Effects of vegetation patterns and grazers on tidal marshes

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4 Positive effects of small-scale topographic heterogeneity on plant diversity and grazers throughout marsh development

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ABSTRACT

Heterogeneity in ecosystems can strongly enhance plant diversity as it can increase the number of niches allowing more species to co-exist on a smaller scale. However, it remains relatively unknown how heterogeneity affects plant diversity as well as grazers and how this changes throughout long-term ecosystem development. At coastal foreshores, small-scale (few m^2) topographic heterogeneity in marsh morphology is observed consisting of higher elevated hummocks alternating with lower elevated depressions. In this study we *i*) estimated the effects of this topographic heterogeneity on plant diversity and grazers, such as hare and geese, and *ii*) how persistent these effects are during ecosystem development by comparing marshes of different ages along a 120-year chronosequence. In the pioneer stage, we found higher elevated hummocks on the intertidal flat. These patterns of hummocks and depressions enhanced plant diversity (number of species, equitability and Shannon diversity index) throughout ecosystem development, ranging from pioneer stage up to 120 year old marsh. Once hummocks were present in the marsh morphology they provided an additional niche facilitating the establishment of plant communities of later successional stages, thus enhancing not only plant diversity but also the suitability of early successional stages of marshes for small grazers.

INTRODUCTION

Ecological theory predicts that environmental heterogeneity within an ecosystem can boost local plant diversity (Ricklefs 1977, Costanza et al. 2011). When resources are distributed unevenly throughout an ecosystem, inter-specific competition is reduced, allowing more species to co-occur on a smaller scale (Ricklefs 1977, Snyder and Chesson 2004). In turn, plant diversity can have a major impact on the functioning of the ecosystem, affecting e.g. primary production and ecosystem resilience (e.g. Chapin et al. 2000; Wacker et al. 2008; Cardinale 2012). Even small-scale environmental heterogeneity can increase the resilience of ecosystems, enabling them to better cope with changing environmental conditions and extreme events such as long-term drought (Hopkins and Del Prado 2007, Godfree et al. 2011). When environmental conditions change rapidly, a wide range of species responding differently can stabilize important ecosystem processes (Hooper et al. 2005). This increased resilience will be of growing importance as rapid climate-driven changes pose a major threat to many ecosystems worldwide, and in particular those in areas where global change impacts may be expected to be the largest (Thomas et al. 2004). There is thus need for understanding the nature of heterogeneity, and how this affects diversity, especially in vulnerable ecosystems.

An important example of environmental heterogeneity is heterogeneity in soil morphology. This topographic heterogeneity can be the result of geological processes e.g. rock outcrops (Wohlgemuth 1998) or it can be biotically induced, e.g. mounds created by badgers in steppe-ecosystems or burrowing by prairie dogs in temperate grasslands (Davidson and Lightfoot 2006, Baker et al. 2013). The heterogeneity may also result from bio-geomorphic interactions between organisms and physical processes (Langlois et al. 2003, Mclaren and Jefferies 2004, Balke et al. 2012). For example, in dune ecosystems the presence of local vegetation patches catching wind-transported sand, results in the formation of large dunes alternating with dune slacks (Baas and Nield 2007). In most of these biotic and bio-geomorphic examples one or a few keystone species induce the topographic heterogeneity. Studies investigating the effect of topographic heterogeneity on diversity have mostly been short-term and limited to one trophic level (e.g. Davidson and Lightfoot 2006, Costanza et al. 2011, Baker et al. 2013) but see for example Van der Heide et al. (2012). However, especially in bio-geomorphic ecosystems, heterogeneity may evolve over time due to the interactions between organisms and physical processes. Thus, there is a strong need for studies focused on the effects of spatial heterogeneity on diversity in developing ecosystems where trophic interactions are expanding (Hooper et al. 2005, Peh and Lewis 2012 and references therein).

In this study we focus on salt marshes, which are bio-geomorphic ecosystems where the interplay of tidally introduced sediment and vegetation growth for a large part determine the long-term development of the marsh platform (Temmerman et al. 2007, Fagherazzi et al. 2012). Many European marshes contain areas with strong topographic heterogeneity, consisting of higher elevated "hummocks" surrounded by lower elevated "depressions" (Gray and Bunce 1972, Balke et al. 2012). This heterogeneity in the marsh platform can be found in marshes of different ages. The diameter of hummocks can range between 1 m and 10 m and elevational differences between hummocks and adjacent depressions can be up to 20 cm. Elevation of the marsh platform determines for a large part the distribution of plant species on the marsh (Olff et al. 1997, Davy et al. 2011) and presence of topographic heterogeneity could strongly boost plant diversity. We investigated how presence of topographic heterogeneity affects i) local plant diversity (number of species, equitability and Shannon diversity index), ii) grazers (abundance and impact), and iii) how both parameters change over time from pioneer stage to mature marshes of 120 years old.

METHODS

Study sites

To cover the entire age span, ranging from pioneer to mature marshes, we used two study sites (Fig. 4.1), a back-barrier marsh located on Schiermonnikoog (53 30'N, 6 10'E, The Netherlands) and the Cefni marsh (53°10'N, 4°23'W, United Kingdom). Schiermonnikoog has a unique natural chronosequence (Van de Koppel et al. 1996, Olff et al. 1997). Due to gradual expansion towards the east, an age and productivity gradient exists ranging from 15 to 120 yrs-old marsh (Fig. 4.1). The pioneer stage is currently lacking on Schiermonnikoog so we included the Cefni marsh which has a large pioneer zone located in front of the marsh. Both marshes are mineral based marshes where fine-grained sediment (silt) is accumulating on top of an underlying coarse-grained (sandy) substrate. Increasing fine-grained sediment layer thickness results in an increasing local productivity and this process determines for a large part the change in vegetation composition during succession (Olff et al. 1997). The marsh of Schiermonnikoog is located on a barrier island and the Cefni marsh is located in an Estuary. Schiermonnikoog is a mesotidal marsh with tidal amplitude of 2.3 m, while the Cefni marsh is a macrotidal marsh with tidal amplitude of 4.7 m. Both marshes show similar heterogeneity in soil morphology (Fig. 4.2). No livestock was present on the marsh areas we used for this study.

SCHIERMONNIKOOG

Along the chronosequence, marsh age was estimated by Olff et al. (1997) using a time-series of aerial photographs. Marsh age was based on the first establishment of vegetation. We selected five marsh ages including: 15, 30, 45, 55 and 120 years old marshes.

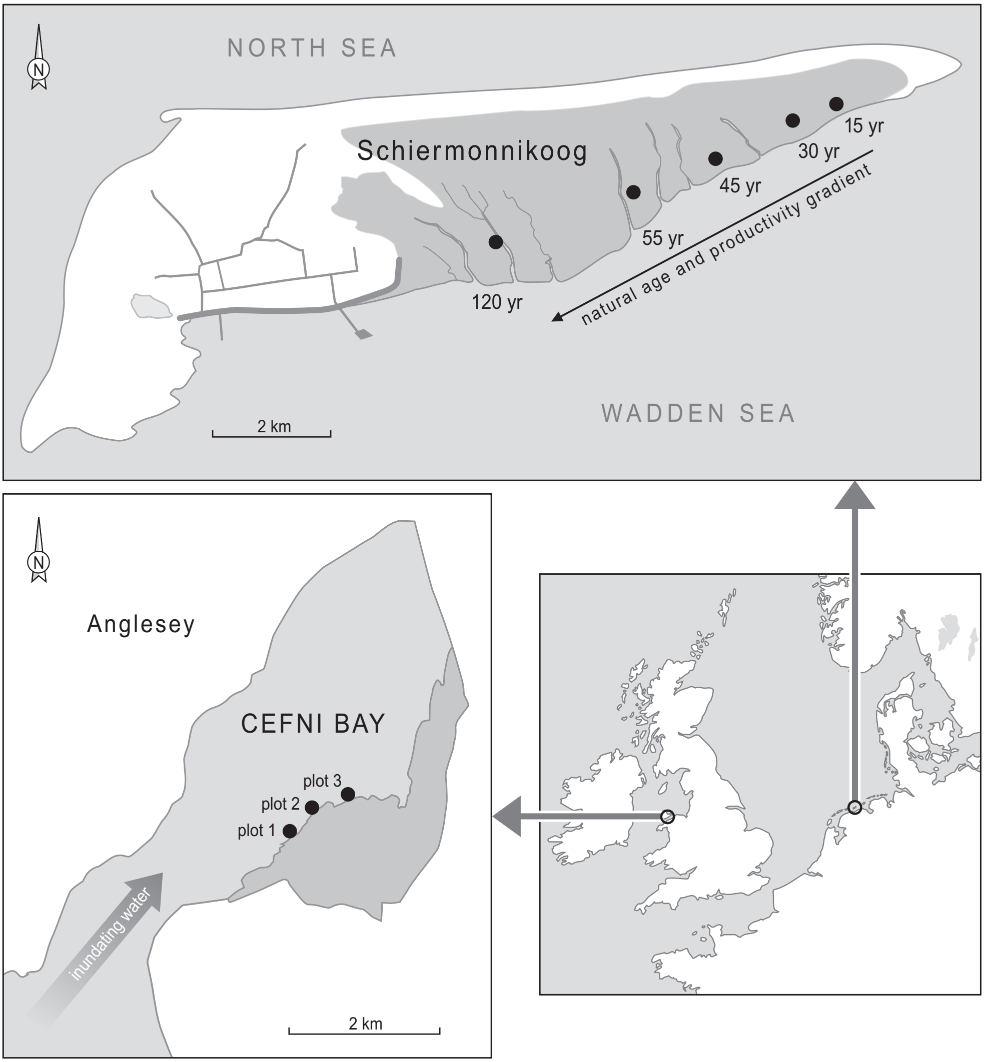

Figure 4.1. A map showing the back-barrier marsh of Schiermonnikoog (The Netherlands) and the Cefni marsh in Northern Wales (United Kingdom). The marsh area is shown in dark grey and water is shown in light grey. All plots included in this study are indicated with black dots. On Schiermonnikoog approximate age (in years) since the start of salt marsh development is given for each site.

Within each of the marsh ages, we compared zones with topographic heterogeneity present to zones without any topographic heterogeneity present, hereafter referred to as the homogeneous marsh. All were located on approximately the same marsh elevation. Several different migratory birds such as Barnacle goose, *Branta leucopsis*, and Brent goose, *Branta bernicla*, are present on the marsh during winter. Additionally, the European brown hare, *Lepus europaeus*, is present on the marsh throughout the year.

CEFNI MARSH

The Cefni marsh was included to study the formation of topographic heterogeneity in the pioneer stage. Due to continuous marsh expansion, a large pioneer zone is present in front of the marsh (Fig. 4.1). Salt-marsh development only started since the 1960s (Packham and Liddle 1970). In the pioneer zone we found elevated pioneer hummocks of varying sizes and heights, which had similar morphological characteristics as the topographic heterogeneity on Schiermonnikoog (Fig. 4.2). The main pioneer species present on the pioneer hummocks was *Puccinellia maritima*, which is an important pioneer plant species recorded on the Cefni marsh (Packham and Liddle 1970) and on Schiermonnikoog (Olff et al. 1997).

For classification purposes we refer to the sites as pioneer zone consisting of pioneer hummocks alternating with bare intertidal flat, as long as no fine-grained sediment is accumulated on top of the coarse-grained substrate of the intertidal flat. Once fine-grained sediment started accumulating on the coarse-grained substrate, and morphology of the marsh platform is conserved, we refer to these sites as marsh. From this point on the topographic heterogeneity is referred to as hummocks alternating with lower elevated depressions. When no elevated hummocks alternating with depressions were found, we refer to it as homogeneous marsh.

Figure 4.2. Topographic heterogeneity observed in pioneer stage on the Cefni marsh (left) and at 30 yrs-old-marsh on Schiermonnikoog (right). The left picture shows higher elevated pioneer hummocks alternating with the lower elevated bare intertidal flat. The right picture shows topographic heterogeneity consisting of higher elevated hummocks alternating with lower elevated depressions.

Effects of topographic heterogeneity in the pioneer stage (Cefni marsh)

In August 2011, we selected three plots on the Cefni marsh within the pioneer zone. These were 50 m × 50 m and at least 200 m apart from each other (Fig. 4.1). The three plots were all located on the bare intertidal flat, starting within 10 m of the salt marsh edge. They were present on different elevations of the underlying coarse-grained substrate: plot 1: 4.5 ± 0.5 cm, plot 2: 5.7 ± 0.4 cm and plot 3: 12.0 ± 0.2 cm above Mean High Tide (MHT). Plot 1 was located closest to the Bay mouth, while plot 3 was located furthest away (Fig. 4.1). Per plot we randomly selected about 30 hummocks of pioneer hummocks and paired each of them with controls taken on the adjacent bare intertidal flat. Controls were of similar size as the adjacent pioneer hummock, which ranges from a few cm up to 200 cm in diameter. To prevent any bias in choosing the location of the control plots, we assigned them consistently 0.5 m on the eastside of each hummock. Per paired measurement we estimated vegetation composition using a decimal scale (Londo 1976), fine-grained sediment layer thickness and surface elevation (cm above MHT). Fine-grained sediment layer thickness was measured using a small corer (1 cm in diameter), which allowed us to estimate it to an accuracy of 0.5 cm. The surface elevation was estimated using an optical levelling instrument (Spectra Precision® Laser LL500 and Spectra Precision® Laser HR500 laser receiver by Trimble), with an accuracy of 0.5 cm.

Development of topographic heterogeneity (Schiermonnikoog)

TOPOGRAPHIC HETEROGENEITY DEVELOPMENT BETWEEN 4 AND 15 YEAR OLD MARSH

In 2000, one plot of 7 m × 7 m was set up on the youngest marsh age of Schiermonnikoog (4 yrs old). The plot included both elevated hummocks and depressions. The plot was divided in smaller subplots of 0.25 m × 0.25 m. And for each subplot we estimated the fine-grained sediment layer thickness and the three most dominant plant species. In 2011, we repeated these measurements for 100 of these subplots: 50 on hummocks and 50 within depressions. This allowed us to determine changes in vegetation and fine-grained sediment layer thickness after eleven years of succession.

TOPOGRAPHIC HETEROGENEITY DEVELOPMENT BETWEEN 15 AND 120 YEAR OLD MARSH

In June 2011, we estimated the effects of topographic heterogeneity on the number of plant species, equitability and Shannon diversity index along the chronosequence on Schiermonnikoog. Equitability is used to indicate the evenness in distribution of the species present, (see for example Tuomisto 2012). We included five marsh ages: 15, 30, 45, 55 and 120 yrs-old-marsh. We chose ten random plots per site, five in marsh zones with topographic heterogeneity present and five in homogeneous marshes. The plots were chosen at approximately the same elevations. To prevent any bias from choosing a scale, we mapped at an increasing logarithmic scale: 0.5, 1, 2, 4, 8 and 16 m² of surface area. We randomly threw sticks on the marsh. In the zone with topographic heterogeneity present we started mapping from the centre of the nearest hummock. In the homogeneous marsh we started where the stick had landed. We estimated vegetation composition using a decimal scale (Londo 1976).

Effects of topographic heterogeneity on grazer abundance and impact throughout ecosystem development (Schiermonnikoog)

Dropping counts are a good estimate for grazing pressure for both hare (Langbein et al. 1999) and geese (Owen 1971). Hence, we estimated in June 2011 the hare and goose presence by counting number of droppings per 4 m^2 on three different marsh types: on hummocks, in adjacent depressions and in homogeneous marsh. We included all five marsh ages (i.e., 15, 30, 45, 55 and 120 yrs-old) and replicated each measurement ten times. We marked each plot with a stick and removed all 'old' droppings approximately two weeks prior to counting day. To calculate the number of droppings per day, we divided total number of droppings by the number of days between removal date and counting date.

To determine impact by the grazers on the topographic heterogeneity, we set-up 20 exclosures (6 m × 12 m) divided between the 15, 30, 45 and 55 yrs-old-marsh (n = 5 per marsh age). These exclosures were set-up in 2009 and located on top of the topographic heterogeneity including both hummocks and depressions within each treatment. Per exclosure we included three treatments: 1) no grazing, 2) only hare grazing present by goose exclusion and 3) both hare and goose grazing present. Geese were excluded using ropes at 25 and 50 cm above the ground, while both hare and geese were excluded using wire mesh. This set-up was used successfully before (Kuijper & Bakker 2005). In June 2011, we selected 0.25 m^2 plots within each treatment. We removed all biomass 1 cm above the marsh surface, sorted the samples per plant species, dried them at 70°C and weighted them afterwards. This resulted in six biomass samples per exclosure and 120 samples in total (n = 5 per treatment). To compare marsh with topographic heterogeneity present to homogeneous marsh, we included data derived from literature that had been collected on the homogeneous marsh areas of Schiermonnikoog at an earlier year (Van Wijnen and Bakker 2000).

Data analyses

To compare vegetation composition between pioneer marshes (measured at Cefni in 2011), 4 yrs-old-marsh (measured at Schiermonnikoog in 2000) and 15 yrs-old-marsh (measured at Schiermonnikoog in 2011) we had to transform the data of the pioneer marsh from the decimal scale to the three dominant plant species (Table 4.1). Based on the vegetation composition, including marshes between 15 and 120 yrs-old marsh (using the decimal scale), we calculated number of species (s), equitability (Eh) and the

Shannon diversity index (H). This enabled us to characterize the effects of topographic heterogeneity presence on plant diversity throughout long-term ecosystem development.

The Shannon diversity index (H):

$$H' = - \Sigma p_i \ln (p_i) \quad (1)$$

P_i = being the proportion of each species present within the plot

Equitability (Eh) was calculated as follows:

$$Eh = H' / \ln (s) \quad (2)$$

Statistical analyses

In the pioneer stage we analyzed the relation between surface elevation change and diameter of the pioneer hummocks with a general linear model, using diameter and plot as predictor variables. Differences in number of species between the three plots were analyzed with a generalized linear model (Poisson distribution), using hummock size and plot as predictor variables. Differences in total biomass on hummocks and depressions between 15 and 120 yrs-old-marshes were analyzed with an ANOVA, using marsh age and type (hummock or depression) as categorical predictors. Number of species was analyzed with a generalized linear model using a Poisson distribution. Diversity characteristics were analyzed using ANCOVA for Equitability and the Shannon diversity index. Numbers of droppings were analyzed with Tukey-tests for each marsh age separately, using type (hummock, depression or control) as categorical predictor. The effect of 1.5 years of grazer exclusion on biomass production was analyzed with a Mixed Effect Model, using grazing treatment and marsh age as fixed factors and exclosure as random factor. Values of $p < 0.05$ were considered significantly different. All analyses were performed using R, version 2.13.0 (R Development Core Team 2011).

RESULTS

Effects of topographic heterogeneity in the pioneer stage (Cefni marsh)

In the pioneer zone all hummocks were covered pre-dominantly by *Puccinellia maritima* and no fine-grained sediment had accumulated yet (Table 4.1). On the adjacent intertidal flat the main species present was *Salicornia europaea* (Table 4.1). The difference in surface elevation between hummocks and the adjacent intertidal flat significantly increased with diameter of the hummock ($t = 11.7$, $p < 0.001$). This relationship was only found in two of the three plots (plot 1 and 2, Fig. 4.3A), where hummocks increased in surface elevation up to 15 cm. Plot 3 diverged from this relationship as hummocks did not significantly increase in height with increasing size (Fig. 4.3A, significant interaction effect between plot and diameter ($t = -6.7$, $p < 0.001$)). Difference in surface elevation in plot 3 was limited to 3 cm. When we focus on the numbers of species found on the hummocks, all three plots showed the same relation: numbers of species increased significantly with diameter of the hummocks (Fig. 4.3B, $z = 10.9$, $p < 0.001$). Up to twelve species were present at a hummock size of 2 m in diameter, whereas on the adjacent bare intertidal flat a maximum of three species was found. The three plots did not differ significantly from each other ($z = 1.56$, $p = 0.12$).

Development of topographic heterogeneity (Schiermonnikoog)

TOPOGRAPHIC HETEROGENEITY DEVELOPMENT BETWEEN 4 AND 15 YEAR OLD MARSH

Pioneer hummocks present on the bare intertidal flat in the Cefni marsh (pioneer) and hummocks on Schiermonnikoog at 4 yrs-old-marsh had in common that *Puccinellia maritima* is one of the dominant plant species (Table 4.1). There were differences in vege-

Table 4.1. The difference in vegetation composition found at pioneer stage (Cefni marsh, UK) compared to 4 and 15 yrs-old-marsh (Schiermonnikoog, NL). The numbers represent the percentage of all plots where that specific plant species is ranked as one of the three most dominant present. This leads to a total of 300% per column, with the exception of the depressions in the pioneer stage as there were not always three species present. Bare soil was included as a "species" during measurements. The three most dominant plant species per age class are shown in bold.

	Hummocks			Depressions		
Marsh age (years)	**pioneer***	**4****	**15**	**pioneer***	**4****	**15**
Fine-grained sediment layer thickness (cm)	0	4 ± 1	6 ± 1	0	3 ± 1	7 ± 1
Bare soil	96	99	0	100	100	100
Armeria maritima	**11**	0	0	0	0	0
Artemisia maritima	0	4	**100**	0	0	**22**
Aster tripolium	7	3	4	0	0	0
Atriplex portulacoides	0	12	4	0	1	**58**
Festuca rubra	0	0	**100**	0	0	0
Glaux maritima	0	0	2	0	0	0
Limonium vulgare	0	**97**	**46**	**4**	18	**100**
Plantago maritima	0	8	40	0	0	0
Puccinellia maritima	**100**	**27**	4	0	**51**	2
Salicornia europaea	**78**	9	0	**93**	**59**	0
Spartina anglica	4	0	0	**33**	23	0
Spergularia media	4	**29**	0	0	3	6
Suaeda maritima	0	12	0	**4**	**45**	12

*Measurements taken on the Cefni marsh (UK), measurements on 4 and 15 yrs-old-marsh were taken on Schiermonnikoog (NL). **Measurements taken in 2000, at pioneer stage and 15 yrs-old-marsh were taken in 2011.

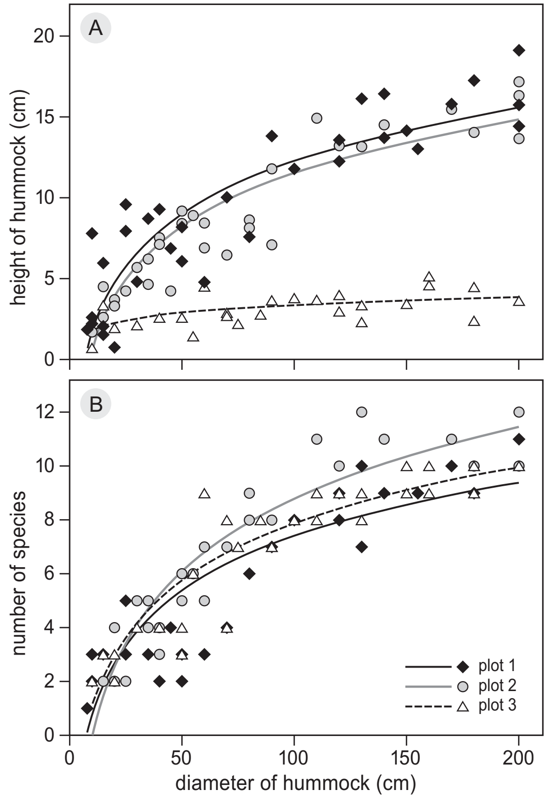

Figure 4.3. Differences in height between hummock and depression (A) and number of species (B) with increasing hummock size of the pioneer vegetation (Cefni marsh). Three plots were established on the intertidal flat located at least 200 m apart from each other. Per plot 30 pioneer hummocks were randomly selected ranging in diameter from a few cm up to 2 m. Each hummock was measured pair wise with an adjacent control plot on the bare intertidal flat. The diameter of the control plot was equal to the diameter of the hummock. Height of the hummock was measured in the centre of each hummock and indicated relative to the control plot. Numbers of species were estimated on the entire hummock.

tation dominance, for example: *Limonium vulgare* was more dominant on the hummocks at 4 yrs-old marsh. Plant succession continued between 4 and 15 years of marsh development. A clear difference in successional stages was found on top of higher elevated hummocks compared to the adjacent lower elevated depressions (Table 4.1 and Table 4.2), implying that two alternative successions had taken place on a small scale of only a few m².

Topographic heterogeneity development between 15 and 120 year old marsh

When topographic heterogeneity was present, the number of species (Fig. 4.4A-B), the equitability (4.4C-D) as well as the Shannon diversity index (4.4E-F) increased compared to the homogeneous marsh. These effects generally increased with surface area

(4A-C-E), but did not change with age of the marsh (Fig. 4.4B-D-F). The significant interaction effects found for equitability and the diversity index (Fig. 4.4C-E) showed that they only increased when topographic heterogeneity was present. Total biomass (g m^{-2}) on the hummocks was higher compared to the depressions and the homogeneous marsh (Fig. 4.5). As we derived the biomass estimates for the homogeneous marsh from literature, we could not perform any statistics comparing homogeneous vs. marsh with topographic heterogeneity present. However, based on the trend we concluded that both depressions and homogeneous marsh had approximately similar biomass estimates, whereas hummocks had more biomass, especially in the youngest and at the older sites (Fig. 4.5). The hummocks had significantly more biomass than depressions ($F_{1,95} = 59.7$, $p < 0.001$). Total biomass was also significantly different per marsh age ($F_{3,95} = 3.5$, $p = 0.02$) while no significant interaction effect was found ($F_{3,95} = 1.2$, $p = 0.31$).

Table 4.2. Change in vegetation composition on marshes with topographic heterogeneity present compared to homogeneous marsh along the chronosequence (15 to 120 yrs-old-marsh). All vegetation compositions were mapped on 16 m^2 plots (n = 5). Vegetation cover was estimated using a decimal scale (Londo 1976). All measurements were taken in 2011 on Schiermonnikoog. The dominant plant species are indicated in bold.

	Topographic heterogeneity present					**Homogeneous marsh**				
	15	**30**	**45**	**55**	**120**	**15**	**30**	**45**	**55**	**120**
Bare	20	1	0	6	15	30	3	6	10	18
Armeria maritima	0	0	0	0	0	0	0	0	0	0
Artemisia maritima	**15**	**16**	**15**	3	10	**4**	**13**	10	**8**	1
Aster tripolium	2	4	2	2	2	**4**	0	0	0	0
Atriplex portulac.	2	4	6	7	12	**24**	4	0	**12**	1
Atriplex prostrata	0	0	1	0	0	0	1	2	1	**5**
Cochlearia sp.	1	1	0	0	0	1	0	0	0	4
Elytrigia atherica	0	0	0	**11**	4	0	**40**	**44**	**56**	**66**
Festuca rubra	**28**	**32**	**32**	**23**	**26**	1	4	**21**	7	**5**
Glaux maritima	3	3	3	**11**	8	1	1	1	0	0
Juncus gerardii	0	6	0	9	**17**	0	4	**15**	1	**12**
Limonium vulgare	**32**	**32**	**38**	**32**	**16**	**42**	**24**	6	1	0
Plantago maritima	10	3	0	0	1	1	0	0	0	0
Puccinellia maritima	6	5	5	5	0	1	10	0	1	0
Salicornia europaea	1	3	2	1	0	1	1	0	2	0
Spartina anglica	0	1	0	0	0	1	0	0	0	0
Spergularia media	1	1	0	0	1	1	0	0	0	0
Suaeda maritima	2	2	1	1	0	**4**	1	0	0	0
Triglochin maritima	0	4	2	1	1	0	1	0	3	0
Nr. of species	**12**	**15**	**11**	**12**	**11**	**13**	**12**	**7**	**10**	**7**

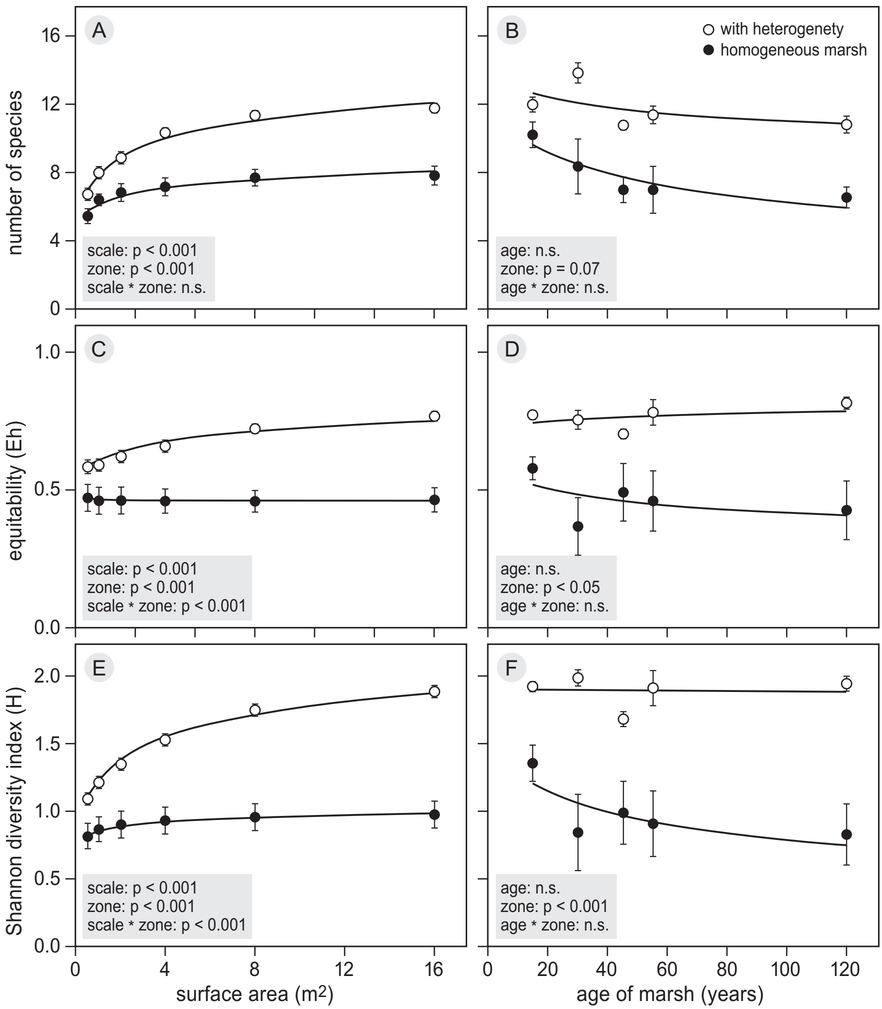

Figure 4.4. Number of plant species (A-B), equitability (C-D) and Shannon diversity index (E-F) determined on plots with increasing surface area (A, C, E) and along the chronosequence (B, D, F) ranging between 15 and 120 yrs-old-marsh on Schiermonnikoog. Open circles indicate heterogeneous marsh with topographic heterogeneity present and closed circles indicate homogeneous marsh. Data shown along an increasing surface area (A-C-E) were averaged over all marsh ages. Along the chronosequence only data measured on 16 m² are shown (B-D-F). Zone represents the differences between the two marsh zones: homogeneous or heterogeneous marsh zone.

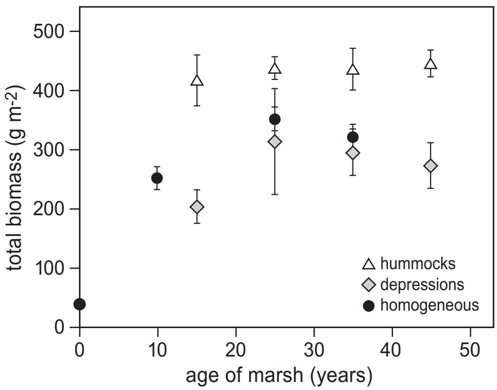

Figure 4.5. Total biomass (g m^{-2}) estimated in homogeneous marsh, on depressions (n = 5) and on hummocks (n = 5) along the chronosequence (up to 55 yrs-old-marsh). Biomass estimates on the homogeneous marsh (n = 3) were derived from literature (Van Wijnen & Bakker 2000). All data were collected with hare and geese grazing present.

Effects of topographic heterogeneity presence on grazer abundance and impact throughout ecosystem development (Schiermonnikoog)

In homogeneous marsh the hare abundance increased with age and productivity to a maximum value at medium-aged-marsh of 45 years old, after which the hare abundance again decreased (Fig. 4.6A). When topographic heterogeneity was present this pattern changed, with the highest hare abundance found in the youngest marshes, and hare abundance decreased with age of the marsh. Hare preferred hummocks above depressions ($p < 0.01$, $p < 0.01$) or homogeneous marsh ($p < 0.01$, $p < 0.01$) at 15 and 30 yrs-old-marsh. At 45 yrs-old-marsh, however, they had a strong preference for homogeneous marsh compared to hummocks ($p < 0.001$) or depressions ($p < 0.01$). Geese seemed to prefer the youngest site and mainly the zone where no topographic heterogeneity was found though these differences were not significant (Fig. 4.6B).

Impact of the small grazers on vegetation characteristics was highest on hummocks (Fig. 4.7). In ungrazed marsh, i.e. where both hare and geese were excluded, total biomass increased significantly on the hummocks (Fig. 4.7A, $t = 3.8$, $p < 0.001$). Biomass on hummocks was unaffected by marsh age or when only hare grazed (Fig. 4.7A, $t = 0.29$, $p = 0.76$). Within ungrazed depressions, total biomass increased significantly (Fig. 4.7B, $t = 3.0$, $p < 0.001$). Within depressions, biomass increased significantly with age of the marsh and all older sites differed significantly from the youngest site ($t = 2.16$, $p = 0.05$, $t = 2.5$, $p = 0.03$ and $t = 2.3$, $p = 0.04$ for 30, 45 and 55 yrs-old-marsh, respectively).

When topographic heterogeneity was present, *Festuca rubra* was already present in high cover at a much earlier successional stage compared to homogeneous marsh, and cover remained relatively stable between 15 and 120 years of marsh succession (table 4.2

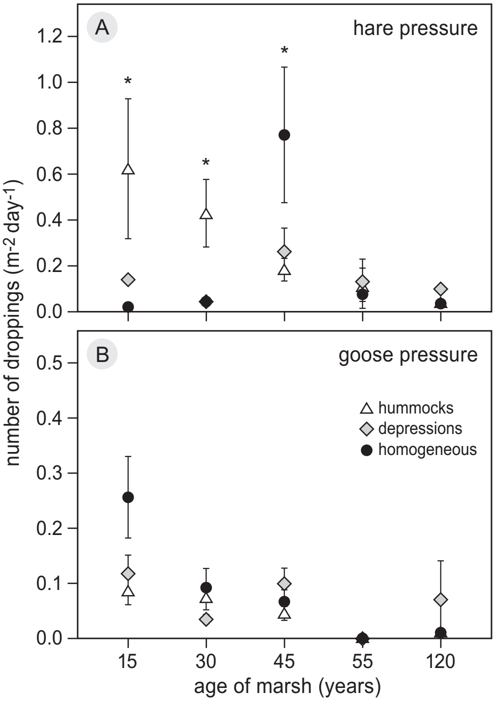

Figure 4.6. Grazer pressure of hare (A) and goose (B) estimated with number of droppings (m^{-2} day^{-1}) along the chronosequence (15 to 120 yrs-old-marsh). Data is collected per 4 m^2 plots. All droppings were removed 14 days prior to counting date.
* indicates this treatment was significantly different ($p < 0.05$) from both other treatments at that marsh age.

and fig. 4.7C). In the homogeneous marsh a clear optimum was shown at 45 year old marsh, thereafter, cover of *Festuca rubra* was quickly reduced again with increasing age (table 4.2). On ungrazed hummocks the biomass of *Festuca rubra* increased significantly (Fig. 4.7C, $t = 5.2$, $p < 0.001$). Hare grazing, i.e. when only geese were excluded, did not result in significant differences ($t = -0.54$, $p = 0.59$). Biomass reduced with age, as it was significantly lower at 55 yrs-old-marsh compared to 15 yrs-old-marsh ($t = -2.55$, $p = 0.02$). *Festuca rubra* was only marginally present in depressions and biomass was not significantly affected by marsh age or grazing treatments (Fig. 4.7D). On hummocks, *Puccinellia maritima* was unaffected by grazing treatment or age of the marsh. Within depressions, the biomass of *Puccinellia maritima* increased with marsh age as both 45 and 55 yrs-old-marsh differed significantly from the 15 yrs-old-marsh ($t = 3.0$, $p < 0.01$ for both 45 and 55 yrs-old-marsh).

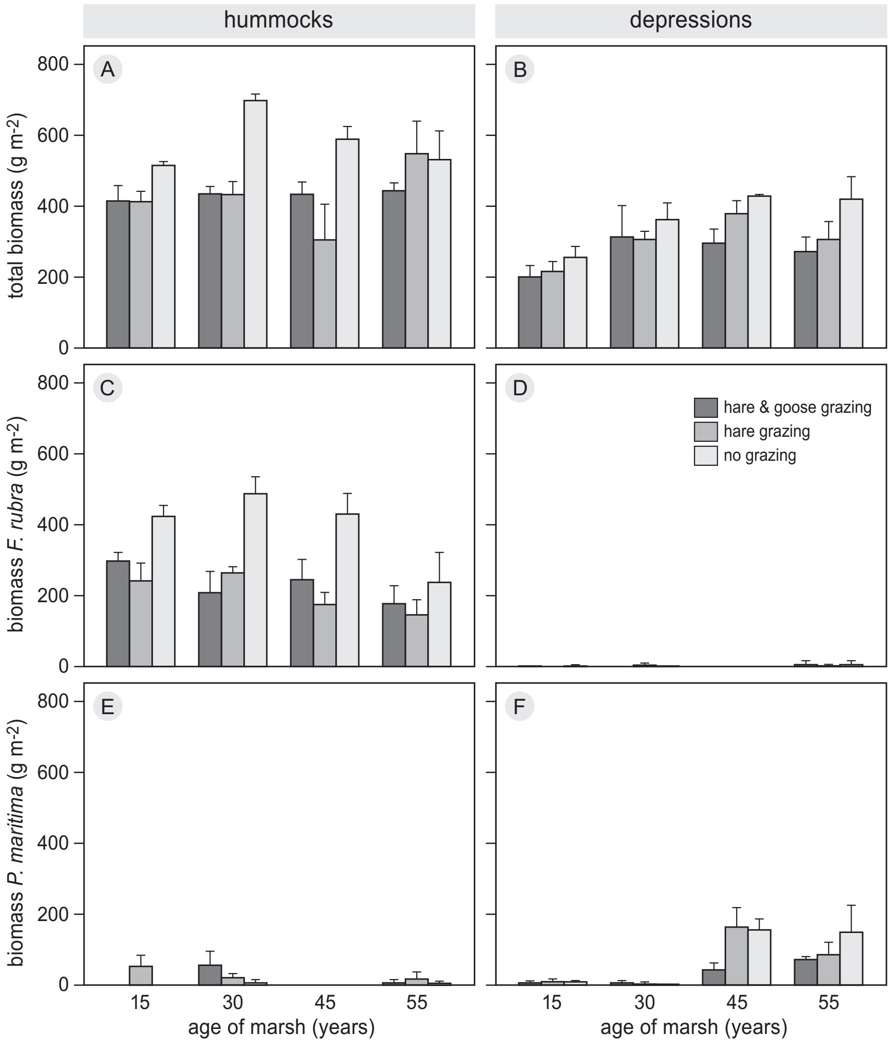

Figure 4.7. Total biomass (A, B), biomass of *Festuca rubra* (C, D) and biomass of *Puccinellia maritima* (E, F) estimated on hummocks and depressions along the chronosequence (15 to 55 yrs-old marsh). Differences are shown after small gazers (hare and geese vs. only geese) were excluded for approximately 1.5 years.

DISCUSSION

Our results clearly showed that the presence of topographic heterogeneity in the marsh soil enhanced plant diversity (number of species, equitability and Shannon diversity index) throughout long-term ecosystem development. Furthermore, it increased grazer abundance especially in early successional stages. Grazers had a large impact on the vegetation on hummocks as well as in depressions. They removed a significant proportion of the biomass present, with largest impact on hummocks in the younger marshes (Fig. 4.7). The hummocks were present already in the pioneer stage before fine-grained sediment was accumulated. The patterns got subsequently conserved under the fine-grained sediment layer in the older stages of marsh development. In young marshes the hummocks provided an additional niche, thereby facilitating the establishment of plant communities of later successional stages. As a result, the hummocks not only enhanced plant diversity, but also enhanced the suitability of marshes for small grazers, i.e. hare, early in succession.

Effects of topographic heterogeneity in the pioneer stage

In the pioneer stage we found higher elevated hummocks on the bare intertidal flat and all were dominated by *Puccinellia maritima*. Several pioneer species in marshes, e.g. *Spartina anglica* and *Puccinellia maritima*, are known to modify their environment by accumulating sediment (Figueroa et al. 2003, Van Wesenbeeck et al. 2008, Balke et al. 2012). Previous studies showed *Puccinellia maritima* can form higher elevated hummocks in the pioneer zone by decreasing erosion and increasing local sediment accumulation (Gray and Bunce 1972, Langlois et al. 2001, 2003). Repeated burial by sediment even enhanced clonal growth (Langlois et al. 2001). This would explain the strong positive correlation we found between increasing surface elevation with an increase in diameter of the hummocks. Plot 3 did not show the same correlation, but according to Langlois et al. (2003) hummock formation depends for a large part on the local hydrodynamic conditions. Limited sediment supply or too strong currents could reduce hummock formation.

Many studies in bio-geomorphic ecosystems have focused on the formation of topographic heterogeneity due to an interaction between vegetation and tidally introduced sediment (Stribling et al. 2007, Van Wesenbeeck et al. 2008, Fagherazzi et al. 2012, Balke et al. 2012). However, studies determining the effect of topographic heterogeneity on plant diversity have been limited so far (with exception of e.g. Ruifrok et al. 2014). In this study we showed that hummock presence facilitated establishment of other salt-marsh species in the pioneer zone. The number of species increased up to twelve species with increasing diameter of the patch (Fig. 4.3). Whereas, we never found more than four plant species on the adjacent bare intertidal flat. Stressful environmental conditions limit many salt marshes species from establishing in the pioneer zone (Davy et al. 2011). In harsh environments, positive interactions between plant species generally are more important in structuring local plant communities than negative interaction such as competition (Bertness and Leonard 1997, He et al. 2013). Stabilization of the soil by *Puccinellia maritima* could facilitate for the other salt-marsh plant species to successfully establish thereby enhancing plant diversity in the pioneer zone (Bertness and Leonard 1997, Langlois et al. 2003).

Development of topographic heterogeneity and the interaction with grazers throughout ecosystem development

Along the entire successional gradient the presence of topographic hummocks and depressions increased local plant diversity (enhancing number of species, equitability and Shannon diversity index, Fig. 4.5). As elevation is an important factor controlling species distribution in marshes (Olff et al. 1997, Davy et al. 2011), presence of the topographic heterogeneity resulted in multiple niches to co-occur on a small scale of a few square metres. A higher elevation generally results in a locally better drained and therefore more oxygen-rich soil (Davy et al. 2011). This will enhance the mineralization rate in the soil (Aller 1994) and hence plant production. An increase in productivity will speed up succession (Olff et al. 1997), allowing later successional species to become dominant at a much earlier stage (Table 4.1). Species such as *Puccinellia maritima* and *Limonium vulgare* first dominated on the hummocks but were found to become dominant in the depressions only in a later stage (Table 4.1 and 4.2). Thus, two co-occurring successional stages within this small-scale topographic heterogeneity of a few square metres will explain the increase in local plant diversity found throughout ecosystem development (Fig. 4.4).

Even at 120 yrs-old-marsh presence of topographic heterogeneity enhanced plant diversity. Presence of this heterogeneous pattern in soil morphology could be preventing *Elytrigia atherica* from becoming a dominant mono-culture. The high (66%) cover of *Elytrigia atherica* we found in homogeneous marsh (Table 4.2), is in line with previous studies that show that *Elytrigia atherica* becomes dominant at mature marshes (Veeneklaas et al. 2013, Wanner et al. 2014). Lower elevated areas generally have more water-logged soils, less oxygen in the soil, and hence more stressful environmental conditions (Davy et al. 2011). Depressions with these high-stress conditions surrounding the hummocks could be forming natural barriers preventing *Elytrigia atherica* from clonally expanding beyond the hummocks (Bouma et al. 2001, Scheepens et al. 2007). Based on our results we conclude that the presence of topographic heterogeneity not only boosts plant diversity in young marshes, but also maintained plant diversity in older mature successional stages.

In contrast to previous studies showing a maximum grazer abundance at marshes of intermediate ages (Van De Koppel et al. 1996, Olff et al. 1997), we found a high grazer abundance at young marshes when topographic heterogeneity was present. A high cover of *Festuca rubra* as well as an increased primary production on hummocks resulted in young marshes to become suitable for grazers at an earlier stage. *Festuca rubra* forms an important part of the diet of the grazers, i.e. hare and goose, in this ecosystem (Van Der Wal et al. 1998, Kuijper and Bakker 2005). Presence of topographic heterogeneity increased the cover of *Festuca rubra* throughout ecosystem development and this enhanced the suitability for the small grazers. On top of hummocks, we found a reduction in total biomass, ranging between 20% and 50%, when grazers were present (Fig. 4.7). This implies a very high grazing pressure on top of hummocks throughout ecosystem development.

Management implications

For conservation purposes and coastal defence many coastal ecosystems are currently being restored and created (Lithgow et al. 2013, Beauchard et al. 2013). They become increasingly important due to the effects of global climate change and the risk of flooding disasters that is increasing worldwide (Temmerman et al. 2013). With ecosystem restoration it is important to restore all ecosystem functions, which has been proven to be a difficult task (Mossman et al. 2012, Staszak and Armitage 2013). Especially a full recovery to similar biotic composition and diversity can take a very long time (over 50 years), if complete recovery is even possible (Borja et al. 2010, Mossman et al. 2012). Promoting the formation and/or actively creating small-scale topographic heterogeneity could speed-up recovery as it will positively affect plant diversity. With increasing plant diversity we could potentially increase the resilience of marshes to changing environmental conditions (Godfree et al. 2011), increasing human disturbances and loss of biodiversity (Hopkins and Del Prado 2007).

Many European marshes are grazed by livestock to increase plant species richness (Bouchard et al. 2003, Wanner et al. 2014). Previous studies showed large grazers can induce heterogeneity in the vegetation (Loucougaray et al. 2004, Nolte et al. 2013a) as well as topographic heterogeneity (Ruifrok et al. 2014) to form in marshes. This positively affects plant species richness (Loucougaray et al. 2004, Ruifrok et al. 2014) as well as invertebrate and avifauna abundance (Bakker et al. 1993). In this study we showed topographic heterogeneity is already present in (livestock-) ungrazed marshes, and that this topographic heterogeneity positively affected not only plant diversity but also grazer abundance. A next step is to study the development of the topographic heterogeneity when livestock is introduced in coastal marshes. This could impact plant diversity and grazers (vertebrate as well as invertebrate grazers) even more.

Long-term persistence of diversity in developing ecosystems

Similarly as in this study, many other studies in different ecosystems showed that environmental heterogeneity increases plant diversity (Stein et al. 2014). Additionally, it can impact other trophic levels as well: e.g. it increases insect-herbivore richness (de Araújo 2013) or alter the presence and impact of mammals within that ecosystem (Davidson and Lightfoot 2006). However, many studies do not take long-term ecosystem development into account (e.g. Wohlgemuth 1998, Davidson and Lightfoot 2006, Baker et al. 2013). In this study we found that the impact of environmental heterogeneity changed with age of the ecosystem. In young marshes, topographic heterogeneity enhanced grazer presence. In contrast, at intermediate age, grazers preferred the zones without topographic heterogeneity present. At mature marsh, the main impact of topographic heterogeneity was to maintain plant diversity and we did not find an impact on grazer presence anymore. Thus, it is important that we include long-term studies, when we want to determine the role of topographic heterogeneity in ecosystems and when we want to include multiple trophic levels.

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