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SPATIAL AND TEMPORAL DYNAMICS OF
SALT MARSH VEGETATION ACROSS SCALES:
IMPLICATIONS OF SEA-LEVEL RISE
AND SITE-SPECIFIC PROCESSES

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Abstract

*This study aimed to investigate spatial patterns and pathways of salt marsh vegetation succession in relation to sea-level rise and subsequent changes in tidal and sedimentation regimes under broad spatial and temporal perspectives on the Skallingen salt marsh, Denmark. There was a unique opportunity of using data on plant species frequency, sea-level, and sedimentation acquired since the early 1930's. I used hierarchical cluster analysis and nonmetric multidimensional scaling to identify vegetation associations and their gradient structure, respectively. The cluster analysis produced four vegetation associations, dominated by 1) *Puccinellia maritima*, *Sueda maritima*, *Salicornia herbacea*, 2) *P. maritima*, *S. maritima*, *Limonium vulgare*, 3) *Festuca rubra*, and 4) *Halimione portulacoides*. These associations indicated different successional stages observed in salt marshes of the Wadden Sea. In general, the Skallingen salt marsh recently illustrated convergent succession into an ecological state where one key species, *H. portulacoides* dominated. There were, however, some sites with other phases deviating from the general trend of succession in the whole marsh area. I interpret this variation as the result of site-specific processes such as grazing and retrogressive succession at cutbank edges along tidal creeks. The conventional understanding of vegetation succession on salt marshes has been associated with the increase of surface elevation and reduced number of tidal inundation. Although our study marsh has been showing constant increase of surface elevation, however, the frequency of over-marsh high tide did not reduce, probably due to sea-level rise. The current dominance by *H. portulacoides* implies that sea-level rise and subsequently increased tidal inundation have halted successional processes. On the one hand, recognizing the significance of site-specific processes, I suggest that a flexible hierarchical approach is necessary in order to take into consideration different ecological processes operating across various spatial scales in the salt marsh ecosystem. On the other hand, I conclude that increased frequency of sea water flooding is a more important determinant of vegetation dynamics than increased surface elevation in the salt marsh where sea-level rise has caused the effect of the former to overwhelm that of the latter.*

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INTRODUCTION

A fundamental question in biogeography is how plant species composition changes over space and time responding to dynamic environmental conditions. The dynamic nature of geomorphic and hydrologic processes that are the main drivers of plant succession in coastal salt marshes makes such locations excellent laboratories for the study of vegetation change. Recently, there has been growing recognition that geomorphic and hydrologic processes in salt marshes are altered by sea-level rise (Dijkema et al. 1990; Reed 1990; van Wijnen and Bakker 2001; Hartig et al. 2002), which in turn produces vegetation dynamics that differ from our conventional expectations (Warren and Niering 1993; Leendertse et al. 1997; Olf et al. 1997).

Traditionally, succession on salt marshes has been associated with the increase of surface elevation and consequently decreased frequency of tidal flooding (Ranwell 1972; Beeftink 1977; Rozema et al. 1988). This linkage is based on the notion of a positive feedback between plant growth and sediment accumulation in which the presence of vegetation increases sedimentation thereby facilitating growth due to lowered tidal inundation and salt stress (Bertness et al. 1992; Srivastava and Jefferies 1995; van de Koppel et al. 2005). As sedimentation and elevation increase, this feedback process facilitates the establishment and growth of later successional species by further reducing the physical stress imposed by sea water.

These temporal changes in salt marsh vegetation play out over space and result in shifting zonation along an elevation gradient from outer to inner areas of the marsh. In general, the gradual gradient has been considered as the key indicator of zonal vegetation change (Sánchez et al. 1996; Olf et al. 1997) and typical of many salt marshes' surface configuration. Much of our knowledge about the succession of salt marsh vegetation has consequently been derived from studies at broad spatial scales that inferred successional dynamics from the underlying elevation gradient (e.g. Pielou and Routledge 1976; Snow and Vince 1984; Vince and Snow 1984; Pennings and Callaway 1992; Sánchez et al. 1996; Costa et al. 2003).

Despite the advances in our understanding of the dynamics of salt marsh vegetation in relation to changing environmental factors, some significant

knowledge gaps still exist. First, questions about how plant communities on salt marshes respond to sea-level rise remain unanswered. According to the conventional view of the positive feedback, sea-level rise probably speeds up vegetation dynamics due to an increased rate of sedimentation and thus enhanced nutrient availability (Olf et al. 1997). In an alternative scenario, changes toward a later successional stage halt because the sea-level rise induces an increase of tidal flooding occurrences (cf. Dijkema et al. 1990; Leendertse et al. 1997). Moreover, retrogressive succession toward an earlier seral stage may eventually occur if the rate of sea-level rise overwhelms that of sedimentation for a long time (e.g. Warren and Niering 1993).

Second, the significance of site-specific processes in creating spatial variation of vegetation changes has not been appreciated enough. The conventional concern of outer-to-inner marsh plant zonation has been useful because at broad spatial scales, salt marshes in general, do not display any conspicuous topographic relief that may cause spatial variation of vegetation and environmental factors coincident with something other than the cross-shore gradient. However, different ecological processes nested within a hierarchy are operating in salt marsh environments (cf. Allen and Starr 1982). For example, tidal creeks are the most notable salt marsh agents that alter vegetation away from the zonal patterns expected when only the cross-shore gradient in elevation is considered. These creeks can often interrupt the overall successional patterns of a whole marsh (Adam 1990). This fine-scale topographic effect (meters to tens of meters; Beeftink 1966) may be one of the main reasons why the outer-to-inner marsh gradient of surface elevation is a useful but incomplete proxy for local variations of plant species and environmental factors (Zedler et al. 1999).

The primary aim of this study is to characterize spatial patterns and long-term pathways of vegetation succession in relation to sea-level rise and subsequent changes in tidal and sedimentation regimes on a salt marsh. One common frustration in salt marsh ecology has been that there are few studies documenting long-term changes in vegetation, consequently most models of succession in salt marsh environments have not been tested (Adam 1990). Although there are some long-term studies of vegetation change in salt marshes (e.g. Roozen and Westhoff 1985; Westhoff 1987), there

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are relatively few that have good long-term environmental data to which the vegetation data can be compared. The data that we present here fill this void. Our research site, the Skallingen salt marsh in Denmark provides a unique opportunity for long-term ecological research in that vegetation surveys have been done at the same locations for a minimum of three times since the early 1930's, and data describing the sedimentation and flooding regimes are also available.

In this research, we address the following two specific questions: 1) *How has sea-level rise affected tidal regime, sedimentation rate, and successional processes on the study marsh? Did it speed up or halt changes in species composition?* 2) *Are spatial patterns of vegetation dynamics created by site-specific processes significant for the patterns of the whole marsh area?*

MATERIALS AND METHODS

STUDY AREA

The Skallingen salt marsh, located on a peninsula in southwestern Denmark lies at the northern end of the Wadden Sea (Figure 1), and is one of the largest undiked coastal salt marshes in Europe.

The peninsula is often characterized as a barrier island or barrier spit (Aagaard et al. 1995) which was formed during the last 400 years. It possesses a

geomorphological zonation that is a typical pattern observed across the Wadden Sea islands (Bartholdy 1997). From the ocean (west) to the backbarrier lagoon (east), the depositional sequences are as follows: beach, dune, salt marsh, and tidal flat. Our study marsh is situated on the backbarrier side of the spit. The marsh is relatively young: it started to develop in the beginning of the 20th century synchronously with the formation of tidal creeks (Nielsen 1935; Jacobsen 1952). Currently, there is a complex and actively migrating tidal creek system in the salt marsh (Christiansen et al. 2002; Bartholdy et al. 2004).

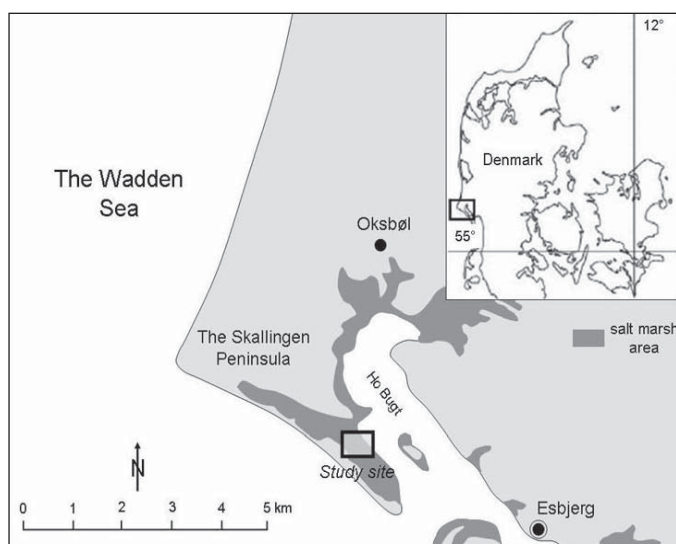
The tidal range is about 1.7 m at spring and 1.3 m at neap tides with a mean of 1.5 m. This area is thus classified as micro-tidal (Davis 1964). In addition, Skallingen often experiences wind-induced sea-level variations up to 4.4 m above Danish Ordnance Zero (DNN) during storm surges.

The Skallingen salt marsh is characterized by a clear division into a natural and a grazed area with the fence between the two parts running roughly parallel to the shoreline. The grazed zone has experienced the change from sheep to cattle grazing and the use of fertilizers leading to significant changes in the composition of plant species (Jensen 1985a). Ecological research on the effect of grazing was conducted by Jensen (1985a) and Morris and Jensen (1998) on this area.

The yearly mean sea-level in the Wadden Sea near Skallingen has generally been increasing since the early 20th century (Table 1). The rate of mean sea-level rise has increased through time with the exception of the period, 1961-1976. Most recently, there has been a mean rise of 5.0 mm year⁻¹ between 1991 and 2006, while an overall rate between 1931 and 2006 was 2.3 mm year⁻¹.

The number of over-marsh high water levels has also gradually been increasing since 1931 (Table 1). Using a quadratic regression model based on recent differences in high water levels of Skallingen and Esbjerg, Bartholdy et al. (2004) estimated high water levels at Skallingen in the early 20th century. Although the difference in the number of over-marsh flooding events between periods was small in the case of higher level events (e.g. 2.0-2.4 m DNN), there were distinct differences in lower level events (e.g. 0.8-1.2 m DNN).

FIGURE 1



Map of the Skallingen Peninsula, Denmark.

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In accordance with the gradual increase of mean sea-level, there has been constant sedimentation and increase of surface elevation on the study marsh since 1933 (Bartholdy et al. 2004). In the outer part of the marsh (close to the tidal flat), the mean accretion rate was 4 mm year⁻¹ and it was 2 mm year⁻¹ in the inner part. The accretion rates have been related to the frequency and levels of high tidal waters.

HISTORICAL FLORISTIC DATA

In the early 1930's, Niels Nielsen (1935) began conducting studies of sedimentation in the Skallingen salt marsh. Four transects were established in the marsh and sampled for both vegetation characteristics and sedimentation. Three of these transects were perpendicular to the shoreline and one was roughly parallel to the shore. The perpendicular transects extended from the tidal flat across the outer marsh and into the grazed area beyond the fence. At each sampled point along these transects, Nielsen recorded the vegetation present using the circular method suggested by Raunkiær (1912). At each sampled location, a 2 m² circular sampling plot was used to characterize the vegetation. 10 randomly located 100 cm² areas within the plot were surveyed for the presence and absence of all species (Nielsen 1935). The primary goal of Nielsen's study was to report sedimentation rates and to do this he leveled sampling locations along his transects and laid down a layer of red sand that could be used as a reference for measurement of future sedimentation (Nielsen 1935). The sand was laid down in plots adjacent to the vegetation survey locations.

In 1949, Helge Nielsen (unpublished data) revisited the originally sampled locations established by N. Nielsen (Nielsen 1935) and resurveyed the vegetation using the same method as N. Nielsen. Qualitative comparison of vegetation cover between the 1930's and the 1950's are also available from an independent source (Iversen 1953).

VEGETATION SAMPLING

In the summer of 2006, we revisited 29 points along the three transects on the Skallingen salt marsh (Figure 2) where N. Nielsen (1935) in 1933 and H. Nielsen (unpublished data) in 1949 surveyed

the vegetation. Finding the previously surveyed locations was possible because the end points of the three historic transects that are perpendicular to the shoreline are known (Bartholdy et al. 2004). The sample points were located by navigating to their locations using a global positioning system (GPS) in conjunction with detailed notes from the 1949 resurvey.

We used a 2 m × 1 m rectangular quadrat that was sub-divided into 200 subdivisions of 10 cm × 10 cm each to sample the vegetation. 10 of the small subdivisions were randomly chosen and the presence of species in each subdivision was recorded. Species nomenclature followed Tind (2003). In order to repeat this procedure at each sampled location, we threw the quadrat around each location three times and averaged the data from the three samples.

Our sampling procedure differed only slightly from the one used in the 1930's and 1940's studies. First, we used a rectangular rather than a circular sampling area. The original rationale for the circular sampling was for more practical transport and to avoid catching branches and thorns in the quadrat (Raunkiær 1912). We did not encounter either of these problems with our survey and due to the ease of construction we used the rectangular survey grid. Furthermore, we surveyed three quadrats at each location whereas the previous studies were based on only a single quadrat at each point. We increased the number of quadrats sampled at each site and averaged the results from the three quadrats to minimize any effect of having resampled a site that was slightly offset from the originally sampled location. However, we believe that with the combination of GPS and detailed notes from the 1949 survey, we were able to be within 2 m of each originally sampled location.

IDENTIFICATION OF VEGETATION ASSOCIATIONS AND GRADIENT STRUCTURE

Prior to statistical analyses, we pooled all samples of the three time steps (1933, 1949, and 2006) into one dataset and performed logarithmic transformation because each species (variable) showed a positively skewed curve. Hierarchical agglomerative cluster analysis was used to classify the samples into a reasonable number of vegetation associations. We selected Ward's Method (= minimum variance method) and

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Euclidean squared distance as the cluster method and our similarity coefficient, respectively. This combination is one of the approaches recommended for avoiding distortion of a dataset and for maximizing defensibility (McCune and Grace 2002).

We used nonmetric multidimensional scaling (NMDS) to extract the potential environmental gradients. NMDS is a distance-based ordination technique well suited for non-normal ecological datasets (Clarke 1993; McCune and Grace 2002). It aims to minimize the discrepancy (i.e. 'stress') between ecological dissimilarities among samples calculated from an original dataset and those calculated from a new dataset created by ordination. After iterative trials to find out a state of the lowest stress, NMDS defines a new configuration of sample units in the ordination space. Because NMDS is a distance-based approach, the distance between sample units can be used as a direct indicator of dissimilarities between them. Samples closer to each other in the ordination diagram are showing more similar ecological characteristics (e.g. species composition). We used Sørensen's distance to calculate sample dissimilarities with a random starting configuration. In order to lower the likelihood of local minima, we performed multiple runs of NMDS ($n = 40$) and a Monte Carlo test ($n = 40$). The Monte Carlo (randomization) test determined the minimum number of dimensions necessary to produce the lowest stress. All statistical procedures were performed in PC-ORD Version 4.14 (MjM Software Design, Gleneden Beach, Oregon, USA).

RESULTS

TEMPORAL TRANSITION OF CLASSIFIED VEGETATION ASSOCIATIONS

We classified vegetation cover of the Skallingen salt marsh into four types using hierarchical cluster analysis. Table 2 lists the average frequency (0-10) of the main plant species of each group. We describe these vegetation associations using established syntaxonomical categories (see Westhoff & den Held, 1969; Roozen & Westhoff, 1985; Westhoff, 1987). Group A was dominated by *Puccinellia maritima*, *Suaeda maritima*, and *Salicornia herbacea* that comprise typical pioneer communities on low salt marshes of the Wadden Sea. One unexpected result was that the average frequency of *Spartina townsendii*, another representative early successional species, was quite low (0.83).

We understand this low abundance as a unique situation of the Skallingen salt marsh and also do not exclude a possibility that our quadrat did not catch its presence adjacent to the shoreline. Second, Group B was characterized by the decrease of these three dominant species' cover (esp. *S. herbacea*) and the emergence of new significant species, *Limonium vulgare* and *Halimione portulacoides*. A similar phase to this was also detected by Roozen and Westhoff (1985) who regarded it as a relatively early successional stage, restricted to higher sites on low salt marshes. *Festuca rubra* dominated Group C with *Plantago maritima* and *Juncus gerardi* being secondary dominants. All other species were markedly reduced relative to Groups A and B. Communities belonging to this group were, in general, located at high salt marsh areas. Last, Group D was predominantly occupied by *H. portulacoides* while other species' cover was quite low. It is known that this community initially begins from the early phase of Group B in which *L. vulgare* still possesses a significant coverage, but through time, *H. portulacoides* becomes dominant by its competitive ability and ecophysiological advantages (Jensen 1985b). The stage of Group D is thus considered a later phase of Group B (Beefink 1965; Roozen and Westhoff 1985).

In order to quantify the pattern and magnitude of changes in species composition, we constructed transition matrices of vegetation dynamics among the four vegetation classifications for the three time steps (1933, 1949, and 2006). In 1933, there were 25 samples belonging to Group A among a total of 29 (Table 3a). Over the next 16 years, 52 % of the locations classified in Group A changed to belong to Group B. Also over this period, sites classified as Group C showed only a slight change in frequency. For the period, 1933-1949, vegetation changes were summarized as 1) reduced frequency of *P. maritima*, *S. maritima*, *S. herbacea* and the appearance of *L. vulgare*, *H. portulacoides* and 2) a general maintenance of the dominance by *F. rubra* at sites with relatively high elevations.

Transition in species composition between 1949 and 2006 was notable in that over 70% of all groups shifted to become members of Group D (Table 3b). Currently, the majority of samples (22 of 29) were dominated by a single species, *H. portulacoides*. This change of dominance was considerable since Group D was not present at all in 1933

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and only one site was classified as Group D in 1949. In addition, there were five locations classified as of Group A in 2006, three of these were previously classified as Groups B or C in 1949.

SPATIAL VARIATION OF CHANGES IN SPECIES COMPOSITION

The spatial pattern of the classified vegetation associations and their temporal transitions varied across the Skallingen salt marsh. Figure 2 illustrates a complex tidal creek system around the three transects and shows the clear difference of vegetation cover between grazed (lower-left side) and ungrazed (upper-right side) parts. In both 1933 and 2006, there was a clear dominance by species belonging to Groups A and D, respectively, although there were some site-specific exceptions. The map of 1933, for instance, contained four samples of Group C only along transect three, while that of 2006 showed a few samples of Groups A and B at sites that were grazed or adjacent to tidal creeks. On the other hand, the map of 1949 indicated a transitional stage in that the number of points characterized as Group A has declined and there was an increase in the number of locations classified as Group B, an intermediate state between Groups A and D. An important aspect of this spatial arrangement of the classified groups was that there is no ecological gradient of vegetation associations with distance from the seashore at any transect for all three dates.

GRADIENT STRUCTURE

The NMDS on the salt marsh vegetation data revealed a temporal differentiation of samples along axis one (Figure 3). Although there were some exceptions, most samples of contemporary vegetation (labeled as 3), in general, were distributed at the left part of the ordination diagram, while those of 1949 (labeled as 2) and 1933 (labeled as 1) toward the right side. We therefore posit that axis one well correlated with time since the first floristic data were collected.

The second NMDS axis likely corresponded to site-specific elevation differences of the marsh surface. According to the survey for topographic profiles of transects on the Skallingen salt marsh (Bartholdy et al. 2004), samples in the upper half of the NMDS diagram were mainly from areas with

relatively uniform elevation, whereas those in the lower half from local heights along transect three. Specifically, there were four local heights along the third transect and the changes in species composition at such sites were illustrated as four sets of trajectory arrows in the ordination plot (Figure 3).

DISCUSSION

SEA-LEVEL RISE AND SUCCESSION OF SALT MARSH VEGETATION

Our general understanding of vegetation succession in salt marshes has been based on process-response sequences: sedimentation → increase of surface elevation → decreased number of tidal inundation and thus decreased salt stress (Ranwell 1972; Beefink 1977; Rozema et al. 1988). According to the notion of a positive feedback between plant growth and sediment accumulation (see **Introduction**), the sequences facilitate the incoming of later successional species (Bertness et al. 1992; van de Koppel et al. 2005). However, this established knowledge has rarely been explicitly tested in relation to sea-level rise due to the lack of long-term field data (but see Leendertse et al. 1997). Here, we first discuss how the environmental history of the Skallingen salt marsh has been in broad agreement with the conventional knowledge in part, and then discuss how the area provided new insight into long-term vegetation dynamics through its unique history of tidal regime and floristic change.

The available data indicate that our study marsh has experienced continuous sedimentation and consequent increase of surface elevation since the early 1930's (Bartholdy et al. 2004), which is well accordance with the trend of salt marshes in the Netherlands (Dijkema et al. 1990; Leendertse et al. 1997; Olf et al. 1997) and beyond Europe (e.g. Morris et al. 2002 in South Carolina, USA). Specifically, Bartholdy et al. (2004) divided the period of 1933-1999 into three sub-periods and reported a simulation modeling result showing that the average yearly accretion has increased from 2.7 mm year⁻¹ over 3.8 mm year⁻¹ to 4.6 mm year⁻¹ on the Skallingen salt marsh. They suggested that the accretion rates have been related to the frequency and levels of high tidal waters. The high water levels responsible for the largest sediment deposition, for instance, were those belonging to the interval be-

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tween 1.2 and 1.4 m DNN. The frequency of such levels has been increasing through time (Table 1).

Despite the increase of surface elevation, our study site is unique in that there has been no decrease of sea water flooding events (Table 1) probably due to sea-level rise (cf. Dijkema et al. 1990), and thus little facilitation of the incoming of later successional species during the long period over 70 years. The contemporary dominance by *H. portulacoides* (Table 3b, Figure 3c) implies that the Skallingen salt marsh is not yet characterized by a late phase of vegetation succession in which species such as *F. rubra* dominates (Group C of Table 2).

This current state of vegetation cover on our research marsh is considered as a relatively earlier stage of succession occurring lower part of salt marshes (Beefink 1965; Roozen and Westhoff 1985). Very similar floristic and environmental situations have also been observed on salt marshes in the Netherlands (e.g. Leendertse et al. 1997). This implies that we, to some degree with care, may extend our insights from Skallingen to the northern part of European coast.

There has been an unanswered question about how vegetation communities on salt marsh respond to sea-level rise. Among the two suggested scenarios dictating speeding up (Olff et al. 1997) and halting (Leendertse et al. 1997) vegetation dynamics, respectively (see **Introduction**), our research on Skallingen advocates the latter view. This is because, although sea-level rise led to the increase of both surface elevation through enhanced sedimentation and tidal flooding occurrences, the study area has showed apparent delay of the incoming of later successional species. Therefore, we conclude that increased frequency of sea water flooding is a more important determinant of vegetation dynamics than increased surface elevation in coastal salt marshes with similar floristic and environmental conditions of Skallingen, assuming that sea-level rise has caused the effect of the former to overwhelm that of the latter. Our conclusion, however, may not fit well estuarine salt marshes with high sediment discharge where relative sea-level is falling (Stevenson et al. 1986; Reed 1990).

Although retrogressive succession toward an earlier phase (e.g. Warren and Niering 1993) is not a dominant phenomenon in our study area, there are some plausible geomorphic and ecological sto-

ries in the near future. Bartholdy et al (2004), on the Skallingen salt marsh, tested three scenarios of the speed of sea-level rise: 2.3 mm year⁻¹, 4.2 mm year⁻¹, and 6.4 mm year⁻¹. If the salt marsh would follow the first two predictions, we expect that the *H. portulacoides*-dominated communities (Group D) could continue for the time being because these rates of sea-level rise have been characteristic of Skallingen until recently (Table 1). However, if the rate becomes between the last two cases, wide retrogression may occur. In the last case, the marsh itself, as well as its plant communities, would gradually drown under the 'worst' scenario for the 21st century, which is also suggested elsewhere (e.g. Hartig et al. 2002 in New York, USA).

PATHWAYS OF SUCCESSION AND SIGNIFICANCE OF SITE-SPECIFIC PROCESSES

Divergent, convergent, and individualistic models (see Frelich & Reich, 1995) of succession derived from forest ecology may also be applicable to the vegetation dynamics in the Skallingen salt marsh. The divergent model indicates that one vegetation community, or a landscape in general, diverges into two or more states over time with no single destination (Phillips 1999). It implies the magnification of initial minor differences within the community. We see such divergence on the Skallingen salt marsh between the years of 1933 and 1949 (Table 3a, Figure 2a,b). During this period, the main initial community characterized by three pioneer species (*P. maritima*, *S. maritima*, and *S. herbacea*; Group A) persisted through time or changed into one of the states of Groups B, C, or D. Theoretically, once the differences become large, the divergent model would allow their perpetuation (Wilson and Agnew 1992). However, Skallingen does not fit this expectation in that there has been convergent succession since 1949.

In convergent succession, regardless of the starting points or the variation in initial conditions, vegetation in two or more states, or a landscape in general, converge into one particular endpoint of species composition (Phillips 1999). It is the key notion of Clements' (1936) classic model of plant succession and still remains implicit in recent studies (e.g. Margalef 1963; Drury and Nisbet 1971; Pickett 1976; Christensen and Peet 1984). In general, we see clearly increased uniformity of species composition at the Skallingen sites

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with the dominance by *H. portulacoides* (Group D) since 1949 (Table 3b, Figure 2c). Although there was site-to-site variation in species composition, chiefly due to micro-scale elevation differences in previous years (esp. four samples of Group C at transect three in 1933), such an initial variation became decreased with community maturation. This general convergence of the Skallingen salt marsh may be due to its unique lack of clear elevation gradient perpendicular to the shoreline, which provides relatively uniform environmental conditions across the whole research field. We suggest that our study area is one exemplary case where both convergence and divergence occur during the same successional sequence, but at different times (cf. Christensen and Peet 1984).

In addition to these general patterns of succession at a broad spatial scale, the spatial variation of changes in species composition at local scales should be considered as the result of site-specific stochastic processes following an individualistic model with multiple pathways (Cattelino et al. 1979). This model considers that stochastic factors such as disturbances interact leading individual local communities to change along multiple pathways at different times at the same location with no stable endpoint (Frelich and Reich 1995). For example, above we found that in 2006 there were still five samples classified as Group A and characteristic of early successional environments (Figure 2c). Three of these were in grazed areas and two were in ungrazed locations. We interpret this site-specific dominance by earlier successional species (esp. *P. maritima*; Group A) in terms of grazing and retrogressive succession due to cutbank erosion along tidal creeks.

First, the *P. maritima*-dominant community is observed nearly all north Atlantic salt marshes grazed by domestic animals such as cattle or sheep (Westhoff 1987). While many studies have reported plausible negative impacts of grazing on salt marsh plant species including soil compaction and physical damage due to trampling, they commonly accepted the positive influence of grazers on *P. maritima* (Jensen 1985a). One explanation of the persistence of the species is 'tread-planting' that favors its vegetative propagation strategy (Ranwell 1972). Trampling by the domestic animals produces quantities of discarded fragments of *P. maritima* which then root readily when trodden into the damp marsh surface. When an over-marsh tidal inundation oc-

curs after a period of grazing, it irrigates the newly 'planted' species and aids its establishment. Grazing therefore is an important factor in maintaining the predominance of *P. maritima*, and thus retarding the process of succession (Jensen 1985a).

Second, the two samples belonging to the earliest successional phase (Group A) and located in the ungrazed portion of the salt marsh represent retrogression in that they have changed from the later stages of Groups B and C, respectively (see transects one and three in Figure 2c). These sites are located adjacent to cutbank edges where erosional processes by tidal flows are relatively intensive. Cutbank edges are often characterized by succession in reverse, a retrogressive change of species and communities (cf. Firth and Hooker 1989; Kupfer and Malanson 1993). When a laterally migrating tidal creek gradually erodes a cutbank edge, sites once located in the salt marsh interior, dominated by relatively later successional species, become adjacent to the channel edge. The term, 'retrogressive succession' is used here because newly developing individuals and communities on the newly formed creek-side are mainly edge-oriented and tend to be in the early stage of succession. There is ample geomorphic evidence illustrating that the Skallingen salt marsh has experienced active cutbank erosion due to the channel migration (Christiansen et al. 2002; Bartholdy et al. 2004). We therefore posit that the presence of the two samples of Group A inside the ungrazed area is the result of site-specific channel erosion. In other words, it is plausible that they would belong to other later successional groups such as D if the two sampled sites were located well inside the marsh area without any cutbank erosion effect.

It is apparent that different ecological processes across broad and local spatial scales are operating on the Skallingen salt marsh (cf. Allen and Starr 1982). Recognizing the significance of site-specific processes, we address a need of adopting flexible hierarchical strategies in managing salt marsh ecosystems that take such various processes into consideration.

CONCLUSIONS

It would be premature to conclude that the three directional models of succession reported here are characteristic of salt marshes in general because the models are probably produced by the unique-

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ness of our study area. First, we consider that the ecological succession at the Skallingen salt marsh is still in progress rather than having achieved a terminal state. This is particularly important when considering the dominance by *H. portulacoides*, which is not a late successional species (Roozen and Westhoff 1985; Westhoff 1987). The convergent succession toward a *H. portulacoides*-dominated phase regardless of distance from the seashore may not be applicable to other salt marshes with a stronger cross-shore elevation gradient and subsequently different physical stresses from outer to inner marshes (e.g. Pielou and Routledge 1976; Snow and Vince 1984; Vince and Snow 1984; Pennings and Callaway 1992; Sánchez et al. 1996; Costa et al. 2003). In addition, the extensive tidal creek system within the Skallingen salt marsh creates a complicating geomorphic constraint that leads to site-specific erosion processes and retrogressive succession. It should, however, be noted that there are also some marshes with almost no such systems (Glooschenko 1980; Adam et al. 1988), although tidal creeks may occupy a large portion of the salt marsh area in many salt marshes.

In addition to the uniqueness of Skallingen above, to our knowledge, this is the first report explaining successional pathways on the salt marsh based on long-term ecological data acquired from the field. We have collected data on the history of plant species abundance and acquired ancillary sedimentation and tidal regime data that detail environmental conditions on Skallingen since the early 1930's. Therefore, our new insights on vegetation succession in relation to changing physical settings help to explain the dynamic nature of a salt marsh ecosystem.

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TABLE 1

Mean water levels and the number of high water levels around the study site in m DNN,
the Danish Ordnance Zero.

Period (years)	1931-1946	1946-1961	1961-1976	1976-1991	1991-2006*
MWL†	0.086	0.119	0.116	0.157	0.214
0.8~1.2 m HWL‡	2193	2563	2610	2856	3229
1.2~1.6 m HWL	510	590	662	774	866
1.6~2.0 m HWL	136	160	160	242	272
2.0~2.4 m HWL	29	32	55	73	77

† measured at Esbjerg, a city near to Skallingen

‡ All high water levels were corrected for the Skallingen salt marsh.

* Extrapolated from statistics based on 1991-2000

TABLE 2

Average frequency (0-10) of main plant species of each group†

Species‡	pucmar	suemar	salher	limvul	fesrub	plamar	halpor
Group A	9.46 (1.43)	6.26 (3.95)	7.43 (3.59)	1.41 (2.60)	0.00 (0.00)	1.45 (2.93)	0.28 (0.88)
Group B	8.07 (2.66)	5.18 (3.68)	1.60 (2.54)	6.18 (2.41)	0.20 (0.56)	2.11 (2.97)	6.09 (3.20)
Group C	1.33 (2.06)	0.78 (1.56)	0.00 (0.00)	2.22 (2.86)	10.00 (0.00)	4.56 (4.33)	0.33 (1.00)
Group D	1.00 (1.64)	0.12 (0.26)	0.13 (0.33)	0.57 (0.57)	0.67 (1.80)	0.59 (0.89)	8.75 (2.34)

† Standard deviations are in parentheses.

‡ pucmar – *Puccinellia maritima*, suemar – *Sueda maritima*, salher – *Salicornia herbacea*,
limvul – *Limonium vulgare*, fesrub – *Festuca rubra*, plamar – *Plantago maritima*, halpor –
Halimione portulacoides

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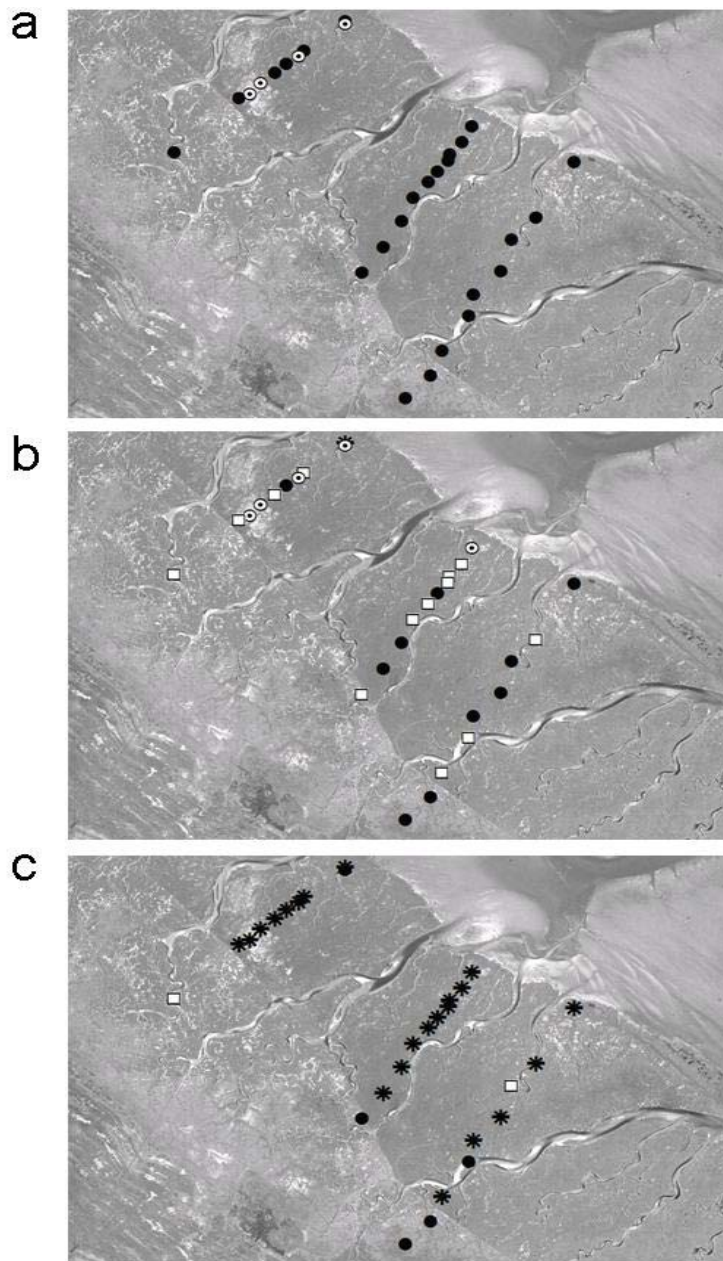
TABLE 3

Transition matrices of vegetation dynamics during years of 1933-1949 and 1949-2006

a) Raw tally matrix (1933-1949)						Transition probabilities (1933-1949)				
	To A	B	C	D	Row total		To A	B	C	D
From A	10	13	1	1	25	From A	0.40	0.52	0.04	0.04
B	0	0	0	0	0	B	0.00	0.00	0.00	0.00
C	0	0	4	0	4	C	0.00	0.00	1.00	0.00
D	0	0	0	0	0	D	0.00	0.00	0.00	0.00
Column total	10	13	5	1	29					
b) Raw tally matrix (1949-2006)						Transition probabilities (1949-2006)				
	To A	B	C	D	Row total		To A	B	C	D
From A	2	1	0	7	10	From A	0.20	0.10	0.00	0.70
B	2	1	0	10	13	B	0.15	0.08	0.00	0.77
C	1	0	0	4	5	C	0.20	0.00	0.00	0.80
D	0	0	0	1	1	D	0.00	0.00	0.00	1.00
Column total	5	2	0	22	29					

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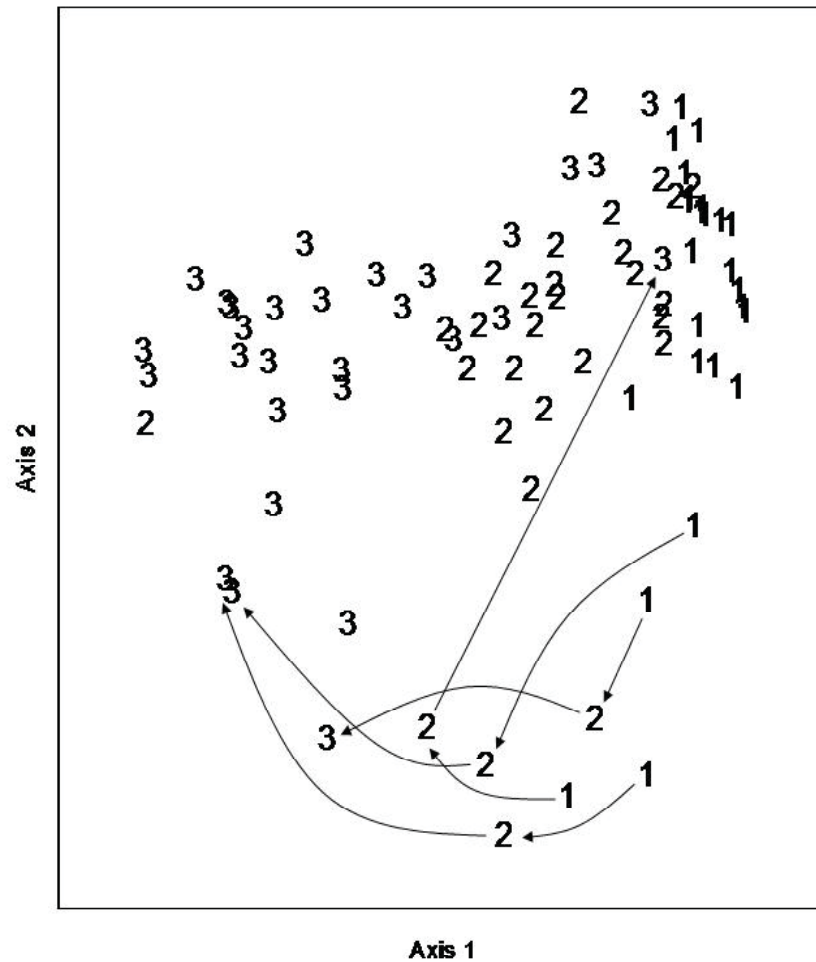
FIGURE 2



Spatial patterns of vegetation dynamics on the Skallingen salt marsh, Denmark. Solid circles, blank squares, blank circles with a dot in the middle, and asterisks belong to Group A, Group B, Group C, and Group D, respectively. Maps at the top (a), middle (b), and bottom (c) represent the year of 1933, 1949, and 2006, respectively. The four points of Group C along the third transect in the map of 1933 indicate local heights. The aerial photograph was taken in 1995.

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FIGURE 3



Nonmetric multidimensional scaling diagram with a total of 87 points from the three time steps (1933, 1949, and 2006), each having 29 points. Points labeled as 1, 2, and 3 represent quadrats of 1933, 1949, and 2006, respectively. There are four sets of trajectory arrows, indicating how each of four local heights along transect three (see Fig. 2) has been showing changes in species composition.



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