The role of dispersal constraints in the assembly of salt-marsh communities

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Summary

The presence and population size of different species in plant communities can be influenced by a number of different factors. The environmental conditions of the site where the community is located may predispose whether species are able to establish or not. The interactions between species (*e.g.* competition or facilitation) at a site may also determine whether species persist, spread or disappear from a community. For the past few decades, ecologists have focussed on these types of local-scale explanations for community patterns. However, species may also have to travel to a site in order to have the possibility of joining a community. Using a sequence of communities increasing in age (*i.e.* chronosequence) on a coastal Dutch island, Schiermonnikoog, as a model system, I explored how the mobility of plant species (*i.e.* dispersal constraints) can influence the composition of salt-marsh communities.

Soil seed bank generally reflects plant community

Studying the relationship between patterns in the vegetation (*i.e.* plant community) and soil seed bank (*i.e.* reserve of seeds stored in the soil) along a community sequence can predict which types of factors influence community composition (Chapter two). Three possible relationships are proposed: the similarity between the vegetation and soil seed bank is a) relatively high and does not consistently increase or decrease with age, b) decreases as communities age and c) is relatively low and does not consistently increase or decrease with age.

The Sørenson similarity index ranged between 0.47 and 0.73 with no consistent patterns along the age gradient. Multivariate analysis indicated that the most important factor in explaining species variance in the vegetation (75.1 %) and soil seed bank (61.4 %) in these communities was the age of the community. Also, the positions of species along the age gradient were similar for the vegetation and soil seed bank, indicating similar trends in abundance of species both above-and-below ground. The relationship between the vegetation and soil seed bank for the salt-marsh communities on Schiermonnikoog most closely resembled the first proposed relationship, thus indicating that seeds of many species remain close to their parent plants despite regular tidal inundations.

Small herbivores (hares and geese) less important than tidal water in dispersing seeds

Having established that limited mobility of seeds may influence communities, the effectiveness of different agents that transport seeds was compared in Chapter three. I studied how seeds move through the digestive systems of hares and geese

(endozoochory) on Schiermonnikoog by examining the contents of their droppings a) collected along the community sequence and b) after experimentally feeding them a set amount of seeds. I also trapped seeds dispersed by tidal water using Astroturf® mats.

Hares deposited more seeds of mid-successional, perennial, high-marsh species than geese, which deposited more seeds of early-successional, annual, low-marsh species. Seed survival and germination of salt-marsh species were higher after ingestion and passage through the digestive system of hares (10 % to 40 %) compared to geese (2 % to 13%). However, small herbivores dispersed two orders of magnitude fewer seeds than those dispersed by tidal water. Therefore, they are not likely to be important factors influencing community composition at this coastal island in the Netherlands.

Storms strongly affect seed movement

Results indicated that hydrochory (*i.e.* seed dispersal by water) is more effective than endozoochory (*i.e.* internal seed dispersal by animals) on Schiermonnikoog. In Chapter four, I further explored the factors influencing the movement of seeds by tidal water including timing of dispersal. Species compositions of vegetation, seed rain, seed production and driftlines along a sequence of communities were compared on Schiermonnikoog.

Storm surges had a positive significant effect on seed-rain patterns as the highest density and diversity of captured seeds were found after a stormy period. Seed rain of youngest communities was more influenced by storms than that of older communities. Results suggested mostly local dispersal of seeds during normal tides (as predicted by Chapter two). However, there was some evidence of long-distance dispersal occurring during storm surges in younger communities that are regularly inundated with tidal water. The role of seed retention in constraining community development, rather than dispersal *per se,* was further examined.

Retention of dry vs. wet seeds

The studies in hydrochory suggested that the important ecological issue concerning seed transport during storm surges may not be whether seeds move but whether they stay in suitable sites. In Chapter five, factors influencing retention of seeds were explored. I examined interactions between seed morphology (floating capacity), moisture conditions, vegetation structure and hydrodynamic variables and the relative role of each factor in determining seed retention based on factorial experiments. Experiments were conducted in a tidal salt marsh (Schiermonnikoog)

and in a flume facility where hydrodynamic variables could be controlled.

Moisture condition of seeds greatly influenced which factors were most important in determining seed retention. Floating capacity was the most significant factor when seeds were dry. In contrast, hydrodynamic effects dominated retention processes when seeds were waterlogged. Results suggest that buoyancy traits appear to determine whether seeds move in the drier summer and autumn months, after initial detachment from parent plants but the intensity of wave action will determine whether waterlogged seeds stay in a microsite during the wetter months of late autumn to early spring.

Conclusions

In short, studies conducted indicate that the distribution of species (*i.e.* presence or absence in communities) is most strongly constrained by establishment conditions at a site, whereas the abundance of species is influenced by processes controlling seed deposition and retention rather than those regulating dispersal per se in coastal, temperate, salt-marsh communities. The high transport potential of storm surges likely enhances distribution of species but restricts their abundance, as many seeds are washed away.