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ECOSYSTEMS

Potential for Sudden Shifts in Transient Systems: Distinguishing Between Local and Landscape-Scale Processes

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ABSTRACT

Thorough understanding of the potential for threshold dynamics and catastrophic shifts to occur in natural systems is of great importance for ecosystem conservation and restoration. However, verifying the presence of alternative stable states, one of the theoretical explanations for sudden shifts in natural systems, has proven to be a major challenge. We examine processes on local and landscape scales in salt-marsh pioneer zones, to assess the presence of alternative stable states in this system. To that end, we investigated the presence of typical characteristics of alternative stable states: bimodality and threshold dynamics. We also studied whether vegetation patches remained stable over long time periods. Analysis of false-color aerial photographs revealed clear bimodality in plant biomass distribution. By transplanting *Spartina anglica* plants of three different biomass classes on three geographically different marshes, we showed that a biomass threshold limits the establishment of *Spartina* patches, potentially explaining their patchy distribution. The presence of bimodality and biomass thresholds points to the presence of alternative stable states and the potential for sudden shifts, at small, within-patch scales and on short time scales. However, overlay analysis of aerial photographs from a salt marsh in The Netherlands, covering a time span of 22 years, revealed that there was little long-term stability of patches, as vegetation cover in this area is slowly increasing. Our results suggest that the concept of alternative stable states is applicable to the salt-marsh pioneer vegetation on small spatio-temporal scales. However, the concept does not apply to long-term dynamics of decades or centuries of heterogeneous salt-marsh pioneer zones, as landscape-scale processes may determine the large-scale dynamics of salt marshes. Hence, our results provide the

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interesting perspective that threshold dynamics may occur in systems with, on the long term, only a single stable state.

Key words: alternative stable states; catastrophic shifts; positive feedback; salt marshes; patchiness; transient systems; thresholds; *Spartina*.

INTRODUCTION

Alternative stable state theory provides the basis for the ability of ecologists to explain some of the sudden and dramatic changes observed in ecosystems. Catastrophic shifts between different ecosystem states may occur in response to gradual change of external conditions (Scheffer and others 2001; Scheffer and Carpenter 2003; Rietkerk and others 2004; van Nes and Scheffer 2005), even in the absence of any significant disturbance. Catastrophic shifts have been found in many different systems, such as shallow lakes (for example, Scheffer and others 1993), arid ecosystems (for example, van de Koppel and others 1997), forests (for example, Augustine and others 1998) and various coastal ecosystems (coral reefs, Knowlton 1992; rocky shores, Petraitis and Dudgeon 1999; mudflats, van de Koppel and others 2001) and are generally considered to occur in systems that have two different stable equilibria, or so-called alternative stable states.

Alternative stable states and, thus, catastrophic shifts, are considered to be a consequence of positive feedbacks (Rietkerk and van de Koppel 1997; Scheffer and others 2001). Positive feedbacks occur when disturbances are amplified by ecological or environmental processes, driving the system away from equilibrium. In theory, positive feedbacks may explain alternative stable states in community composition (Scheffer and others 1993), vegetation biomass (Walker and others 1981; Rietkerk and van de Koppel 1997), or animal numbers (Persson and others 2003). Positive feedbacks have been convincingly demonstrated in the field (Wilson and Agnew 1992). However, experimental verification of alternative stable states in natural systems has proven to be much more of a challenge. Dynamic changes in ecosystems typically occur at large spatial and temporal timescales, making thorough testing intrinsically difficult (Petraitis and Latham 1999; Schroder and others 2005).

Salt-marsh pioneer zones in the Netherlands have a number of typical features indicating the potential for alternative stable states. First of all, they are characterized by a patchy distribution of either dense stands of the common cordgrass *Spartina anglica* or unvegetated intertidal flats which are inhabited by benthic invertebrates (Figure 1). On the intertidal flat benthic invertebrates, especially lugworms, impede settlement of *Spartina* seedlings (van Wesenbeeck and others 2007). The boundaries between *Spartina* patches and sediment of the intertidal flat are abrupt, with *Spartina* density dropping from about 250 stems per m^2 to 0 over 10–20 cm. Secondly, salt marshes exist entirely by the grace of positive feedback between plants and sediment deposition (Allen 2000). Plants typical of lower salt-marsh zones, such as *Spartina anglica*, reduce hydrodynamic energy from currents and/or waves locally, thereby enhancing sedimentation and decreasing sediment erosion (for example, Leonard and Luther 1995; Bouma and others 2005). The increased sediment deposition increases surface elevation, thereby lowering inundation frequency and increasing nutrient availability. These changes improve conditions for plant growth, constituting a positive feedback between the density or biomass of *Spartina* and its growth potential (Wilson and Agnew 1992; Castellanos and others 1994). This feedback is scale-dependent, especially under conditions of high flow velocity, implying that reduced water flow inside tussocks results in increased water flow at the edges of tussocks, explaining the presence of erosion gullies there (van Wesenbeeck and others 2008). These erosion gullies may hinder expansion of existing tussocks, and arrest tussock development (van Wesenbeeck and others 2008).

Despite the clear positive feedback, salt-marsh pioneer zones typically develop toward closed

Figure 1. Photograph of a salt-marsh pioneer zone with tussocks of *Spartina anglica* in the southwest of The Netherlands.

vegetation on a multi-decadal timescale (Allen 2000). Moreover, a number of recent studies have indicated that salt marshes may reveal complex spatial dynamics in response to internal feedback relations (Silliman and others 2005; van de Koppel and others 2005). Hence, the literature reveals little evidence for the presence of alternative stable states in salt-marsh ecosystems. Here, we investigate to what extent criteria for alternative stable states apply to the structure and dynamics of salt-marsh pioneer zones. We address short-term indicators of alternative stable states, such as presence of bimodality and thresholds and compare these with a GIS study on the long-term stability of *Spartina* vegetation in salt-marsh pioneer zones. We discuss whether the current concept of alternative stable states allows ecologists to assess the potential for sudden shifts in both salt marshes and other transient ecosystems.

METHODS

The theoretical literature proposes a number of indicators for the presence of alternative stable states (Scheffer 1998; Schroder and others 2005). For example, inspection of state variables using a large set of randomly distributed samples should reveal a bimodal distribution of key variables, focusing around the equilibrium values that characterize each state (Scheffer and Carpenter 2003; Schroder and others 2005). Further, experimental testing for biomass thresholds that need to be crossed before a switch to another state is initiated, is an alternative way of examining the presence of alternative stable states (Scheffer and Carpenter 2003; Schroder and others 2005). Finally, both states should persist on relevant time scales, typically defined by the generation-time of the involved organisms, to be considered stable (Connell and Sousa 1983; Peterson 1984; Sousa and Connell 1985; Sutherland 1990; Petraitis and Latham 1999). We investigate for the presence of the above indicators in Dutch salt-marsh ecosystems.

Bimodality

To investigate vegetation distribution along the stress gradient from intertidal flat to salt marsh, we carried out an observational study on aerial photographs. False-color aerial photographs from 1998 of salt marshes in the Westerschelde (51°21′ N and 003°42′ E), were used to determine bimodality. To obtain an estimate of vegetation biomass the Normalized Difference Vegetation Index (NDVI) was used. NDVI is composed of red and near infrared reflectance differential ratios (NIR-R/NIR+R) (Pettorelli and others 2005), allowing it to be used as a measure of plant biomass. False-color photographs (scale 1:5,000) were scanned at high resolution. They were rectified, geo-referenced, and mosaicked in a Geographical Information System (GIS) to yield images with a pixel size of 0.25 m by 0.25 m. Distribution of vegetation was examined using NDVI values at three zones along a gradient from high marsh, salt-marsh pioneer zone, to intertidal flat. The intertidal flat is the zone without vegetation. The high marsh is the zone with high vegetation cover close to the dike and the salt-marsh pioneer zone is the vegetated zone in front of the retreating cliff of the old marsh (van de Koppel and others 2005). All these zones are easily distinguishable in the field as well as on aerial photographs. In this article, pixel values for the red and infrared from the original scanned photographs have been used. No attempt has been made to retrieve values for surface reflectance in the red and infrared as no comparisons between different pictures were made.

Thresholds

We tested the hypothesis that the establishment of *Spartina* is controlled by a threshold in biomass, above which a plant or tussock has to grow before it has a reasonable chance of persistence in the field. Experiments were performed at three geographically different locations in The Netherlands: a salt marsh in the Westerschelde (Paulinapolder: 51°21′ N and 003°42′ E), in the Oosterschelde (Krabbekreek: 51°37′ N and 004°07′ E), and one of the Dutch barrier islands (Schiermonnikoog: 53°29′ N and 006°18′ E) was used. Transplants of three different *Spartina* biomass classes were planted into open sediment; small seedlings in groups of three, small clonal fragments (underground root and one or two aboveground stems), and large clonal fragments of 20 cm × 20 cm consisting of 15–20 stems. These three different biomass classes were considered representative for natural ways of recruitment. *Spartina* reproduces sexually by seeds. As seed germination failure tends to be high in the field (Ranwell 1964; van Wesenbeeck and others 2007), seeds were germinated under ideal conditions first and then transplanted to the field. As *Spartina* is a clonal plant most vegetation expansion occurs vegetatively. Rhizomes or ramets (small clonal fragments) can break off and disperse by themselves (Ranwell 1964), explaining why they constituted our intermediate biomass class. Finally, whole chunks of *Spartina* can be dislodged and displaced by storms, erosion, or ice-rafting (pers. obs.), clarifying our choice of the largest biomass class. Note that naturally, however, most dispersal seems to be with seedlings.

Seeds and clonal fragments were obtained from natural *Spartina* from a single salt-marsh location in the Westerschelde. Small fragments of 10–15 cm length were taken with sufficient roots and one or two green stems of approximately 10 cm length. Seedlings were germinated a week before planting. For 18 months presence, absence, and size (height for stems and diameter for large fragments) for all transplanted units were scored every month in the beginning, but later every other month. To address the importance of variation in underlying abiotic factors, we planted the tussocks, rhizomes, and seedlings in both high and low areas that were present in natural topography on the intertidal flat, following a randomized block design. High and low transplants were generally less than 5 m apart and low transplants were planted between 10 and 20 cm lower than high transplants. Size and elevation treatments, forming one block, were repeated ten times each, in each location ($n = 300$). Survival data were analyzed applying a Cox Proportional Hazard regression model. Three new variables were created to determine the effect of the three biomass classes on survival independent of location or elevation. To correct for effects of location and elevation a so-called confounding variable (Sokal and Rohlf 1995) was created that incorporated all possible combinations of high and low transplants and geographic location. This confounding variable ranged from 1 to 6 (2 high and low transplants × 3 locations = 6) and was analyzed as a grouping factor. Two other dummy variables, consisting of 1 and 0, represented the three biomass classes (seedlings = 0 1; small units = 1 0; large units = 0 0) and were analyzed as the dependent variables. To determine the effects of biomass on survival, an analysis on both dummy variables (all three biomass classes) was executed ($n = 300$). To distinguish between small fragments and seedlings, large fragments (represented by a 0) were omitted from the last dummy variable. This dummy variable then only consisted of seedlings (represented by a 1) and small units (represented by a 0). The regression analysis was repeated with this dummy variable ($n = 240$).

We extended the aforementioned experiment to test the null hypothesis that areas occupied by *Spartina* would recover from a removal disturbance by developing new vegetation, against the alternate hypothesis that those areas would remain bare, meaning they would shift to another state. We were not allowed to remove tussocks that were naturally present, because of the importance of *Spartina* for coastal protection. To avoid this problem, large clonal units of *Spartina* were first planted into the two salt-marsh pioneer zones in the southwest Netherlands that were used for previous experiments. In each pioneer zone, 5 units were planted and left to establish for 2 years. All planted pieces established and were expanding slowly. After 2 years the entire fragments were removed by digging out above- and below-ground biomass. A small part of each of these fragments was replaced and planted in another bare spot to control for environmental conditions preventing vegetation re-growth. Removal areas were examined for *Spartina* re-growth after one (6 months) and two (18 months) growing seasons. The newly transplanted pieces were checked for survival.

To gain insight in natural recruitment processes, emergence and survival of natural seedlings were measured in one of the Southern locations (Krabbekreek) over a period of 2 years. Four permanent plots of 10 m × 5 m were established. In these plots, seedling presence was monitored by recording exact seedling location using a large grid with a maze width of 0.5 m × 0.5 m. Every 3–4 months seedling mortality and recruitment were monitored using this grid.

Long-Term Stability

We used infrared aerial photographs of the salt-marsh area near Paulinapolder to obtain an estimate of *Spartina* tussock stability on large spatial and temporal scales. False-color photographs (scale 1:5,000, pixel size 0.25 m × 0.25 m) of 1982, 1998, and 2004 were used that were scanned and geo-referenced in the same way as for analysis of bimodality. Based on the pixel values in the images, a supervised classification was carried out to map salt-marsh vegetation. No distinction was made between vegetation types. Two change maps were produced by overlaying two classifications (1982 and 1998 plus, 1998 and 2004), revealing areas in which vegetation disappeared or expanded between 1982 and 1998, and between 1998 and 2004. To quantify patterns of growth and erosion in the pioneer zone, a polygon was cut out that only contained pioneer vegetation and no high marsh. In the overlay map of 1982 and 1998 a polygon was drawn in the pioneer zone. The polygon bordered the erosion zone of the high marsh and on the other side the bare intertidal flat. The same polygon was used in the overlay map of 1998 and 2004. Within the polygons, we quantified the surface area of vegetation that emerged, disappeared, or persevered, respectively, from the number of pixels in each class.

RESULTS

Bimodality

Our results provided a number of indications for the occurrence of alternative stable states in salt-marsh pioneer zones. Analysis of aerial photographs indicated that plant biomass is bimodally distributed. High NDVI values are dominating in high marshes (Figure 2A), indicating high vegetation biomass. Low NDVI values are dominating on intertidal flats (Figure 2C), reflecting the absence of vegetation here. In the salt-marsh pioneer zone a bimodal distribution of both high and low NDVI values can be distinguished (Figure 2B), confirming visual information that vegetation mostly occurs with high biomass or not at all. The lack of intermediate NDVI values, thus intermediate biomass of vegetation implies that transitions between vegetation and bare soil are sharp instead of gradual. The right peak, representing the frequency of pixels with high NDVI values, thus, pixels with vegetation, is somewhat lower than the left peak that represents the frequency of pixels with low NDVI values. This implies that the analyzed area consisted of more intertidal flat than vegetation, which does not interfere with our observation that vegetation distribution is bimodal.

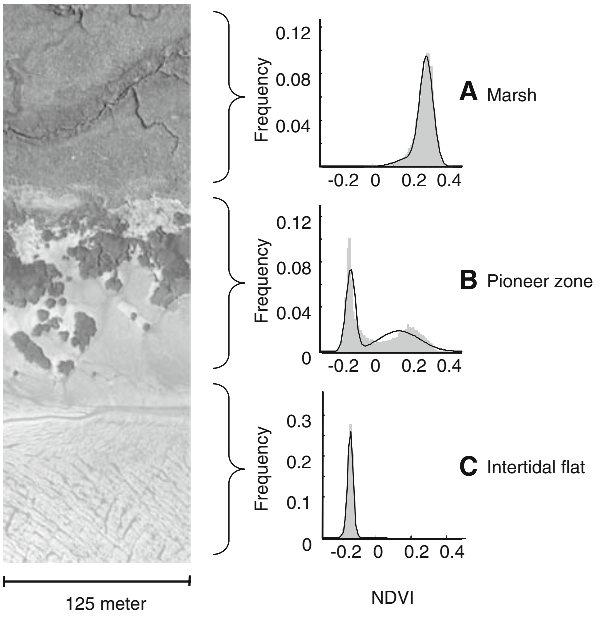

Figure 2. Example of transect through a marsh taken from an aerial photograph of Paulina polder (Westerschelde). Graphs represent the frequency distribution of the NDVI for the high marsh (**A**), pioneer zone (**B**), and tidal flat (**C**).

Thresholds

Our experimental results provide clear evidence of threshold dynamics in the establishment of vegetation. Transplants were capable of sustaining themselves in bare patches, provided that the transplanted units were large enough (Figure 3A, B, C). Seedlings did not survive to become adult plants in any of the locations. Mortality of small fragments was especially high in the beginning. Most large fragments survived for the time monitored and were mostly expanding (Figure 4). Differences in survival were significantly explained by differences in transplant biomass (t-value 6.20, $P < 0.01$; t-value 8.02, $P < 0.01$). Differences in survival between seedlings and small fragments were also significant (t-value -4.78, $P < 0.01$). These experimental results coincide with monitoring of natural seedling recruitment and survival (Figure 5). Natural recruitment is very episodic. In 2003, 89 seedlings settled in this area as opposed to

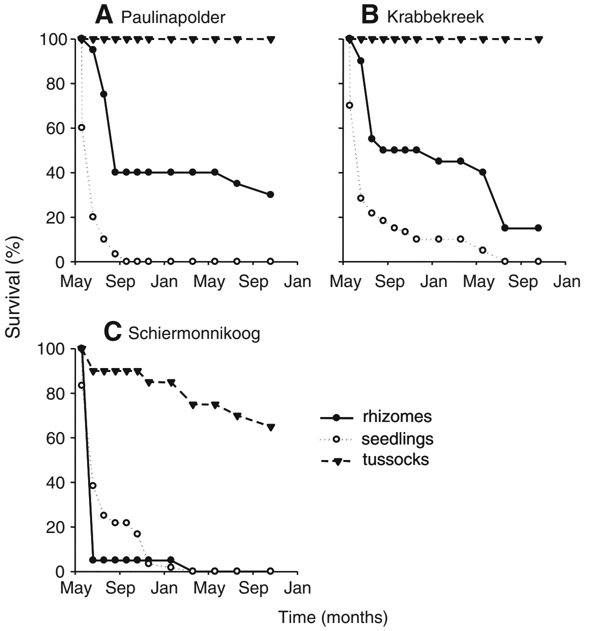

Figure 3. Survival of planted seedlings (*open circles*, $n = 60$), small fragments (*closed circles*, $n = 20$), and large fragments (*closed triangles*, $n = 20$) during 18 months in Paulinapolder (**A**), Krabbekreek (**B**), and Schiermonnikoog (**C**). Differences between survival of large and small fragments (t-value 6.20, $P < 0.01$) and large fragments and seedlings (t-value 8.02, $P < 0.01$) and seedlings and small fragments (t-value -4.78, $P < 0.01$) were all significant.

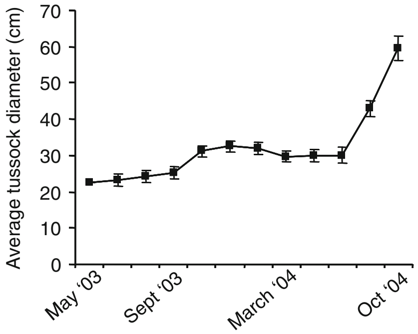

Figure 4. Average diameter of transplanted large fragments that survived, over a period of 18 months in Paulinapolder, Krabbekreek, and Schiermonnikoog. Error bars represent standard errors.

2 in 2004 (not represented in figure). However, none of the seedlings seem able to survive and form a new *Spartina* patch during the 2 years of observation. In our disturbance experiment, where we removed five *Spartina* tussocks in two different areas (n = 10), no re-growth was recorded in any of the cleared patches. All fragments that were transplanted as a control, survived and established (n = 10).

Long-Term Stability

Examination of changes in the spatial structure of *Spartina* tussocks in salt-marsh pioneer zones over a period of 22 years revealed little evidence for long-term vegetation stability (Figure 6A, B). Overlay analysis made clear that for this particular area in the same time span some tussocks were extending (light gray areas), whereas others were contracting (black areas). Moreover, vegetation loss and growth were recorded on the same tussock and a number of tussocks disappeared, whereas others established. Vegetation cover more than doubled between the years 1982 and 1998, although considerable loss was still occurring locally (Figure 6A). Nevertheless, very little vegetation loss was observed between 1998 and 2004 (Figure 6B); in this short period, vegetation growth was extremely high (Figure 6B). Large tussocks merged and were predominantly growing, whereas small tussocks appeared and disappeared.

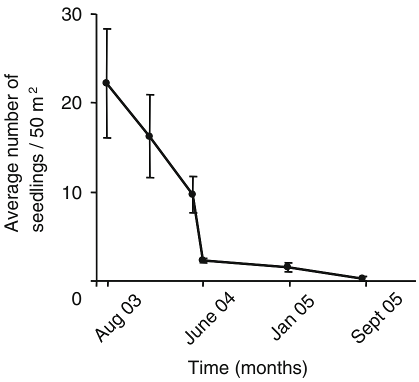

Figure 5. Number of *Spartina* seedlings monitored in four 10 × 5 m^2 plots, in a salt-marsh pioneer zone (Krabbekreek, Oosterschelde) during a period of 2 years.

DISCUSSION

In this article, we assessed to what extent the concept of alternative stable states is relevant in patchy salt-marsh pioneer zones. Our results reveal clear indications for the presence of alternative stable states in observations of vegetation characteristics and manipulative experiments. We found a bimodal vegetation distribution and a threshold in the establishment of *Spartina* vegetation, both of which are linked to the presence of positive feedbacks and alternative stable states by ecological theory (for example, Wilson and Agnew 1992; Scheffer and others 2001; van de Koppel and others 2001; Rietkerk and others 2004; Schroder and others 2005). Moreover, positive feedback between vegetation and sediment, a potential cause of bistability, has been described for a number of salt marshes (Chater and Jones 1957; Ranwell 1964; Scholten and Rozema 1990) and is considered to play an important role in salt-marsh dynamics (van de Koppel and others 2005; van Wesenbeeck and others 2007; van Wesenbeeck and others 2008). Hence, our empirical evidence combined with the evidence from the literature, seems to indicate the presence of alternative stable states in salt-marsh vegetation and thereby the potential for sudden shifts between vegetation and bare sediment. However, GIS analysis of vegetation development over 22 years gave a completely different picture, revealing a dynamic and transient ecosystem characterized by ongoing contraction and disappearance of some, and expansion of most vegetation patches. These patches probably develop toward a homogeneous vegetated state. Although alternative stable states theory adequately describes dynamics of salt-marsh pioneer zones on the scale of individual tussocks, on landscape scales and over longer periods of time, salt-marsh pioneer zones appear to be in a transient state. Nevertheless, threshold dynamics govern early vegetation establishment, and hence there is potential for sudden shifts to occur during pioneer vegetation development, for instance in the form of episodic estab-

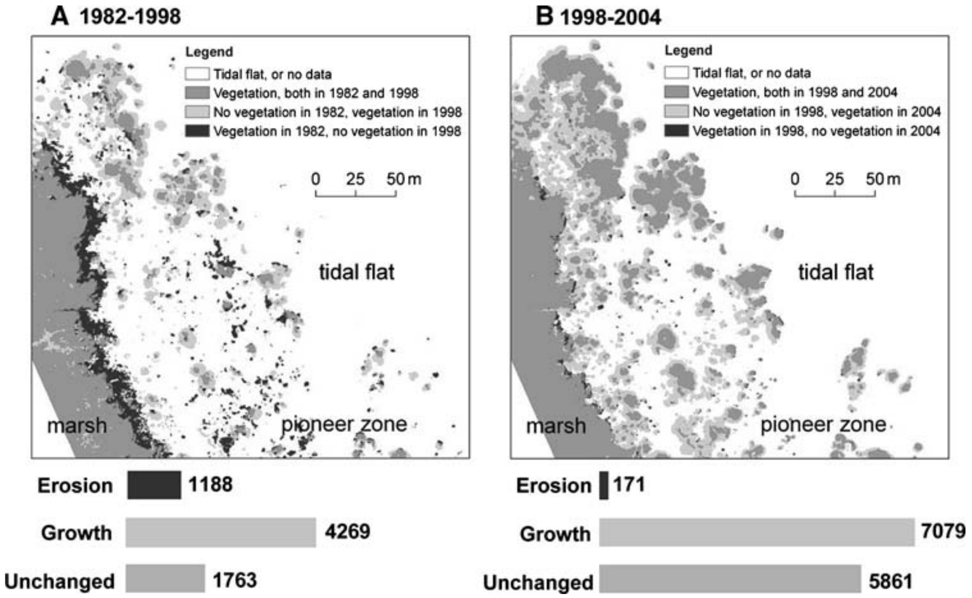

Figure 6. Growth and erosion of *Spartina* tussocks in a salt-marsh pioneer zone (Paulinapolder, Westerschelde). The picture shows vegetation that had been present between an interval (dark gray), vegetation that has developed in this period (light gray), and vegetation that has eroded in this interval (black). (**A**) shows the interval from 1982 to 1998 and (**B**) shows the interval from 1998 to 2004. Bars and numbers underneath the pictures show the exact amount of vegetation (in m^2) in the pioneer zone (from the black erosion zone in (**A**) to the right) that has been eroding or growing in both periods.

lishment of pioneer vegetation, or sudden and (on the short term) irreversible disappearance of vegetation patches.

Our experimental results show that although seedlings emerging more-or-less evenly over the area will not result in quick vegetation establishment, vegetation can successfully establish in a high-density patch (Figures 3 and 4). Such a patch may expand and grow out to cover, eventually, the entire area, even though initial biomass is quite small when averaged over the entire pioneer zone. Hence, the mudflat state is resistant to small disturbances on small spatial scales, but is vulnerable to spatially concentrated invasion of vegetation. This result highlights the importance of lateral expansion of tussocks as a spatially explicit process in limiting the stability of the bare-mudflat state on larger spatial and temporal scales. Our study, however, provides only a limited assessment of the determinant of initial vegetation establishment, and more research is required to clarify the stability of the mudflat state.

The lack of stability in patchy pioneer vegetation can have many potential causes. First, stability might have been prevented by changes in external factors, such as dredging or changed hydrodynamics (Pringle 1995; Van der Wal and others 2008). A second and more likely cause explaining long-term developments, however, are feedbacks occurring at larger spatial scales (Scheffer and others 2005; Dekker and others 2007; Janssen and others 2008). Changes in tussock configuration will influence hydrodynamic conditions by reducing the total amount of water flowing into the area (Temmerman and others 2005). This will favor development toward closed vegetation, dissected by drainage channels, increasing the stability of the homogeneously vegetated state. As a consequence, long-term stability may only be reached at a single large-scale equilibrium characterized by nearly homogeneous vegetated salt marsh. This equilibrium might be reached very slowly, as it is set back regularly by disturbances, such as storms, that cause erosion. Concluding, although within-patch feedback processes explain the presence of strongly contrasting patches with sharp boundaries (Van Wesenbeeck and others 2008) landscape-level processes that integrate the effects and interactions between small-scale patches may determine the large-scale, long-term development of the salt-marsh pioneer zone.

The possibility of processes at multiple spatial scales interacting to generate complex dynamics in ecosystems has been well established in the theoretical literature (Levin 1992; Rohani and others 1997; Aguiar and Sala 1999). Multi-scale interactions between feedback processes have, for instance, been studied in arid ecosystems, where small, micro-scale feedbacks interact with feedback processes at the landscape level, amplifying nonlinear dynamics, and leading to alternate stable states and considerable hysteresis at large spatial scales (Foley and others 2003; Scheffer and others 2005; Dekker and others 2007; Janssen and others 2008). These multi-scale feedback processes are suggested to explain shifts from perennial vegetation to deserts (Scheffer and others 2005; Dekker and others 2007; Janssen and others 2008). Other theoretical studies show that scale-dependent feedback processes may induce regular spatial patterns, increasing ecosystem resilience and buffering against large-scale ecosystem shifts (Rietkerk and Van de Koppel 2008). In a prior article, we presented evidence for similar scale-dependent relations affecting tussock expansion in salt-marsh pioneer zones (van Wesenbeeck and others 2008). However, although these processes likely delay the development of pioneer salt marsh vegetation (van Wesenbeeck and others 2008), they are unable to completely arrest development in the pioneer vegetation state for most salt-marshes, as landscape-scale feedbacks may lead to development of a full vegetation cover (Allen 2000).

Concluding, our study suggests that the concept of alternative stable states can be regarded as an approximate explanation for vegetation patchiness on short temporal and small spatial scales, but is not well adapted to predict the long-term dynamics of heterogeneous salt-marsh pioneer zones. This coincides with the idea that positive feedback may lead to hysteresis on short timescales, but may not necessarily cause bistability on the long run if there is dependence between fast-changing state variables (for example, local vegetation density) and slowly changing forcing factors (for example, landscape-scale processes) (Schroder and others 2005). A number of recent studies pointed at the potential for dramatic vegetation collapse in salt-marsh systems that have clear positive feedbacks, but evidently did not have two alternative stable states (Silliman and others 2005; van de Koppel and others 2005). The above literature, in combination with our own work, suggests that for sudden vegetation collapse to occur, bistability may not be a prerequisite. Moreover, systems that are not stable on longer timescales may have dynamics that resemble alternative stable state systems closely (Schroder and others 2005; Van Geest and others 2007). This has important implications for current theory on catastrophic shifts in ecosystems, as sudden changes that are difficult to reverse (at short timescales) may result from human interference in such systems despite the (evident) lack of alternative stable states.

Although small-scale processes do not always accurately predict large-scale dynamics, exploration of small scale processes, and especially acknowledging the presence of small-scale thresholds, is helpful for adequate conservation and restoration of ecosystems. In our system that is clearly in flux when viewed on larger spatial and temporal scales, we revealed typical characteristics of alternative stable states on smaller scales. This points to the possibility for sudden shifts in this ecosystem, in response to small human disturbances, which may require long time periods (decades in our system) to recover (Suding and others 2004). Criteria developed for detecting alternative stable states can provide useful tools in detecting the presence of thresholds in development of ecosystems. In addition, acknowledging that positive feedback can generate threshold dynamics, despite the absence of long-term bistability, will be an important step forward in the application of alternative stable state theory in ecology, and help in the conservation of complex ecosystems.

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