Effects of grazing management on biodiversity across trophic levels – The importance of livestock species and stocking density in salt marshes

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Highlights:

- Optimal grazing management on salt marshes for plants and animals is unclear
- A grazing experiment with cattle and horses at two stocking densities was set up
- Plants, pollinators, birds and voles all responded idiosyncratically
- Choice of livestock species is of less importance than stocking density
- We recommend concurrent application of different grazing regimes

Summary

European coastal salt marshes are important for the conservation of numerous species of specialist plants, invertebrates, breeding and migratory birds. When these marshes are managed for nature conservation purposes, livestock grazing is often used to counter the dominance of the tall grass *Elytrigia atherica*, and the subsequent decline in plant species richness. However, it remains unclear what is the optimal choice of livestock species and stocking density to benefit biodiversity of various trophic levels.

To fill this knowledge gap, we set up a triplicate, full factorial grazing experiment with cattle and horse grazing at low and high stocking densities (0.5 or 1 animal ha^{-1}) at the mainland coast of the Dutch Wadden Sea. Here, we present the results after 4 years and integrate these with previously published results from the same experiment to assess effects of livestock grazing on various trophic groups.

Stocking density affected almost all measured variables: high stocking densities favoured plant species richness and suppression of *E. atherica*, whereas low stocking densities favoured abundances of voles, pollinators and flowers. Densities of different functional groups of birds showed no significant response to the regimes, but tended to be somewhat higher under 0.5 horse and 1 cattle ha^{-1}.

Choice of livestock species had fewer and smaller effects than stocking density. Horse grazing was detrimental to vole density, and showed an interactive effect with stocking density for Asteraceae flower abundance. Multidiversity, a synthetic whole-ecosystem biodiversity measure, did not differ among regimes. These results are discussed in the light of other results from the same experiment.

Because of these contrasting effects on different trophic groups, we advise concurrent application of different grazing regimes within a spatial mosaic, with the inclusion of long-term abandonment. High density horse grazing, however, is detrimental to biodiversity.

1. Introduction

To maintain high plant species richness and to counter the encroachment of tall, competitive plant species, livestock grazing is a frequently used management tool in European semi-natural grasslands. It is becoming increasingly clear, however, that not all trophic groups respond equally positively to this type of management. Grazing is often beneficial to plant species richness (Olff and Ritchie, 1998), but detrimental to species richness of many arthropod groups (Foster et al., 2014; van Klink et al., 2015), molluscs (Boschi and Baur, 2007) and small mammals (e.g. Villar et al., 2014), while mixed effects are reported for species richness of meadow birds (e.g. Atkinson et al., 2005; WallisDeVries et al., 2007). Holistic management approaches, designed to benefit various trophic and taxonomic groups are therefore urgently needed (WallisDeVries et al., 2002).

Coastal salt marshes in north-western Europe represent a case in point. These ecosystems are of high conservation interest because of the numerous plant- and invertebrate species confined to this specific habitat, some of which are endemic to the region, and therefore protected under the EU Habitats Directive (Doody, 2008; EC Habitats Directive, 1992). Additionally, salt marshes are of high importance to large numbers of breeding and migratory birds, among which several species classified as vulnerable on the Dutch, German and British red lists, such as Redshank (*Tringa totanus*) and Oystercatcher (*Haematopus ostralegus*).

Mainland salt marshes have been used for livestock grazing for millennia, because of their productive clay soils. However, over the past 50 years many marshes fell to abandonment as livestock grazing became less profitable (Bakker et al., 2002). Abandonment usually results in a dominance of competitive plant species such as the tall-statured Sea couch grass (*Elytrigia atherica*) on higher salt marshes, Sea purslane (*Atriplex portulacoides*) on lower marshes (Bos et al., 2002; Wanner et al., 2014), or Common reed (*Phragmites australis*) on brackish marshes (Esselink et al., 2000). Such encroachment endangers populations of short-statured plants (Bos et al., 2002) and some invertebrate species (van Klink et al., 2013), and changes nesting and foraging conditions for birds, which are key issues according to the EU Habitats Directive. Livestock grazing can maintain species-rich plant communities and prevent, or decrease, the dominance of *E. atherica* (Bakker et al., 2002), but will under high stocking densities create a homogeneous short-grazed vegetation structure, which is unfavourable to many species of invertebrates (Pétillon et al., 2007; Rickert et al., 2012) and breeding birds (Mandema et al., 2015; Norris et al., 1998). Therefore it remains unclear, how grazing can be implemented best with respect to stocking density and livestock species to benefit various trophic and taxonomic groups, and to prevent the dominance of competitive plant species, thus promoting biodiversity. To fill this knowledge gap and to optimise salt-marsh conservation management, we installed a four-year grazing experiment on a mainland salt marsh at the Dutch Wadden Sea coast, using cattle and horse grazing at 0.5 and 1 animal per hectare, each. Here, we present new findings on plant, bird, pollinator and vole communities at the field scale, and compare these to previously reported results on vegetation structural complexity, nest survival, staging geese, survival of flowering forb *Aster tripolium*, and sediment accretion.

On salt marshes, the most important mechanisms by which livestock grazing affects biodiversity are biomass removal (defoliation) and trampling (Bakker et al., 1985). The impacts of both these processes increase with stocking density, but can also be expected to differ between livestock species due to differences in digestive system and mouth morphology. Horses, as hind-gut fermenters, have higher food intake rates than ruminants of the same size, and are able to digest more low-quality, high-fibrous grasses (Illius and Gordon, 1992; Menard et al., 2002). Additionally, horses can forage closer to the ground and are more active than cattle (Menard et al., 2002). Therefore, we hypothesise that the effects of horse grazing on the system will be greater than those of the more placid cattle.

The direct effects of livestock on their habitat can be expected to cascade up the food-chain (Evans et al., 2015). We hypothesise that plant species richness benefits from higher stocking densities as grazing opens the canopy and decreases light competition (Borer et al., 2014). Such a short and open vegetation canopy will be beneficial for spring staging geese, as these small herbivores require high-quality forage (Mandema et al., 2014b). By contrast, protective cover for voles will decrease under high stocking densities (Villar et al., 2014), hence, voles are hypothesised to be more abundant under low stocking densities. Also pollinators can be expected to be more abundant under low stocking densities, as their most important floral resource, *Aster tripolium*, is sensitive to grazing (Kiehl et al., 1996; Nolte et al., 2013). The thus expected high abundance of invertebrates and seeds under low stocking densities should in turn be attractive for breeding and wintering birds foraging on the salt marsh. By contrast, birds that forage on the intertidal flats, but roost on the salt marsh, are hypothesised to utilise the more heavily grazed marsh, because of the higher detectability of predators. Raptors and owls, in turn, can thus be expected to forage under low stocking densities, where their vertebrate prey, such as voles, are most abundant (Baker and Brooks, 1981). Our aim was therefore to determine which grazing regime (i.e. species and stocking density) is most optimal in terms of biodiversity.

2. Material and Methods

2.1 Study area and experimental design

We established a triplicate grazing experiment in 2010 (year 1) on the salt marshes of Noord-Friesland Buitendijks at the mainland coast of the Dutch Wadden Sea (N53°20', E5°43'). The site is a typical example of a Western European mainland salt marsh, which has established on marine clay deposits (up to 80% clay and silt) within man-made sedimentation fields. The average yearly temperature is 11 °C, with an average yearly rainfall of 785 mm (2005-2015; Royal Dutch Meteorological Institute). The study area is characterised by a distinct vegetation zonation from the frequently flooded pioneer zone, over the low marsh, to the higher elevated and seldom flooded high marsh, and is managed for nature-conservation purposes. The historic management of the experimental area was cattle grazing at relatively high densities (Esselink et al., 2009), with several rotations per year. This management type was continued until the start of the experiment in the central and eastern replicates, but in the western replicate grazing was ceased for eight years prior to 2009. In 2009 (year 0), high-density grazing was installed in the western replicate for one season to enhance comparability with the other two replicates at the start of the experiment in 2010.

Each replicate was subdivided into five paddocks of approximately 11 ha (Fig. 1), in each of which a different summer grazing regime (June-October) was installed: horse and cattle grazing at two stocking densities each (0.5 and 1 animal ha^{-1}), and a rotational grazing regime (one fallow year followed by 1 cattle ha^{-1}; not considered here due to limited data). Livestock were obtained from local farmers. Cattle were all 2-3 year old non-lactating cows (breed: Holstein-Friesian; ca. 600 kg). The horse herds consisted of animals of both sexes, all above 2 years of age (breed: Dutch Warmblood (KWPN); ca. 700 kg). The regimes were randomly assigned to the paddocks, with the restriction that horse grazing was not applied to two adjacent paddocks to avoid interactions between the two herds. Ungrazed paddocks were not included in the experiment, since the effects of grazing cessation on various biotic groups have been studied extensively elsewhere (e.g. Ford et al., 2013; Irmler and Heydemann, 1986; Kiehl et al., 1996; Wanner et al., 2014). In addition, the ecological changes are most pronounced under such a severe management regime, making it an ineffective control. The high density cattle grazing regime thus best reflects the historic management, and can be regarded as control regime.

2.2 Data collection

2.2.1 Vegetation

The spread of *E. atherica* was assessed by vegetation mapping of each paddock in year 0 and 4, based on aerial photographs. Vegetation types were identified according to the Trilateral Monitoring and Assessment Program (TMAP) vegetation classification (Esselink et al., 2009). The maps were digitised and the area of the *E. atherica* vegetation type (>50% cover of *E. atherica*) was calculated using ArcGIS 10.1. We analysed change in the percentage cover of the *E. atherica*-type per paddock between year 0 and year 4.

To study changes in plant species richness, permanent plots (PPs, 4 m x 4 m) were installed in year 0. In each paddock eight PPs were placed, stratified equally over the high and the low marsh (Appendix A). PPs within the same block and marsh zone were positioned on a comparable surface elevation along the gradient, within homogeneous vegetation. The minimum distance between PPs and the fence was ten metres. Each year in late August / early September (year 0-4) the vegetation height was measured to the nearest cm at five random locations within each PP using a Styrofoam drop disc (diameter 25 cm, weight 75 g), and all plant species were recorded. Nomenclature of plant species follows Van der Meijden (2005). We analysed mean vegetation height and plant species richness per PP.

2.2.2 Flowers and pollinators

Pollinators were chosen to represent invertebrates because they play an important role in plant reproduction, and are easily visually assessed at the scale of our experimental paddocks. This contrasts to other invertebrate groups, which are typically trapped at small scales and are difficult to identify. Because very few pollinator species can reproduce on the salt marsh, all individuals should be considered immigrants in the system.

Pollinator and flower abundance were assessed three times per year (early June, mid-July and around September 1st of years 2-4), along 500 m long transects laid out diagonally through each paddock (Appendix A). Using a modified version of the Pollard walk (Pollard, 1977) all Macrolepidoptera (butterflies and day-active moths) were counted and identified by walking along each transect at moderate speed and counting all specimens within a 5 m x 5 m x 5 m imaginary cube. Every 25 m, for one minute all pollinators (Macrolepidoptera to species level, bumblebees, honeybees and hoverflies at family level) in a 2 m x 2 m sub-plot were counted, and flower abundance of all forb species was estimated on a simple scale: 1: 1-10; 2: 10-50; 3: 50-100, 4: >100 (see WallisDeVries et al., 2012). For analysis, we used total pollinator abundance per paddock per year. Total flower abundance per species per paddock was calculated by summing the minimum value of its abundance class over all sub-plots. Flower abundance can thus be seen as a lower boundary estimate.

2.2.3 Birds

From April of year 1 to December of year 4, bird censuses were conducted biweekly at sunrise along a permanent transect in each paddock (Appendix A). All birds sighted (i.e. on the ground, flying up or landing), except overflying birds, were identified and their locations marked on a map, which was later digitised.

All observed birds were classified into one of five functional groups, based on whether they use the salt marsh for foraging or not, *viz*.: (1) foraging (PB-forag) and (2) non-foraging potential breeding birds (PB-nonforag), (3) foraging (NB-forag) and (4) non-foraging non-breeding birds (NB-nonforag), and (5) raptors (including owls). The functional group of PB was only used for observations in the breeding season (April 1st - July 31st) for those species known to breed at the site according to Bos et al. (2015), excluding raptors (no raptors bred within the experimental area during the research period). Outside this period, these species were classified as NB. The analyses were also performed for Meadow Pipits

(*Anthus pratensis*), the only species observed in each paddock each year, and all bird species combined. The complete list of all bird species, their classification and their total abundances can be found in Appendix B.

2.2.4 Voles

Voles (predominantly *Microtus arvalis* and to a lesser degree *M. agrestis*) occur on the high marsh and only during the summer season (C. Smit unpublished data). This is due to frequent inundations of the low marsh, and floods during winter storms. Therefore, the effects of grazing on voles were only assessed on the high marsh. In October of year 4, 60 circular plots of 2 m^2, spaced 10-20 m apart along three to ten transects depending on the width and length of the high marsh within the paddock, were surveyed once within each paddock (Appendix A, Fig. A1). Each plot was scanned for signs indicating the presence of voles: runways, fresh plant fragments, or faecal pellets (see Villar et al., 2014). For analysis, the proportion of subplots with vole presence was calculated per paddock (N = 3 replicates per treatment). In the eastern replicate, 24 plots (10%) were excluded from analysis, due to flooding at the time of sampling.

2.3 Statistical analysis

All analyses were done in R 3.2.5 (R Core Team, 2016). For all analyses of species richness, presence, abundance, and plant vegetation height, we used generalised linear mixed models (GLMM) with backward model selection based on Akaike's Information Criterion (AIC) using the lme4 package (Bates *et al.* 2014). As explanatory variables in all models we used livestock species (cattle or horse), stocking density (0.5 or 1 animal ha^{-1}) and their interaction, and as random factors we included a nested design of paddock nested in block. Year was included as a separate random factor (except for voles, which were only assessed in year 4) to account for yearly differences, and possible non-linear cumulative effects. For the analyses of treatment effects, data from year 1-4 were used. We checked for differences in plant diversity among paddocks before the experiment started (year 0), and found no differences (P = 0.31). Final model significance was compared to the null-model of no explanatory variables. Multiple comparisons between all four regimes were done post-hoc by running the GLMM with the same random structure, but with ‘regime’ (factorial, four levels) as explanatory variable. On this model Tukey’s HSD test was performed to test specifically for differences among the four grazing regimes, using the Multcomp library (Hothorn et al., 2008).

For the change in cover of *E. atherica* and vegetation height (log transformed to correct for heteroscedasticity) the error structure followed a normal distribution. The models for plant species richness, flower abundance, pollinator abundance, and bird species richness and abundance had a Poisson error structure, and the presence of voles was analysed using the binomial distribution. Overdispersion of the residuals in the Poisson and binomial models was dealt with using individual level random effects and tested for significance against the model not accounting for overdispersion for improvement of fit.

For the analysis of plant species richness and vegetation height per PP, we included marsh zone (high or low) and its interactive effects as additional fixed variable, and PP in the random structure (PP nested in paddock nested in block). When marsh zone showed a significant interaction with any other variable, the dataset was split and analysed separately per marsh zone.

The relationship between the abundances of pollinators and floral resources was assessed using linear models with log-transformed pollinator abundance as dependent variable, and flower abundance and year (factorial) as explanatory variables. Log transformation provided a better fit of the data than a Poisson error distribution. Four different classes of flowers were assessed, *viz*.: (1) total flower abundance, (2) flower abundance of *A. tripolium* (i.e. the most abundant Asteraceae species), (3) abundance of all Asteraceae flowers (*A. tripolium*, *Cirsium arvense*, *Sonchus arvensis* and *Leontodon autumnalis*), (4) flowers of other forbs (mostly *Potentilla anserina*, *Glaux maritima* and *Spergularia* spp.).

We used distance sampling (Thomas et al., 2009) to estimate total density of all bird functional groups within the experimental paddocks. In order not to inflate density estimates due to flocking behaviour, only incidence data were used to obtain estimates. From the mapped positions, perpendicular distances to the transect line were calculated using ArcGIS 10.1, after which density per 11 ha paddock was estimated using the Distance package for R (Miller, 2015). Model selection of the appropriate distance function (half-normal or hazard rate) and covariates (livestock species, stocking density, replicate or paddock) was based on AIC. For three out of five functional groups (PB-nonforag, NB-nonforag and Raptors), no individuals were seen in some paddocks in some years, therefore estimates were obtained by pooling all four years per paddock for these groups. The estimated densities were then entered into mixed effects models with the structure described above. Probability distributions and model parameters can be found in Appendix C.

To obtain a synthetic number of biodiversity per year for each paddock, we calculated multidiversity (Allan et al., 2014) over plants, butterflies and the five functional bird groups using their total species richness per paddock per year. This is a novel diversity metric covering multiple taxonomic or functional groups. For each group, the proportion of species relative to the maximum observed number of species was calculated for each paddock, after which these proportions were averaged over all groups.

3 Results

3.1 Vegetation

The cover of the *E. atherica* vegetation type tended to be lower under high stocking densities (*P* = 0.08; Table 1), but differed strongly among replicates. In the eastern replicate the *E. atherica* vegetation type was not present in three paddocks after four years. By contrast, in the western replicate, and to a lesser extent in the central replicate, the *E. atherica* type was already widespread at the start of the experiment.

In total 38 plant species were recorded, among which 18 halophytes (Appendix B). On both the high and the low marsh, mean vegetation height was higher under low stocking densities, but was not affected by livestock species (Table 1, Fig. 2a,c). Plant species richness differed among the regimes on the high marsh only, and was higher under high stocking densities (Table 1, Fig. 2b,d).

3.2 Flowers and pollinators

Over years 2-4, we counted 15 flowering plant species and 11 butterfly species over a total of 598 individual butterflies. Additionally, 1874 hoverflies, 143 bumblebees and 42 honey bees were counted (Appendix B). Total flower abundance was lower under high stocking densities, but did not differ between livestock species (Table 1). Abundance of Asteraceae flowers did not differ between stocking densities under cattle grazing, but was under horse grazing highest under low density grazing (Table 1, Fig. 3a). Flower abundance of the most abundant Asteraceae species, *A. tripolium*, was significantly higher under low stocking densities than under high densities (Table 1). Abundance of non-Asteraceae flowers was not affected by the regimes (Table 1).

Pollinator abundance was highest under low stocking densities (Table 1). However, post hoc comparisons among the four specific treatments showed only effects of stocking density under horse grazing (lower pollinator abundance at high stocking density), but not under cattle grazing (Fig. 3b). There was a strong positive relationship between flower and pollinator abundance (Fig. 3c). Of all floral groups tested, the pooled Asteraceae reached the highest explanatory power (t = 8.50, $P<0.001$, adjusted $R^2 = 0.86$, Fig. 3c), whereas the abundance of pollinators was not related to the flower abundance of other species ($P = 0.87$). The abundance of *A. tripolium* alone also had strong explanatory power for pollinator abundance (t = 6.91, $P<0.001$, $R^2 = 0.82$), whereas all flowers combined had less explanatory power (t = 2.83, $P<0.008$, $R^2 = 0.64$). Year was a highly significant factor in all models ($P<0.001$) due to strongly differing weather conditions. Year 2 was characterised by cold and wet weather, resulting in very low pollinator numbers. In contrast, year 4 was warm and dry with a 'blanket' of pollinators covering the area, with little discrimination among regimes (Fig. 3c).

3.3 birds

Over the four years, 4870 observations of 60 bird species over 14423 individuals were made (Appendix B). Overall, effects of the grazing regimes on bird densities were weak. Although the models of several functional groups showed significant estimates for some of the factors, including the interaction between livestock species and density, the models did not significantly differ from null models at the 5% level (Table 1, Fig. 4).

3.4 Voles

Overall, voles were present in 29% of the 696 plots checked. Vole presence was significantly higher under low stocking densities ($P<0.001$), and under cattle grazing ($P<0.001$; Table 1, Fig. 5).

3.5 Multidiversity

Multidiversity did not significantly differ among the grazing regimes (Table 1). Graphs of the species richness of each group per paddock can be found in Appendix A (Fig. A2).

4 Discussion

Overall, we found significant effects of stocking density on almost all measured variables, and some differences between livestock species. Our hypothesis that effects of horse grazing are always greater than those of cattle at the same stocking density was not supported, since for most variables no differences or differences contrasting over the two densities were found. Evidence for cascading effects beyond pollinators and voles were not found. The multidiversity metric showed no differences among regimes, which was probably caused by the contrasting trends for plants and pollinators in combination with non-significant differences for all bird groups (Fig. A2). Its usefulness in conservation science thus needs further validation.

We found a trend for suppression of the grass *E. atherica* under high density grazing, but high variability between the replicates makes it hard to draw strong conclusions. In a large scale experiment such as ours, such variability (i.e. *E. atherica* well established in the western replicate, but little cover in eastern replicate) is impossible to avoid. Nevertheless, this trend concurs with research at other sites showing that high-density grazing can prevent the spread of *E. atherica* (Bakker, 2014).

4.1 stocking density

Stocking density had strong effects on almost all variables measured here and in other publications on the same experiment (summarised in Table 2). This is in agreement with experiments both on salt marshes (e.g. Andresen et al., 1990; Kiehl et al., 1996; Rickert et al.,

2012) and in other grassland systems (e.g. Dennis et al., 1997; Evans et al., 2015; Kruess and Tscharntke, 2002; WallisDeVries et al., 2007).

As hypothesised, plant species richness was higher under high stocking density, as vegetation height decreased. This suggests that competitive exclusion among plant species is indeed strong under low stocking densities, which may lead to future plant species losses. However, this was only found on the high marsh, while on the low marsh no differences in species richness were found. This is probably due to the already low overall plant species richness of the low marsh (average 7 and maximum 12 species per 16 m^2), and the short duration of the experiment relative to the gradual effects of competitive exclusion on plant species richness. The greater plant species richness on the high marsh may also be due to the lower cover of *E. atherica* under high stocking densities.

Suppression of the competitive grass *E. atherica* tended to be most successful under high stocking densities. However, under such conditions, vegetation structural heterogeneity and complexity is strongly reduced (Nolte et al., 2014), with unfavourable consequences for other biota. Structurally heterogeneous vegetation supports more invertebrate species (Dennis et al., 1997; van Klink et al., 2013), and nest sites for birds (Mandema et al., 2015, 2014a; Norris et al., 1998) than homogeneous short-grazed vegetation does, and is thus preferable from a conservation perspective. By contrast, staging geese may benefit from a homogeneous short-grazed vegetation structure because of its high nutritional value (Mandema et al., 2014b), and can thus be expected to become less abundant on marshes grazed at low stocking densities where the vegetation is higher (Bos et al., 2005).

As was also predicted, the abundance of voles and pollinators decreased with increasing stocking density due to a decrease in vegetation cover and flower abundance. For the pollinators, this was explained by the abundance of Asteraceae flowers, which are a high quality resource. This was expected, since for pollinators reproduction does not take place on the salt marsh, and thus the abundance of floral resources together with weather conditions will determine the abundance of pollinators on the salt marsh. Because of their importance for plant reproduction and as potential food source for birds, a decrease in pollinator abundance can have severe consequences for ecosystem processes. The results of voles should be interpreted with some caution, as we sampled voles only once (at peak population), while voles show multi-annual cycle dynamics (Villar et al., 2014). However, we are confident that our results give a good representation of the relative effects of the grazing regimes, since the processes by which the voles are affected (most importantly defoliation and trampling) should be independent of vole population cycles.

Our experimental regimes had no significant effect on the abundances of the different functional groups of birds. This was surprising, since we previously found strong evidence of habitat deterioration in the short-grazed vegetation, especially under high density horse grazing: decreased vegetation height and heterogeneity (Nolte et al., 2014), increased nest trampling risk (Mandema et al., 2013), and decreased prey abundance (van Klink et al., 2014). It must be noted, however, that also under low stocking densities, nest trampling can be substantial (Sharps et al., 2015). Such a lack of detectable effects on birds is not uncommon in grazing experiments (e.g. WallisDeVries et al., 2007), but somewhat contrasts other research, where highest densities of breeding Meadow Pipits and other breeding birds were found under intermediate (Evans et al., 2006) or high sheep grazing densities (Loe et al., 2007). However, these studies were conducted with a different livestock species and in different biotopes, complicating generalisations.

Several factors may have contributed to the general absence of detectable effects on birds. First, the scale of our experimental paddocks in comparison to the foraging range and nest density of birds was relatively small. The number of breeding territories counted in year 2 was ca. 1 and 0.5 territories per hectare in the central and eastern replicates, respectively (data from Esselink et al., 2015). Second, the complex relation between abundance and accessibility of food resources in grazed systems (Evans et al., 2006) may have obscured the relation between birds and their resources. Also the different grazing histories of the replicates may factor into this, if the resource abundance was differently affected by grazing in the different replicates. A final reason may be that breeding sites had been chosen before grazing commenced in late May/early June.

4.2 livestock species

Choice of livestock species was of less importance than stocking density, which is in line with previous research (e.g. Boschi and Baur, 2007; Jerrentrup et al., 2015; Öckinger et al., 2006). However, we did find some significant differences between cattle and horses. The foremost difference is that more trampling takes place under horse than under cattle grazing (Mandema et al., 2013). This results in higher probabilities of bird-nest losses, and can also account for the lower densities of voles and lower sediment accretion rates (Nolte et al., 2015). Additionally, trampling was shown to significantly affect flower abundance of *A. tripolium* (Nolte et al., 2013). Here, trampling interacted with dietary differences: under high stocking densities *A. tripolium* was damaged more by horses due to their greater mobility, but under low densities more by cattle due to their selective foraging for *A. tripolium*. Experimental grazing on German salt marshes has shown that sheep have an even higher preference for *A. tripolium*, and can almost completely remove the species from the system (Kiehl et al., 1996). Trampling and consumption of *A. tripolium* have strong detrimental effects on its rich herbivorous insect community (van Klink and van Schrojenstein Lantman, 2015) and its pollinators. Lastly, some evidence was found that cattle induce a more fine-grained vegetation patchiness compared to horses (Nolte et al., 2014).

4.3 relevance to other systems and conclusion

Many of our results are likely applicable to a range of other grassland types where grazing is used for conservation management. Despite the obvious differences in species pool characteristics, environmental conditions such as productivity and soil type, and ecological complexity, the mechanisms involved can be expected to be similar. Consequently, the responses of the studied species groups to different grazing regimes (low vs. high stocking density, ruminant vs. hindgut feeder) may be comparable. Additionally, our results highlight the importance of studying different trophic groups in order to avoid erroneous management decisions based on single taxa.

No single management type (i.e. grazing regime) was beneficial to all studied groups. Horse grazing at high densities does not provide many benefits to biodiversity and can therefore be discarded as a management option for conservation purposes. In contrast, long-term abandonment, which has been intensively studied elsewhere, proves to have beneficial effects on many, but not all invertebrate species (Rickert et al., 2012; van Klink et al., 2013). Therefore we thus recommend several types of management to be applied concurrently, including long-term abandonment, in order to maximise the biodiversity potential of an area.

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Table 1. Summary statistics of all GLMMs. *P*-values in bold indicate significant effects at $P < 0.05$.

				livestock density			livestock species			species*density			MODEL	
		unit	distribution	estimate	test statistic	*P*	estimate	test statistic	*P*	estimate	test statistic	*P*	χ^2	*P*
Plants														
Cover change *E. atherica*		% per paddock	Gaussian	-0.19±0.09	t = -1.99	0.08			ns			ns	3.99	**0.046**
Log mean vegetation height (cm)	high marsh	per PQ	Gaussian (log)	-1.02±0.26	t = -3.98	**<0.01**			ns			ns	11.12	**<0.001**
	low marsh	per PQ	Gaussian (log)	-1.21±0.38	t = -3.19	**0.01**						ns	7.40	**0.006**
Plant species richness	high marsh	per PQ	Poisson	0.40±0.09	z = 4.39	**<0.001**			ns			ns	11.13	**<0.001**
	low marsh	per PQ	Poisson			ns			ns			ns	0.27	0.6
Flowers and pollinators														
Total flower abundance		per 80 m^2	Poisson^1	-0.28±0.14	z = -2.09	**0.04**			ns			ns	3.55	0.06
Asteraceae flower abundance		per 80 m^2	Poisson^1	-0.06±0.04	z = -1.61	0.1	0.90±0.42	z = 2.12	**0.03**	-0.13±0.05	z = -2.42	**0.02**	15.83	**0.001**
A. tripolium flower abundance		per 80 m^2	Poisson^1	-0.18±0.04	z = -4.44	**<0.001**			ns			ns	12.03	**<0.001**
Other flower abundance		per 80 m^2	Poisson^1			ns			ns			ns	1.71	0.19
Pollinator abundance		per 500 m transect	Poisson^1	-0.12±0.03	z = -3.5	**<0.001**			ns			ns	6.83	**0.004**
Birds														
Meadow pipit (density)	all year	per paddock*	Poisson^1	0.73±0.44	z = 1.65	0.1	0.64±0.50	z = 1.29	0.19	-1.24±0.64	z = -1.95	**0.05**	6	0.097
PB foraging on marsh (density)	(spring)	per paddock*	Poisson^1			ns			ns			ns	4.01	0.26
PB not foraging on marsh (density)	(spring)	per paddock**	Poisson^1			ns			ns			ns	0.02	0.88
NB foraging on marsh (density)		per paddock*	Poisson^1	0.23±0.18	z = 1.29	0.2	0.44±0.21	z = 2.14	**0.03**	-0.59±0.26	z = -2.26	**0.02**	4	0.246
NB not foraging on marsh (density)		per paddock**	Poisson^1	2.00±0.70	z = 2.84	**<0.01**	1.76±0.80	z = 2.20	**0.03**	-2.35±0.98	z = -2.40	**0.02**	6.47	0.09
Raptors (density)		per paddock**	Poisson^1			ns			ns			ns	0.26	0.61
All birds (density)	all year	per paddock*	Poisson^1			ns			ns			ns	4.47	0.22
Voles														
Vole presence		per 60 subplots	Binomial	-0.18±0.04	z = -4.91	**<0.001**	-1.35±0.19	z = -7.15	**<0.001**			ns	76.9	**<0.001**
Multidiversity														
Multidiversity of 7 functional groups		per paddock	Gaussian			ns			ns			ns	1.84	0.61

* Density estimated by distance sampling per paddock per year. **Estimated per paddock per four years. [1]Overdispersion was corrected using individual level random effects. PP = permanent plot, PB = potential breeding birds, NB = non-breeding birds.

Table 2: Summarised effects of livestock species and density in this experimental setup, reported here and elsewhere: ↓: negative effect, ↑: positive effect, =: no effect, ↕: interactive effect, and causal mechanism per group. 'H' indicates that the direction of the effect relates to horse grazing. PB: potential breeding birds; NB: non-breeding birds. Symbols between parentheses represent marginally significant effects (0.1>P>0.05).

		Effect of increasing stocking density	**Effect of livestock species**	mechanism(s)	**source** (if other than this paper)
Plants					
Cover *E. Atherica* vegetation type		(↓)	=	trampling / defoliation	
Vegetation height	high marsh	↓	=	trampling / defoliation	
	low marsh	↓	=	trampling / defoliation	
Plant species richness	high marsh	↑	=		
	low marsh	=	=		
Patch size		(↑)	↑H	selectivity	a
flowers and pollinators					
Aster tripolium flowers		↕	↕	trampling / defoliation	b
Total flower abundance		↓	=		
Asteraceae abundance		↕	↕	trampling / defoliation	
Other flower abundance		=	=		
Pollinator abundance		↓	=		
Birds					
Meadow pipits		=	=	defoliation	c
PB foraging on marsh		=	=		
PB not foraging on marsh		=	=		
NB foraging on marsh		=	=		
NB not foraging on marsh		=	=		
Raptors		=	=		
All birds		=	=		
Nest trampling		↑	↑H	trampling	d
Geese abundance	autumn	↑	↑H		e
	spring	=	=		e
Voles					
Presence		↓	↓H	trampling(?)	
Multidiversity		=	=		
Sediment accretion		↓	(↓H)	defoliation / trampling	f

Sources: (a) Nolte et al. (2014); (b) Nolte, Esselink & Bakker (2013); (c) van Klink et al. (2014); (d) Mandema et al. (2013); (e) Mandema et al. (2014b); (f) Nolte et al. (2015).

FIGURES

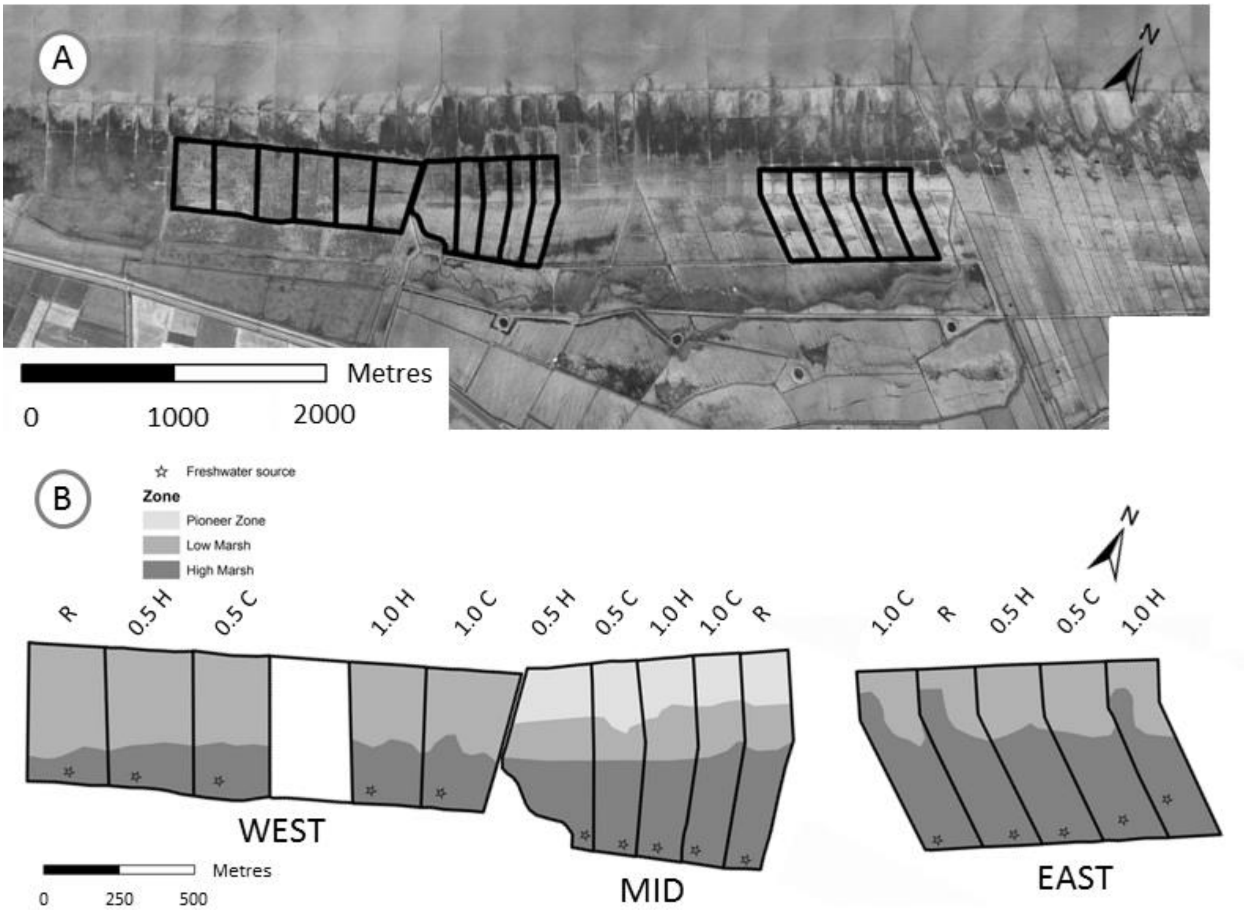

Figure 1: Overview of the grazing experiment at the salt marshes of Noord-Friesland Buitendijks (A). Experimental setup (B) with grazing regimes indicated as 0.5 = 0.5 animal ha^{-1}; 1.0 = 1.0 animal ha^{-1}; H = horse; C = cattle and R = rotational regime. Locations of the PPs and pollinator, bird, and vole transects can be found in Appendix A.

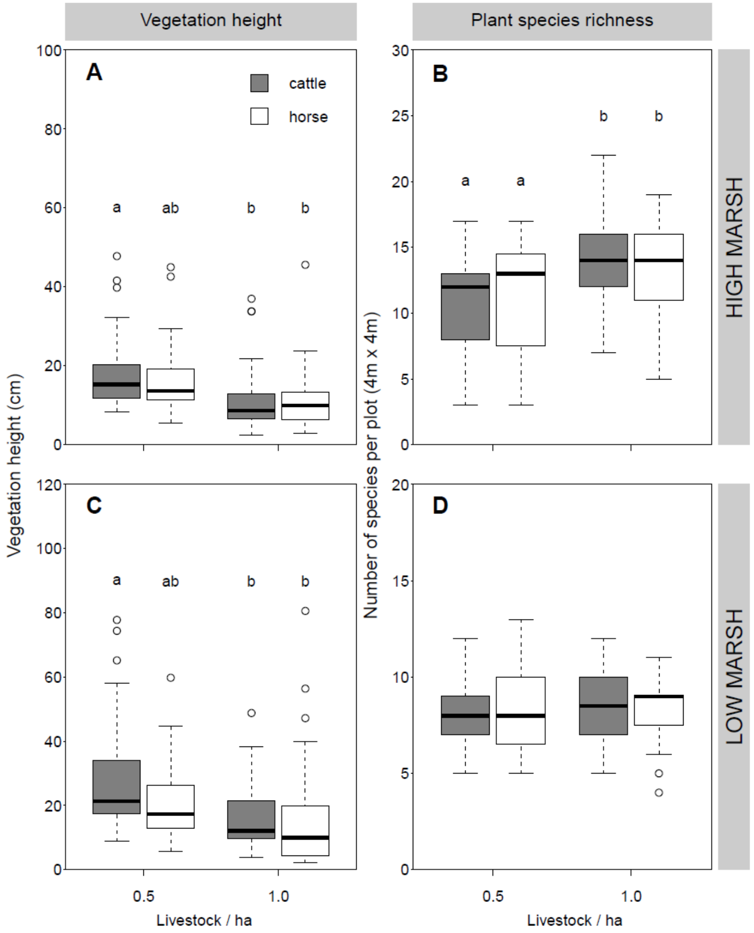

Figure 2: Effects of grazing by different livestock species (cattle or horse) at two densities (0.5 and 1 animal per hectare) on vegetation height and plant species richness. Boxes represent the raw data: 25% and 75% quartiles from the median (thick line), whiskers represent the maximum or minimum values, excluding outliers, and outliers are defined as more or less than 1.5 times the interquartile range. Significant differences among regimes indicated by post-hoc Tukey tests with all regimes as separate factors are indicated by different letters.

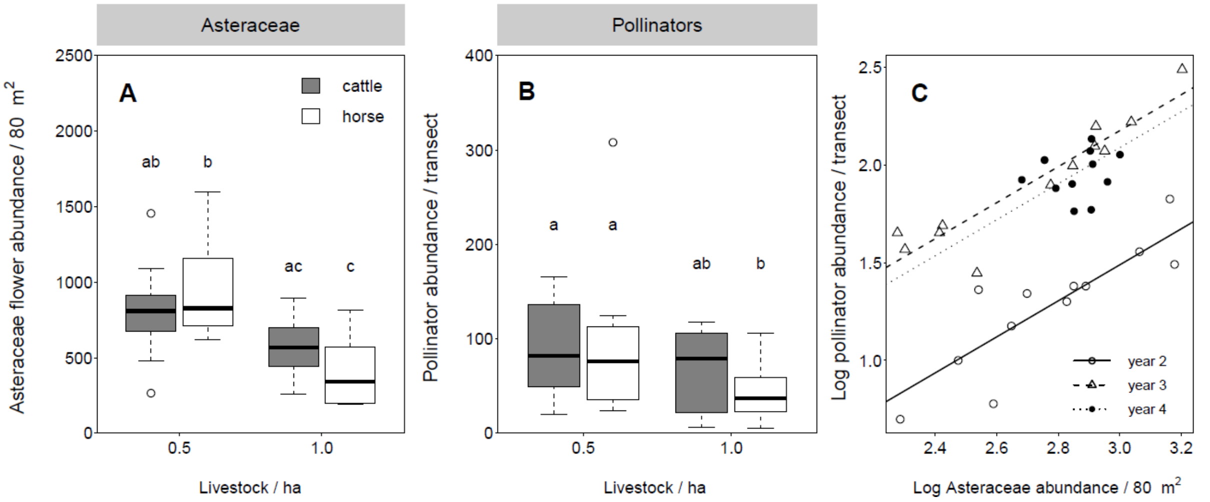

Figure 3: The estimated abundance of Asteraceae flowers (A) and pollinators (B) under four grazing regimes. (C) The relationship between Asteraceae and pollinator abundance per transect. The large annual differences can be ascribed to strong differences in weather conditions, where year 2 was particularly cold and wet. Boxplot and letter attributes as in Fig. 2.

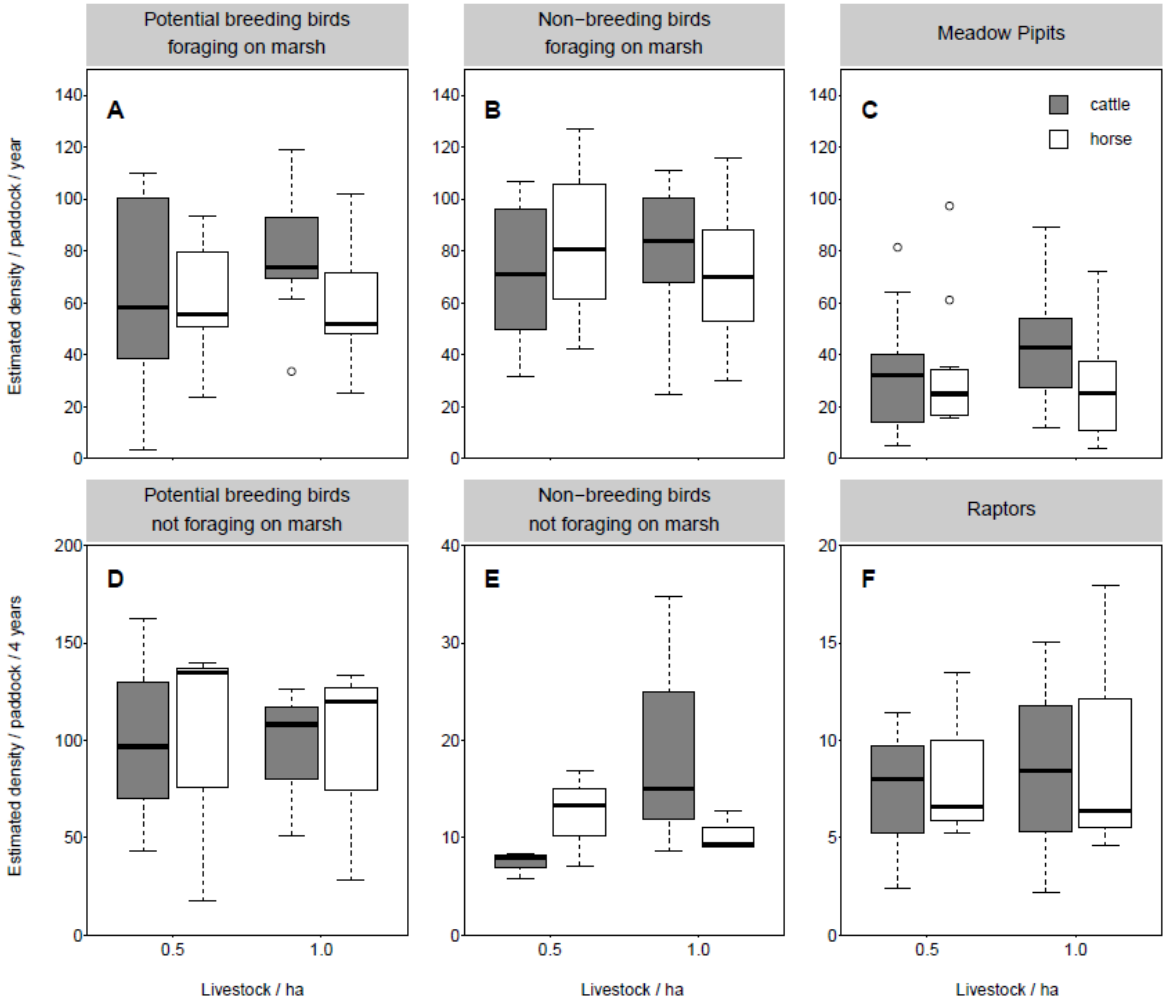

Figure 4: Estimated density of birds (number of individuals per 11 ha) of different functional groups over the four grazing regimes. Due to low numbers of sightings per year, densities of the functional groups on the second row were estimated per four years. Boxplot attributes as in Fig. 2.

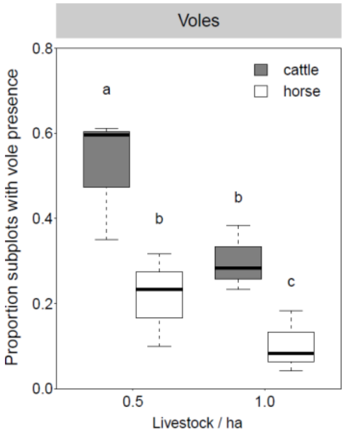

Figure 5: Proportion of subplots (60 subplots per paddock) with vole presence in year 4. Boxplot and letter attributes as in Fig.2.