

THRESHOLDS AND SHIFTS: CONSEQUENCES OF HABITAT MODIFICATION IN SALT-MARSH PIONEER ZONES

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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. 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. 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. 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). 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. 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 common 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*. *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.