Thresholds and shifts:
consequences of habitat modification in salt-marsh pioneer zones

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Contents

Chapter 1

General introduction

Interactions between species and their environment

Species distribution can reflect underlying abiotic variability (Clements 1916), but in turn, abiotic variability can actively be influenced by species themselves (Darwin 1881). Presently, interactions between species and their environment are a major theme in ecological research, with a focus on the influence that organisms can exert on their surroundings (e.g. Dawkins 1982, Wilson and Agnew 1992, Bertness and Callaway 1994, Jones *et al.* 1994, OdlingSmee *et al.* 1996, Jones *et al.* 1997). Despite this overwhelming attention for the potential of organisms to transform and construct their habitats, implications of this aspect for ecosystem dynamics, species interactions and spatial structure, have received relatively little attention.

Currently several terms dealing with interactions between organisms and abiotics are circulating: the extended phenotype (Dawkins 1982), positive feedback (switches) (Wilson and Agnew 1992), ecosystem engineering (Jones *et al.* 1994) and niche construction (OdlingSmee *et al.* 1996). Of these terms, the extended phenotype and niche construction are usually used in an evolutionary context, dealing with evolutionary implications of habitat modification by species (Dawkins 1982, OdlingSmee *et al.* 1996). The ecosystem engineering concept is by far the most widely applicable as ecosystem engineers are described as “organisms that change biotic or abiotic materials, thereby controlling availability of resources to other organisms” (Jones *et al.* 1994). The most well-known example of an ecosystem engineer is the beaver that slashes trees and causes them to barricade rivers, thereby creating ponds of stagnant water (Jones *et al.* 1997). However, practically any organism in any system can function as an ecosystem engineer (Jones *et al.* 1997).

The generality and ubiquity of ecosystem engineering constitutes the main criticism on the concept. Critics state that all species affect their surroundings in one way or another (Lawton 1994), and that only very few of these impacts will significantly alter or contribute to ecological processes, which is taken as a measure for relevance of engineering (Reichman and Seabloom 2002). In fact, engineering can be an accidental by-product of the mere presence of an organism in an ecosystem (Jones *et al.* 1994, Reichman and Seabloom 2002), not encompassing further consequences on the species itself or on ecological processes. Another point of concern is the suggestion that ecosystem engineering is a very context-dependent principle (Wright and Jones 2006). Whereas, principles, such as positive feedback and facilitation, have resulted in the development of general assumptions of their effects (Wilson and Agnew 1992, Bruno *et al.* 2003), there seems to be little consensus, however, on the common effects of ecosystem engineering. Here I distinguish between intraspecific and interspecific consequences of ecosystem engineering on species, community and landscape scales.

By changing environmental circumstances an ecosystem engineer can ameliorate conditions for itself (positive feedback loop) and for others (facilitation). The concept of positive feedback switches establishes a link between ecosystem engineering and other ecological processes. This link is extremely useful for describing intraspecific effects of ecosystem engineering and for understanding implications on ecosystems. First, effects of ecosystem engineering are expected to magnify, if the transformed property induces a positive feedback loop with the ecosystem engineer. In this case ecosystem engineering constitutes a relevant influence on ecosystem processes and functioning, thereby effectively eliminating the main point of criticism on the ecosystem engineering concept. Second, positive feedbacks connect ecosystem engineering with evolutionary principles, such as niche construction, when the transformed property increases the fitness of the engineer. Third, implications of positive feedback on ecosystem dynamics are well-studied and ecosystem engineering might bring about similar effects. For example, positive feedbacks are generally limited by some factor, such as a negative feedback on larger scales (scale-dependent feedbacks) (Lejeune *et al.* 1999, van de Koppel *et al.* 2005a), or by reaching another equilibrium (alternative stable states) (Rietkerk and van de Koppel 1997, van de Koppel *et al.* 2001). It will be important for understanding and predicting ecosystem dynamics of systems dominated by ecosystem engineers, to detect whether these consequences also arise in relation with ecosystem engineers.

Habitat modification can strongly affect community structure (e.g. Rhoads and Young 1970, Bertness and Callaway 1994, Jones *et al.* 1997, Crooks 2002). The most well-known interspecific effect of ecosystem engineering is facilitation, a process that already was recognized before ecosystem engineering became in vogue (e.g. Chandler and Fleeger 1987, Bertness 1989, Callaway *et al.* 1991, Bertness and Shumway 1993). Facilitation deals with positive species interactions, and is often mediated by alleviation of environmental stress (Bruno *et al.* 2003). Accordingly, facilitation has been shown to play an important structuring role under conditions of high physical stress (Bruno *et al.* 2003). Previously, physical forces were assumed to structure communities under stressful conditions, while species interactions, such as predation and competition, were thought to be the main structuring force under benign conditions (Menge and Sutherland 1976). In the light of ecosystem engineering, facilitation is one of the few consequences of habitat modification that is known, to a certain extent predictable, and well-documented.

Several small attempts to generalize interspecific consequences of ecosystem engineering on spatial structure of ecosystems have already been made. Ecosystem engineering is often suggested to induce habitat heterogeneity by creating patches that differ from the surroundings (Hui *et al.* 2004, Gutierrez and Jones 2006, Wright *et al.* 2006). On landscape scales, encompassing both modified and unmodified patches, an increase in biodiversity will be observed (Wright *et al.* 2002, Castilla *et al.* 2004, Wright *et al.* 2006). Conclusively, patchiness and heterogeneity seems to be one of the possible effects of ecosystem engineering. Landscape-scale patchiness might point at other ecosystem engineering effects, such as thresholds and alternative stable states (e.g. Walker *et al.* 1981, Peterson 1984, Rietkerk and van de Koppel 1997, van de Koppel *et al.* 2001, Scheffer and Carpenter 2003, D'Odorico *et al.* 2005). This can probably even link ecosystem engineers with catastrophic shifts (Rietkerk *et al.* 2004) but this has not been developed any further. Finally, it has been suggested frequently that ecosystem engineers should be a target for successful conservation and restoration of ecosystems (Boogert *et al.* 2006, Byers *et al.* 2006, Crain and Bertness 2006). A more thorough knowledge of effects of ecosystem engineering on community structure, landscape scale patterns and species interactions, will enhance our understanding of the consequences of ecosystem engineering, and benefit conservation and restoration of natural systems with the use of ecosystem engineers.

Aim of this thesis

The main aim of this thesis is to enhance our mechanistic understanding of the structuring role of ecosystem engineers on different scales. Therefore, I evaluate the mechanisms by which habitat modification affects species interactions, community composition, the development of spatial patterns, and the potential for catastrophic shifts, using the salt-marsh pioneer zone as a model system.

What are salt marshes and why are they important?

Salt marshes are coastal grasslands that are situated on the interface of land and sea, and are flooded periodically with seawater during high tides. They are considered to belong to the most productive systems in the world and are characterized by a gradient in elevation that determines inundation duration and vegetation presence. Salt marshes are home to plant species that are only found in areas with high levels of salinity. Additionally, salt marshes and adjacent intertidal flats are popular breeding and feeding grounds for different bird species.

Conservation of salt-marsh landscapes is not only important from a biological point of view, but salt marshes also play an important role in coastal protection and defense, implying there are important economic reasons to protect salt marshes. Evidence is increasing that presence of large marsh areas in front of the seawall dissipates wave energy, thereby reducing hydrodynamic forces on the seawalls (Möller *et al.* 1996, Möller *et al.* 1999). Seawalls that are protected by salt marshes can be considerable lower and smaller than dikes without marshes in front (King and Lester 1995). Hence, presence of salt marshes can substantially reduce costs for coastal defense.

Studies confirm severe losses of salt-marsh area all over the world (Schwimmer 2001, Bromberg and Bertness 2005, Wolters *et al.* 2005). In many areas salt marshes are squeezed in between shipping channels on the front and fixed coastlines at the back (Figure 1A). This so-called ‘coastal squeeze’ (Winn *et al.* 2003) might form a large problem for salt marshes adapting to sea-level rise, as they can not retreat more inland. This illustrates the importance of scrutinizing salt-marsh response to changes in environmental variables.

Figure 1.1. A. Typical Dutch salt marsh bordering the seawall. B. Salt-marsh pioneer zone with scattered *Spartina anglica* tussocks. Photographs by: J. van Soelen

Salt-marsh pioneer zones

A salt marsh is the result of interactions between physical and biological processes (Dijkema *et al.* 2001). Salt-marsh formation starts in the pioneer zone, where the first vascular plants invade the intertidal flat (Figure 1.1B). These plants mostly are *Spartina* spp. and *Salicornia* spp. However, of these plants only the perennial *Spartina* (see Box 1) induces salt-marsh formation by trapping sediment and increasing soil elevation. The lower level of *Spartina* occurrence is set by immersion time, which limits light availability (Hubbard 1969).

Pioneer salt-marsh vegetation consisting of *Spartina anglica* is generally characterized by a patchy vegetation structure. *Spartina* forms round shaped tussocks that are found scattered over the mudflat (Figure 1.1B). These patches are considered to expand, forming a homogeneous vegetation cover dissected by drainage structures (Olff *et al.* 1997, Allen 2000, van de Koppel *et al.* 2005b, Temmerman *et al.* 2007).

Nevertheless in reality salt-marsh pioneer zones can be dominated by *Spartina* patches that seem fairly stable for decades. Considering this, several scenarios are possible once *Spartina* patches are present in a salt-marsh pioneer zone. Patches can expand gradually, patches can expand suddenly or patches can erode gradually and patches can erode suddenly, or patches can both expand and erode simultaneously either gradually or abrupt.

The importance of positive feedback and facilitation for salt-marsh formation

Salt marshes are merely created by a positive feedback between vegetation and sediment deposition and retention (Yapp *et al.* 1917, Allen 2000, van de Koppel *et al.* 2005b). This process is generally starts in the pioneer zone by plants of the genus *Spartina* (see Box 1 and Figure B1.1). This grass exhibits a positive feedback loop with sedimentation. Aboveground stems and leaves reduce current velocities inside the vegetation, thereby decreasing erosion and increasing sedimentation of small particles from the water column (Ranwell 1964, Castellanos *et al.* 1994, Cahoon *et al.* 1996). This process results in higher elevations within vegetation, which has a positive effect on *Spartina* growth by a reduction in submersion times, thus enhancing light availability for photosynthesis (Hubbard 1969).

Similar to most salt-marsh plants, the lower level of occurrence for *Spartina* is set by stress and the higher level by competition. By increasing elevation, *Spartina* facilitates the community of salt-marsh plants that live in the higher marsh areas. Once elevation inside vegetation becomes higher other species, that can not tolerate stresses in the pioneer zone, invade *Spartina* vegetation. These species are generally better competitors for light and resources and ultimately replace *Spartina* (Bertness and Ellison 1987). Although *Spartina* also prefers the less stressful conditions of the high marsh, it is competitively excluded from these more benign areas (Bertness 1991).

Salt marshes: a model system

Salt-marsh pioneer zones are generally situated between the vegetated platform of a high marsh and the bare intertidal flat that is mainly inhabited by benthic invertebrates. This zone is a good model system as it is a transition between these two distinct habitats, resulting in stressful conditions for organisms that are characteristic of both habitats. Further, the zone is characterized by strong physical forcing and variability on landscape scales, but does not show strong underlying abiotic heterogeneity on smaller scales. It is occupied by a limited number of plant and animal species from which the most prominent are strong ecosystem engineers. Benthic fauna, characteristic of the intertidal flat is known for the large influences they impose on their surroundings, mostly by bioturbation (Meysman *et al.* 2006) and the main plant species, from the genus of *Spartina*, is a famous ecosystem engineer, increasing soil elevation by sediment input (Wilson and Agnew 1992, Chung 1993). Although no large differences in abiotic conditions are expected to be found within the pioneer zone initially, the zone is usually characterized by patchy configurations, which are expected to be caused by ecosystem engineering effects.

Outline of this thesis

In this thesis I try to enhance the understanding of implications of ecosystem engineering for ecosystem dynamics, species interactions and spatial structure. Therefore, intraspecific consequences of ecosystem engineering on different scales are studied, by examining implications of positive feedbacks in *Spartina* patches characteristic of salt-marsh pioneer zones. It is tested whether possible factors, such as negative effects on larger scales, or alternative stable states can limit these positive feedbacks. Interspecific consequences of habitat modification are examined by investigating if opposite positive feedbacks can counteract each other. This process can be seen as the negative alternative of facilitation, affecting other species negatively via the environment. Finally, the effects of stress and facilitation on species interactions are investigated.

First, it is investigated if habitat modification results in scale-dependent effects that explain the occurrence of *Spartina* patches, and have a structuring potential on

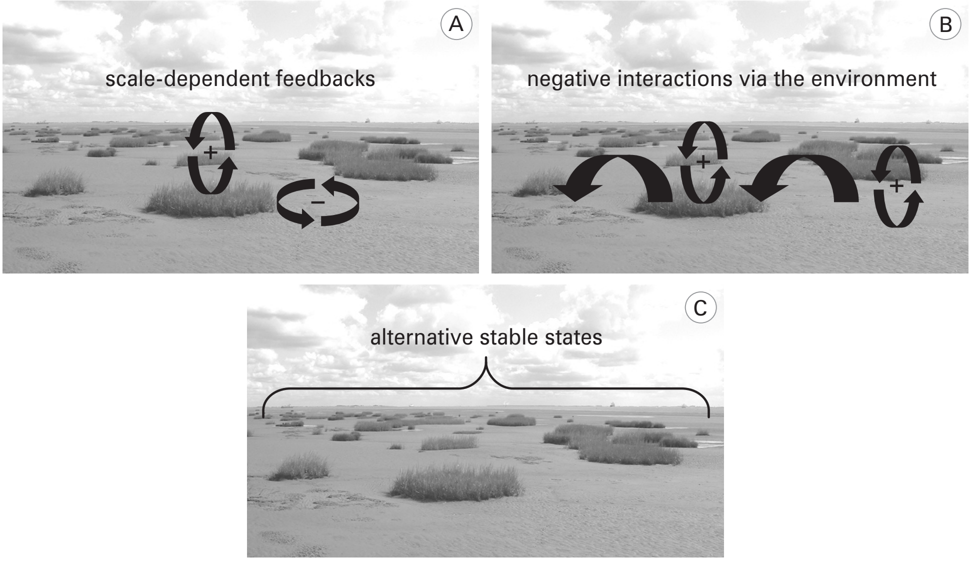

Figure 1.2. Schematic representation of expected consequences of ecosystem engineering that play a role in structuring salt-marsh pioneer zones, such as A. Scale-dependent feedbacks, B. Negative species interactions by habitat modification, C. Alternative stable states.

landscape scales (Figure 1.2A). Positive feedback effects within patches may result in negative effects just outside patches, which might function as a stabilizing force on patch borders (Chapter 2). These small-scale effects can possibly explain large-scale complexity of salt-marsh systems (Chapter 2). Second, it is examined whether ecosystem engineering might be a mechanism for negative species interactions, besides positive effects of habitat modification by facilitating other species (Chapter 3, Figure 1.2B). These negative interactions via the environment inhibit invasion of one species in patches occupied by the other, offering a possible explanation for the patchy structure of the salt-marsh pioneer zone (Chapter 3). In the appendix by chapter 3, species interactions via habitat modification are modeled, trying to explain the potential for exclusion and coexistence compared to other forms of competition, such as competition for resources. This is further explored in a literature study, in which recent studies on ecosystem engineering are reviewed (Chapter 4). Here, ecosystem engineering by one species is considered as a mechanism underlying ecological invasions, and ecosystem engineering in opposite directions by multiple species, creates habitat heterogeneity through patchiness. Patchiness often points at the presence of thresholds and alternative stable states in a system. So, in chapter 5 the presence of biomass thresholds for settlement is tested and stability of patches is studied over decades (Chapter 5, Figure 1.2C) to asses the potential for sudden shifts in salt-marsh pioneer zones. Finally, a landscape-scale approach is taken, evaluating effects of changing environmental stresses on competition and facilitation in distinct coastal habitats (Chapter 6). Positive and negative species interactions in a community facilitated by *Spartina* are examined along a gradient of hydrodynamic stress to measure which processes determine community structure with differing stresses.

Box 1
Spartina anglica

The dominant plant species in salt-marsh pioneer zones in Europe is the common cordgrass, *Spartina anglica* (Figure B1.1A + B1.1B). *Spartina anglica* is a cross between the smooth cord-grass *Spartina alterniflora*, which was introduced from the North East coast of the US at the end of the nineteenth century, and Europe's native cordgrass *Spartina maritima* (Lacambra *et al.* 2004). This cross first resulted in a sterile hybrid (*S. x townsendii*), which gave rise to the fertile allopolyploid *Spartina anglica* (Ayres and Strong 2001). Nowadays *Spartina maritima* is mostly out-competed by *Spartina anglica*, which is a fierce grower and has high fecundity (Lacambra *et al.* 2004). The rapid colonization potential of *Spartina anglica* and its ability to increase soil elevation by capturing sediment have often been used by man for salt-marsh protection, creation of new salt marshes and for stabilization of coastlines (Dijkema *et al.* 2001, Chung 2006).

Figure B1.1. A/ *Spartina anglica* stand (canopy height approximately 50 cm), B/ *Spartina anglica* getting submerged. Photographs by: I.E. Hendriks

Chapter 2

Does scale-dependent feedback explain spatial complexity in salt-marsh ecosystems?

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submitted

Abstract

Complexity theory highlights scale-dependent feedback mechanisms as an explanation for regular spatial patterning in ecosystems. To what extent scale-dependent feedback clarifies spatial structure in more complex, non-regular systems remains unexplored so far. We report on a scale-dependent feedback process generating patchy landscapes at the interface of intertidal flats and salt marshes. Here, vegetation was characterized by *Spartina anglica* tussocks, surrounded by erosion gullies. Field surveys revealed that larger tussocks have deeper gullies, suggesting that gully erosion is caused by increased water flow around tussocks. This was confirmed by flume experiments. Transplantation of small clumps of *Spartina* revealed that the growth of *Spartina* transplants compared to transplant growth on bare sediment was higher within *Spartina* tussocks, but lower in the gully just outside *Spartina* tussocks, providing clear evidence of scale-dependent feedback. Our results emphasize that scale-dependent feedback is a more general explanation for spatial complexity in ecosystems than previously considered.

Introduction

What determines the spatial structure of ecosystems? This simple question addresses one of the most complex issues in ecology for over a century now. For long it has been assumed that underlying abiotic variability explains spatial patterns of species distribution, either directly (Clements 1916; Tilman 1982), or indirectly by dictating the strength of biological interactions along gradients, such as the rocky intertidal (Menge 1976; Bertness 1998). Although this theory is valid for many ecosystems, it fails to explain the occurrence of spatial patterning within ecosystems with little underlying abiotic heterogeneity.

Recently, a body of theory has emerged emphasizing the presence of heterogeneous species distribution in systems with little variety in environmental background conditions, such as regular vegetation patterning in arid zones (Klausmeier 1999; Couteron & Lejeune 2001; von Hardenberg *et al.* 2001), vegetation patterning in boreal and temperate bogs (Rietkerk *et al.* 2004b), and regular patterning of mussels on intertidal flats (van de Koppel *et al.* 2005). These studies propose that a scale-dependent feedback between localized facilitation and large-scale inhibition induces spatial self-organization, and explains the observed spatial structure. In arid systems, for example, infiltration of water is locally enhanced by plant presence, while on landscape scales competition for water between plants is the dominant process explaining observed vegetation patterns (Couteron & Lejeune 2001; Rietkerk *et al.* 2002). So far, scale-dependent feedback mechanisms have mostly been linked to regular patterns, such as banded, spotted or labyrinth structures (Rietkerk *et al.* 2004a). This is consistent with the activator-inhibitor principle that was originally introduced by Turing (1952) and which is considered the basis of scale-dependent theory (Rietkerk *et al.* 2004a). It is still unknown whether scale-dependent feedbacks also play a role in structuring systems that have more complex non-regular spatial patterning and, thus, whether the concept is more generally applicable.

In stressful environments, such as coastal ecosystems, habitat modification is an important mechanism by which many species are known to improve the living conditions for themselves and for other species. A good example of this is attenuation of wave and current stresses by the cordgrass *Spartina anglica* in salt-marsh pioneer zones, a mechanism that is known to facilitate other species (Bruno 2000; van de Koppel *et al.* 2006), but also has beneficial effects on *Spartina* itself (Bouma *et al.* 2005b). Reduced hydrodynamics within the vegetation increase sedimentation, leading to higher soil elevation in *Spartina* vegetation (Yapp *et al.* 1917; Ranwell 1964; Castellanos *et al.* 1994; Cahoon *et al.* 1996). Increased soil elevation shortens inundation time, increases aeration and lowers salinity, improving conditions for plant growth. This constitutes a positive feedback between the density and size of *Spartina* and its growth potential (Wilson & Agnew 1992). However, despite local positive feedback within patches, negative effects may occur on larger scales, just outside the patches. Small gullies, that are observed just outside *Spartina* patches (Figure 2.1A), indicate that current velocities may be increased around *Spartina* tus-

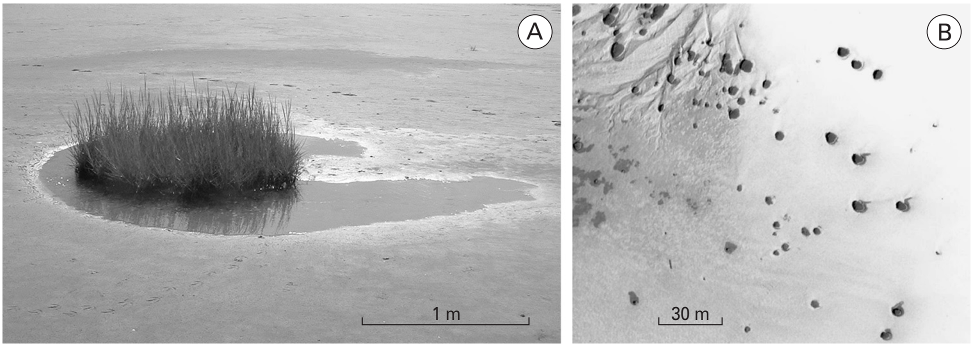

Figure 2.1. (A) Typical example of an elevated tussock with erosion gullies on the side on intertidal flat in the Westerschelde. (B) Aerial photograph representing a 600 by 600 m area of an intertidal flat in the Westerschelde. Black patches are vegetation in a matrix of bare sediment (white-gray). Gray patches on the left of the picture are microphytobenthos.

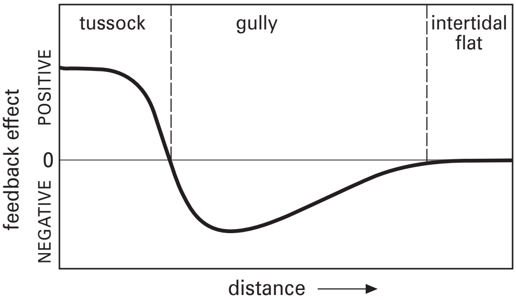

Figure 2.2. Schematic representation of expected feedback effects at different distances from tussock centre. Dashed line represents zero feedback effect. If the black line rises above the dotted line feedback effects are positive, below the dashed line feedback effects are negative. The variable distance refers to distance from the tussocks' center.

socks, leading to erosion of the gullies and possibly preventing tussocks from expanding laterally. Hence, divergence of flow may induce a scale-dependent feedback determining the patchy structure of pioneer salt-marsh vegetation (Figure 2.1B).

Here we ask the question if scale-dependent feedbacks might affect ecosystem structure in a system without regular patterning. We hypothesize that feedback effects on plant growth are scale-dependent; effects are positive within vegetation patches but negative just outside, relative to plant growth on bare sediment (Figure 2.2). These hypotheses were tested by exploration of aerial photographs to investigate whether distribution of *Spartina* tussocks was random or regular, by executing flume studies to explore relationships between physical stress and feedbacks effects, and by transplanting experiments in the field to assess influence of feedbacks effects on vegetation development under natural conditions. We discuss the implications of our results as indicative for the importance of scale-dependent feedbacks in complex, non-patterned ecosystems.

Methods

Field site

Pioneer salt-marsh vegetation consisting of *Spartina anglica* is, in early stages of salt-marsh development, characterized by a patchy vegetation structure (Figure 2.1B). Although under ideal growth conditions a homogeneous vegetation cover will develop, there is growing evidence that vegetation expansion can be inhibited by interactions with abiotic processes, such as nutrient availability and hydrodynamics (Hemminga *et al.* 1998). This might explain the sometimes stable appearance of *Spartina* tussocks over periods of more than ten years.

To examine whether scale-dependent feedback processes might retard tussock expansion field experiments were conducted on the Plaat van Walsoorden (N 51° 22, 6’, E 4° 04, 7’) in the Westerschelde, The Netherlands. This is an intertidal flat of approximately 2 kilometers width with patchy distributed tussocks of the English Cordgrass, *Spartina anglica* (Figure 2.1B). Although some erosion and expansion of tussocks was recorded, tussocks generally have been present for over ten years (unpublished data). Most tussocks are characterized by a dome-shaped appearance and by erosion gullies running along their edges (Figure 2.1A). Transitions between tussocks and surrounding sediment are sharp and sometimes tussock edges seem vulnerable to erosion because of their slightly elevated position.

Pattern analysis of aerial photographs

To determine if tussock distribution in salt-marsh pioneer zones was random, clustered, dispersed or regular, we examined tussock distribution by calculating Ripley’s K (Ripley 1977) from aerial photographs from the same intertidal flat where we executed experiments. Photographs were selected based on their clarity and absence of benthic macro algae, allowing us to easily extract vegetation from the surrounding sediment using color information from red and blue bands. Photographs from 2004 were selected, which were the most recent ones that were usable and were between 500 and 700 meters in width and length. This way there was no interference with edges of the flat, with areas without vegetation or with areas with other vegetation types. The photographs were scanned and middle points of all vegetation patches were determined using Matlab, Version 7.1. Ripley’s K was calculated using R, version 2.2.1. Inter-tussock distances were used to calculate K(d), which compares distances between neighboring tussocks with random values and uses this to obtain a measure for spatial distribution of point data for different inter-tussock distances. 100 Monte Carlo iterations were used to calculate the 95% confidence intervals for spatial randomness. Instead of K(d) the more robust function L(t) was plotted ($L(t)= \sqrt{K(d)/\pi}$). L(t)-values represent the number of points that are expected to be found at certain distances if point data are randomly distributed (based on Poisson distribution). L(t)-values that rise above the upper confidence limit imply that for these specific inter-tussock distances more points are found than would be expected based on a Poisson distribution, pointing at clustering of point data. L(t)-values below the lower confidence limit indicate a dispersed distribution as the number of points encountered for that specific inter-tussock distance are less than expected. L(t)-values that stay between the confidence intervals imply randomness.

Field surveys of mound volume and gully depth

We investigated if any relationship exists between the volume of a tussock and the depth of erosion gullies along the tussock edges by measuring gully depth and tussock volume of 13 tussocks in the field. To obtain an estimate of tussock volume we measured tussock surface area and height of the mound in the field and multiplied these parameters. Tussock size was determined by measuring the diameter in both North-South and East-West direction. Tussock mound elevation and gully depth were calculated by measuring soil height in the middle of the tussock and then measuring the deepest point of the gully and a point at 5 meters distance from the tussock center. Height in the middle of the mound was measured only once, but the elevation of the gully and 5 meter from the tussock were measured in all four wind directions: North, East, South, and West. To obtain the height of the mound we calculated the average altitude of the four points at 5 meter distance North, East, South and West from the mound and subtracted this average from the altitude of the mound middle. For calculating gully depth mean elevation of the gully was subtracted from the mean altitude at 5 meters. The resulting four gully depth values for each tussock were averaged for all 13 tussocks. Finally, mound volume and gully depth were correlated using Statistica, Version 7.1.

Flume experiments

We examined whether scale-dependent effects were caused by hydrodynamic forces in a flume study. To test whether scale-dependent effects varied with changing physical stress the effects of current velocity and water height on tussock border erosion were measured. A flume is an artificial channel used for studying the flow of fluids. In the test section, objects such as vegetation can be placed to study the effects of the object on hydrodynamics. Our measurements were done in a racetrack flume at the NIOO-CEME in Yerseke. This flume has a total length of 17.5 m and a volume of about 10 m^3. Current velocity can be regulated between 0 and 0.6 m s^{-1} respectively. The test section of the flume is 0.6 meter wide and 2 meters long. For further details on this flume system see Van Duren *et al.* (2006). For our flume study, we used vegetation densities representative of *Spartina* densities in the field (1600 shoot per m^2) on mixed sandy silt sediments. *Spartina* was grown from seed. Seeds were obtained from *Spartina anglica* in the field six months earlier (September/October) and stored in salt water at 7 °C. For germination seeds were rinsed with fresh water and put in a warm, moist and light place. Small seedlings were planted in trays that fitted the flume test section widthwise (0.6 m), but were shorter than the test section lengthwise (tray 1.0 m compared to test section of 2.0 m). In these trays seedlings were grown to adult *Spartina* plants (average plant height was comparable to natural *Spartina* plants under salt conditions), while being watered with a mixture of fresh and salt water to mimic field conditions. Finally, half of the tray was filled with vegetation (0.3 meter wide and 1 meter long), so that vegetation bordered one side of the flume while filling half of the test section. The other half consisted of bare sediment. For the flume experiment, trays were put in the middle of the test section, leaving 0.5 m open space on each end of the tray. This allowed us to remove front and back plates of the tray, fill the remainders of the test section with sediment that was similar to the sediment used in the trays (comparable to sandy silt) and make soils in the complete test section level with the flume bottom. All this was done to prevent the front and back plates of the tray from interfering with occurring erosion.

To detect if erosion was caused by diversion of current stress to tussock borders, as the tussock acts as a barrier for water flow, erosion was measured after running the flume with six different water heights (12, 15, 17, 20, 22.5, 25 cm), but with a constant flow velocity of 0.3 m s^{-1} for 30 minutes. Data from flume studies were only used to obtain a qualitative understanding of ongoing processes, as increased current velocities alongside vegetation patches will differ quantitatively from currents in the field, where lateral water movement is not restricted by the width of the flume channel. However, velocities that were imposed in the flume are representative for velocities observed in the field (Bouma *et al.* 2005a). To determine the influence of current velocities with incoming tides on tussock border erosion, we used six different flow velocities (0.2, 0.23, 0.25, 0.27, 0.3, 0.4 m s^{-1}) with a constant water height of 12 cm. After running the flume with a unidirectional flow, erosion was measured manually. This was done by laying out a grid of 120 cm in the x-direction and 60 cm in the y-direction measuring sediment height with a measuring stick every 5 centimeters. After each measurement sediment was restored by adding (and removing) sediment where necessary. Two multiple regression analyses were performed in Statistica, with eroded volume as the dependent variable in both and water height and current velocity as independent variables respectively.

Transplanting experiments

The presence of a scale-dependent feedback in the field was established by executing transplanting experiments. To test whether growth of *Spartina* was affected by erosion in a scale-dependent way, we planted small *Spartina* clumps (15-20 stems) at various distances from the center of tussocks in the field. Transplant units were obtained from a single *Spartina* tussock growing at the same field site. To determine if *Spartina* tussocks facilitate growth of con-specifics within a tussock, transplants were planted inside existing tussocks (0 meter). To test whether plants have lower survival next to tussocks a second clump of vegetation was planted just next to existing tussocks in the gully (0.5 meter). As a control, the last piece of vegetation was planted outside the influence area of the tussock (4 meter). To eliminate effects of competition for light we added a treatment of clumps that were transplanted inside tussocks into small areas where aboveground biomass of other plants was repeatedly removed up to 20 cm from the transplant. All treatments were repeated twelve times in different randomly chosen tussocks. Transplant success was monitored every two months by scoring presence/absence of transplanted units, measuring diameter, counting stems and measuring height of five random stems of each transplant. After 14 months all transplants were harvested. Biomass was dried in an oven at 50 degrees Celcius for 48 hours and weighed afterwards. Analysis of variance was applied, with competition treatments nested in the 0 distance class, to determine if variances in biomass of transplants were explained by distance from the tussock. Post hoc comparisons were done using a Tukey HSD test.

Results

Extracting middle points for all tussocks from the four aerial photographs resulted in a point pattern (Figure 2.3A) that was used to calculate L(t) for inter-tussock distances using Ripley's K-test for determining randomness of spatial point data (Figure 2.3B). Inter-tussock distances that form a wave around the confidence intervals expose a regular pattern. Although not all trends are similar, L(t)-values derived from photograph 2 lie completely in between the confidence intervals (Figure 2.3B2), pointing at a random tussock distribution. L(t) values in Figure 2.3B1 and 2.3B3 rise slightly above the upper-confidence limit, pointing at clustering of tussocks. In figure 2.3B3 clustering only occurs for inter-tussock distances above 50 m and below 300 meter. Above 300 meter L(t) values are in between the confidence intervals again. Hence, our analysis did not provide any evidence for regularity in tussock distribution.

Our field survey of tussock surface area, mound height and gully depth shows a significant positive correlation between tussock volume and depth of the erosion gullies next to the tussock ($R^2 = 0.32$, $P < 0.05$). So, tussocks with large volumes are surrounded by deeper gullies. Our flume studies, testing if erosion next to tussocks could be linked with current velocity and water height, showed a positive linear relationship between current velocity and eroded volume (Figure 2.4A: $R^2 = 0.86$, $P < 0.01$). This implies that faster water flow generates deeper erosion gullies alongside tussocks. Furthermore, these erosion gullies are mainly generated with low water levels; our flume study revealed a perfect negative linear relation between border erosion and height of the water column (Figure 2.4B: $R^2 = 0.96$, $P < 0.001$).

Biomass of transplants in the field fluctuated with distance from the naturally present tussocks. Significant effects of distance from the original tussock on transplant performance were detected (Figure 2.5: nested-ANOVA, $F_{1,44} = 30.49$, $P < 0.001$). Average biomass was highest inside the tussock, whereas lowest biomass was recorded in the 0.5 meter class, just next to the original tussock. This class differed significantly from all other classes (Figure 2.5: Tukey HSD test, $P < 0.001$). Transplants in this class stand in the erosion gully, that is waterlogged, which probably

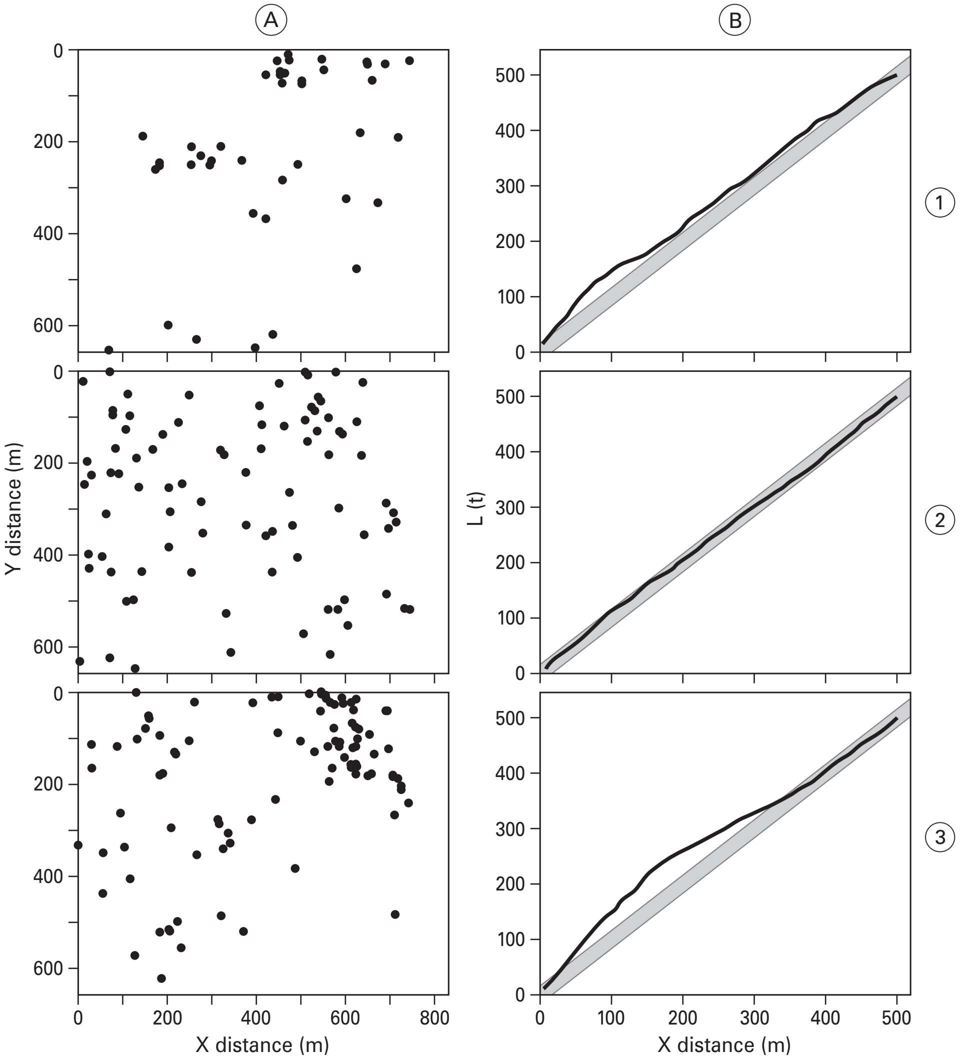

Figure 2.3. (A) Point patterns derived from aerial photographs which were used to calculate (B) L (t) values for inter-tussock distances using Ripley's K-test for determining randomness of spatial point data. Dotted lines represent confidence intervals (95%) and solid lines represent L(t) values. If the solid line rises above the upper confidence limit points are clustered, if it goes below the lower confidence limit points are showing a regular pattern. If L(t) values are in between both confidence limits points are randomly distributed.

caused their mortality. The transplants at 4 meters from the tussocks perform better than those at 0.5 m from the tussock but worse than transplants within the tussock (Figure 2.5). No significant effect of above ground competition on tussock performance was encountered for the transplants in distance class 0 (Figure 2.5: nested-ANOVA, $F_{2,44} = 1.66$, $P = 0.21$). The 0 m class without competition, differed only

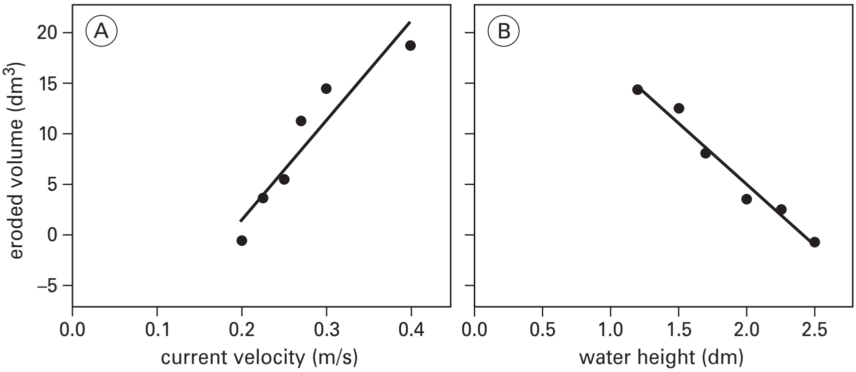

Figure 2.4. Correlation of the eroded volume next to *Spartina* vegetation with (A) current velocity (R^2=0.86), and (B) water height (R^2=0.96), in a race-track flume.

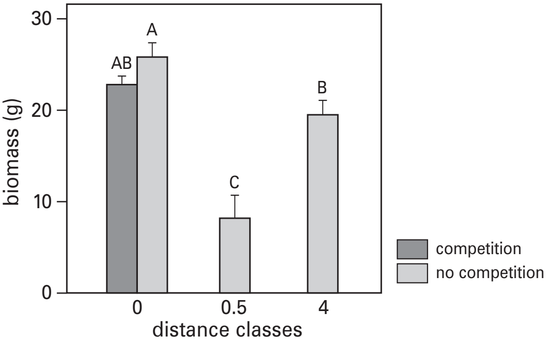

Figure 2.5. Average biomass (dry weight) of transplanted vegetation units per distance class (0, 0.5 and 4). In the 0 category competition and without competition treatments are depicted. Letters indicate significant differences (Tukey test) and bars represent standard errors (+1 SE).

marginally from the furthest distance class of 4 meter (Figure 2.5: Tukey HSD test, $P = 0.05$). The 0 m class with competition did not differ significantly from this class (Figure 2.5: Tukey HSD test, $P = 0.53$).

Discussion

The results of our study reveal that scale-dependent feedback processes, previously described exclusively in systems with regular spatial patterns, can also be an important cause of spatial structure in systems with a more random distribution of vegetation. In salt-marsh pioneer zones, tussocks divert stresses imposed by water currents, resulting in sedimentation and improved growth within the tussocks, but also in erosion and deprived growth conditions next to tussocks. Tussocks with larger volumes were found to have deeper erosion gullies and flume experiments showed that deeper erosion gullies are created by larger current velocities. In the field, survival and growth of transplanted *Spartina* units was severely suppressed inside erosion gullies. Despite of clear evidence for the presence of a scale-dependent feedback in our system, analysis of aerial photographs revealed that tussock distribution was either random or close to random, and little evidence of regularity was found. Hence, our study indicates that scale-dependent feedback mechanisms can be an important cause of spatial structure, even in systems that lack the regular patterns that are typically linked to scale-dependent feedback.

Most examples in literature, linking regular patterning to scale-dependent feedbacks, originate from systems under close to relatively homogeneous underlying (abiotic) conditions (Klausmeier 1999 (arid systems); see Rietkerk *et al.* 2004b (peatlands); van de Koppel *et al.* 2005 (musselbeds); but also see van de Koppel *et al.* 2006 for scale-dependent feedback influencing community structure along abiotic gradient). In salt-marsh pioneer zones, the main abiotic force, being hydrodynamic stress, is particularly variable in space and time, which might be a possible cause for the generation of irregular patterns. Hence, the presence of scale-dependent feedbacks in these more heterogeneous systems might lead to development of complex spatial structures. A recent modeling study emphasized that the presence of vegetation fixated dynamic creek structures on intertidal flat, resulting in formation of unvegetated tidal channels and a vegetated platform (Temmerman *et al.* 2007). Here, similar to our results, spatial structure (creek formation) was proposed to result from scale-dependent effect of plant growth on sedimentation. Our combined findings strongly suggest that scale-dependent interactions between plant growth and hydrodynamics play a key role in the formation of the extensive networks of creeks and gullies that are typical for salt marshes (Allen 2000), implying that scale-dependent feedbacks on small scales can possibly influence complex structures at larger scales.

Scarcity of resources is generally stressed as an important condition for the formation of regular patterns, generated by scale-dependent feedbacks (von Hardenberg *et al.* 2001; Lejeune *et al.* 2002; Rietkerk *et al.* 2002). In our study scale-dependent feedback is caused by diversion of physical stress at small scale within tussocks, which inevitably results in magnification of physical stress at larger scales, outside of the tussocks. This is illustrated by our flume study that shows that, in particularly at low water levels, strong erosion is observed along tussock borders. Hence, scale-dependent feedback can not only arise from the redistribution of scarce resources but may also have other underlying processes such as divergence of physical stresses. These seemingly different processes have in common that local stress is reduced (larger availability of nutrients or water, reduction of current velocities), resulting inevitably in enhanced stresses on larger scales (smaller availability of nutrients or water, increased current velocities). Hence, our study highlights a new class of scale-dependent feedback, broadening their generality as a cause of spatial complexity in ecosystems.

Scale-dependent feedbacks are density dependent processes, where scale-dependent positive and negative effects fluctuate with density or biomass, as was found in arid vegetation or in mussel beds (Rietkerk *et al.* 2002; van de Koppel *et al.* 2005). In salt-marsh pioneer zones feedback effects vary with volume of the mound (this study), but have also been shown to vary with stem density (van Hulzen *et al.* 2007). Higher shoot densities inside tussocks cause more sedimentation inside the tussock but deeper erosion gullies next to the tussock. Effects of scale-dependent feedbacks differ with varying physical stress. In arid vegetation the amount of rainfall, which logically is the main stressor, determines the final vegetation pattern and the vulnerability of the system to sudden and catastrophic shifts (Klausmeier 1999; Rietkerk *et al.* 2004a). Similarly, in salt-marsh systems, stress levels depend on current velocities, and high current velocities were found to generate strong erosion patterns around tussocks. Hence, our experiments, combined with other data (van Hulzen *et al.* 2007), emphasize the feedback nature of plant-current interactions: effects become stronger with increased density and higher flow velocity.

Concluding, we demonstrated the presence of scale-dependent feedbacks, between vegetation and current velocity, in salt-marsh pioneer zones where *Spartina* tussocks are patchily distributed on the intertidal flat. In these zones, tussocks were distributed in a random or slightly clustered fashion, implying that occurrence of scale-dependent feedbacks in ecosystems is not necessarily limited to systems with regular spatial patterns. Moreover, the physical stressor is current velocity, suggesting that scale-dependent feedbacks may act through a wider range of potential mechanisms than previously thought. These findings suggest that scale-dependent feedbacks might be a widely applicable mechanism causing spatial complexity in a broad range of ecosystems.

Acknowledgements

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Chapter 3

Biomechanical warfare in ecology; Negative interactions between species by habitat modification

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Abstract

Since the introduction of the term ecosystem engineering by Jones *et al.* (1997) many studies have focused on positive, facilitative interactions caused by ecosystem engineering. Much less emphasis has been placed on the role of ecosystem engineering in causing negative interactions between species. Here, we report on negative interactions between two well known ecosystem engineers occurring at the interface of salt marsh and intertidal flat (i.e., common cordgrass *Spartina anglica* and lugworms *Arenicola marina*), via modification of their joint habitat. A field survey indicated that, although both species share a common habitat, they rarely co-occur on small spatial scales (< 1 m). Experiments in the field and in mesocosms reveal that establishment of small *Spartina* plants is inhibited in *Arenicola*-dominated patches because of low sediment stability induced by the lugworms. In turn, *Arenicola* establishment in *Spartina*-dominated patches is limited by high silt content, compactness and dense rooting of the sediment caused by *Spartina* presence. Our results show that negative interactions by modification of the environment can result in rapid mutual exclusion, particularly if adverse effects of habitat modification are strong and if both species exhibit positive feedbacks. This illustrates the potential for negative interactions via the environment to affect community composition.

Introduction

It has long been recognized that organisms can have a substantial influence on their abiotic surroundings and that this can have large impacts on community structure (Darwin 1881, Clements 1916). Recently, the topic regained attention when Jones *et al.* (1994) launched the term 'ecosystem engineering' for the ability of organisms to cause physical state changes in biotic or abiotic materials. Since then, studies on the effects of ecosystem engineers mostly emphasize positive effects of modification of habitats, such as increasing biodiversity and complexity (Wright *et al.* 2002, e.g. Gilad *et al.* 2004). In particular in stressful environments, amelioration of adverse environmental conditions is believed to result in facilitative interactions between species (Bertness and Callaway 1994, Bertness 1998, Bruno *et al.* 2003).

Less attention has been paid to structuring capacities of negative interactions between ecosystem engineers in spite of the long history of research on negative effects of habitat modification, particularly in marine habitats (for a review see Peterson 1980, Peterson 1991). A classical example originates from the trophic group amensalism hypothesis, which states that deposit feeders on tidal flats negatively affect filter feeders by making sediment more erosive which will clog filters (Rhoads and Young 1970, Peterson 1980). Moreover, deposit feeders also limit recruitment of larvae of filter feeders by burying them (Woodin 1976, Gray 1981, Snelgrove and Butman 1994). Furthermore, several forms of allelopathic interactions can be considered a negative interaction via the environment (Naveh 1967, Webb *et al.* 1967, Janzen 1969). Many examples of negative effects originate from research on non-native and invasive species that out compete the native community by substantially transforming environmental conditions (Crooks 2002, Levine *et al.* 2003, Cuddington and Hastings 2004). Typically, most of the aforementioned studies focus on effects of habitat modification by a single species on biodiversity.

We report on an example of ecosystem engineering as a mechanism for bilateral and negative species interactions at the interface of salt marsh and intertidal flat in the Netherlands. In these areas a large variety of engineering species can be found, such as bioturbating infaunal species, and sediment stabilizing grass species. Two of the most obvious engineers that dominate the interface of the salt marsh and intertidal flats are the pioneer plant *Spartina anglica* and the bioturbating worm *Arenicola marina*. Both species are known to exhibit positive feedback loops with environmental factors that stimulate their own growth. The cord grass *Spartina anglica* is known for its ability to capture fine-grained sediment by reducing current velocities and to increase sediment compactness or bulk density (Ranwell 1964, Castellanos *et al.* 1994, Cahoon *et al.* 1996). *Arenicola* affects the environment in the opposite way, as its bioturbation profoundly reduces the silt content and decreases the bulk density of the sediment (Krüger 1959, Cadée 1976, Levinton 1995, Riisgard and Banta 1998, Goni-Urriza *et al.* 1999, Reise 2002).

In this paper we examine negative interactions between two ecosystem-engineers that modify the same environmental variable to their own benefit, but in opposite directions, and the implications of these interactions for community structure. We present an experimental study that investigates whether reverse effects of both species on sediment properties prevent both species to coexist on small spatial scales within an ecosystem. We discuss the potential for mutual exclusion that results from this type of interaction and the differences with conventional forms of competition.

Methods

Field site

We conducted a field study at the interface of a salt marsh and the adjacent tidal flat, at the northern part of the Krabbekreek, which is an arm of the Oosterschelde in the SW Netherlands (N 51°36.838' and E 004°07.440'). At this interface *Arenicola marina* dominates the intertidal flat, while *Spartina anglica* dominates the low salt-marsh zone, also called pioneer zone. Generally, *Spartina* prefers habitats without salt water influence but there it is competitively excluded (Bertness 1988, Scholten and Rozema 1990, Bertness and Shumway 1993, Huckle *et al.* 2002). *Arenicola* prefers areas that are submerged with salt water most of the time (Krüger 1959, Beukema and De Vlas 1979). Although the preferred habitat of both species is different both species are commonly found together at the outer limits of their preferred habitat, at the interface of salt marsh and tidal flat.

To investigate the extent to which *Arenicola* and *Spartina* co-occur, *Arenicola* and *Spartina* densities were counted in September 2003 along a number of transects. Each measurement along these transects consisted of counting of *Arenicola* heaps, droppings deposited at the tube opening, and *Spartina* shoots in 0.25 m by 0.25 m plots. Plot size is below the typical scale of patchiness in the system. Perpendicular to the seawall three transects of 100 m were sampled. Transects were 50 m apart and sampled 8 times every 5 m. Adjacent to this area transects through five circular tussocks of *Spartina* vegetation were surveyed. Transects varied in length between 8 and 19 m, depending on the size of the tussock and were sampled twice every 0.25 m. In total 868 plots were measured. As not all of these samples are independent, data were analyzed by building a 2*2 table, which shows the quantity of plots where each species is encountered alone, together, or none of the species are encountered. This table was used to perform a Fisher exact test, which tests if *Spartina* and *Arenicola* occurrence is independent based on their occurrence with and without each other (Sokal and Rohlf 1995). To establish the relation between the numbers of *Arenicola* heaps that are visible at the surface and the number of lugworms that are present in the sediment, in the field we extracted the lugworms for eleven plots that varied in the number of heaps in the same period as transects were surveyed. The number of heaps proved to be a good predictor of the number of lugworms in the sediment ($R^2 = 0.94$, $P < 0.05$).

Effects of Arenicola on Spartina

To look at the potential of both species to establish in habitat dominated by the other species, we took those life stages of either species that were thought to be able to colonize unoccupied area, and were encountered in the field frequently. This implies we tested the potential of *Spartina* seedlings to colonize *Arenicola* patches and the potential of large and mature *Arenicola* to invade *Spartina* tussocks.

The effect of *Arenicola* on settlement and survival of *Spartina* seedlings was determined both in the field and in a mesocosm experiment. In the field, 20 seedlings were planted at least 5 cm from each other, in three patches with lugworms (controls) and three patches where lugworms were excluded by a 1 m x 1 m fine-meshed net (1 mm2 mesh) buried at 50 mm depth. The control plots were located directly adjacent to the exclusion plots, and contained natural densities of *Arenicola*. To eliminate effects of the establishment of the net, three nets were buried nine months prior to seedling planting. The number of surviving seedlings was recorded over time. After 40 days the experiment was finished, and the sediment in all exclosure and control plots was searched for lugworms in a 1 m x 1 m area to a depth of 30 cm. In the exclosures on average 7 worms per plot were found while in natural plots on average 63 worms per plot were encountered (n = 3, ANOVA, F = 37.59, $P < 0.01$). Survival trends of seedlings with and without *Arenicola* present were compared using a Gehan's Wilcoxon test. An earlier experiment was conducted using seeds instead of seedlings. However, due to harsh conditions in the field, almost none of the seeds germinated independent of treatment type.

To increase control on the variables influencing seedling survival, we investigated the interaction between *Arenicola* and small *Spartina* plants in a mesocosm experiment. Six tanks (0.9 m long * 1.1 m wide * 0.6 m deep) were filled with 0.4 m sediment collected in an area with a natural abundance of *Arenicola*. To kill all benthos, the sediment was submerged in fresh water for one week. Before the onset of the experiment, the sediment was thoroughly rinsed with seawater. In three tanks, 80 lugworms were added per tank, which is close to maximum densities in the field, whereas no lugworms were added to the other three tanks. All tanks were exposed to a tidal regime of six hours submergence in seawater, followed by six hours of emergence. During emergence, the sediment was exposed to artificial illumination. Under the sediment, a drain was present that allowed groundwater levels to drop approx. 10 cm beneath sediment surface during emergence. Lugworms established themselves pretty quick judging from the number of dropping heaps in the tanks. Two weeks after the lugworms were added to half of the tanks, ten large seedlings (approx. 10 cm), 20 intermediate seedlings (approx 5 cm) and 20 small seedlings (approx. 1 cm) of *Spartina anglica* were planted in each tank, using different random planting schemes. All plants were at least 10 cm apart. Again, due to high germination failure of *Spartina* we had to germinate seeds first before using them. Presence and absence of all plants was recorded every day, specifically after every two tides. Survival trends in tanks with and without *Arenicola* present were compared using a Gehan's Wilcoxon test for each different size of seedlings.

Effects of Spartina on Arenicola

To investigate the potential of *Arenicola* to invade sites currently occupied by *Spartina*, we quantified settlement of lugworms inside and outside natural *Spartina* stands. In four *Spartina* tussocks aboveground biomass was removed. In each cleared patch a plastic ring of 12 cm high was pushed 5 cm into the ground. Between 2 to 4 m from the first ring a second ring was put in sediment that was naturally dominated by *Arenicola* and devoid of *Spartina* vegetation. Differences in elevation between rings in tussocks and on bare mud were less than 20 cm. Lugworms that naturally occurred in the surrounding area were dug out of the sediment and within each ring 10 lugworms were released. All rings were covered with a net to prevent *Arenicola* disappearance due to bird predation and migration during high tide. The number of lugworms that settled in the sediment was recorded after 0.5, 2 and 28 hours, respectively. Settlement was characterized by a worm being able to penetrate the top-layer of the sediment and a worm was considered to be settled once it had completely disappeared into the beginning of a new burrow. The Mann-Witney U test was used to compare burrowing success of *Arenicola* in *Spartina* patches and in natural lugworm patches, because of low variation (Sokal and Rohlf 1995).

To test if *Spartina*, once it has established with high biomass, could exclude *Arenicola*, a second experiment was carried out by planting 20 cm by 20 cm *Spartina* tussocks (15-20 stems) inside an *Arenicola* dominated environment. After two years the number of lugworms in and outside the tussock was counted to test if *Spartina* excluded *Arenicola* from its habitat. The comparison between lugworms living in and outside transplanted tussocks was done using a one-way Analysis of Variance. Data was log(x+1) transformed to meet the assumption of homogeneity of variance. This was tested using a Cochran's C-test.

Engineering effects on abiotic parameters

To assess the influence of *Spartina* and *Arenicola* on silt content and bulk density, we collected sediment samples of 50 ml of the upper sediment layers in *Spartina* versus *Arenicola* dominated patches in the field. Four samples were taken in four *Spartina* patches and in four *Arenicola* patches. To limit other factors influencing sediment composition we collected four 50 ml samples from each of our *Spartina* and *Arenicola* dominated mesocosms, where both species initially were placed in the same type of well-mixed sediment without infauna. Four tanks (0.9 m long x 1.1 m wide x 0.6 m deep) were put outside in June so that light conditions were natural and precipitation could enter the tanks. Otherwise, the set-up was as described for the previous mesocosm experiment. At the start of the experiment the same sediment was put in all tanks. Then we planted *Spartina* rhizomes in two tanks, while in the two other tanks *Arenicola* was added (control). After two months four soil samples were taken in all tanks.

In the lab, the samples were weighed, freeze dried and weighed again. Bulk density was calculated as the ratio between the dry weight and the volume (Birkeland

1984). Silt content of these samples was determined using a Malvern Mastersizer 2000. The influence of *Spartina* and *Arenicola* on the critical erosion threshold of the sediment was quantified using a Cohesive Strength Meter (CSM) in both the field plots and the mesocosm tanks. For detailed information on the CSM and the processing of CSM data, see Tolhurst *et al.* (1999, 2000), and Patterson *et al.* (2000).

A one-way nested Analysis of Variance was used to examine differences in sediment characteristic in patches dominated by *Arenicola* and in patches dominated by *Spartina*. Homogeneity of variances was tested using a Cochran's C-test. Statistics for the bulk density in the mesocosms experiment were calculated using a repeated measurements Analysis of Variance. For comparing silt fraction and stability a nested one-way Analysis of Variance was used. Here, homogeneity of variances was also tested with a Cochran's C-test.

Results

Transect surveys clearly demonstrated that *Arenicola marina* and *Spartina anglica* occur spatially separated (Figure 3.1). Generating a 2*2 table of occurrence of both species indicated that *Spartina* was found in 271 plots and *Arenicola* in 404 plots. 160 plots contained neither of both species and they co-occurred in 28 plots. Fishers' exact test was highly significant, pointing at dependence of occurrence of both species (df = 1, $P < 0.0001$). This implies that *Spartina* and *Arenicola* do not co-occur in general. However, they border each other closely and transitions between both habitats are sharp.

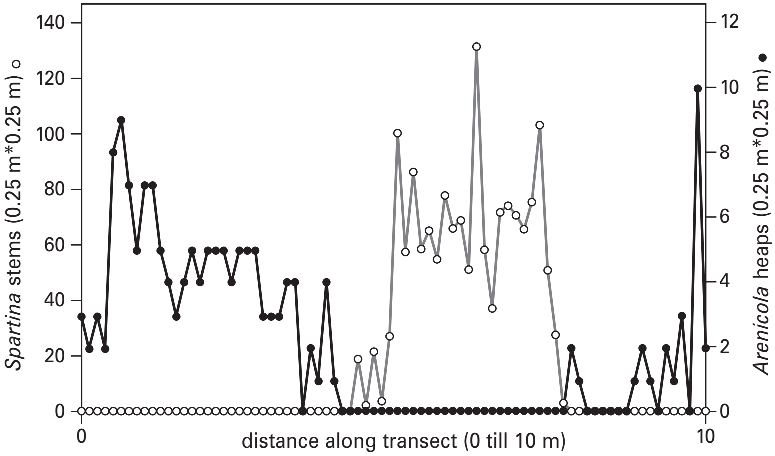

Figure 3.1. Example of one transect showing *Spartina anglica* (open symbols) and *Arenicola marina* (closed symbols) distribution over an intertidal flat with salt-marsh pioneer vegetation. In general, the species did not co-occur in the same patch (n = 866, $P < 0.0001$).

Several physical parameters were measured in both habitats. In *Arenicola* patches in the field the critical erosion threshold was significantly lower than in *Spartina* tussocks (Figure 3.2A, nested ANOVA, $F_{1,\,24} = 37.76$, $P < 0.01$). The same held for *Arenicola* and *Spartina* in mesocosms (Figure 3.2A, nested ANOVA, $F_{1,\,12} = 4718.63$, $P < 0.001$). Bulk density was not significantly different in *Spartina* tussocks compared to *Arenicola* patches in the field (Figure 3.2B, ANOVA, $F_{1,\,24} = 3.95$, $P = 0.09$), but a slight difference between means can be seen. This difference was significant in the tanks though (Figure 3.2B, Repeated measures ANOVA, $F_{1,\,12} = 17.89$, $P < 0.01$). For the silt content of the sediment in the field the values were significantly higher in *Spartina* tussocks than in *Arenicola* patches (Figure 3.2C, nested ANOVA, $F_{1,\,24} = 9.17$, $P < 0.05$). In the mesocosms no differences in silt content were observed between *Spartina* and *Arenicola* tanks (Figure 3.2C, nested ANOVA, $F_{1,\,12} = 0.16$,

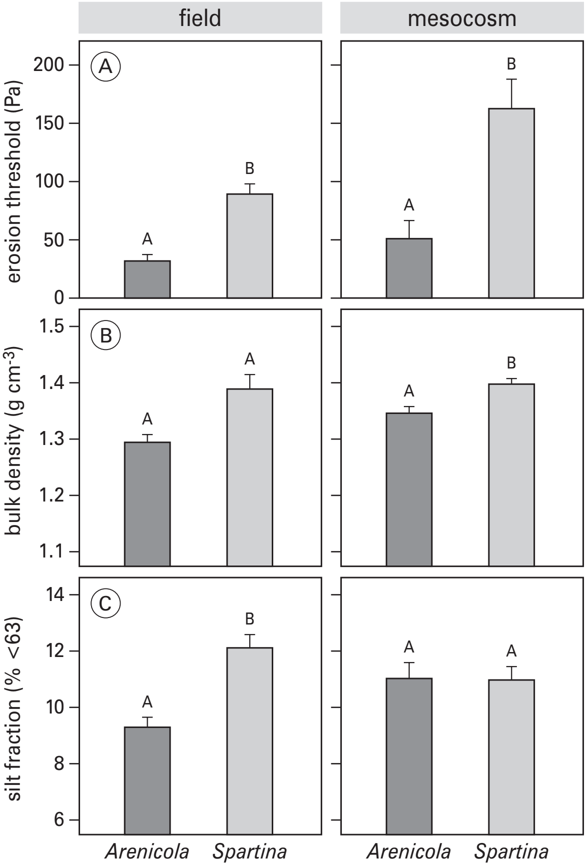

Figure 3.2. Difference in soil stability (A), bulk density (B) and silt content (C) of the soil between plots with a high density of *Arenicola marina* (dark grey) and plots with a high density of *Spartina anglica* (light grey) stems in the field (n = 16) and in the mesocosms (n = 8). Different letters indicate significant differences between pairs ($P < 0.05$). Error bars represent standard errors (±1 SE).

$P = 0.73$), which is most likely due to the closed circulation system, that does not allow silt to be removed from the system or imported into it. This restriction does not apply to the open flow system in the field.

Survival analysis revealed that mortality rate over time of *Spartina* seedlings in the field was higher in the *Arenicola* patches than in patches without *Arenicola* (Gehan's Wilcoxon test statistic = 3.84, $P < 0.01$). Although seedling survival in the field was low in general, the negative effect of lugworm presence was clearly detectable (Figure 3.3A, test statistic = 3.84, $P < 0.01$). Also in our mesocosms studies, the survival trends differed significantly for the *Arenicola* treatment and the control (Figure 3.3B (small seedlings): test statistic = -4.77, $P < 0.01$; Figure 3.3C (intermediate seedlings): test statistic= -4.28, $P < 0.01$; Figure 3.3D (large seedlings): test statistic = -2.29, $P < 0.05$), meaning that mortality rates were higher with lugworm presence than without. Trends became less significant with increasing size of *Spartina* seedlings. The graphs show that there was an increasing time-lag in mortality with increasing size of the *Spartina* plants. Mortality was mainly caused by burial of plants by the sediment that lugworms excreted or by plants sinking away or

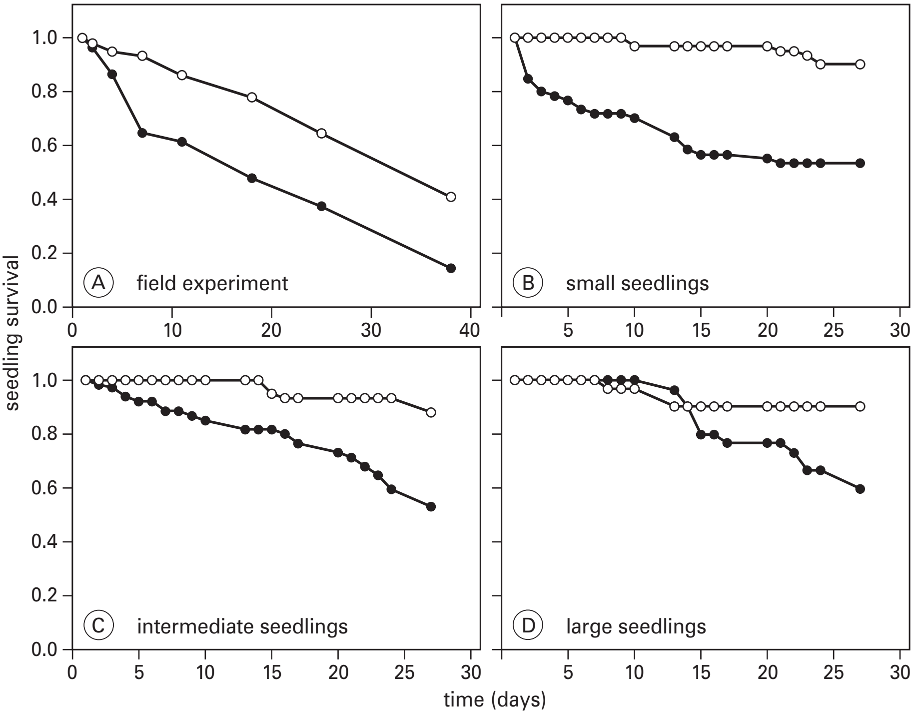

Figure 3.3. Survival of planted seedlings in plots with *Arenicola marina* (closed circles) and in control plots without *Arenicola* (open circles), in the field (A) and in the mesocosms planted with small (1-2 cm) seedlings (B), intermediate (5 cm) seedlings (C) and large (10 cm) seedlings (D), respectively. Seedling survival in the controls was significantly higher than in the treatments for all graphs.

tumbling over because of instability of the substrate (pers. obs. Van Wesenbeeck). This explains why larger plants took longer to die and disappear.

A clear effect was found of *Spartina* presence on the potential for lugworms to penetrate the sediment. In the lugworm addition experiment in open sediment, all lugworms penetrated the sediment and disappeared completely in plots where lugworms were already present. However, none of the worms managed to dig deeper into the sediment than 0.5 cm within 28 hours in areas occupied by *Spartina* tussocks, even though aboveground vegetation had been removed (Figure 3.4: Z-score= -2.31, $P < 0.01$).

Once *Spartina* was transplanted with high biomass to lugworm patches it was able to survive and even to limit *Arenicola* presence. Moreover, *Arenicola* seems to prefer soil outside the *Spartina* patch rather than in it (Figure 3.5: ANOVA, $F_{1, 20} = 152.7$, $P < 0.001$).

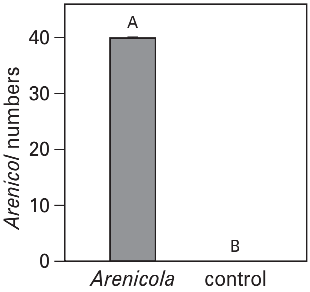

Figure 3.4. Digging success of *Arenicola marina* added to plots with Arenicola (dark grey) and plots with *Spartina anglica* (light grey) in the field (n = 8). Different letters indicate significant differences ($P < 0.01$). Error bars represent standard errors (±1 SE).

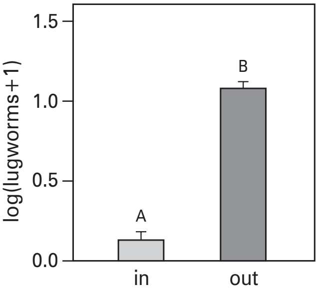

Figure 3.5. Numbers of *Arenicola marina* encountered within and outside planted *Spartina* tussocks (n = 11). Different letters indicate significant differences ($F_{1, 20} = 152.7$, $P < 0.001$). Error bars represent standard errors (±1 SE).

Discussion

Our results demonstrate that in intertidal communities, habitat modification can induce negative species interactions, thereby greatly affecting community structure. Although sharing a common habitat, we observed a striking spatial segregation between common cord grass *Spartina anglica* and the lugworm *Arenicola marina* at the interface of salt marsh and intertidal flat. Dense *Spartina* patches, several meters in diameter, were found scattered on the intertidal flat, which is dominated by numerous lugworms. Despite of their close proximity, the two species do not mix, pointing at a potential negative interaction between both species. Our experiments revealed that *Spartina* and *Arenicola* inhibit each other from invading occupied habitat by modifying habitat properties. Although species exclude each other from local patches in our system, they co-occur, though spatially segregated, on ecosystem scales. This might be a property that sets apart negative interactions via the environment between two species from negative effects induced by a single ecosystem engineer. In the last case, when engineering effects are strong a single engineer can potentially exclude other species on larger ecosystem scales as well (Crooks 2002).

Habitat modification in intertidal systems

The effects of *Arenicola* and *Spartina* on silt content, bulk density and sediment stability, described in our study, concur with former studies in the literature and have previously been shown to influence establishment of other species. In *Spartina* tussocks, higher critical erosion thresholds of the sediment surface, higher silt content and higher bulk density were measured than in the *Arenicola* patches. The root system of *Spartina* aerates, dries and compacts sediment, and root mats form dense and solid structures (Angers and Caron 1998). The increased erosion threshold and bulk density of sediment occupied by *Spartina* may explain the inability of *Arenicola* to penetrate the soil and construct a feeding funnel. Even if *Arenicola* was able to construct a tube, high silt contents would make it impossible for the worms to pump water through the sediment and feed (Meysman *et al.* 2005). *Spartina* is known to have a negative effect on soil organisms by changing soil structure (Gribsholt and Kristensen 2002). On the West coast of the US, where *Spartina* is an invasive species, cordgrass has detrimental effects on the native benthic species assemblage of the intertidal flat (Patten 1997). Besides *Spartina* also eelgrass is shown to exhibit small negative effects on infauna (Brenchley 1982). The root mat of eelgrass retards movement of burrowing deposit feeders, but indirect mechanisms, such as increased silt input, might play a role here as well.

Besides *Spartina*, *Arenicola* affects the environment noticeably. In *Arenicola* patches stability and bulk density are lower, because of the continuous mixing of sediment by lugworms. This continuous stirring of the substrate results in burial of small *Spartina* plants. More examples can be found in the literature that support the idea that lugworms, and other bioturbators, inhibit recruitment and settlement of other organisms (Flach 1992). They were thought to limit recruitment of larvae of filter feeders by consuming or burying them according to the principle of trophic group amensalism (Rhoads and Young 1970, Woodin 1976, Gray 1981). Burying and sediment mixing may have negative effects on small plants, seeds and seedlings as well. Lugworms are known to restrict eelgrass presence by burying the eelgrass leaves (Philippart 1994). Like in our study, eelgrass and lugworms seem to exclude each other implying that they are in general not found together in the same patch (Philippart 1994).

In addition to *Spartina* and *Arenicola*, many other organisms living in intertidal soft sediment habitats also have substantial influence on sediment composition and thereby, they will affect the potential for other species to occupy these areas.

Peterson (1980) names these interactions 'indirect interference through alteration of the physical environment' while Wilson (1991) labels them 'sediment-mediated interactions' and considers them common to many infaunal communities. Both refer to the trophic group amensalism theory for good examples of indirect negative interactions on intertidal flats. Summarizing, there is ample support that negative interactions by habitat modification are an important force in structuring intertidal communities.

Negative interactions by habitat modification in a more general perspective

Negative interactions via habitat modification may have similarities with conventional forms of competition, such as competition for resources. However, when species interact via modification of a common environmental factor, as shown in the present paper, modification of this environmental factor by one species increases its own growth, but decreases the growth rate of its competitor. As a consequence, replacement will commence with increasing rate as one actor becomes more dominant. Species that compete by exploiting a common resource, limit the growth potential of the other species as well as for itself. As a consequence, competitive exclusion typically occurs at a slow rate, determined by the difference in the break-even levels (R^*) of both species for the common resource (Tilman 1983). This explains why we expect the potential for (mutual) exclusion to be higher in case of negative interactions by habitat modification relative to competition for resources.

Negative interactions by habitat modification may in some aspects resemble competition for space or interference competition. At small spatial scales, modification of the environment by the founding species strongly decreases the potential for other species to invade. Hence, as in competition for space, it leads to priority effects, in which the first organism to arrive dominates the locality. However, as space can be considered a resource (e.g. Yodzis 1978, Paine 1984), depletion of space leads to decreased population growth of both species, when viewed at larger spatial scales. In a similar way, interference competition, where one species negatively affects the growth of another species for instance via aggressive interactions (Crombie 1947, Brian 1956), poses a cost on the aggressor and the receiver, and hence depresses the growth of both species. As explained before, negative interactions via habitat modification do not entail any costs, and hence replacement rates are expected to be higher. To fully understand the implications of these distinct types of interactions for community structure, it is important for future research to formalize the conceptual differences between negative interactions by habitat modification and various forms of competitive interactions.

The realization that negative interactions via the environment can function as a mechanism for exclusion bears important consequences for community ecology. In stressful habitats, physical factors and facilitation are considered to be the main structuring forces (Menge 1976, Bertness and Callaway 1994, Bertness and Leonard 1997, Hacker and Gaines 1997, Bruno *et al.* 2003). However, negative interactions by means of modifying the environment, as presented in this paper, might in particular apply to communities in stressful habitats where engineering is thought to be of main importance (Jones *et al.* 1997). Although competition for resources was regarded of smaller importance in these habitats, negative interactions via habitat modification might take its place as the dominant negative interaction, as is observed in our study system. Elucidating the relative importance of different competition mechanisms in relation to environmental conditions will be a major challenge for future research on the structure of ecological communities.

Acknowledgements

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Appendix 3
A general model of species interactions via habitat modification

Although ecosystem engineering was a recurring topic in ecological studies from the last decade, not much theoretical studies set out to model implications of ecosystem engineering (Hastings *et al.* 2007). Nevertheless, development of ecosystem engineering models will allow us to distinguish generalities between implications of ecosystem engineering, and point out differences between ecosystem engineering and direct biotic interactions. So, additional to the large body of literature pointing out examples of ecosystem engineers in a wide variety of ecosystems, there is a strong need for multi-species modeling of ecosystem engineering (Hastings *et al.* 2007).

Previous research reveals that ecosystem engineering can function as a mechanism to inhibit invasion by other organisms or by other ecosystem engineers (van Wesenbeeck *et al.* 2007). This might explain observed patchiness in systems with two strong ecosystem engineers that modify environmental variables in opposite ways (Eppinga *et al.* 2007, van Wesenbeeck *et al.* 2007). To examine how negative interactions via modification of a common habitat can, in principle, influence the dynamics of a two-species interaction, we formulated a conceptual model. First, we derive a general, mathematical framework in which negative interactions via modification of a joint habitat are defined. This framework is based on the commonly used Lotka-Volterra competition model. Next, we analyze this model to investigate whether and when this type of interaction leads to coexistence or competitive exclusion.

In the commonly-used Lotka-Volterra model for competition between two species, interspecific effects are included as a direct, linear negative effect of one species on the other. Here, we adopt this model as a framework, replacing the inter-specific interaction terms by functions determining the effects of the environment on net population growth:

$$\frac{dA}{dt} = r_A\left(1 - \frac{A}{K_A} - f_A(E)\right)A \qquad (1)$$

$$\frac{dB}{dt} = r_B\left(1 - \frac{B}{K_B} - f_B(E)\right)B \qquad 2)$$

Here, A and B are the biomasses of the two interacting species, r_A and r_B are the intrinsic growth rates of species A and B, and K_A and K_B are the maximum biomass of both species. The functions $f_A(E)$ and $f_B(E)$ represent the effects of environmental variables on the biomass change of both species, and can either be positive or negative.

Most environmental conditions (e.g. pH, oxygen content, silt content) are determined by concentrations of physical or chemical species, and are hence controlled by source-sink dynamics. Their local state is determined by input and output rates, referred to as I and O. In principle, both I and e are functions of the local environmental conditions, and can be influenced by the local biota (e.g. A and B). Hence, the dynamics of some environment parameter E can be described in general terms as:

$$\frac{dE}{dt} = I(E,A,B) - O(E,A,B)E \tag{3}$$

In principle, the functions $f_A(E)$, $f_B(E)$, $I(E,A,B)$ and $O(E,A,B)$ can have many shapes. We are, however, only interested in negative interactions via habitat modification, which allows us to further specify the constraints on the above set of functions without losing generality. The effects of species A and B on the environment are defined to be opposite ($\partial E(A,B)/\partial A$ and $\partial E(A,B)/\partial B$ are of opposite sign, where E(A,B) is defined as $I(E,A,B)/O(E,A,B)$ (assuming $E(A,B)$ to be near equilibrium); one species has a positive effect on the environment, whereas the other affects it negatively. The effect that a species has on the environment is beneficial to its own growth, but negatively affects the growth of the competitor (both $\mathrm{d}f_A(E)/\mathrm{dE}$ and $\partial E(A,B)/\partial A$, and $\mathrm{d}f_B(E)/\mathrm{dE}$ and $\partial E(A,B)/\partial B$ have the same sign). These constraints define negative interactions between two species via habitat modification in general terms. Below, we analyze a specific example of this system, reflecting interactions between two ecosystem engineers on the interface of salt marshes and intertidal flats (van Wesenbeeck *et al.* 2007).

On the interface of salt marshes and intertidal flats benthic species that inhabit the intertidal flat and vascular plants that induce salt-marsh formation meet. The most common plant species found there is *Spartina anglica*, or common cordgrass that forms patchy tussocks in a matrix of bare sediment. One of the characteristic species inhabiting this sediment is the lugworm *Arenicola marina*. Both species are strong ecosystem engineers and affect several environmental parameters once they are present. A review of the literature on both species (Chater and Jones 1957, Krüger 1959, Ranwell 1964, Reise 1985, Castellanos *et al.* 1994, Levinton 1995, Angers and Caron 1998, Reise 2002, van Wesenbeeck *et al.* 2007) identifies sediment composition (i.e. bulk density and erosion threshold in our experiments), sediment movement and sediment stability as important environmental parameters that are on the one hand highly influential to the dynamics of both species and, on the other hand, strongly influenced by the dynamics of both species. Sediment composition in turn, consists of several components such as grain size (silt content), porosity, bulk density and permeability (potential for water to penetrate the soil). Moreover, these components are correlated in various ways. As silt content rises, for example, soil permeability decreases and bulk densities increases. To provide a conceptualized view on the interaction between *Arenicola* and *Spartina*, we choose silt content as a proxy for the effects of both species on the environment. *Arenicola* prefers soils with 2-12% silt content. Higher silt contents reduce permeability (Beukema and De Vlas 1979), which results in high sediment resistance and low oxygen supply, in turn inhibiting the pumping capacity of *Arenicola* (Meysman *et al.* 2005). *Spartina*, on the other hand, shows higher growth rates and shoot densities at high silt contents, because rhizomes penetrate easier in muddy soils (Chater and Jones 1957, Scholten and Rozema 1990) or possibly because higher silt contents coincide with higher nutrient levels. Note, however, that this is a simplified, conceptualized view on the effects of both species on their environment.

Sediment silt content is influenced by both species in opposite directions (van Wesenbeeck *et al.* 2007). *Arenicola* decreases the silt fraction of the sediment by excreting silt on top of the sediment where it is more vulnerable to being flushed away once the intertidal flat is submerged (Levinton 1995, Goni-Urriza *et al.* 1999, Reise 2002). *Spartina*, on the other hand, increases silt fraction by protecting the sediment from erosion and increasing precipitation of silty particles from the water column by reducing current velocities inside the vegetation (Ranwell 1964, Castellanos *et al.* 1994, Cahoon *et al.* 1996). To limit model complexity, we chose to incorporate the effect of vegetation on sedimentation but we did not include the effects of vegetation on sediment retention. These specifications lead to a more explicit version of equation 3:

$$\frac{dE}{dt} = I(1 + g_B B) - [O_0(1 + g_A A)]E \tag{4}$$

Here E represents silt content, I is the inflow of silt from the overlying water during submergence, which is enhanced by *Spartina* presence, Oe_0 is the rate of sediment erosion when both A and B are zero, g_A represents the effect of *Arenicola* on the erosion and g_B expresses the effect of *Spartina* biomass on silt input.

The functions $f_A(E)$ and $f_B(E)$ that represent the effects of silt on the biomass change of both species, are defined as follows:

$$f_A(E) = \alpha_A \frac{E}{E + n_A} \tag{5}$$

$$f_B(E) = \alpha_B \frac{n_B}{E + n_B} \tag{6}$$

Here, α_A and α_B represent the maximal limiting effect of environmental factors on the growth of the species, n_A and n_B are those environmental conditions where limitation is half of its maximal value. If $\alpha = 0$, species growth is not affected by the environment. For $0 < \alpha \leq 1$, the species has only a limited sensitivity to environmental stress; the maximal negative effects of the environment are insufficient to significantly reduce growth of both species, independent of their effects on the environment. However, for $\alpha > 1$, severe environmental conditions can completely block growth when the density of the involved species is low. Here, the interaction between species and their environment can be crucial in determining survival under these conditions.

To simplify model analyses, we have applied a quasi steady-state assumption: we assume that the environment is near equilibrium when analyzing the dynamics of the interacting species (Edelstein-Keshet 1988). This quasi-steady-state assumption reduces the number of equations to two, which allows us to use the standard phase-plane approach that is commonly used to analyze Lotka-Volterra-class competition models (Yodzis 1989). The zero-growth isoclines of both *Spartina* and *Arenicola* are plotted in a *Spartina* vs. *Arenicola* density plane (Figure 1). On both isoclines, the rate of change of the involved species equals zero. If the isoclines intersect at positive values, an internal equilibrium exists. Two boundary equilibria occur at the intersection of an isocline with the axis of the species for which the isocline depicts zero growth.

We investigated the potential dynamics of this model for different parameter values. To focus on those parameter settings essential to the model's behavior, we have

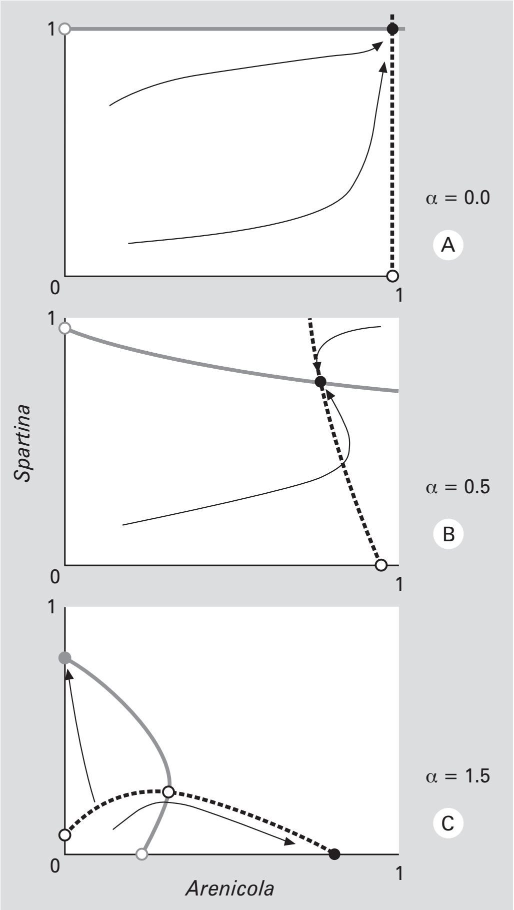

Figure A3.1. Density planes for the model where both species interact via the environment and effects of the environment on species growth potential for three different α-values that represent no effects of environment on species growth (A), small negative effect of environment on species growth (B) and strong suppression of species growth by environment (C). Open circles indicate unstable equilibria and closed circles indicate stable equilibria.

reduced the parameter complexity of system 1. We redefine species biomass relative to their own maximal biomass (e.g., $K_A = K_B = 1$). As the isoclines are defined as $(1 - X - f_X(E)) = 0$, where X labels either species, the value of species growth rate r_X is inconsequential to our graphical analysis. Hence, we adopt $r_A = r_B = 1$. In the first analysis (figure 1A), we assume that the effects of the environment on the growth of both species is negligible (e.g., aA and aB are zero). In this setting, the species do not interact. Consequently, we observe that both isoclines are straight lines intersecting at $A, B = 1, 1$. Both species can invade when the other is dominant, and they will reach the equilibrium $A, B = 1, 1$ for any initial condition. Once effects of the environment on both species are moderate (e.g., α_A and $\alpha_B = 0.5$), we observe that the isoclines slightly bend inwards: each species slightly limits the growth of the other (figure 1B). Again, both species can invade at all times, and a single stable equilibrium is found at the intersection of both isoclines. When the effects of the environment on each species are severe (e.g., α_A and $\alpha_B = 1.5$), both isoclines severely bend inwards, and intersect with both axes (figure 1C). The boundary equilibria are stable now, which implies that species A can not invade once species B is present and vice versa. So, our model predicts that strong interactions of a species with their environment lead to mutual exclusion, and domination depending on initial conditions. For a limited range of parameter settings, the isoclines intersect in multiple places. This leads to a situation where for instance both boundary equilibria and the internal equilibrium are stable.

We analyzed a conceptual, mathematical model for negative species interaction via habitat modification. This model shows that when species affect environmental conditions in opposite ways to benefit their own growth, there is a high potential for mutual exclusion especially when engineering effects are strong. This is in agreement with our experimental results. Moreover, our model provides a conceptual definition of negative interactions through habitat modification that allows this interaction to be investigated and experimentally tested in a wide range of ecosystems.

For most of the parameter space in our model, growth of one species results in rapid exclusion of the other. This property sets apart negative interactions by modifying the environment, as discussed in this paper, from resource competition, which does not allow mutual exclusion based on a single resource. This can be understood as follows: when species compete by exploiting a common resource, each species limits the growth potential of the other species as well as for itself. As a consequence, competitive exclusion typically occurs at a slow rate, determined by the difference in the break-even levels (R^*) of both species for the common resource (Tilman 1983). However, when species interact via modification of a common environmental factor, as discussed in this article, modification of this environmental factor by one species increases its own growth, but decreases the growth rate of its competitor. This explains why the potential for (mutual) exclusion is much higher in case of negative interactions by habitat modification relative to competition for resources.

Chapter 4

Negative species interactions through ecosystem engineering

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submitted

Abstract

Since its introduction, the ecosystem engineering concept has primarily emphasized the positive role of engineering organisms in creating habitats for other species. However, evidence is growing that habitat modification by engineers can also act as a negative form of interspecies interaction. In this paper we discuss recent research suggesting that transformation of the environment by ecosystem engineers can be an important cause of species exclusion. Two cases are considered; one-way negative interactions, where modification of the environment by a single species results in exclusion of other species, and two-way negative interactions, where two species interact by modifying the same environmental variable. We conclude that one-way interactions can be a mechanism underlying biological invasions and two-way interactions can create environmental heterogeneity through patchiness.

One-way and two-way negative interactions by ecosystem engineering

Since the introduction of the ecosystem engineering concept by Jones *et al.* (1994), the tendency has been to consider ecosystem engineering as a constructive force that maintains and creates habitats (Wright *et al.* 2004). As a consequence, research until now has mainly focused on positive effects of habitat modification/ecosystem engineering on other species (Wright *et al.* 2002, Bruno *et al.* 2003, Gilad *et al.* 2004). Nevertheless, construction of new habitat will inevitably lead to destruction of old habitat, posing negative effects on the inhabitants of the original habitat, possibly even resulting in exclusion (Rhoads and Young 1970, Peterson 1980, Bertness 1999, Crooks 2002, Cuddington and Hastings 2004). Exclusion of other species might have beneficial effects on the ecosystem engineer by reduction of interspecific competition. In this respect, the concept of ecosystem engineering relates to the concept of positive-feedback switches in communities, which was introduced in the early 1990s (Wilson and Agnew 1992). Positive feedback switches occur if vegetation modifies the environment making it more suitable for itself and/or less suitable for other species (Wilson and Agnew 1992). Here we aim to examine the consequences of negative species interactions through habitat modification on community structure, by linking the concepts of ecosystem engineering and positive feedback switches (Box 1).

Box 1
The link between ecosystem engineering and positive-feedback switches

The concepts of positive-feedback switches and ecosystem engineering were introduced in the ecological literature in the first half of the 1990s (Wilson and Agnew 1992, Jones et al. 1994). Wilson and Agnew (1992) defined positive feedback switches as “a process in which a community modifies the environment, making it more suitable for that community” (Wilson and Agnew 1992). Ecosystem engineering was described by Jones et al. (1992) as “directly or indirectly modulating the availability of resources (other than themselves) to other species, by causing physical state changes in biotic or abiotic materials”. The papers introducing both concepts have frequently been cited, although the trend in number of citations suggests that the ecosystem engineering concept is currently more embedded in ecological theory (Figure B1.1). A possible explanation for this trend is that the paper of Wilson and Agnew (1992) has mainly focused on positive feedback switches in plants, while Jones et al. (1994) introduce examples of animals as well. However, the concept of positive-feedback switches also applies to (slow-moving or sessile) animals (van de Koppel et al. 2005, van Wesenbeeck et al. 2007b). Nevertheless, ecosystem engineering may appear to be a more generally applicable mechanism, as all organisms for which positive feedbacks have been described are ecosystem engineers, but not all ecosystem engineers induce positive feedback switches. In any case, both mechanisms are clearly linked.

The paper of Wilson and Agnew (1992) is more specific than the paper of Jones et al. (1994) in defining in defining possible consequences. For example, positive feedback switches are subdivided in four different type of switches; the one-sided switch, the reaction switch, the symmetric switch, and the two-factor switch (Wilson and Agnew 1992). The most common type is the one-sided switch. Here a community changes the environment in patches where it occurs. Boundaries with the surroundings are unstable because nothing limits the community from further invading unmodified space. The other three switches can lead to a stable mosaic situation, where in an initially homogenous environment, two different communities occur in different patches separated by sharp boundaries (Wilson and Agnew 1992).

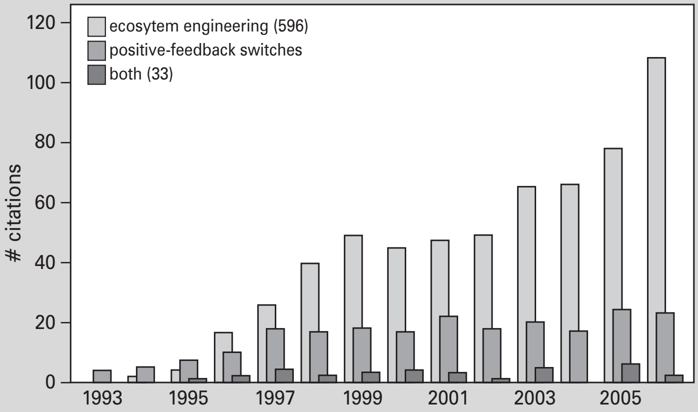

Figure B1.1. Number of citations of the papers introducing the concepts of ecosystem engineering (Jones *et al*. 1994) and positive-feedback switches (Wilson and Agnew 1992). Categories display, papers that refer to Wilson and Agnew (1992) only, papers that refer to Jones et al 1994 (or Jones *et al.* 1997) only, and papers that refer to both these papers.

In this review, we discuss the importance and implications of ecosystem engineering as a cause of negative interactions between species. We distinguish between one-way and two-way negative species interactions. We speak of one-way negative interactions if habitat modification by an ecosystem engineer negatively affects other species that do not have a profound modifying effect on their habitat (Fig. 4.1A). Two-way negative interactions refer to the situation in which two ecosystem engineers modify the same environmental variable but in opposite directions, thereby

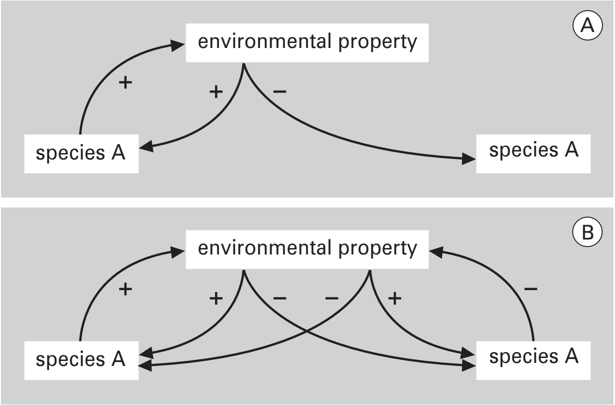

Figure 4.1. Conceptual diagrams of possible relationships between species and their abiotic environment. A) One-way effects; one species acts as an ecosystem engineer modifying the habitat, which in turn negatively affects the other species. B) Two-way effects; both species exhibit positive feedbacks with the environment but in opposite directions.

inhibiting each other's growth (Fig. 4.1B). One-way negative interactions are highly asymmetrical, as most ecosystem engineering effects (Jones *et al.* 1997), and have been proposed as a driving mechanism of exotic invasions (Crooks 2002, Cuddington and Hastings 2004). Two-way negative interactions by habitat modification might prevent one ecosystem engineer from taking-over, as effects are more symmetrical. Thus, two-way interactions might result in a patchy distribution of the different engineer species that create a heterogeneous landscape on landscape scales.

Negative interactions by one-way ecosystem engineering provoking exotic invasions

Most examples of negative interactions by ecosystem engineering in the literature deal with one-way effects, in which a single species modifies an environmental variable in patches where it is present, resulting in reduced growth or fitness of other species. This type of interaction is very similar to the one-sided switch of Wilson and Agnew (1992), where a single community modifies an environmental variable in the patches it occupies. Well-documented mechanisms of one-way interactions include for example the deposition of toxic litter by trees, inhibiting seedling emergence (Facelli and Kerrigan 1996, Facelli *et al.* 1999, Dzwonko and Gawronski 2002), and changing of fire-regimes by grasses, excluding native shrubs (Brooks *et al.* 2004). Other examples come from species that change chemical properties of a system, causing allelopathy, where organisms change their surroundings by releasing a chemical substance, and thereby inhibit the growth of other species (Naveh 1967, Webb *et al.* 1967, Janzen 1969).

Many mechanisms of habitat modification have been demonstrated with non-native invaders. Possibly native species also affect other species negatively by transforming the environment, but negative effects become particularly conspicuous once an exotic species invades a community, thereby eliminating native species. Some recent literature stresses that invasive engineers ease their spread by indirectly affecting native species through habitat modification (Crooks 2002, Levine *et al.* 2003, Cuddington and Hastings 2004). Complementary to this work, it has been suggested that species exhibiting a positive feedback loop with the changed environmental property can be extremely fierce invaders (Wilson and Agnew 1992, Levine *et al.* 2003, Cuddington and Hastings 2004, Strayer *et al.* 2006). So, the invasive species transforms the environment and this has a positive effect on the invasive species itself, either directly by exhibiting a positive effect on the fitness of the invader, or indirectly, by reducing competition with natives, because native species cannot tolerate the change in environmental variables. This might result in domination of the exotic invader (Keane and Crawley 2002). Here below, we present some examples of exotic invaders for which it has been shown that the modified a-biotic variable has a negative effect on native species, resulting in a positive effect on the invader.

An early study on impacts of invaders on their new habitat considered habitat modification by the common iceplant (*Mesembryanthemum crystallinum*), native to the Namibian desert in South-Africa, but invasive to the US and Australia (Vivrette and Muller 1977, Bohnert and Cushman 2000). Presence of the common iceplant increases soil salinity, because of salt leakage from its senescent tissue (Kloot 1983). The common iceplant is able to withstand high levels of soil salinity, because under such conditions it can switch to Crassulacean Acid Metabolism (CAM). CAM allows the plant to keep the stomata closed during the day, which enables a much more efficient use of water (Bohnert and Cushman 2000). High salinity levels are tolerated by the iceplant itself, but will exclude native species that lack the possibility to switch to CAM (Vivrette and Muller 1977, Bohnert and Cushman 2000). Similar mechanisms are used by other plant species as well and often enables them to invade and dominate in large areas, as long as salt levels are sufficiently high (Wilson and Agnew 1992).

A more homogeneous species composition has been described to result from alteration of fire-regimes, induced by alien grasses, with detrimental effects on the native community (D'Antonio and Vitousek 1992, Brooks *et al.* 2004). The alien grass often changes fuel properties, for example by producing large amounts of dead biomass, thereby inducing changes in fire intensity, size or frequency (D'Antonio and Vitousek 1992, Brooks *et al.* 2004). The grass life-form allows rapid re-growth after the fire, whereas other species, especially tree species, are less resistant to fire and recover more slowly (D'Antonio and Vitousek 1992). In this respect the grass constitutes a positive feedback with the changed fire regime and, similar to the example of the iceplant, the invasive grass takes over the community, being the only species that can withstand the new stressful conditions. Many other invasive species might initiate one-way negative interactions by altering different ecosystem properties. For example many stands of invasive tree species lack an understorey community due to lowering of water tables (Zavaleta 2000) and excretion of toxic substances by dead leaves (Souto *et al.* 1994). However, the ecology of these species has not been put in this perspective so far.

These examples illustrate that one-way interactions by the engineer are highly asymmetrical as predicted by Jones *et al.* (1997). Because of the resulting positive feedback loop, there is no direct limit to expansion of the invader (Wilson and Agnew 1992), explaining why exotic species that are strong ecosystem engineers can become the dominant species in a community, resulting in loss of native species. Concluding, alteration of ecosystem properties is a successful mechanism promoting invasions and this might result in a more homogeneous landscape, where the invasive species is dominant.

Negative interactions by two-way ecosystem engineering inducing patchiness

Ecosystem engineering might be a rather unbalanced process in the case of one-way negative interactions exerted by invasive species. In case of two species transforming the same environmental variable in the opposite direction, engineering actions might create a mosaic of different patches, preventing habitat take-over of a single species. Such a balanced interaction is similar to the so-called ‘symmetric switch’ as introduced by Wilson and Agnew (1992). They defined a symmetric switch as “community X changes an environmental factor in its patches, and community Y simultaneously changes the same factor but in the opposite direction”. This is what we defined as two-way negative interactions by ecosystem engineering and from now on we will on refer to it as ‘two-way interactions’.

Although Wilson and Agnew (1992) propose two-way interactions to exist, they do not give a conclusive example illustrating the idea. Recently, two papers emerged that show clear cases of two-way interactions mediated by the environment (Eppinga *et al.* 2007, van Wesenbeeck *et al.* 2007a). In both these papers, a species or functional group of species changes an environmental property to its own benefit, while another species or functional group of species changes the same property in the exact opposite direction possibly to its own benefit as well. Thus, both species change an environmental variable in a direction that is favorable for itself, but unfavorable for the other species, resulting in exclusion of the other species from occupied patches.

An example of a two-way interaction comes from the interface of salt marshes and intertidal flats, where English cordgrass and lugworms transform sediment properties in opposite directions (Figure 4.2A). The English cordgrass *Spartina anglica* locally decreases current velocities, resulting in an increase in silt input, sediment compactness, bulk density and elevation, which is positive for plant growth as submergence time is decreased and nutrients input is increased (Ranwell 1964, Castellanos *et al.* 1994, Cahoon *et al.* 1996). The lugworm *Arenicola marina* has an

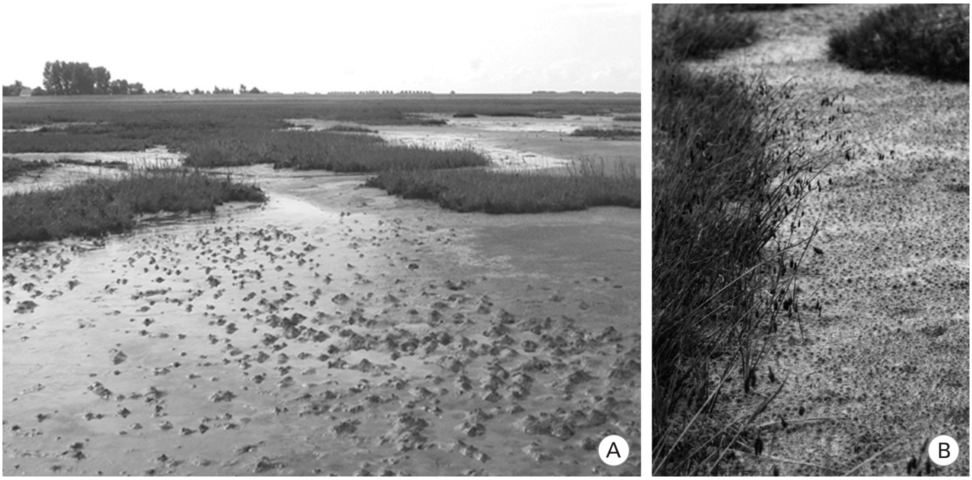

Figure 4.2. Patchy ecosystems with two ecosystem engineers that modify the environment in opposite directions. A. Salt-marsh pioneer zones where *Spartina* and *Arenicola* modify silt content and stability of the sediment (photograph by: B.K. van Wesenbeeck), B. Peatlands in Argentina with separated patches of *Spaghnum imbricatum* and *Carex magellanicum* (photograph by: E. Adema).

exact opposite effect on sediment composition, as it stimulates output of silt from the system by bioturbation of sediment (Krüger 1959, Cadée 1976, Levinton 1995, Riisgard and Banta 1998, Goni-Urriza *et al.* 1999, Reise 2002), which is positive for the lugworm itself as high silt contents restrict the capacity of the lugworm to pump water through the sediment (Meysman *et al.* 2005). However, silt output is expected to have an adverse effect on *Spartina* establishment and growth. On this interface between salt marshes and intertidal flats species co-occur on a landscape scale of hundreds of meters, but on local scales of several meters they occur spatially separated in patches that they create themselves by transforming the environment (van Wesenbeeck *et al.* 2007a). Thus, on local scales both species exclude each other by transforming environmental conditions, resulting in a patchy landscape on landscape scales.

A similar example originates from bog systems (Figure 4.2B). *Sphagnum* and vascular plants modify several environmental factors in opposite directions, stimulating their own growth, but repressing growth of the other functional group (Eppinga *et al.* 2007). *Sphagnum* promotes a higher water table (van Breemen 1995) and lowers nutrient availability for vascular plants (Malmer *et al.* 1994, Malmer *et al.* 2003), whereas vascular plants induce lower water tables (Ingram 1983, Marschner 1995, Frankl and Schmeidl 2000) and higher nutrient levels (Rietkerk *et al.* 2004b, Wetzel *et al.* 2005), which they prefer. These two-way effects amplify slight initial differences in landscape variation, into the formation of sharply bounded patches of vascular plant-dominated hummocks and *Sphagnum*-dominated hollows (Belyea and Clymo 2001, Rietkerk *et al.* 2004b, Eppinga *et al.* 2007). Although these different micro-environments alternate on a spatial scale of meters, they can differ substantially in environmental conditions (Bragazza *et al.* 1998, Gunnarsson and Rydin 1998, Malmer *et al.* 2003).

These examples illustrate that patchiness is not necessarily the result of underlying abiotic heterogeneity, but it could be the result of two-way negative interactions between species or functional groups of species that modify an initially relatively homogeneous habitat in opposite directions. Concluding, two-way negative interactions may alter habitat conditions in opposite ways, inducing a symmetric switch that creates a mosaic of contrasting communities (Wilson and Agnew 1992). Such mosaics have been linked with alternative stable states (Wilson and Agnew 1992), but in theory a one-sided positive feedback can also induce alternative stable states (Scheffer and Carpenter 2003). For diversity, patchiness means a more heterogeneous habitat, which could possible lead to an increase in diversity on ecosystem-scales.

Future challenges and Conclusions

The utility of the ecosystem engineering concept depends on knowing when habitat modification needs to be explicitly considered, as a potential underlying cause for observed patterns (Hastings *et al.* 2007). Evidence is growing that negative species interactions through habitat modification can act as an important structuring force in a large variety of ecosystems. The various examples discussed in this paper particularly show that negative interactions by habitat modification may induce positive feedbacks that have a large structuring effect in ecosystems, also by affecting community interactions. More specific, one-way negative interactions may act as a possible mechanism facilitating species invasions, resulting in more homogeneous species assemblages. Also, two-way negative interactions may structure ecosystems by triggering spatial heterogeneity through patchiness. To identify such causal relationships and evaluate implications of ecosystem engineering into more detail, there is a need for combined field experiments and mathematical modeling.

Until now, incorporation of habitat modification in mathematical modeling has been surprisingly limited (Hastings *et al.* 2007). Further progress in this area could stimulate the development of theory on the importance of habitat modification as compared to biotic interactions and resource competition (see box 2). Furthermore, our examples illustrate the need for a multispecies approach in evaluating effects of ecosystem engineering, as opposed to estimating effects of single species upon their environment. A multispecies approach will also reveal interactive effects that may arise. These different avenues of research could increase our understanding of the role of habitat modification in determining community structure, specifically with respect to exotic invasions and ecosystem patchiness. Such better understanding may be particularly helpful to increase the success of restoration efforts to eradicate exotic invaders (Byers *et al.* 2006, Hastings *et al.* 2007), and to predict the response of patchy ecosystems to future global change (Rietkerk *et al.* 2004a).

Box 2
Extending models of community organization with negative interactions by habitat modification

Generally, it is assumed that physical stresses and relieve from these physical stresses (facilitation) structure communities in stressful environments (Menge and Sutherland 1976, 1987, Bertness and Callaway 1994). Under less stressful conditions competition and predation are considered important structuring forces (Menge and Sutherland 1976, 1987) (Figure B2.1). Recently, ecosystem engineering is incorporated into these models of community organization (Crain and Bertness 2006). Where would negative interactions between species via the environment fit in these models?

Positive feedback switches and ecosystem engineering are typically linked with communities under stressful conditions, where it is of main importance to ameliorate a-biotic conditions (Jones *et al.* 1994). Hence, negative interactions by ecosystem engineering might in particular apply to communities in stressful habitats, where other negative interactions, such as competition for resources, are thought to be trivial. This would actually simplify models of community structure along stress gradients with the generalization that under stressful conditions species interactions, negative or positive, are mediated by the environment (Figure B2.1). Consequently, direct interactions between species, such as predation and associational defenses, would be the main determinant of community structure under more benign conditions (Crain and Bertness 2006).

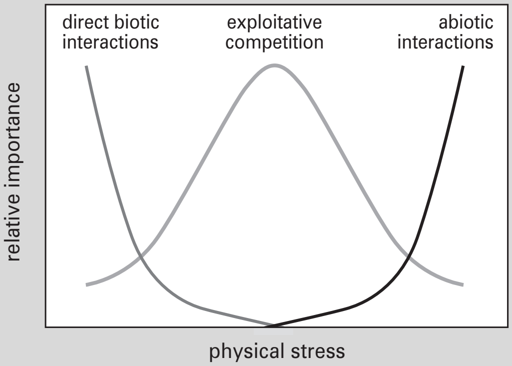

Figure B2.1. A simplification of community assembly models. Direct species interactions, such as predation or associational defenses, might play a dominant structuring role in communities, with low stress (dark gray). With high stress conditions indirect species interactions, mediated by the environment, such as facilitation or negative effects of ecosystem engineering, might be the dominating force structuring a community (black). Competition may still be the dominant process with intermediate stress levels, coinciding with the traditional Menge-Sutherland model (1976, 1978, light gray).

Chapter 5

Potential for sudden shifts in transient systems; distinguishing between local and landscape-scale processes

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submitted

Abstract

A better understanding of the potential for alternative stable states and catastrophic shifts to arise in natural systems is of great importance for ecosystem conservation and restoration. However, the applicability of the concept of alternative stable states to natural systems is ambiguous. We examine processes on local and landscape scales in salt-marsh pioneer zones, to determine to what extent the concept of alternative stable states applies to this system, and hence to asses the potential for sudden shifts in this system. Therefore, we investigated the presence of three typical features of alternative stable states: bimodality, threshold dynamics and bistability. 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 at the presence of alternative stable states at small, within-patch scales and 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 may be applicable to the salt-marsh pioneer zone, but is only relevant on short temporal and spatial scales. However, the concept is unable to predict long-term dynamics of heterogeneous salt-marsh pioneer zones. Present findings underline that threshold dynamics (e.g. sudden shifts in response to human interference) can be an important characteristic of systems with transient dynamics that may, on the long run, only have a single stable state.

Introduction

One of the most useful applications of the alternative stable states theory in natural systems is to predict the potential of an ecosystem to switch to another state without showing any warning signs. These sudden and catastrophic shifts between different ecosystem states occur in response to disturbances or gradual change of external conditions (Scheffer *et al.* 2001, Scheffer and Carpenter 2003, Rietkerk *et al.* 2004, van Nes and Scheffer 2005). Catastrophic shifts have been found in many different systems, such as shallow lakes (e.g. Scheffer *et al.* 1993), arid ecosystems (e.g. van de Koppel *et al.* 1997), coral reefs (e.g. Knowlton 1992) and forests (e.g. Augustine *et al.* 1998) 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 thought to be generated by positive feedbacks (Scheffer *et al.* 2001, Rietkerk *et al.* 2004). Positive feedbacks occur when an organism amplifies disturbances or environmental processes, driving the system away from equilibrium. In theory, positive feedbacks are considered to cause alternative stable states in community composition (Scheffer *et al.* 1993), vegetation biomass (Walker *et al.* 1981, Rietkerk and van de Koppel 1997), or animal density numbers (Persson *et al.* 2003), within systems. Positive feedbacks have been convincingly demonstrated in the field (Wilson and Agnew 1992). However, experimental verification of alternative stable states in natural systems is hampered by disagreement on how to determine stability of alternative states (Connell and Sousa 1983, Peterson 1984, Sutherland 1990, Petraitis and Latham 1999) and by the lack of long-term studies (Petraitis and Latham 1999, Schroder *et al.* 2005).

The original alternative stable state concept, as developed by Lewontin in the 1960's, proposes that a system can occur and stably persist, when not perturbed, in two or more states under the same environmental conditions (Lewontin 1969). The theoretical literature proposes a number of indicators for the presence of alternative stable states (Scheffer 1998, Schroder *et al.* 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 *et al.* 2005). Further, experimental testing for biomass thresholds above or below which a system has to be perturbed before a switch to another state is initiated is an appropriate way of examining presence of alternative stable states (Scheffer and Carpenter 2003, Schroder *et al.* 2005). Finally, both states should be stable on relevant time-scales, typically defined by the generation-time of the involved organisms (Connell and Sousa 1983, Peterson 1984, Sousa and Connell 1985, Sutherland 1990, Petraitis and Latham 1999).

Recently, a number of theoretical studies pointed at the potential for catastrophic shifts to occur in systems that do have positive feedback, but are not confirmed to have two alternative stable states (Silliman *et al.* 2005, van de Koppel *et al.* 2005). Hence, for catastrophic shifts to occur, long-term bistability seems not to be a prerequisite. Furthermore, it has been suggested that systems that are not stable on longer

Figure 5.1. Photograph of a salt-marsh pioneer zone with tussocks of *Spartina anglica* in the southwest of The Netherlands.

time-scales may have dynamics that resemble alternative stable state systems closely (Schroder *et al.* 2005, Van Geest *et al.* in press). Here we ask to what extent criteria for detecting alternative stable states are useful for predicting ecosystem development and sudden shifts in ecosystems.

Salt-marsh pioneer zones are considered to develop into closed vegetation on the long term (Olff *et al.* 1997, Allen 2000). Moreover, a feedback between vegetation and sedimentation is considered to result in complex long-term dynamics, as salt-marsh formation is followed by lateral erosion and salt-marsh degeneration on time-scales of several hundreds of years (van de Koppel *et al.* 2005). Nevertheless, salt-marsh pioneer zones in the Netherlands have a number of typical features indicating potential for alternative stable states and sudden shifts. First of all, they are characterized by a patchy distribution of either dense stands of the common cordgrass *Spartina anglica* or un-vegetated intertidal flat which is inhabited by benthic invertebrates (Figure 5.1). On the intertidal flat benthic invertebrates, especially lugworms, impede settlement of *Spartina* seedlings (van Wesenbeeck *et al.* 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 (e.g. Leonard and Luther 1995, Bouma *et al.* 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 *et al.* 1994). This feedback is scale-dependent, especially under conditions of high flow velocity, implying that reduced water flow inside tussocks results in increased water flows at the edges of tussocks, explaining the presence of erosion gullies there (Van Wesenbeeck *et al.* submitted). These erosion gullies may hinder expansion of existing tussocks (Van Wesenbeeck *et al.* submitted), and arrest tussock development.

Here we investigate to what extent criteria for alternative stable states explain structure and dynamics of salt-marsh pioneer zones. We address short-term indicators of alternate 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 the applicability of using the alternative stable state concept to predict potential for sudden shifts in stable and transient ecosystems.

Methods

Bimodality

To investigate vegetation distribution along the stress gradient from intertidal flat to salt marsh, we carried out an observational study on aerial photographs. A false-color aerial photograph from 1998 of Paulinapolder, a salt marsh in the Westerschelde (51°21’ N and 003°42’ E), was used to determine bimodality. Suitable aerial photographs of the other areas, where field experiments were performed, could not be found due to the fact that either these aerial photographs were taken during high tide, while the pioneer zone was completely submerged, or high algal biomasses were present that could not be distinguished from vegetation. To obtain an estimate of vegetation biomass the Normalized Difference Vegetation Index (NDVI) was used. NDVI is composed of red and near infra-red reflectance differential ratio (NIR-R / NIR+R) (Pettorelli *et al.* 2005), allowing it to be used as a measure of plant biomass. False color photographs (scale 1:5000) 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, till intertidal flat. The intertidal flat is the zone without vegetation presence. 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 *et al.* 2005). All these zones are easily distinguishable as well as in the field as on aerial photographs. In this paper, 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. Three different *Spartina* biomasses were transplanted; small seedlings in groups of three, small clonal fragments (underground root and one or two aboveground stems), and large clonal fragments of 20 cm x 20 cm consisting of 15 to 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 *et al.* in press), 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 till 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 was 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 meters apart and low transplants were planted between 10 till 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. For creating disturbances it was 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 two years. All planted pieces established and were expanding slowly. After two 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* regrowth 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 two years. Four permanent plots of 10 m x 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 x 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 1:5000, pixel size 0.25 m*0.25 m) of 1982, 1998 and 2004 were used that were scanned, geo-referenced and classified 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 in this zone. High NDVI-values are dominating in high marshes (Figure 5.2A), indicating high vegetation biomass. Low NDVI-values are dominating on intertidal flats (Figure 5.2C), 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 5.2B), 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

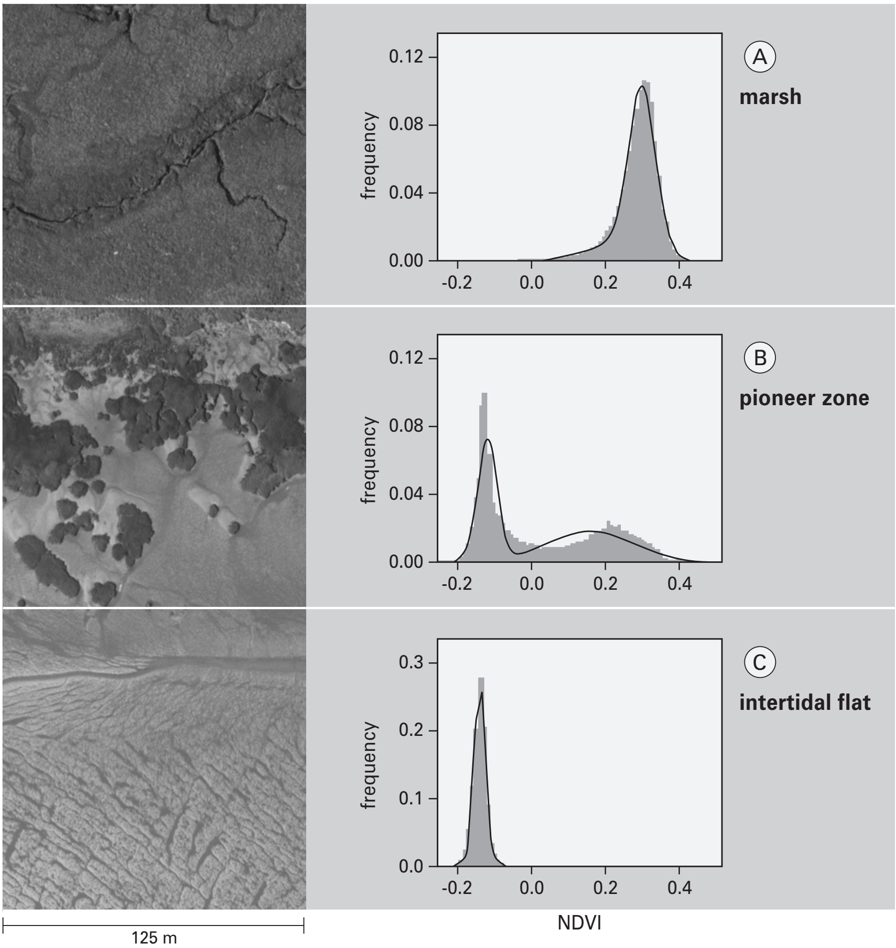

Figure 5.2. Example of transect through a marsh taken from an aerial photograph of Paulina polder (Westerschelde). Graphs represent the frequency distribution of the NDVI for the high marsh (A), pioneer zone (B) and intertidal flat (C).

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.

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 5.3 A, 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 were surviving for the time monitored and were mostly expanding (Figure 5.4). Differences in survival were significantly explained by differences in transplant bio-

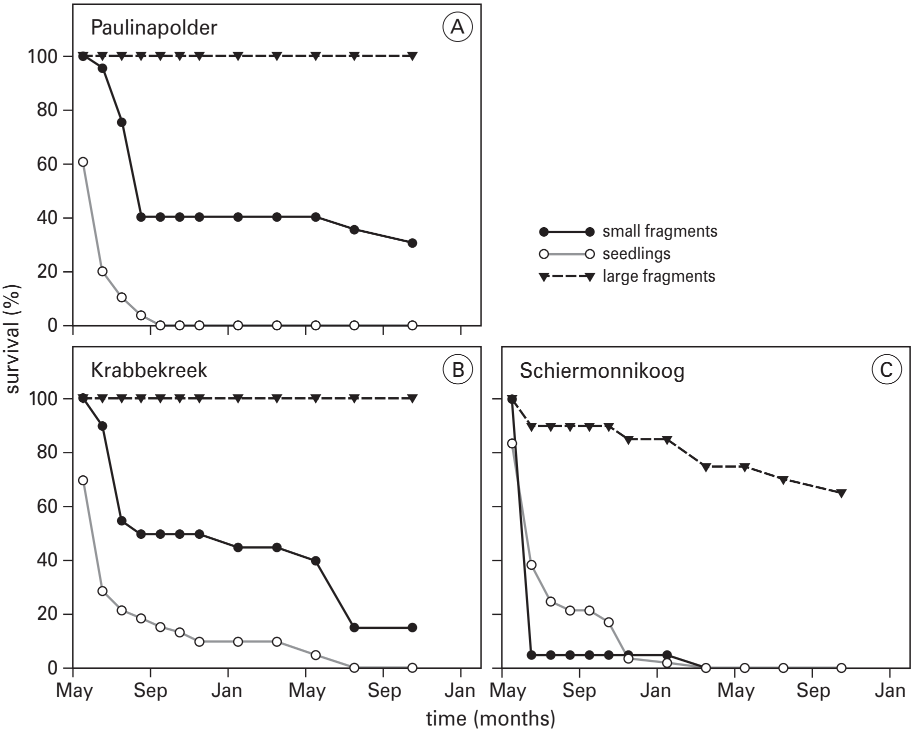

Figure 5.3. Survival of planted seedlings (open circles, n = 60), small fragments (closed circles, n = 20) and large fragments (closed triangles, n = 20) during 18 months in Paulinapolder (A), Krabbekreek (B) and Schiermonnikoog (C). Differences between survival of large and small fragments (t-value: 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.

mass (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 5.5). Natural recruitment is very episodic. In 2003, 89 seedlings settled in this area as opposed to 2 in 2004 (not represented in figure). However, none of the seedlings seem able to survive and form a new *Spartina* patch during the two 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).

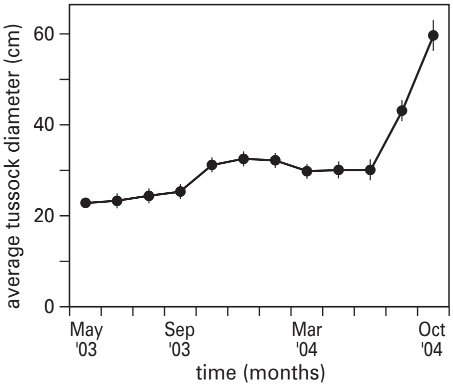

Figure 5.4. Average diameter of transplanted large fragments that survived, over a period of 18 months in Paulinapolder, Krabbekreek and Schiermonnikoog. Error bars represent standard errors.

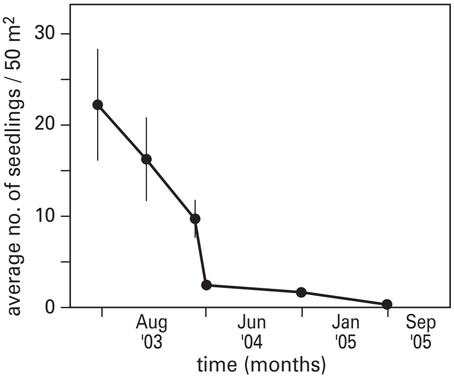

Figure 5.5. Number of *Spartina* seedlings monitored in four 10x5 m^2 plots, in a salt-marsh pioneer zone (Krabbekreek, Oosterschelde) during a period of two years. Error bars represent standard errors.

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 5.6A+B). Overlay analysis made clear that for this particular area in the same time span some tussocks were extending (light grey areas), while others were contracting (black areas). Moreover, vegetation loss and growth were recorded to occur on the same tussock and a number of tussocks disappeared, while others established. Vegetation cover more than doubled between the years 1982 and 1998, while still considerable loss was occurring locally (Figure 5.6A). Nevertheless, very little vegetation loss was observed between 1998 and 2004 (Figure 5.6B), while in this short period, vegetation growth was extremely high (Figure 5.6B). Large tussocks merged and were predominantly growing, while small tussocks appeared and disappeared.

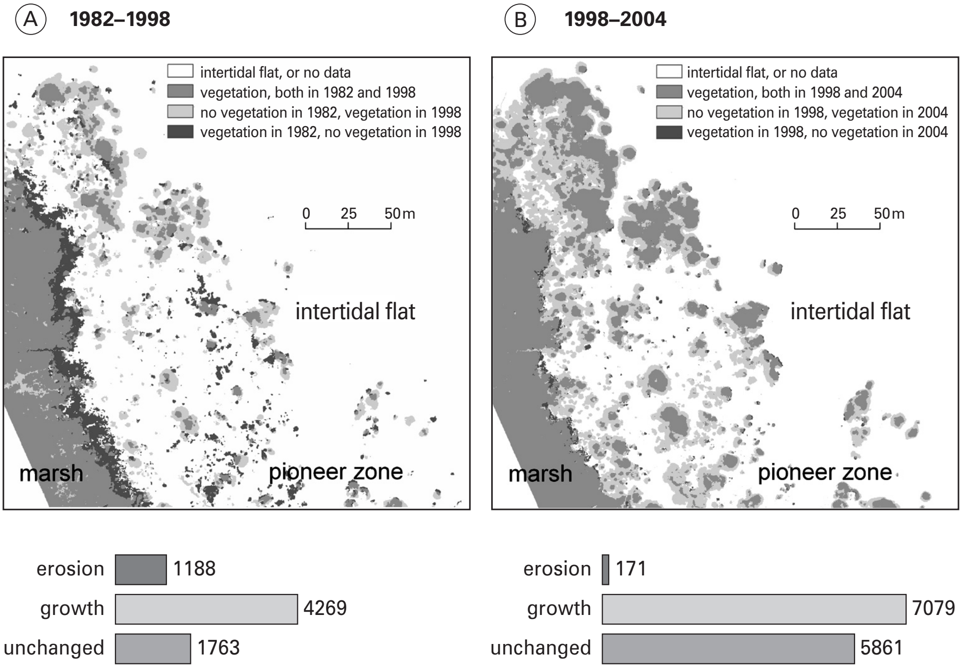

Figure 5.6. Growth and erosion of *Spartina* tussocks in a salt marsh pioneer (Paulinapolder, Westerschelde). The picture shows vegetation that had been present between an interval (dark gray), vegetation that has developed in this period (light gray) and vegetation that has eroded in this interval (black). Figure 5.6A shows the interval from 1982 till 1998 and Figure 5.6B shows the interval from 1998 till 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 Figure 5.6A to the right) that has been eroding or growing in both periods.

Discussion

In this paper, we assessed possible application of the alternative stable states concept within salt-marsh pioneer zones. Our results are twofold: We found clear indications for the presence of alternative stable states in observations of vegetation characteristics and manipulative experiments, suggesting the presence of two separate attractors. However, analysis of vegetation development over 22 years gave a completely different picture, revealing a dynamic and transient ecosystem characterized by ongoing contraction and mostly expansion of vegetation patches. 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 are transient systems. Nevertheless, threshold dynamics govern early vegetation establishment, and hence there is potential for sudden shifts to occur during pioneer vegetation development, particularly at small scale. Our study emphasizes that the frame-work of the alternative stable state theory might be useful for understanding dynamics of transient systems that linger in an unstable situation for considerable time.

The concept of alternative stable states is generally considered to apply to systems that show long-term stability. However, recently the suggestion was made that in some systems, dynamics resemble alternative stable state situations, but one of the two equilibria is seldom found in a stable situation under natural conditions (Schroder *et al.* 2005, Van Geest *et al.* in press). It has been put forward that alternative stable states can influence structure of transient states (Schroder *et al.* 2005) or that the presence of an 'almost stable state' may slow down ecosystem development towards the only true stable equilibrium (Van Geest *et al.* in press). Moreover, the existence of two attractors is considered to lead to hysteresis, but not necessarily to bistability (Schroder *et al.* 2005). This coincides with our findings in salt-marsh pioneer zones, where for example conditions for settlement are different from conditions for vegetation persistence or expansion, pointing at the presence of hysteresis. Below, we discuss the limitations of the concept of alternative stable states to detect potential for sudden, catastrophic shifts, in relation to spatial and temporal scale.

Many mathematical studies relate positive feedback to the presence of alternative stable states (Walker *et al.* 1981, Rietkerk and van de Koppel 1997, van de Koppel *et al.* 1997). The presence of a bimodal biomass distribution suggests the presence of a threshold effect in the growth of *Spartina* in the interface zone (Wilson and Agnew 1992, Scheffer and Carpenter 2003, Schroder *et al.* 2005). The occurrence of thresholds, brought about by positive feedbacks, induces potential for sudden unannounced shifts, where a slight change in environmental parameters or a slight disturbance pushes the system over the threshold and causes it to collapse (Scheffer *et al.* 2001, Rietkerk *et al.* 2004). Our results reveal a bimodal vegetation distribution and a threshold in the establishment of *Spartina* vegetation, both of which are indicative for the presence of positive feedbacks and alternative stable states (e.g. Wilson and Agnew 1992, Scheffer *et al.* 2001, van de Koppel *et al.* 2001, Rietkerk *et* *al.* 2004, Schroder *et al.* 2005). Positive feedback between vegetation and sediment has been described for 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 *et al.* 2005). Hence, our empirical evidence for bimodality and thresholds in salt-marsh vegetation, combined with evidence from 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. Nevertheless, there seems little basis for the occurrence of alternative stable states on larger time scales.

Hughes *et al.* (2005) stated that system wide collapse could be an emergent property of small scale dynamics. In our study, within-patch feedback processes determine biomass stability, and may induce the presence of alternate attractors on short time scales, while landscape-scale forcing, however, is independent of the state of each individual patch. This explains the presence of strongly contrasting patches with sharp boundaries, bimodality of biomass distribution, and the threshold effects which we found in our short-term empirical study. On longer timescales, landscape-level processes that integrate the effects of many small-scale patches may determine the external conditions that any individual patch experiences. These may, in the long run, affect the persistence of alternate attractors, and cause instability at the landscape level. For example, in salt-marsh pioneer vegetation, changes in tussock configuration will influence hydrodynamics on larger scales (Temmerman *et al.* 2005). This coupling of processes occurring on different scales has previously been hypothesized and complicates experimental and theoretical exploration of ecosystem stability (Rinaldi and Scheffer 2000, Foley *et al.* 2003, Scheffer *et al.* 2005). Thus, our study suggests that the concept of alternative stable states can be used as an approximation of ecosystem dynamics on short temporal and spatial scales, but is unable to predict the long-term dynamics of heterogeneous salt-marsh ecosystems, because of spatial feedback processes occurring at landscape scales. So, critical in the adoption of the alternative stable states concept for a particular ecosystem, is the a-priory definition of the relevant spatial and temporal scale, before experimental investigation of the presence of alternative stable states is started (Paine and Trimble 2004)

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 at the possibility for sudden shifts in this ecosystem, in response to small human disturbances, which may take long (decades in our system) to recover (Suding *et al.* 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 positive feedback and threshold dynamics as indicators for potential catastrophic shifts in transient as well as stable systems, will be an important step forward in the application of alternative stable state theory to natural systems, and help in the conservation of complex ecosystems.

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Chapter 6

Distinct habitat types arise along a continuous hydrodynamic stress gradient due to interplay of competition and facilitation

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Abstract

Though species interactions across local environmental gradients are well studied, the way in which species interactions shift between different habitats on a landscape-scale has received less attention. We hypothesized that interactions among a suite of shoreline plant species shift across a hydrodynamic-exposure gradient, leading to generation of apparently distinct habitat types (e.g. bare cobble beaches, vegetated cobble beaches, fringing marshes, and salt marshes). We examined hydrodynamic forcing, and found that it was strongly correlated with shoreline habitat type. A transplant experiment revealed that all plants were rapidly crushed and abraded in bare cobble areas with high hydrodynamic energy, and were out-competed by grasses in the low energy salt marshes. Vegetated cobble beaches inhabit the largest amount of plant species under intermediate conditions, where hydrodynamic energy is sufficiently low to allow the establishment of the ecosystem engineer *Spartina*, and sufficiently high to prevent the monopolization of space by competitively dominant, but stress intolerant grasses. Experimentally reducing physical and biotic stresses (hydrodynamics and interspecific competition) on bare cobble beaches and salt marshes respectively enabled forbs to persist across the whole gradient. These results demonstrate that the outcome of interspecific interactions at landscape scales is driven by background physical conditions, and that this can result in development of what are considered distinct habitats.

Introduction

How species interactions shift across environmental gradients has been a fruitful ecological inquiry (e.g. Menge & Sutherland 1976, Bertness & Callaway 1994, Huckle *et al.* 2000, Pugnaire & Luque 2001, Maestre & Cortina 2004). However, most studies have focused on single habitat types and/or small scale gradients. Recent research has begun to scale-up and investigate shifting species interactions across landscape-scale gradients (e.g. alpine gradients, Callaway *et al.* 2002, estuarine salinity gradients, Crain *et al.* 2004). Despite this recent trend, the potential for shifting species interactions to result in what are traditionally considered distinct habitats has received considerably less attention.

Coastal shorelines are ideal systems for testing questions across large-scale environmental gradients as stress conditions, such as hydrodynamic forcing or salinity, vary predictably. The biological communities of coastal habitats are relatively easy to manipulate, their community ecology has been extensively explored, and they are exposed to multiple environmental stressors, such as wave exposure, changes in salinity, and desiccation (Bertness *et al.* 2000). Shoreline geology and oceanography largely determine the degree to which coastal environments are exposed to these stresses in a predictable manner. For instance, exposed rocky headlands experience greater wind and hydrodynamic stresses than nearby protected shores, while protected bays accrete sediments and form salt marshes (Allen 2000). In Narragansett Bay, Rhode Island, USA, coastal habitats include salt marshes, cobble beaches and rocky shore habitats that have each been well studied independently (e.g. Bertness 1999, Bruno 2000, Kennedy & Bruno 2000). Thus, community ecology and species interactions within each of these habitats are relatively well understood. However, many of the same plant and animal species live in all of these separate habitats, but the way in which their interactions shift between those habitat types and the consequent community outcomes and patterns have not been experimentally examined.

Menge and Sutherland (1976, 1987) developed a conceptual model predicting how the importance of ecological processes, such as disturbance, competition and predation, vary predictably in response to environmental stress. Some of the basic predictions of their model are that the abundance of basal trophic levels is limited by physical factors at high levels of environmental stress, by predation at low levels of physical stress, and competition at intermediate levels of physical stress. Bertness and Callaway (1994) extended this model by including facilitation, predicting that positive interactions will be the most important structuring process where physical and biological (predation and/or competition) stress is highest, due to neighbor amelioration of respective stressors. Thus, the background environment is predicted to drive changes in direction and intensity of species interactions along natural stress gradients. The balance between positive and negative interactions has been the topic of several other modeling studies (e.g. Holmgren *et al.* 1997, Wilson & Nisbet 1997, Travis *et al.* 2005) and field studies at local spatial scales, generally within a single habitat (e.g. Menge *et al.* 1986, Bertness 1989, Bertness & Yeh 1994, Greenlee &

Callaway 1996, Callaway 1998, Bertness *et al.* 1999, Callaway & Aschehoug 2000, Pugnaire & Luque 2001, Callaway *et al.* 2002, Maestre *et al.* 2003). Despite this interest, no previous studies have tested models of species interactions under differing environmental stresses across large-scales that actually span distinct habitat types.

In this paper we examine how community composition and species interactions shift with differing hydrodynamic stresses (currents and waves) in Narragansett Bay, RI, and contribute to formation or maintenance of the distinct habitat types found in this bay. By doing so, we test whether models of species interactions developed at local scale environmental gradients (Menge & Sutherland 1987, Bertness & Callaway 1994) accurately predict the shifting nature of species interactions between different habitats at a landscape scale. Scaling up from previous work within salt marshes (Bertness & Ellison 1987, Ewanchuk & Bertness 2004) and cobble beaches (Bruno 2000) we hypothesized that at landscape-scales, the dominant factor structuring vegetation patterns would be physical disturbance where hydrodynamic energy is highest, facilitative interactions where hydrodynamic impact is intermediate, and competitive exclusion where hydrodynamic stress is low. Research was conducted in intertidal habitats common to southern New England and other semi-protected coastal areas including bare cobble beaches (BCB) and vegetated cobble beaches (VCB), fringing marshes (FM) and developed salt marshes (SM). We tested the relationship between hydrodynamic energy and vegetative habitat type at different scales, transplanted several species of forbs (flowering plants, mostly non-woody) and grasses along the entire hydrodynamic gradient, and performed manipulative experiments at extreme ends of the hydrodynamic gradient. Together, these approaches provide evidence that interactions between common plant species shift due to varying environmental stress, and result in the formation of distinct coastal habitat types.

Material and Methods

Field site

Surveys were conducted in central Narragansett Bay, Rhode Island, USA and field experiments were located in the same bay in the Narragansett Bay National Estuarine Research Reserve (41°39’ N and 71°21’ W). Narragansett Bay is a well-mixed estuary with near oceanic salinity (28-31 ppt) and semi-diurnal tides ranging from 0.8-2.0m. Waves within the sheltered bay can exceed 1 m, and are generated by local winds and boat traffic (Bruno 2000). Main wind direction is variable and fluctuates on a daily basis (Zhao *et al.* 2006). Experimental study sites were selected as representative of the four common coastal habitats in Narragansett Bay. At the most exposed locations, such as headlands, bare cobble beaches dominate. In areas that are apparently sheltered from prevailing winds and wave action, cobble beaches are colonized by the grass *Spartina alterniflora* with forb communities behind the *S. alterniflora* bed (vegetated cobble beaches). In yet more protected areas such as embayments, cobble beaches are occupied by *Spartina alterniflora* beds with grasses such as *Spartina patens* and *Distichilis spicata* dominating behind the bed (fringing marsh). Finally, on extremely sheltered shores and behind berms, salt marshes occur. In all of these distinct habitats types (except on the most wave-swept bare cobble beaches), *Spartina alterniflora* dominates the low-tidal heights where it facilitates initial establishment of the community in mid- and high-tidal zones. In salt marshes, the facilitative mechanism is the build-up of peat (Bertness 1988), and on cobble beaches it buffers hydrodynamic impact and stabilizes the substrate (Bruno 2000). However, the communities occurring behind *Spartina alterniflora*, at mid-tidal elevations, differ considerably between different habitats.

Large scale coastal vegetative survey & hydrodynamic measurements

A large-scale coastline survey was performed to examine the correlation between coastal habitats and hydrodynamic energy. Approximately 150 km of coastline within Narragansett Bay were visually surveyed from a boat traveling 5km/hr within 20 m of the shoreline. The coastline was categorized as bare cobble beach, vegetated cobble beach, or fringing marsh/salt marsh. Composite beaches comprised of coarse sand and rocks were grouped with the bare cobble category, and salt marshes fronted by sandy berms were assigned to the salt-marsh category. The length and locations of habitats along the shoreline were recorded using a Global Positioning System (Trimble 76CS), downloaded into ArcView (ArcGIS 9.1) and depicted on a coastline map. The vegetation survey data were correlated spatially with an Average Exposure Index (AEI) which ranks shoreline wave energy from 1-20 based on effective fetch, wind direction, and wind speed. This index was calculated previously for 100x100 m grids in Narragansett Bay (see Kopp *et al.* 1995 for details). Differences in AEI among all habitat types were calculated using a one-way Analysis of Variance. Homogeneity of variances was examined using a Cochran's C-test. AEI-values were log-transformed to homogenize variances. Post hoc comparisons were done using a Tukey HSD test.

To examine a qualitative relationship between habitat types and hydrodynamic forcing at greater spatial resolution, and to verify the large-scale application of the AEI, we deployed 5 dissolution blocks to measure relative differences in water flux at ten replicates sites of each habitat type: bare cobble beaches, vegetated cobble beaches, fringing marshes and salt marshes (see Thompson & Glenn 1994, Bruno & Kennedy 2000 for details on dissolution block technique). Dissolution blocks were glued on two layers of mesh, which was pinned to the surface. Blocks were placed intertidally about 10 cm above the soil surface, at the lower border of the *S. alterniflora* bed to avoid measuring potential flow energy reduction behind the bed, and were placed at the equivalent tidal heights in the other habitats. Dissolution blocks were only used as a qualitative measure for general hydrodynamic stress to compare between different habitats. The blocks were deployed at the end of April and collected 14 days later. To account for loss of some blocks due to failure of adhesives, seven locations and four blocks for each location were used in statistical analysis. A two-way nested-ANOVA was used to examine differences in block mass loss for each habitat type (with site replicate nested in habitat type). Homogeneity of variances was tested using a Cochran's C-test. Mass loss from the blocks was natural log-transformed to meet assumptions for normality. Post hoc differences among groups were determined using a Tukey HSD test.

Plant survival across gradient

To test where common shoreline plants grew best, size-standardized plant units (phytometers) of four common coastal species were transplanted to the four habitats (bare cobble beach, vegetated cobble beach, fringing marsh and salt marsh) and their survival was monitored. In each habitat, plants were planted at mid-tidal heights where they are typically found. Individual ramets of the grass *Spartina patens*, 1-2 year old individuals of the perennial *Limonium nashii*, and seedlings of the annuals *Salicornia europaea*, and *Suaeda linearis* were used as phytometers. Four replicates of each species were transplanted into each of four replicate sites of each habitat type. All transplants were obtained from nearby field sites. Seedlings, small plants and ramets were planted into 10x10 cm blocks of peat where they were watered and allowed to stabilize for 3-5 days. Phytometers that survived the stabilization period were then planted into the different communities, buried flush with the surrounding substrate, and their peat base was secured in place with a galvanized steel garden staple. For the perennials there was only one small plant in each transplant, but for the annuals there were 5 seedlings in the *Suaeda* transplants and 20 seedlings in the *Salicornia* transplants. All plants were planted in May. Survival was recorded biweekly for 3 months. Survivorship for each species was analyzed using a survival analysis based on a Gehan's Wilcoxon test. Survival trends were compared among habitats types using pairwise survival test statistics with an adjusted α-value of 0.0033 (Bonferroni adjustment: α-value of 0.01 divided by 3, the number of comparisons for each data point) presented in table 6.1.

Table 6.1. Test statistics and p-values for Gehan's Wilcoxon test. To compare between survival of each species separately in all different habitats, pairwise comparisons were done for all combinations with a p-value of P<0.003 (sm= salt marsh, fm=fringing marsh, vcb=vegetated cobble beach, bcb=bare cobble beach).

	S. patens (n=16)		*Suaeda* (n=80)		*Salicornia* (n=320)		*Limonium* (n=16)	
Habitats	test statistic	P-value	test statistic	P-value	test statistic	P-value	test statistic	P-value
sm-fm	–1.01	0.31	2.10	0.04	3.36	<0.003	0.63	0.53
sm-vcb	–1.05	0.30	5.10	<0.003	4.59	<0.003	3.00	<0.003
vcb-fm	0.92	0.36	4.37	<0.003	3.29	<0.003	3.02	<0.003
bcb-fm	–4.95	<0.003	–10.05	<0.003	20.31	<0.003	–4.71	<0.003
bcb-vcb	–2.90	0.0037	–10.67	<0.003	–17.53	<0.003	–5.08	<0.003
bcb-sm	–4.74	<0.003	–9.42	<0.003	21.17	<0.003	–4.82	<0.003

Stabilization and Competition Experiments

Based on results from previous studies, we performed two experiments to test whether removing community-limiting variables at both ends of the gradient enabled plant persistence in those habitats. On bare cobble beaches, plants are generally limited by physical stress that can be ameliorated by *S. alterniflora* beds which buffer hydrodynamic stresses and allow forbs to occur higher on the beach behind the beds (Bruno 2000). In salt marshes on the other hand, most plants are excluded from the zone above *S. alterniflora* by the competitive dominant *Spartina patens* (Bertness 1991). To test the generality of these results at our study sites, and test the competitive exclusion hypothesis in the fringing marsh habitat, we performed a stabilization experiment on the bare cobble beach and a competition-removal experiment in the salt marsh. For both experiments we transplanted plants in the same way as described for the transplanting experiment.

The stabilization experiment was conducted to investigate if substrate instability associated with high hydrodynamic energy limits survival of forb seedlings on bare cobble beaches. Substrate stabilization was designed to mimic facilitation by *S. alterniflora* beds which can baffle wave energy and minimize cobble movement. Cobbles were stabilized by securing a piece of hardware cloth (mesh size 1x1 cm^2) over the cobbles, and plants were transplanted into stabilized areas ($n = 9$) and into adjacent unstabilized control areas ($n = 9$) (see Bruno 2000 for methods). Three species were used; the perennials *Spartina patens* and *Limonium nashii*, and an annual from the cobble beach forb community, *Suaeda linearis*. For the perennials one plant or stem was used per peat block for *Suaeda* 5 seedlings were planted in each peat block. The experiment was initiated in late May 2005, which is a peak period for the emergence of shoreline plants, and a time when spring storms are common. After three weeks, the aggregate dry biomass of each species in each plot was taken as a measure of plant performance. Biomass data were compared with a one-way ANOVA, and homogeneity of variances was verified using a Cochran's C-test. Data were log $(x+1)$ transformed when necessary to meet assumptions of ANOVA (Sokal & Rohlf 1995).

To test the hypothesis that competition with *Spartina patens* excludes other plants from the higher marsh zones where hydrodynamic stress is benign, competition experiments were performed. Individual ramets of the grass *Spartina patens*, 1-2 year old individuals of the perennial *Limonium nashii*, and seedlings of the annuals *Salicornia europaea*, and *Suaeda linearis* were transplanted into the salt marsh and fringing marsh into areas from which the dominant grass was experimentally removed (no competition treatments), and into unmanipulated control areas (competition treatments). Above-ground biomass of dominant grasses (predominantly *Spartina patens*) was removed by manual clipping of 40x80 cm^2 areas. Bare plots and controls were replicated 10 times in each habitat, and one individual of each of the four species was transplanted to each plot. After 3 months all species were harvested and weighed. Dry biomass per replicate was analyzed as a measure of plant performance. Data were analyzed using the Mann-Whitney U test for non-parametric data.

Results

The survey of Narragansett Bay (Figure 6.1) revealed that fringing marshes/salt marshes are restricted to areas protected from wave exposure (e.g. like coves and bays), and that bare cobble beach is prevalent on more exposed shorelines. Differences in dissolution block weight loss (AEI) of the three habitats (bare cobble beach, vegetated cobble beach and fringing marsh/salt marsh) were significant (F2, 87=17.8, $p<0.05$ for all post-hoc comparisons), revealing that habitat type is correlated with hydrodynamic stress (Figure 6.2A). This relationship was further supported by the dissolution block sampling (Figure 6.2B) which revealed significant differences in water movement between vegetative habitat types ($F_{3,\ 84} = 54.8$ and $P < 0.01$ for all comparisons), except for the difference between bare cobble and vegetated cobble beach. These results imply that community structure is largely influenced by hydrodynamic forces, but that some bare beaches are potentially suitable habitat for *Spartina alterniflora* colonization.

The phytometer transplant experiment revealed that, in general, shoreline plant species perform best on cobble beaches where the forb community is naturally found (vegetated cobble beaches, Figure 6.3A, B, C, D). The three forb species all survived best in the vegetated cobble beach habitat, while *S. patens* survived equally

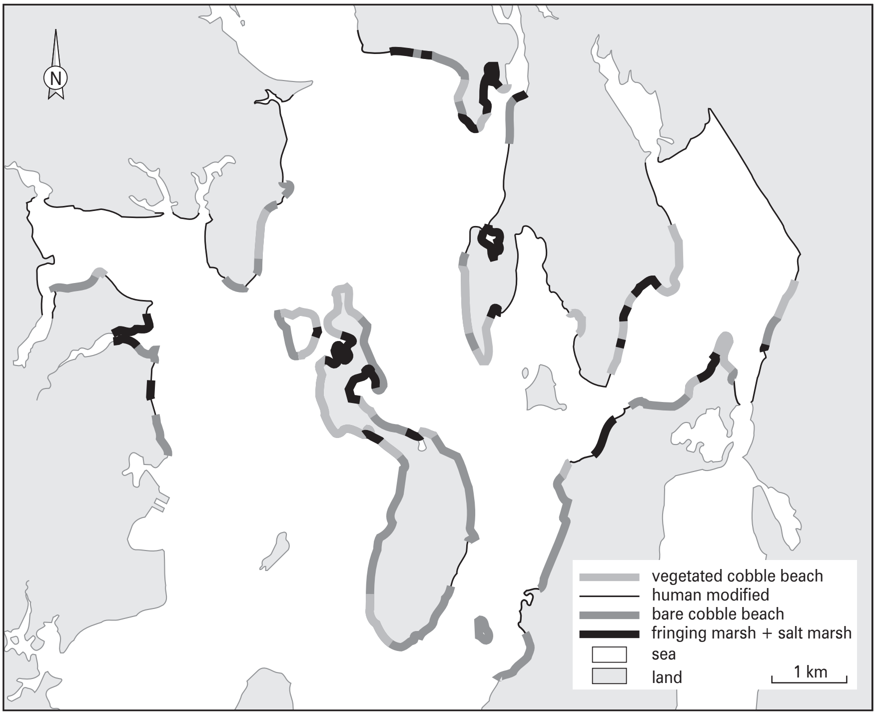

Figure 6.1. Map of a survey of coastline habitats in a part of Narragansett Bay (Rhode Island, US).

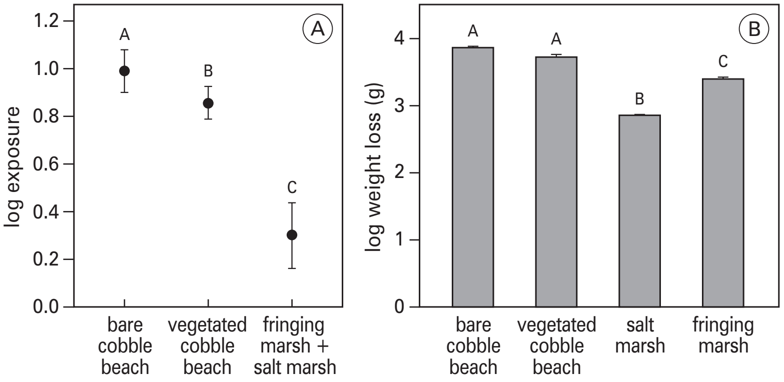

Figure 6.2. The relation between hydrodynamic forces and present community established by (A) using the survey of community types along the coast linked with the log of an exposure index and (B) a dissolution block study on different beaches in the bay. Figure A shows differences in exposure of three categories of coastal habitat ($F_{2,\ 87} = 39.94$, $P < 0.01$) and the letters in figure B indicate significant differences ($F_{3,\ 84} = 54.8$ and $P < 0.01$).

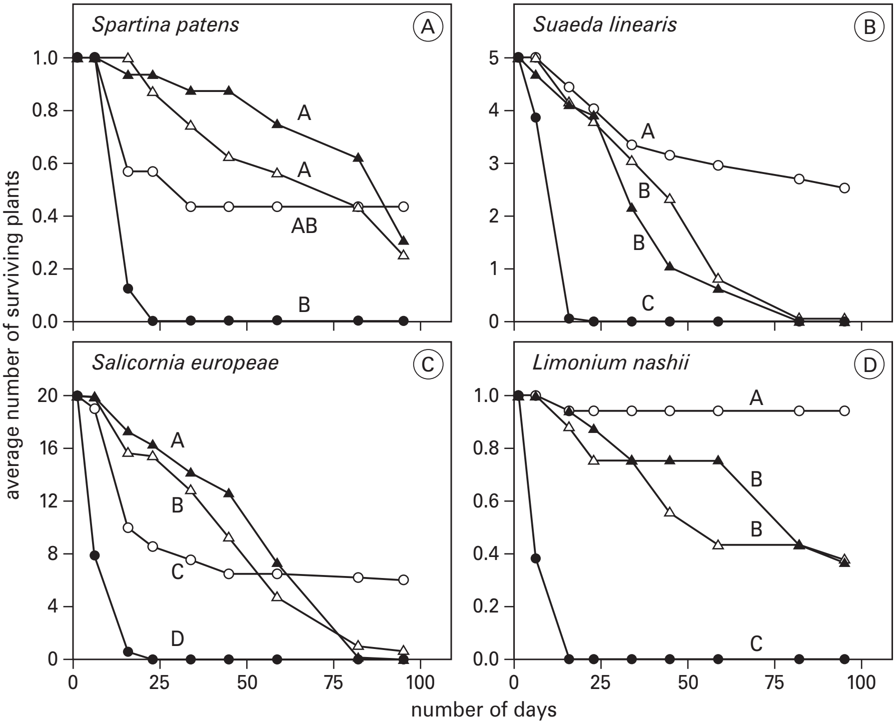

Figure 6.3. Survival trends in four different community types along a hydrodynamic stress gradient of seedlings of four different species, (A) *Spartina patens* (n = 4), (B) *Suaeda linearis* (n = 4), (C) *Salicornia virginica* (n = 4), (D) *Limonium nashii* (n = 4). Letters indicate significant differences between trends for $P < 0.0033$ (see Table 6.1 for test statistics).

well in the vegetated cobble beaches, fringing marsh, and salt marsh. In contrast, there was rapid mortality of all transplanted species on beaches comprised of bare cobble unless the substrate was experimentally stabilized. At the more wave-protected end of the gradient, *Limonium* and *S. patens* persisted through the growing season in the salt marsh and fringing marsh, but *Salicornia* and *Suaeda* failed to do so.

In the stabilization experiment, all three species performed better in stabilized plots than in control plots (*Limonium*: $F_{1,\,16} = 9.4$, $P < 0.05$, *Suaeda*: $F_{1,\,16} = 11.3$, $P < 0.05$ and *S. patens*: $F_{1,\,16} = 6.0$, $P < 0.05$, see fig. 6.4). Transplants in the non-stabilized treatment were crushed by cobbles and shell material after one single storm event. Of the three experimental species, *Spartina patens* was most affected by cobble movement. Of this species no individuals were able to survive in the unstabilized control treatment, whereas of the other species some individuals survived in this treatment (Figure 6.4).

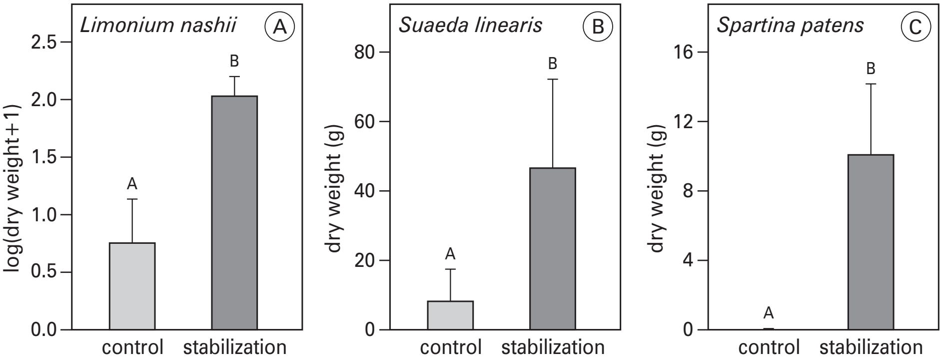

Figure 6.4. Final biomass of seedlings in stabilized and control plots of three different species, (A) *Limonium nashii* ($F_{1,\,16} = 9.4$, $P < 0.05$), (B) *Suaeda linearis* ($F_{1,\,16} = 11.3$, $P < 0.05$) and (C) *Spartina patens* ($F_{1,\,16} = 6.0$, $P < 0.05$). Error bars represent standard errors and letters above bars indicate significant differences for $P < 0.05$.

In the competition experiment, results differ between salt marsh and fringing marsh (Figure 6.5). In the salt marsh, competition suppressed growth of *Salicornia* (Z-adjusted = –2.15, $P < 0.05$) and *S. patens* (Z-adjusted = –2.18, $P < 0.05$), and did not have a detectible effect on *Limonium* (Z-adjusted = 0.65, $P = 0.51$) and *Suaeda* (Z-adjusted = –1.00, $P = 0.32$). For the latter plant species this appears to be due to high variances, because average biomass was lower in competition treatments. In fringing marsh all transplant species had significantly higher biomass without competition than those growing with competition (*Limonium*: Z-adjusted = –2.69, $P < 0.01$, *Salicornia*: Z-adjusted = –3.86, $P < 0.01$, *Suaeda*: Z-adjusted = –3.16, $P < 0.01$, *S. patens*: Z-adjusted = 2.55, $P < 0.05$).

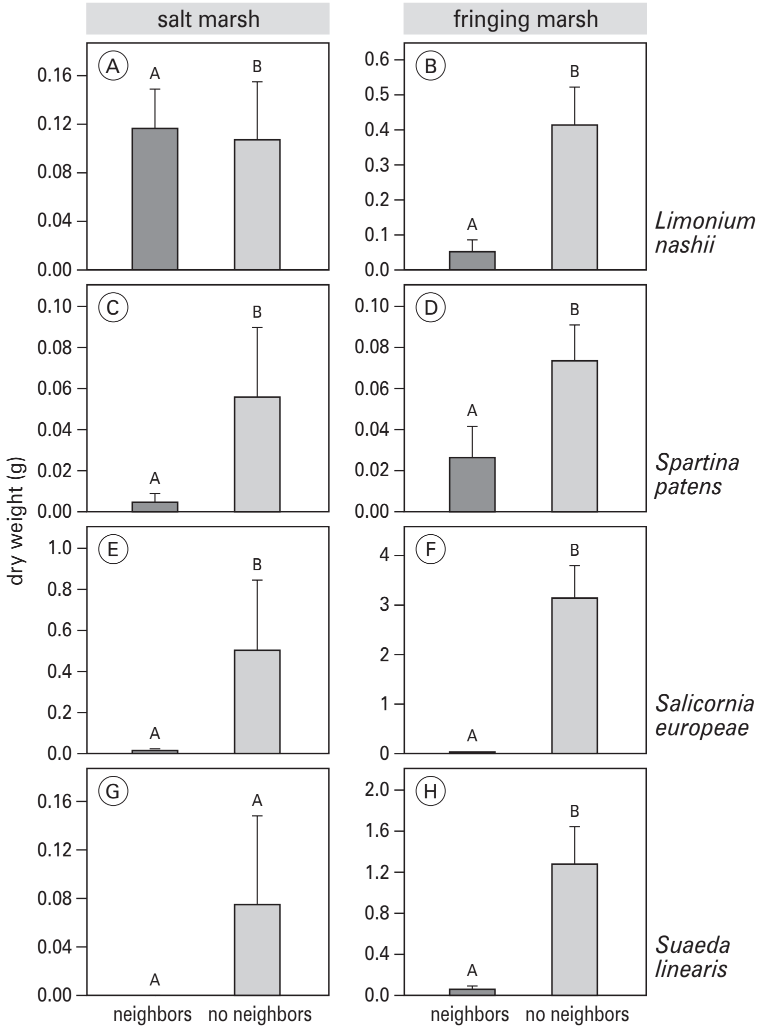

Figure 6.5. Final biomass of seedlings in neighbor removal and control plots with neighbors of four different species, (A+B) *Limonium nashii* (Marsh: Z-adjusted = 0.65, P = 0.51; Beach: Z-adjusted = –2.69, P < 0.01), (C+D) *Spartina patens* (Marsh: Z-adjusted = –2.18, P < 0.05; Beach: Z-adjusted = 2.55, P < 0.05) and (E+F) *Salicornia europeae* (Marsh: Z-adjusted = –2.15, P < 0.05; Beach: Z-adjusted = –3.86, P < 0.01) and (G+H) *Suaeda linearis* (Marsh: Z-adjusted = –1.00, P = 0.32; Beach: Z-adjusted=-3.16, p<0.01) for two different habitats, a protected salt marsh (A, C, E, G) and a fringing marsh developing on a cobble beach (B, D, F, H). Error bars represent standard errors and letters above bars indicate significant differences for p<0.05.

Discussion

Our results revealed that shifting plant interactions lead to creation of distinct habitat types along wave-stress gradients. Interactions shift from primarily facilitative on exposed vegetated cobble beaches to competitive at protected fringing and saltmarsh sites. At intermediate stress the competitive dominant from the marsh was relegated to a minor role. As a consequence of this shift in the nature of interspecific interactions, the community assembly mechanisms and organization of shoreline plant communities vary.

Occurrence of coastal habitats in relation to hydrodynamic stress

The geology of the coastline dictates the exposure of coastline organisms to waves and currents. In the Narragansett Bay ecosystem, glacial retreat, shoreline erosion, and sea-level rise have driven the present outline of the land-sea interface (Donnelly & Bertness 2001). The resulting hydrodynamic context, in turn, determines background environmental stress for interactions among a common suite of halophytic plants and ultimately generates what have always been considered and studied as distinct coastal habitat types. Next to extreme variation in coastal exposure between salt marshes and cobble beaches that drives different habitat types, hydrodynamic variation additionally drives more subtle, yet consistent, differences among cobble beach community types. There are some caveats with using dissolution blocks (Porter *et al.* 2000). However, we deployed all blocks in similar environments and only use results as a qualitative estimate for hydrodynamic stress. Results from our dissolution blocks coincide nicely with results derived from the exposure index. Salt marshes are found in protected bays where hydrodynamic energy is very low, allowing sediment deposition and peat accretion (Wiegert *et al.* 1981, Allen 2000, French *et al.* 2000). In contrast, higher hydrodynamic stress on exposed coastlines leads to open cobble beaches where substrate instability crushes and abrades emerging vegetation (Bruno 2000). In relatively protected cobble areas where wave energy is consistent enough to create a steep beach slope, yet low enough for some sediment deposition and peat accretion, fringing marshes develop that are similar to salt marshes. However, in fringing marshes, vegetation zones are condensed relative to salt marshes as the slope of the beach is steep (Bruno 2000). As wave exposure increases on cobble beaches, *Spartina patens* becomes rare and instead, a community of forbs develops behind *S. alterniflora* beds. These communities, with intermediate hydrodynamic stresses, are the most diverse communities in our spectrum and can contain up to 11 plant species (Bruno & Kennedy 2000).

Hydrodynamic stress measured by our dissolution blocks accurately predicted the presence of all of habitat types described above, except bare cobble and vegetated cobble beaches, which it was unable to resolve. The lack of differences between vegetated and non-vegetated cobble beaches may be due to sampling time. We recorded our dissolution block measurements in spring to target the period critical to the emergence of forbs, and may have missed differences that determine the success of

S. alterniflora among sites in other seasons. An alternative explanation is that *S. alterniflora* colonization of bare cobble beaches is limited by propagule dispersal, and that positive feedbacks promote bed growth and persistence once *S. alterniflora* establishes, as suggested by Bruno and Kennedy (2000). Nevertheless, our analysis of the exposure index (AEI), which does account for seasonal shifts in prevailing winds by integrating conditions throughout the year, revealed differences in exposure between vegetated and non-vegetated cobble beaches.

Once *S. alterniflora* establishes, its role as a foundation species and ecosystem engineer facilitates the establishment of plant communities behind (Bruno 2000), and invertebrate community within (Altieri *et al.* 2007), the bed . This successional development of the coastal environment ultimately climaxes in salt-marsh systems, unless harsh hydrodynamic conditions prevent the peat development necessary for marsh development. Such an interface between successional species interactions and environmental limitations can lead to ‘arrested succession’, which is succession terminated by local environmental circumstances (Graham & Henry 1933). In our study system, the hydrodynamic conditions along the environmental gradient effectively determine prevailing species interactions which combine with positive feedbacks to generate distinct habitats from a common pool of potential component species. The shorelines are thus hierarchically organized (Bruno *et al.* 2001, Altieri *et al.* 2007), where environmental stress in the form of wave-driven substrate instability determines first where the foundation species *S. alterniflora* can establish, which in turn determines the nature of secondary interactions among the plants facilitated by *S. alterniflora*. Alternative hypotheses for variation in community type across the hydrodynamic gradient such as seed dispersal, have been examined previously in our study system, and were shown to not limit distributions of shoreline forbs (Rand 2000, Bruno 2002).

Plant response over the whole gradient

The tradeoff between stress tolerance and competitive dominance is a recurring mechanism in the partitioning of species along stress gradients. This general tradeoff has determined plant distribution patterns across other coastal gradients, such as tidal elevation (Little & Kitching 1996) and salinity gradients (Crain *et al.* 2004), and likely drives species distribution patterns across our hydrodynamic gradient as well. For instance, *Spartina patens*, the best competitor in the low flow environment of marshes where it forms a monoculture (Bertness 1988, La Peyre *et al.* 2001), is not able to dominate in the higher stress environment of cobble beaches, regardless of whether *S. alterniflora* buffers water movement in the low zone. Transplants of *S. patens* experienced high mortality in the *Spartina*-forb cobble beach, and total mortality in the most physically extreme environment. As a result, halophytic forbs that are competitively inferior to *S. patens* in salt marshes (Rand 2000, Ewanchuk & Bertness 2004) exploit a competitive refuge on cobble beaches in the zone behind *S. alterniflora* beds where hydrodynamic stress is sufficiently buffered. *S. patens* is likely more susceptible to physical stress and unable to dominate behind *S. alterni-*

flora beds on cobble beaches, allowing a diverse forb community to proliferate. It seems that coastal forbs and grasses exhibit tradeoffs in stress tolerance and competitive ability that determine their distribution across a hydrodynamic stress gradient, resulting in emergence of different habitats. In our system facilitation by a foundation species drives development of a diverse community under intermediate stress conditions where the competitive dominant species is restricted by physical factors.

Applying models to landscape-scales

Conceptual models that predict shifting outcomes of species interactions along physical stress gradients (Menge & Sutherland 1987, Bertness & Callaway 1994, Bruno *et al.* 2003) have been widely supported by small-scale empirical studies conducted within a given habitat type. For instance, on rocky shores, *Ascophyllum* buffers the intertidal community from extreme desiccation stress at high intertidal environments, but interacts neutrally or negatively with species at lower intertidal elevations where desiccation stress is less extreme (Leonard 1999). Similarly, in high alpine systems, positive interactions between plants are more common at stressful high elevations, and competition prevails at more physically benign lower elevations (Callaway *et al.* 2002). Also, in semi-arid Mediterranean grasslands, the facilitative effects of grasses on shrubs increase with stress (Maestre *et al.* 2003). Together these studies lend support for shifting species interactions across environmental stress gradients on local scales or within a single habitat, whereas the present study provides evidence that these conceptual predictions can be generalized to landscape-scale gradients of environmental stress that span several distinct habitat types.

Our study is among the first to integrate facilitation theory with the intermediate disturbance hypothesis which assumes that species diversity is highest with intermediate physical stress (Connell 1979). For example in our system facilitation by a foundation species drives a highly diverse community at intermediate stresses. The need to integrate models of community organization with theories of diversity and productivity has been previously suggested (Hacker & Gaines 1997, Bruno *et al.* 2003), and will allow the development of a more complete picture of ecosystem functioning and organization. In this respect, our present findings imply a broader application of general community ecology theories: ecosystems and regions which have historically been considered as consisting of independent habitats can be unified by a common mechanistic framework.

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Chapter 7

Synthesis

Organisms changing their environment, also called ecosystem engineering, can be a potentially important process in structuring salt-marsh pioneer zones. In this thesis, I examined this hypothesis by studying the consequences of ecosystem engineering by *Spartina anglica*, on species interactions, ecosystem dynamics, and spatial structure. My aims were twofold: first, I tried to explain the patchy distribution of *Spartina anglica* in salt-marsh pioneer zones, and to provide insight in how ecosystem engineering affects the dynamics of this zone. Second, I generalized these findings for developing a more common knowledge of implications of ecosystem engineering on species, community, ecosystem and landscape scales.

On species scales, *Spartina* is known to develop an intricate feedback with its abiotic environment by reducing current velocities, resulting in increased sedimentation within *Spartina* tussocks (Ranwell 1964, Castellanos *et al.* 1994, Cahoon *et al.* 1996). This improves growth conditions for *Spartina*, constituting a positive feedback. On larger scales, this positive effect within vegetation, results in increased current velocities and gully erosion, which inhibits tussock expansion, just outside tussocks (Chapter 2 and Figure 7.1A). This feedback can influence the development of pioneer zones by retarding patch development, thus generating a heterogeneous landscape. Other research has shown that this feedback can generate the complex structure that is typical of fully-developed marshes, by fixating water run-off routes, which finally develop into channels that dissect high marshes (Temmerman *et al.* 2007).

In many intertidal landscapes, patches of *Spartina anglica* are found to alternate with open areas dominated by *Arenicola marina*. Strikingly, both species are hardly ever found together in the same patch, suggesting a negative interaction between them. Our research revealed that both species transform sediment properties in opposite ways, in the patches that they occupy: *Spartina* increases the accumulation of silt, while *Arenicola* maintains more sandy sediment by increasing silt transport out of the system. This way, both species negatively affect the persistence of the other species. These negative interactions by ecosystem engineering emerged as an important structuring mechanism (Chapter 3, Figure 7.1B), explaining the patchy occurrence of these species. Ecological theory emphasizes facilitation as an important structuring interaction in stressful environments (Bruno *et al.* 2003). However, the research in this thesis reveals that negative interactions by ecosystem engineering can play an equally important role under stressful conditions (Chapter 3). Moreover, a literature survey revealed that these negative effects of ecosystem engineering can be an important mechanism underlying successful biological invasions, if only one species is a strong ecosystem engineer. If ecosystem engineering effects are counteracted by an organism exhibiting an opposite feedback with environmental properties, they can possibly explain patchiness in ecosystems (Chapter 4).

Heterogeneity in the form of strongly contrasting patches is considered an indicator for the presence of thresholds and alternative stable states (Wilson and Agnew 1992, Petraitis and Latham 1999, Handa *et al.* 2002, Konar and Estes 2003, Rietkerk *et al.* 2004, van Nes and Scheffer 2005). In salt-marsh pioneer zones, ecosystem engi-

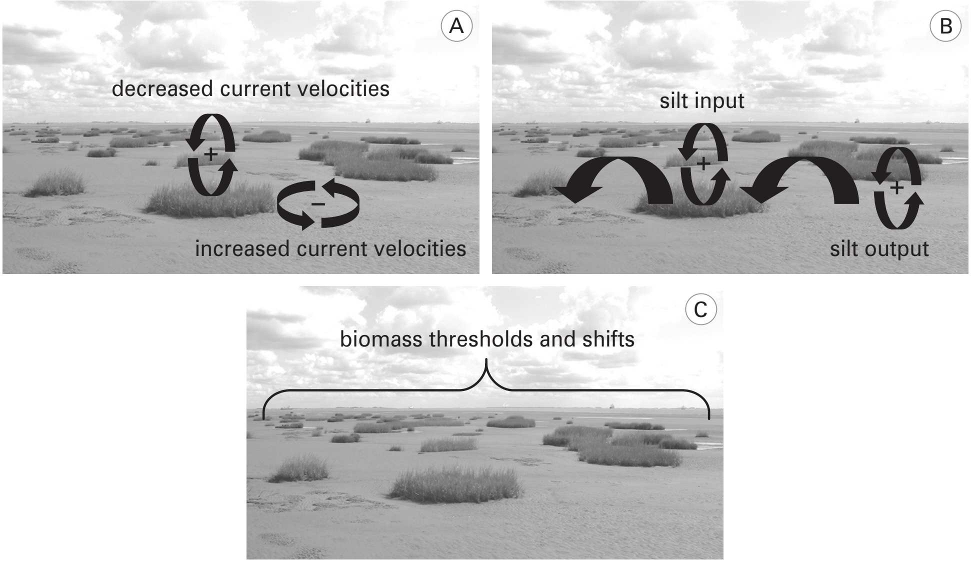

Figure 7.1. Schematic representation of expected processes, induced by ecosystem engineering, that play a role in structuring salt-marsh pioneer zones, such as A. Decrease and increase of current velocities, B. Mutual exclusion by changing sediment properties (stabilization and destabilization), C. Biomass thresholds and shifts

neering by *Spartina anglica*, resulting in a positive feedback, induces a threshold in vegetation response to environmental conditions. This threshold makes it possible for *Spartina* patches to persist, while existing conditions do not support the establishment of *Spartina* seedlings on bare sediment (Chapter 5), suggesting the presence of alternative stable states. Although our experiments confirmed the presence of alternative stable states on local, within-patch scales, a study of long-term vegetation development did not support the idea of alternative stable states, as patches were found to extent and contract simultaneously on longer time scales (Chapter 5). However, the presence of thresholds and non-linear response implies that salt marshes may still show sudden state changes, despite the absence of alternative stable states (Chapter 5 and Figure 7.1C).

Positive feedbacks

The research in this thesis links the frequently-used principles of ecosystem engineering and positive feedback switches. Although these concepts were both launched in the early 1990s, only a limited number of studies establishes a link between the species-oriented engineering concept and system-oriented positive feedback theory (Chapter 4, Wilson and Agnew 1992, Jones *et al.* 1994). Ecosystem engineering can induce positive feedbacks, if the engineered property promotes growth of the engineer. Although positive feedbacks were initially considered to be a mechanism that specifically concerned vegetation (Wilson and Agnew 1992, Rietkerk and van de Koppel 1997), feedback processes were found to be similarly strong in sessile and slow-moving animals that are ecosystem engineers (Chapter 3, van de Koppel *et al.* 2005a). Hence, the concept of positive feedbacks offers a good framework for the potential effects of ecosystem engineers on community and ecosystem dynamics.

The enormous effect that positive feedbacks have on the dynamics of the complete salt-marsh pioneer zone is striking. A null model of our system would predict gradual development of the salt-marsh pioneer zone, where vegetation density and species composition gradually change from the salt-marsh edge towards higher elevations. However, in natural salt-marsh pioneer zones transitions from vegetation to bare sediment are abrupt. If vegetation is present above a certain biomass, entrapment of silt is increased, resulting in a positive feedback that greatly affects plant growth and species interactions. In this thesis, we showed that early vegetation dynamics are strongly influenced by these positive feedbacks. They may propagate vegetation growth, but can also induce strong thresholds for vegetation settlement and disappearance, generating a patchy landscape (Chapter 5). Thresholds provide a potential explanation for the observation that *Spartina* patches do exist in areas where *Spartina* settlement is practically impossible (Chapter 5, Scheffer and Carpenter 2003). Moreover, they can retard vegetation development by gully formation (Chapter 2). The effects of engineering by *Spartina* may be expressed at multiple scales, affecting landscape-level processes and, thus, be of importance for adequate salt-marsh management and conservation. This I will discuss below.

Landscape-scale effects

In addition to positive feedbacks within patches, and negative feedbacks next to patches, feedbacks on a landscape scale may also occur. In salt-marsh pioneer vegetation, processes at local and landscape-scales seem to be coupled. Small-scale changes in tussock configuration will influence hydrodynamics on larger scales. The presence of more biomass is likely to result in a reduction of the amount of water that can enter the pioneer zone (Temmerman *et al.* 2005). This implies that with an increase in total path area, hydrodynamic forces on most tussock edges become smaller creating better opportunities for expansion of individual patches. However, on some tussocks hydrodynamics are expected to increase, as the presence of more vegetation will result in a concentration of flow through certain gullies. These gullies will form the template for future creeks in high marshes (Temmerman *et al.* 2007). This process constitutes a positive feedback between vegetation and decreasing hydrodynamics on landscape scales, which destabilizes patch borders. Overall, landscape-scale feedbacks might destabilize patchy ecosystems, causing patches to expand and merge, or disappear. In salt-marsh pioneer zones patchiness is explained by within patch-dynamics on short temporal scales, whereas landscape-scale forcing is approximately independent of the state of each patch (Chapters 2 and 5). However, it seems that on longer timescales, landscape-level processes that integrate the effects of many small-scale patches, determine the external conditions that any individual patch experiences. These landscape-level effects may, in the long run, influence the persistence of alternate attractors, and cause instability (Chapter 5).

Patchy systems have been shown to exhibit complete ecosystem switches as well. A nice example of this originates from studies on shallow lakes (van Nes and Scheffer 2005). Although most examples of regime shifts in shallow lakes show a sudden and abrupt shift from a clear to a turbid state (Scheffer *et al.* 1993), in Lake Veluwe clear patches developed while the lake was in a turbid state (van den Berg *et al.* 1998). These patches expanded gradually until rather abruptly the complete lake shifted into a clear state again (van Nes and Scheffer 2005). Notably, patches of clear and turbid water are able to coexist within the same lake (Scheffer *et al.* 1994). Development of patchiness with sharp transitions in such a well-mixed system is remarkable and, as patches are able to expand, patchiness only precedes a later shift of the complete ecosystem. Studies in the present thesis and the shallow lake example point at the possibility that local feedbacks inducing patchiness, could also set off cascading effects, resulting in complete ecosystem shifts.

Engineering effects differ with scale and background stresses

Intraspecific and interspecific engineering effects differ considerably depending on which scale they are examined (Hastings *et al.* 2007). In chapter 2 feedbacks between *Spartina* and current velocities changed from positive to negative to neutral with increasing scale. Inside vegetation feedbacks were positive implying that current velocities were reduced and sedimentation increased. Just next to vegetation increased current velocities, resulting in erosion, constituted a negative feedback. This study demonstrates that intraspecific effects of the engineer on the environment vary with scale.

Interspecific effects of ecosystem engineering, for example effects of engineering on biodiversity, also are scale dependent. In many cases ecosystem engineering results in patchiness on landscape scales (Hastings *et al.* 2007). On the scale of these patches effects of engineering on biodiversity can be positive (Wright *et al.* 2006) or negative (Chapter 3, Crooks 2002, Levine *et al.* 2003). However, it is predicted that on ecosystem or landscape scales ecosystem engineering, will result in higher species diversity, due to an increase in habitat heterogeneity (Jones *et al.* 1997, Wright *et al.* 2002, Wright *et al.* 2006). Hence, investigating effects of ecosystem engineers on their environment and on biodiversity can yield rather distinct results depending on the scale on which these effects are examined.

Both intraspecific and interspecific consequences of engineering are likely to depend on the environmental context as well (Hastings *et al.* 2007). In chapter 2, flume studies showed that effects of *Spartina* on sedimentation and erosion became more pronounced with high current velocities and were almost absent with low water currents. This implicates that intraspecific engineering effects of a species on the environment subside with decreasing stress, confirming the idea that engineering is more important with high stress conditions (Jones *et al.* 1997). Interestingly, this suggests that engineering effects of a species on the environment may not exist in the absence of stress.

Similarly, engineering effects on biodiversity are found to change under different stresses. We examined the main structuring processes, facilitation or competition, in communities facilitated by *Spartina* under different stress conditions (Chapter 6). Under intermediate to high stress conditions facilitation by the ecosystem engineer *Spartina alterniflora* supported a diverse community of plant species. However, under low stress conditions most plants of this community were excluded by a competitive dominant grass species. As a result, *Spartina* facilitated a monoculture under low stress conditions. Understanding how ecosystem engineering activities and effects of ecosystem engineering differ with changing environmental contexts will enhance our understanding of the influence of ecosystem engineers on species distribution and ecosystem development (Crain and Bertness 2006, Wright and Jones 2006, Hastings *et al.* 2007). Summarizing, these studies illustrate the need for proper and specific setting of spatial scales and environmental background conditions when examining ecosystem engineering consequences.

Implications for salt-marsh conservation and management

Coastal habitats, such as salt marshes, are threatened by sea-level rise and anthropogenic development of coastlines. Many of these habitats are subject to physically stressful conditions, mostly related to flooding by seawater. For organisms living under such stressful conditions, modifying their abiotic surroundings can be a useful strategy, and thus ecosystem engineering is expected to be an important shaping force in coastal habitats. Here, I discuss implications for management of salt marshes, resulting from effects of ecosystem engineering on the system.

The positive feedback between *Spartina* and sedimentation forms the basis for salt-marsh formation. Under ideal conditions, *Spartina* can rapidly invade a bare intertidal flat and form a homogeneous vegetation cover. Capturing of fine-grained sediment by *Spartina* stands, raises soil elevation and makes the habitat suitable for invasion of other salt-marsh plants. However, many salt marshes in the Netherlands are eroding and *Spartina*, if present at all, is found in scattered patches on the intertidal flat. Several processes that could limit expansion of present *Spartina* tussocks and prevent recruitment with new seedlings were demonstrated in this thesis.

Recruitment of *Spartina* by seedlings does not happen easily in natural systems. Processes of recruitment were demonstrated to be very episodic, implying that in some years massive recruitment events take place, while in other years seedlings are almost absent (Chapter 5). From the established seedlings few are able to survive. Especially in areas that are occupied by the lugworm *Arenicola marina*, seedling survival is low. Lugworms tend to rework the soil intensively, thereby burying and destroying *Spartina* seedlings (Chapter 3). Other studies show *Nereis*, another benthic invertebrate, to inhibit settlement and survival of pioneer vegetation as well (Hughes and Paramor 2004, Paramor and Hughes 2004). However, it is doubted whether these small-scale processes can influence complete salt-marshes (Wolters *et al.* 2005). From our transplanting experiments, where we transplanted different sizes of *Spartina* (seedlings, 1-2 stems and 20 stems), it became clear that in many areas with *Spartina* tussocks settlement by seedlings on bare sediment was unsuccessful (Chapter 5). Transplanted higher biomasses of *Spartina*, small plugs of about 20 stems, almost always survived (Chapter 5). These results underline that the presence of *Spartina* tussocks in salt-marsh pioneer zones does not indicate the potential of *Spartina* to settle by seedlings. This implies that thresholds for *Spartina* disappearance and settlement are present.

The presence of thresholds for vegetation settlement, points at non-linear vegetation dynamics. This implies that vegetation will not respond in a gradual or linear way, to gradual and linear changes in environmental parameters. For example, field observations confirmed the presence of *Spartina* tussocks on an intertidal flat in the Westerschelde estuary in the Netherlands that experienced little growth and erosion for over 15 years. Suddenly these tussocks disappeared completely in one year (pers. obs.). These observations confirm the potential of salt marshes to exhibit sudden shifts between states in response to small changes in external conditions. However, previous studies have shown that processes of salt-marsh formation and erosion may be cyclic (van de Koppel *et al.* 2005b).

Next to problems with settlement, *Spartina* also experiences problems with expansion. It was demonstrated that reduction of current velocities inside tussocks could result in increased current velocities at the borders of tussocks. Increased current velocities lead to enhanced erosion and gully formation at tussock edges, retarding vegetation development (Chapter 2). These effects are extremely important with high current velocities and are not detected if current velocities are low (Chapter 2). Long-term observations of tussock expansion and erosion in salt-marsh pioneer zones revealed that both processes can occur simultaneously (Chapter 5). This complicates prediction of future directions of salt-marsh development from present erosion and expansion data.

Opposed to applied research that is often used in conservation to answer specific questions, we used a rather fundamental approach to explain processes in salt-marsh pioneer zones. Although this approach does not yield direct answers to more applied questions, a more general understanding of processes that structure salt-marsh pioneer zones is gained. In our view, this makes fundamental research a useful tool for understanding ecosystem processes, which will facilitate successful management and conservation of natural systems. For successful restoration and conservation of salt-marsh systems it should be kept in mind that in mind that vegetation development often is a slow process. It might be a profitable strategy to create benign physical conditions for vegetation settlement and growth, on a temporary basis, for example by using groins. Once vegetation is actually present with high biomass it is expected to be rather resilient to changes. Still, our results suggest that salt-marsh pioneer zones have the capacity to suddenly shift from a vegetated to an unvegetated state in response to environmental changes. Although salt-marsh erosion and re-growth might be natural cyclic processes, one can wonder whether sudden disappearance of salt marshes is natural and desirable in systems that are strongly influenced be humans.

Conclusions and recommendations for future research

This thesis highlights several consequences of ecosystem engineering in intertidal habitats. Ecosystem engineering effects were examined on different scales, to determine effects on species interactions, ecosystem dynamics, and spatial structure. Most of this research was driven by the aim to understand the patchy nature of salt-marsh pioneer zones. Therefore, processes that may explain this patchiness were examined, on species, community and landscape scales. Summarizing, it was concluded that small-scale ecosystem engineering could cause positive feedbacks, negative species interactions via the environment, non-linear ecosystem behavior, landscape complexity, and development of distinct habitats along stress gradients.

Ecosystem engineering can induce positive feedbacks on local, within-patch scales, with resultant negative feedbacks on larger, between-patch scales. These feedbacks can give rise to more complex structures on ecosystem or landscape scales. Furthermore, ecosystem engineering can be a mechanism for negative species interactions, resulting in exclusion and patchy species distributions in ecosystems. Also, habitat modification can give rise to thresholds in ecosystems, resulting in unpredictable and irreversible ecosystem changes in response to environmental change. Finally, ecosystem engineering can generate the development of strong contrasting habitats along gradients of stress. For all these effects it should be kept in mind though that they vary considerably depending on environmental background conditions and spatial scale.

Future research should extend on the conceptual framework that we developed for negative species interactions via the environment, including both empirical and modeling studies. There is a need for development of multi-species models that distinguish between biotic interactions and engineering effects (Hastings *et al.* 2007). Furthermore, it will be interesting to examine whether engineering effects of a species on the environment, can only be detected under high stress conditions and are absent when conditions are benign. Then, it can be valuable to investigate whether negative interactions by ecosystem engineering are common to stressful environments and whether this should be incorporated in general models of community organization. These models assume that resources are not limiting with high stresses. However, it is not definite that a causal relationship between stress and resources exists.

Another line of research that is worth pursuing is investigating the implications of patchiness in ecosystems and, specifically, in transition zones between different systems. Possibly effects on transition zones can cascade through a system and affect both ecosystems that border the transition zone. A more thorough understanding of dynamics in transition zones could benefit successful management and conservation of complete ecosystems. Hypotheses should aim to examine if patchiness is a characteristic of transition zones and whether these zones are in general maintained by positive feedbacks. This will give insight into the vulnerability of transition zones to changes and help to estimate response of transition zones to climate change. This line of research will also allow us to predict response of salt marshes, and specifically salt-marsh pioneer zones, to future sea-level rise.

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Summary

Thresholds and shifts: consequences of habitat modification in salt-marsh pioneer zones

The topic of ecosystem engineering received tremendous attention since its introduction a decade ago. However, generalizations on its consequences and effects are still scarce. In this thesis, I examine implications of habitat modification on ecosystem dynamics, species interactions, and spatial structure, with a special emphasis on effects on different scales. Research was conducted in intertidal habitats, mainly in the transition zone between salt marshes and intertidal flats, also called the salt-marsh pioneer zone. This zone is characterized by patchily distributed tussocks of the grass *Spartina anglica* and home to several strong ecosystem engineers. I found that interactions between organisms and the environment are an important shaping force in salt-marsh pioneer zones. Such small-scale engineering activities influence ecosystem structure, and determine ecosystem dynamics, on species, community, and landscape scales.

Field surveying revealed that in areas with strong hydrodynamic forcing, more voluminous *Spartina* mounds are surrounded by deeper gullies than *Spartina* mounds with smaller volumes (**Chapter 2**). Transplantation of small *Spartina* clumps showed that, compared to a control, *Spartina* growth inside tussocks was higher, but next to the tussocks, inside the gully, *Spartina* growth was significantly lower. These scale-dependent feedback effects might restrict tussock expansion and influence large-scale complexity of salt-marsh systems.

Another process causing patchiness in salt-marsh pioneer zones is the interaction between *Spartina* and the lugworm *Arenicola*. Both species occur in alternating patches in the pioneer zone (**Chapter 3**). In these patches they modify soil conditions, thereby inhibiting invasion of the other species. These negative species interactions by ecosystem engineering may be a mechanism underlying invasions once engineering effects of a single species prevail (**Chapter 4**). However, if two engineers affect the environment in opposite ways, a patchy landscape will develop. Thus, habitat modification can be a mechanism for negative species interactions, which can be seen as a negative equivalent of facilitation (changing the environment in a positive way for other species) (**Chapters 3 and 4**). Similar to facilitation one expects to find this process mainly in stressful systems and this bears important consequences for community assembly models. Further, the strong patchiness that can be induced by habitat modification underlines the need for setting the proper scale when investigating ecosystem engineering effects.

Patches in salt-marsh pioneer zones are generally dense and show sharp transitions with surrounding sediment. To test whether *Spartina* could also establish with low biomass or if a threshold for vegetation establishment was present in the system, different size classes of *Spartina* clumps were transplanted into bare patches of several salt-marsh pioneer zones (**Chapter 5**). Only large *Spartina* clumps (more than 20 stems) survived, pointing at the presence of a threshold for vegetation establishment. A threshold effect results in non-linear vegetation dynamics, which complicates prediction of vegetation response in relation to changes in environmental parameters. This leads us to hypothesize that sudden and unexpected shifts can take place between the vegetated and bare state in salt-marsh pioneer zones. If this is a com-

mon characteristic of transition zones between ecosystems in general, the vulnerability of transition zones to environmental change in response to global change will be an important direction for future research.

Finally, ecosystem engineering effects were put into a landscape perspective by studying the effect of hydrodynamic stress on species interactions in a community facilitated by *Spartina* (**Chapter 6**). *Spartina* supported a highly diverse community with intermediate stress conditions, and a monoculture of the competitive dominant grass species with very benign conditions. This demonstrates that ecosystem engineering effects on biodiversity differ with differing physical stresses, illustrating the need to make specific assumptions on background conditions when examining effects of ecosystem engineering.

Concluding, ecosystem engineering effects in salt-marsh pioneer zones vary with changing scale and with differing background stresses. This thesis illustrates that small-scale habitat modification can result in scale-dependent feedbacks, negative species interactions via the environment, non-linear ecosystem behavior, emergent patterns or complexity on landscape scales, and development of distinct habitats along stress gradients.

Samenvatting

Hindernissen en sprongen: gevolgen van habitat modificatie in de pionierzone van schorren en kwelders

Interacties tussen organismen en hun omgeving zijn een centraal onderwerp in ecologisch onderzoek. Organismen die hun omgeving ingrijpend veranderen, worden ook wel *ecosystem engineers* genoemd. Deze ecosystem engineers zijn talrijk en worden aangetroffen in de meest uiteenlopende systemen. De gevolgen van de veranderingen die deze organismen veroorzaken in hun leefomgeving zijn echter vooralsnog weinig onderzocht. In dit proefschrift beschrijf ik mijn onderzoek naar de effecten van ecosystem engineering op soortinteracties en op dynamiek en ruimtelijke structuur van ecosystemen. Deze gevolgen zijn onderzocht op verschillende schalen: soorts-, gemeenschaps-, ecosysteem-, en landschapsschaal.

Het onderzoek is uitgevoerd in intergetijdegebieden. Dit zijn gebieden die tussen zee en land liggen en die tweemaal daags, tijdens vloed, worden overstroomd door de zee. Voorbeelden van intergetijdegebieden zijn stranden en kale slikplaten, maar intergetijdegebieden kunnen ook begroeid zijn met planten en grassen en worden dan schorren of kwelders genoemd. De zone waar een kaal intergetijdegebied overgaat in begroeid schor heet pionierzone. Deze zone wordt in Nederland vaak gekenmerkt door de aanwezigheid van *Spartina anglica*, ofwel Engels slijkgras, dat in gefragmenteerde pollen op het kale slik wordt aangetroffen. Engels slijkgras is bekend als sterke ecosystem engineer, want de plant remt waterstroming zodat kleine sedimentdeeltjes uit de waterkolom neerdalen in de pol. Deze ingevangen sedimentdeeltjes hogen de bodem op, waardoor Engels slijkgras minder lang onder water staat met hoogwater. Dit heeft een positief effect op de overleving en groei van *Spartina* en initieert de aangroei van schorren. Met behulp van het ecosystem engineering concept en de implicaties hiervan, verklaar ik in dit proefschrift waardoor gefragmenteerde *Spartina*-pollen in de praktijk niet altijd snel uitgroeien tot een volwassen schor.

In gebieden met hoge stroomsnelheden zijn naast de ronde *Spartina*-pollen geultjes te zien. Hierom wordt verondersteld dat het remmen van de stroming in de pol waarschijnlijk leidt tot verhoogde stroomsnelheden naast de pol. Veldwaarnemingen tonen aan dat *Spartina*-pollen met meer volume omringd zijn door diepere geulen (**Hoofdstuk 2**). Het aanplanten van kleine stukjes *Spartina*-pol, zowel binnen bestaande pollen als in de geulen er omheen, bevestigt dat, vergeleken met een controlepol die is aangeplant buiten de invloedssfeer van andere pollen, aangeplante pollen beter groeien in bestaande vegetatie en slechter groeien in de geul. In de pol is er een positieve feedback tussen remming van stroming en vegetatie groei. Deze positieve feedback in de pol heeft een negatieve feedback naast de pol tot gevolg, grotere stroomsnelheden naast de pol en de daardoor ontstane geulen, belemmeren gelijkmatige polgroei en dit kan op ecosysteemschaal leiden tot de ontwikkeling van een complex landschap, zoals een volwassen schor met daarin een karakteristiek patroon van kreken.

Een andere mogelijke oorzaak van de gefragmenteerde verdeling van pollen op het slik is de interactie tussen *Spartina* en de wadpier, *Arenicola marina* (**Hoofdstuk 3**). Beide soorten worden in de pionierzone van schorren aangetroffen, maar op een schaal van een vierkante meter komen ze zelden samen voor. *Spartina* maakt over het algemeen lokaal de bodem slibbiger door het invangen van kleine sedimentdeeltjes, terwijl Arenicola juist slib uit het systeem verwijdert. Deze tegengestelde transformaties van de omgeving hebben een positief effect op de soort zelf en kunnen daarnaast werken als mechanisme dat invasie van de ene soort onmogelijk maakt op plekken waar de andere soort al aanwezig is. Dergelijke negatieve soortinteracties via een omgevingsfactor kunnen eveneens een onderliggend mechanisme zijn aan biologische invasies, indien de invasieve soort de binnengedrongen omgeving sterk verandert in zijn eigen voordeel (**Hoofdstuk 4**). Zodra echter een tweede soort aanwezig is die een tegenovergestelde feedback met een omgevingsfactor heeft, zou het juist kunnen leiden tot een gefragmenteerd landschap waar stukken met soort A en soort B elkaar afwisselen. Ecosystem engineering kan dus functioneren als een mechanisme voor negatieve soortinteracties en dit kan ook wel worden gezien als het negatieve equivalent van facilitatie (veranderingen in de omgeving door soort A hebben een positief effect op soort B). Net als in het geval van facilitatie is te verwachten dat ook negatieve interacties via de omgeving voornamelijk onder stressvolle omstandigheden worden aangetroffen, waar het verbeteren van de leefomgeving de meest effectieve overlevingsstrategie is. Deze bevindingen suggereren dat een specificatie van de schaal essentieel is bij het onderzoeken van de effecten van ecosystem engineering. Zo zijn de effecten op biodiversiteit sterk afhankelijk van de ruimtelijke schaal waarop deze effecten worden bestudeerd. Op de (kleinere) schaal van een stuk dat wordt gedomineerd door één soort zijn de effecten van eco-engineering op biodiversiteit negatief. Op de (grotere) schaal van het ecosysteem, waarin fragmenten van meerdere soorten voorkomen, zorgt ecosystem engineering echter voor een grotere heterogeniteit, en dus ook voor een grotere biodiversiteit.

Spartina-pollen in pionierzones vertonen scherpe overgangen naar het omliggende sediment en zijn vrijwel altijd aanwezig met hoge biomassa. Het ontbreken van een graduele overgang van geen vegetatie naar hoge biomassa vegetatie kan erop duiden dat vegetatie enkel met hoge biomassa kan bestaan en dat lage biomassa's van vegetatie niet kunnen overleven. In dit geval zou er een drempelwaarde van biomassa zijn voor vestiging van vegetatie in het systeem. Om dit te testen zijn drie verschillende stadia van *Spartina*-vegetatie aangeplant in gebieden waar al *Spartina*-pollen aanwezig zijn (H**oofdstuk 5**). Deze stadia betreffen zaailingen, scheuten van 1-2 stengels met een wortelstok, en kleine pollen met meer dan 20 stengels met de daaraan verbonden kluit van wortels. Slechts het stadium van meer dan 20 stengels overleefde. Dit duidt op de aanwezigheid van een biomassadrempel voor vestiging van vegetatie. *Spartina* pollen met hoge biomassa kunnen dus blijven bestaan in gebieden waar door stressvolle omstandigheden geen vestiging van jonge *Spartina* vegetatie (met lage biomassa) mogelijk is. Aangezien vestiging onder andere condities plaats vindt dan het verdwijnen van de vegetatie is de respons van vegetatie op veranderingen in omgevingsparameters niet lineair. Gebrek aan lineairiteit lijdt mogelijk tot onverwachte sprongen in vegetatiedynamiek; een kleine verandering in milieufactoren zou kunnen leiden tot het plotseling verdwijnen van alle aanwezige vegetatie. Mogelijkerwijs is dit een algemene eigenschap van overgangszones tussen ecosystemen. De gevoeligheid van deze zones voor veranderingen is een belangrijke richting voor toekomstig onderzoek, onder andere met het oog op klimaatsverandering.

Tot slot zijn de effecten van ecosystem engineering op een landschapsschaal bekeken (**Hoofdstuk 6**). In een gemeenschap die gedomineerd wordt door *Spartina* is een studie gedaan naar het belang van competitie en facilitatie langs een gradiënt van wisselende hydrodynamische stress. Interacties tussen soorten binnen deze gemeenschap worden bepaald door de sterkte van de hydrodynamische stress en dit resulteert uiteindelijk in de ontwikkeling van verschillende habitats. Onder zeer lage stresscondities faciliteert *Spartina* een gemeenschap die voornamelijk uit een competitief dominant gras bestaat. Dit gras kan echter niet domineren onder stressvollere condities, waarbij een veel soortenrijkere gemeenschap ontstaat, die initieel mogelijk wordt gemaakt door *Spartina*. Hiermee wordt aangetoond dat effecten van ecosystem engineering kunnen variëren bij verschillende achtergrondcondities.

Concluderend, effecten van ecosystem engineering variëren met schaal en met achtergrondcondities. Dit proefschrift laat zien dat veranderingen in de omgeving veroorzaakt door organismen kunnen resulteren in schaalafhankelijke terugkoppelingen, ontwikkeling van complexe systemen, negatieve soortinteracties via de omgeving, niet-lineaire respons resulterend in plotselinge verschuivingen in de toestand van het ecosysteem, en ontwikkeling van verschillende habitats onder verschillende stresscondities.

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