	..	.1	.1	.1	..	..	..	..	..	..	..	..	..
Rubus idaeus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	.1	.2	.3	22	23	31	33	12	13	.2	.1	.3	13	..	..	..	1.
Sonchus arvensis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	.1	..	1.	..	..	..	..	..	..	..	..	..	..	..	..	..
Cerastium fontanum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	.1	.1	1.	..	..	..	.1	..	..	..	.1	..	..	..	..	..
Stellaria media	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Elymus caninus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.	1.	11	.1	.1	.1	..	.1	..	..	..	..	..	..	..
E. repens	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	.1	.1	..	.1	.1	..	..	..	..	..	..	..	..	..	..
Silene dioica	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	.1	1.	..	.1	..	1.	1.	..	..	..	..	..	1.	..	..
Mercurialis perennis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.	21	11	51	55	51	53	53	54	55	55	55	55
Allium ursinum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.	1.	4.	44	53	55	55	55	54	55	55	55
Cirsium arvense	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	.1	.1	.2	..	..	..	..	..	..	..	..	..
Milium effusum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.	..	..	..	..	.1	..	..	..	..
Stachys sylvatica	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	.1	.1	.1	..	.1	.1	1.	11	.1	..
Dactylis glomerata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	.1	..	..	..	..	..	..	..	..
Anemone nemorosa	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	.1	1.	11	22	24	55	54	44
Corydalis spp.	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	.1	.1	11	11	11	.2	12	11
Gagea lutea	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	.1	..	.1	.1	11	.1	.1	.1
Acer platanoides seedl.	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	.1	..	.1	.1	1.	..	..
Paris quadrifolia	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1.	.1	1.	.1	..	..
Ranunculus auricomus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	11	1.	..
Urtica dioica	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2.	1.
Ranunculus cassubicus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	11	..



Results

Vegetation of the lower shore

Instead of showing distinct vegetation belts, shore plant populations (in both years) generally had overlapping distributions (cf. Table 1). Lowest on the shore, *Eleocharis uniglumis* dominated, gradually passing over to a *Juncus gerardi* belt. Higher up, *Festuca rubra* dominated. In the shade of the outermost *Alnus glutinosa* bushes, *Calamagrostis epigejos, Filipendula ulmaria* and *Angelica sylvestris* were prominent. In the more sheltered transects, a *Phragmites australis* community occurred, partly in dense stands with hardly any other vascular plant species, partly with more scattered individuals mixed with *Scirpus lacustris* spp. *tabernaemontani, S. uniglumis* and *Galium palustre.*

In the most exposed transect, the lowest parts (at and slightly above mean water level) were poor in species with *Deschampsia bottnica* and also *Phragmites.* In the upper parts, a community with *Phalaris arundinacea* and *Sonchus arvensis* had developed.

Vegetation of the woodland zone

The field and shrub layer vegetation in the woodlands close to the open shore was characterized by *Rubus idaeus* and *Elymus caninus. Rubus caesius* was common both on the shore and in the forest. Higher up, *Mercurialis perennis* and *Allium ursinum* dominated. In the sites with dense spruce forest, the field layer consisted mainly of scattered individuals of *Dentaria bulbifera* and *Trientalis europaea.* The more open woodlands of the exposed transects had a field layer more species-rich and with higher species abundances of, among others, *Geranium sylvaticum, Veronica chamaedrys* and *Laserpitium latifolium.*

Environmental change

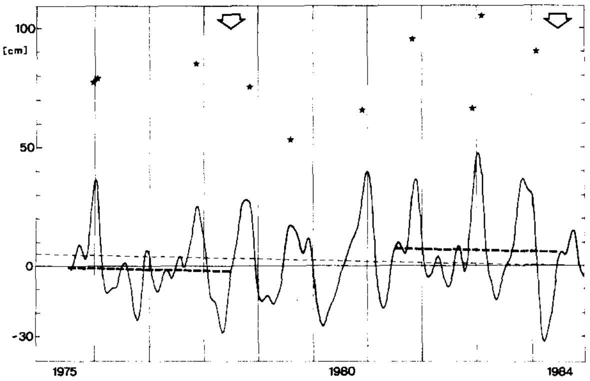


Fig. 1. (Smoothed) curve of water levels at Forsmark, 85 km NNW of the study area from 1975 to 1984. Arrows mark the two sampling dates, stars each year's absolute maximum, the thin dashed line theoretical zero level, the thick dashed lines mean over three year periods prior to each sampling, related to theoretical zero level. Data from the Swedish Meteorological Survey (SMHI).

Time-scales of change. Due to the strong effect of sea levels on the shore environment, changes in habitat conditions can be observed on the various time-scales corresponding to the various time-scales of sea level change (Fig. 1):

1. The seasonal rhythm of low water during spring and summer, variable water levels in late summer and autumn, and high water levels, storm waves and ice-push in winter limit establishment of plants on new areas to early summer and require tolerance against drowning and mechanical destruction for biennial or perennial species.
2. The year-to-year variations of the physical environment, such as water levels, wind velocities, precipitation and radiation, affect the chances for establishment and persistence of coastal plants differentially in different years.
3. The effects of seashore displacement, caused by land uplift, can be observed over periods longer than 10 years and lead to the general apparent 'downward migration of plants' (Ericson, 1980).

Water level changes in the course of our study. During recent centuries, the general trend of land uplift at Skabbholmen resulted in an apparent long-term lowering of sea level of ca. 5.0 mm/yr

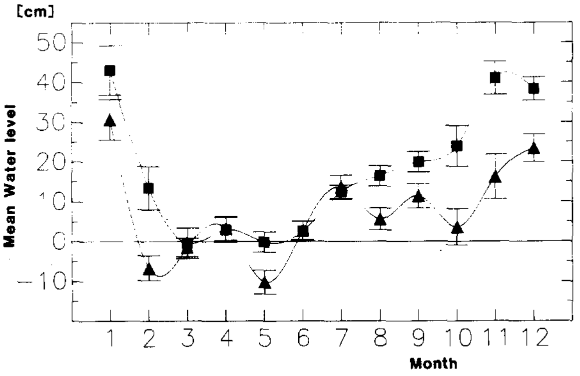


Fig. 2. Mean water levels for months in the three-year periods prior to each vegetation sampling with 95%-confidence intervals. Triangles: July 1975 to June 1978, squares: July 1981 to June 1984. Data from the Swedish Meteorological Survey (SMHI).

(calculated after Åse, (1964)). In the Baltic Sea, there are great differences in mean water level from year to year, however, and these create difficulties in observing the trend of seashore displacement during periods shorter than 10 years.

From the long-term trend, we predicted a mean water level ca. 3 cm lower for the second sampling, compared with the first. Figure 1 shows the difference in the course of water levels during the period 1975 to 1984. The graph illustrates that water levels during the second period have been higher than the predicted value; and in fact higher than during the first period. Comparison of monthly means above theoretical zero level (= mean water level corrected by land uplift, Fig. 2) showed that this difference was levelled out in March, April, June and July; the greatest differences occurred in winter.

Changes in shore geomorphology of the island. We noted the following indications of geomorphological change in the four transects between 1978 and 1984: in transect 3, the stones that 1978 had been bare in the lowest part of the transect (sites 1 to 10) were, in 1984, covered by coarse sand and some drift material. The moss belt in sites 12 to 14 disappeared, another one was now found in sites 16 to 19. The accumulation of drift material around site 22 had been moved to a new belt higher up (sites 24 to 26), leaving more bare stones than before. Much of the litter in this zone was covered by the drift material (Table 1). In transect 4, erosion (most probably during a heavy storm with high water level in January 1983) had affected the middle part, near to the edge of – and inside the woodland: the topsoil had been removed almost entirely, many tree roots now lay bare, and the percentage of stones at the soil surface had increased. In the forest, a new drift accumulation (ca. 20 cm high) was created. In total, there were indications of heavy wave action higher on the shore in 1984 than in 1978. This may be due to both the generally higher water levels in winter and the extreme storm in January 1983.

Field layer response to environmental change

If there is a significant trend of short-term temporal change in species composition of all sites, then the regression coefficient (called the 'canonical coefficient') of time in years on at least one of the ordination axes should be significant. Standardized canonical coefficients and approximate significance levels (as given by CANOCO) are listed in Table 2 for both shore and forest data. The significances show that the first axis is related to both variables in both subsets. The coefficients indicate a strong dominance of elevation on this axis. The second axis is in both cases dominated by year.

Table 2. Canonical coefficients (= standardized regression coefficients of the ordination scores on the external variables) in DCCA of the transect data with year and elevation as external variables.

	Canonical coefficients	
	Shore	Forest
First axis		
Elevation	1.00*	0.68*
Year	0.12*	−0.11*
Second axis		
Elevation	0.04	−0.07*
Year	−0.34*	−0.22*

* significant ($P < 0.05$).

In the ordination diagram (Fig. 3), the main direction of change for each of the external variables in the shore subset is illustrated by the thick arrows in the center of the diagram (called a biplot). The length of these arrows corresponds to the relative importance of these two variables in determining the floristic variation. For the sake of simplicity, only the species and samples from transect 3 are shown in the diagram.

The thin arrows show the actual change of each sample. Relative to the first axis, the direction of these arrows gives an estimate of the relation between six-year change in this site and the main pathway of long-term vegetation change, as far as it can be predicted from elevation. An arrow perpendicular to the first axis indicates that no change corresponding to the long-term trend has occurred at this site. Figure 4 shows the same samples as in Fig. 3, but with numbers to allow their identification with Table 1.

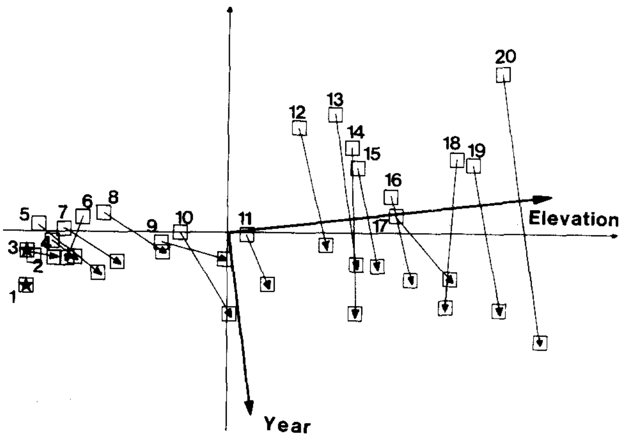


Fig. 4. The site trajectories of transect 3 (shore) with sample numbers, based on the same DCCA ordination of the total shore data as in Fig. 3.

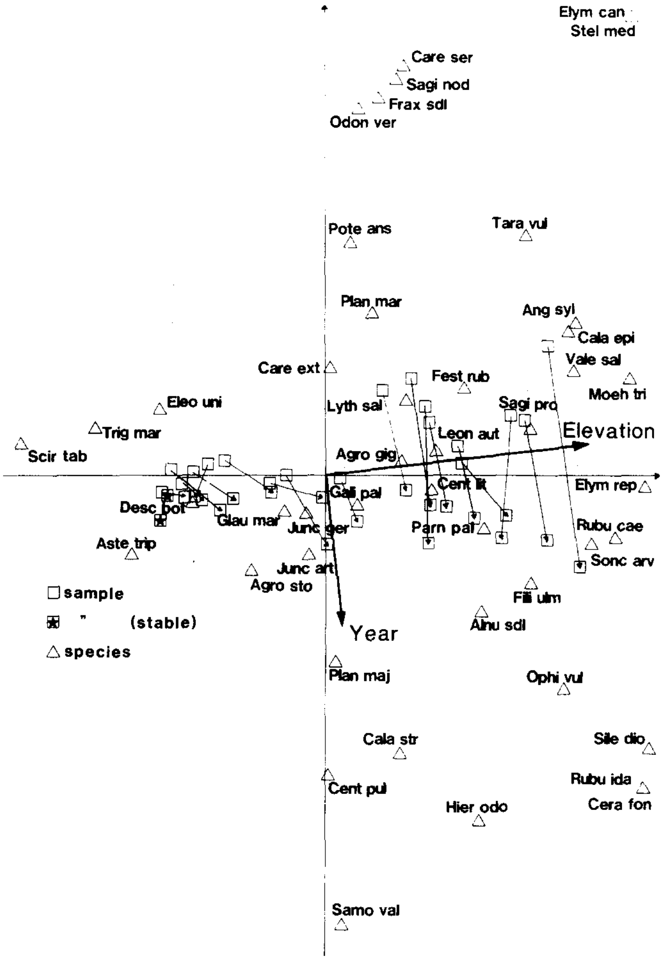


Fig. 3. Diagram of the DCCA ordination for the shore data set (Axes 1 and 2). Triangles mark species occurring in transect 3, squares and thin arrows mark site trajectories of six-year change in transect 3. Thick arrows denote main direction of change and relative importance of the two external variables.

The (standardized) coefficients of the multiple regressions of external variables on ordination scores given in Table 2 can be used to study the relative contribution of the external variables to the dispersion of the sample scores along each of the ordination axes. For this, we calculated the unstandardized coefficients by dividing the standardized coefficients by the standard deviations of the corresponding variables (Table 3).

The resulting equations show the linear combinations of the two variables in their relation to the sample scores:

Table 3. Means and standard deviations for the external variables

	Shore		Forest	
	mean	SD	mean	SD
Elevation (cm)	22.3	18.5	173.0	91.0
Year	3.0	3.0	3.0	3.0

Shore: $x = 0.054\ z_1 + 0.040\ z_2$ (1)

Forest: $x = 0.008\ z_1 - 0.035\ z_2$ (2)

where x is the first axis sample score, z_1 is elevation in cm and z_2 is year in years. x expresses species turnover along the first ordination axis in terms of standard deviations (SD) of the mean species response. The average rate of change along the first axis each site went through from 1978 to 1984 can be estimated by substituting z_1 and z_2 by the elevation and year value for any site in these two years and calculating the difference between the two resulting x-values. As elevation in our model was given the same values for both sampling years, the result will only be dependent on the difference in z_2 values. Substituting 0 and 6 for z_2 will therefore give an average rate of change along the first axis of 0.24 SD (shore) and 0.21 SD (forest).

From the same equations (1) and (2), the ratio of the regression coefficients for year and elevation gives an expression for the average rate of vertical change of species distributions (i.e., the elevation difference that gives an equivalent floristic change as a time lag of one year). The coefficient of variation for this ratio (approximated as the square root of the sum of squares of the two single coefficients of variation) yields 95%-confidence intervals for the results (Ter Braak, pers. comm.):

Shore: 0.74 ± 0.37 cm/yr

Forest: -4.71 ± 3.44 cm/yr

The short-term rate of vertical change of species distributions along the first axis for the shore vegetation was thus (a) different from zero and (b) included the present rate of seashore displacement (0.5 cm/yr). Within the margins of error, we conclude that the shore vegetation had changed significantly during six years in the direction of the long-term floristic trend and that the rate of change in this direction was consistent with the known rate of land uplift.* For the forest vegetation, we attempted no further interpretation of this result, because the negative value and its large confidence interval (resulting from the small regression coefficient with elevation) indicate a low reliability.

The first-axis component of the 'year vector' in Figs. 3 and 4 relates to the change discussed in the previous section. The second, larger component, however, illustrates the relatively large importance of temporal change in floristic composition that is independent from the first component, i.e., changes deviating from the long-term trend. Species in the upper half of the diagram were generally reduced in abundance; those in the lower half gained.

Comparison of direct and indirect gradient analysis

We compared the results of DCCA with those from a standard DCA ordination, unconstrained by external variables. DCCA yielded eigenvalues for the first axes that were slightly lower than DCA for the first axis (Table 4), but considerably lower for the second. A comparison of gradient lengths shows more directly that the DCCA axes (especially the second axis) are related to a smaller amount of (estimated) species turnover than those of DCA. Note that the third and fourth DCCA axes were predefined as residual axes, i.e., they account for components of the floristic variation not accounted for by the two external variables. Table 4 also shows the correlation coefficients between year and elevation and the first two axes of both analyses.

The main conclusion from this comparison is as follows: the first axes in both DCA and DCCA (with similar eigenvalues) were highly correlated with elevation and represent the dominating floristic trend in the data sets. The second axes in

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* After acceptance of this paper, version 2.0 of CANOCO became available. This includes an option to remove between-transect variation prior to CCA and a Monte Carlo significance test for the relation between ordination scores and external variables. For the shore data set, new eigenvalues (Axis 1: 0.510, 2: 0.111, 3: 0.308, 4: 0.199) show that much of the residual variation of the previous analysis was due to between-transect variation. The average rate of change of species distributions on the shore now was still closer to the long-term rate of land uplift: 0.44 cm/year. The significance test indicated significance for $p < 0.01$. Results for the forest subset yielded no further insights.

Table 4. Comparison between DCA and DCCA: eigenvalues, gradient lengths and species-environment correlations.

	Shore		Forest	
	DCA	DCCA	DCA	DCCA
Eigenvalues				
1st Axis	0.654	0.564	0.605	0.410
2nd Axis	0.466	0.104	0.313	0.057
3rd Axis	0.281	0.524*	0.215	0.498*
4th Axis	0.181	0.287*	0.154	0.252*
Gradient lengths (SD)				
1st Axis	5.5	4.4	5.9	3.3
2nd Axis	5.7	0.9	2.8	0.7
3rd Axis	3.8	5.0*	3.1	4.4*
4th Axis	3.2	3.5*	2.4	3.4*
Correlation coefficients with 1st Axis				
Elevation	0.837	0.939	0.766	0.852
Year	0.103	0.068	−0.060	−0.112
With 2nd Axis				
Elevation	0.316	0.142	0.134	−0.183
Year	0.042	−0.737	−0.144	−0.563

* residual axes.

DCCA, however, have smaller eigenvalues, very short gradient lengths and high correlations with year, while the second DCA-axes have higher eigenvalues, longer gradients and no such clear correlations. This, with respect to the relatively high eigenvalues of the (residual) third and fourth axes in DCCA indicates that other environmental variables (e.g., substrate or exposure) result in greater variation in species composition than does the overall change during six years.

Discussion

Rate and direction of vegetation change

In an environment characterized by a high degree of disturbance, we can not expect a clear shift of all species response intervals along the gradient of long term change (elevation) during six years. In the shore subset, the main trend of floristic change could be separated into two parts: (1) a small, but significant trend based on a migration of species populations downward with a vertical rate of ca. 0.7 cm/yr and (2) a greater change that was not related to elevation, and so must reflect a short-term fluctuation. The relative contribution of each of these two aspects of species composition change can also be studied for individual samples. In Figs. 3 and 4, samples changing in agreement with the long-term trend of succession have arrows from left to right, while samples with deviating change move from top to bottom.

The direction of change in sites 3 to 9 was more clearly related to elevation than in the sites higher on the shore. Table 1 and Fig. 3 indicate that this is mostly due to the colonization of a number of graminoids, such as *Deschampsia bottnica, Juncus gerardi, J. articulatus, Agrostis gigantea* and *Festuca rubra.* Some of these species also show corresponding decrease in the higher parts of their distribution, e.g. *Juncus gerardi* and also *Eleocharis uniglumis.* We observe a distinct shift in elevational distribution of most species. Although inundation was more frequent during three years prior to the second sampling, the increase in cover of sediments (reflected by the apparent decrease of stone cover) allowed a higher species richness. Note the deviating behaviour of site 6 that is explained by decrease in cover only (*Plantago maritima* is the only disappearing species).

Sites 10 to 20, by contrast, show very little change along axis 1, their time trajectories gradually turn to positions almost perpendicular to the arrow of change in elevation. On the other hand, the trajectory length is greater here than lower down the shore. A few species act as colonizers again, but they do not come from belts higher up (e.g., *Hierochloe odorata, Ophioglossum vulgatum*, the apparent colonization of *Alnus glutinosa* somewhat misleads here, because the shrub and tree layer had not been sampled). Especially site 12 and also its neighbours showed a loss in species number (also moss cover decreased strongly), but these species were not colonizing elsewhere. In general, the change of species composition in this belt had little to do with the long-term trend of migrating species populations. The main cause for this appeared to be the erosion due to the storm in January 1983. This picture may also be somewhat distorted for those species that had a distribution reaching into the woodland that had been excluded here.

The results from the forest suggest that short term vegetation dynamics (though in the same order of magnitude as on the shore) in the forest were determined by other factors than seashore displacement. An example is given by the change of some species abundances (e.g., the increase of the open shore species *Filipendula ulmaria* and the corresponding decrease of the woodland species *Allium ursinum*) on the organic drift material accumulation (sites 24–26) that was observed in the forest part of transect 3 (Table 1). Due to the great variability in forest types, the probable existence of gap dynamics and the shortage of other external data, we do not discuss the possible pathways of change in the forest vegetation any further here.

Comparison between direct and indirect gradient analysis

The usual interpretation of DCA ordination results (indirect gradient analysis) is built on the idea that the spread of sites along axes reflects successive species replacement along a hypothetical environmental gradient. CCA also fits a unimodal response model, but with respect to combinations of supplied external variables. Due to the extra constraint in CCA, any difference between the floristic gradients related to the external variables and those calculated by DCA will cause lower eigenvalues in CCA than in DCA (Table 4). The ordination axes, although corresponding to a smaller fraction of the total floristic variance, are useful to explore the effect of external variables that are not necessarily dominating the vegetational gradients. A comparison to unconstrained DCA is needed, though, to estimate the importance of floristic trends others than the ones expressed by the constrained axes.

The environmental variable elevation was the basis of our sampling plan and turned out to have the most profound influence on the distribution of species in both DCA and CCA, as it determined the first axes almost completely (Table 4). This is not surprising on a seashore where many species response intervals can be included in their entirety by transects across the shore. Field observations and inspection of our tables gave us little reason to doubt the assumption that most species, in our case, actually do respond with a roughly bell-shaped, unimodal curve to this gradient, as is required for success in the use of DCA as an ordination method (Hill & Gauch, 1980).

Correlations of the short-term time gradient with ordination axes were much more clear in CCA than in DCA: they were both more highly correlated with one of the axes, and the same axis was less related to the other supplied variable. This possible separation of effects gives an advantage of CCA in interpretation for two reasons. First, while DCA aims for ‘maximum floristic variance expressed in the ordination’, CCA aims for ‘maximum correlation between external variables and that part of the floristic variance they can explain’. Hence in CCA a smaller amount of information from the input matrix is expressed in the ordination, but the result is, in turn, better related to the supplied data about the environment. For an ecological study, we thus end up with a less noisy image of the species’ responses. Second, the introduction of more than one gradient can create difficulties in the interpretation of pure species/sample ordinations. These difficulties may be especially troublesome in studies of three-dimensional (species × sites × times) matrices (Williams & Stephenson, 1973). Temporal gradients can then be confused with spatial gradients (as was pointed out by Swaine & Greig-Smith, (1980)). In DCA, the impact of external gradients on the ordination can be studied either graphically or with help of (multiple) regression analyses between axes and external variables. CCA allows a more direct approach to the problem, since it provides (1) clear information on the relations between the external gradients and the ordination scores, (2) ordination diagrams (biplots) that clearly illustrate the relative importance of the supplied external variables and their main direction of change (Fig. 3), and (3) a better separation between the influences of the external variables (cf. Purata, 1986).

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