Disturbance–diversity relationships for soil fauna are explained by faunal community biomass in a salt marsh

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A B S T R A C T

Disturbance–diversity relationships have long been studied in ecology with a unimodal relationship as the key prediction. Although this relationship has been widely contested, it is rarely tested for soil invertebrate fauna, an important component of terrestrial biodiversity. We tested disturbance–diversity relationships for soil meso- and macrofauna in a salt marsh where periodic sea water inundation and cattle grazing occur as stressors. We hypothesized a unimodal inundation frequency–diversity relationship, whereas we expected grazing to overrule the effects of inundation frequency due to its large effects on the habitat of soil fauna. We found a negative relationship between inundation frequency and diversity at the ungrazed sites and no relationship at the grazed sites. Moreover, we found a negative relationship between community biomass and diversity for soil fauna that may have caused this negative disturbance–diversity relationship. Community biomass at the intermediate inundation frequency increased due to the dominance of *Orchestia gammarellus* (a macro-detritivore species), which could exploit low quality litters at the ungrazed sites. We highlight that the negative relationship between faunal community biomass and faunal diversity may influence disturbance–diversity relationships and illustrate that total biomass distribution of feeding guilds of soil fauna can improve our understanding of the soil fauna response to stressors in salt marshes.

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1. Introduction

Disturbances have long been argued to contribute directly and indirectly to species diversity (Kolasa et al., 1989; Maarel, 1993; Buckling et al., 2000). In general, it has been suggested that intermediate levels of disturbances or stress, both in terms of frequency and in intensity, maximize biodiversity, the so-called Intermediate Disturbance Hypothesis (IDH) (Connell, 1978; Huston, 1999; Wilkinson, 1999; White and Jentsch, 2001; Dos Santos et al., 2011). However, the proposed unimodal relationship between environmental disturbance or stress and diversity as suggested by the IDH is often not supported by empirical studies (Mackey and Currie, 2001; Hughes et al., 2008; Fox, 2012). The deviations from the unimodal relationship between disturbance and diversity have been attributed to several factors, such as site conditions, species traits, as well as the frequency and magnitude of the disturbances (Wootton, 1998; Sheil and Burslem, 2003; Shea et al., 2004). Hence, the need for studying the factors that can cause deviations from unimodal disturbance–diversity relationships has been stressed (White and Jentsch, 2001; Shea et al., 2004; Haddad et al., 2008).

Several mechanisms underlying the unimodal relationship between disturbance and diversity have been postulated. One general assumption is that long-living species are not able to thrive in highly disturbed sites, whereas colonizer species, such as *r*-strategists, in less disturbed sites are outcompeted by competitively superior species (Shea et al., 2004). Both long-living and colonizer species are however expected to co-exist in between these extremes, therefore resulting in higher biodiversity at intermediate disturbance levels (Connell, 1978; Zobel, 1997; Martin, 2001; Shea et al., 2004). Mechanisms that promote co-existence among

species may also depend on factors like species' ability to utilize and partition resources (Buckling et al., 2000; Shea et al., 2004; Haddad et al., 2008). The ability of species in communities to utilize and partition resources is often reflected in the net productivity of the communities or the community biomass (total biomass of the co-occurring species within a community) (Post and Pedersen, 2008). Fluctuations in community biomass may provide explanations for the variations in disturbance–diversity relationships (Gough et al., 1994; Huston, 1994; Kondoh, 2001). For instance, the increase in the community biomass due to an increase in dominant species in the absence of disturbance may shift the community composition and thus decrease species diversity (Kondoh, 2001). Moreover, local environmental conditions such as habitat and resource heterogeneity in case for soil fauna could equally determine soil fauna diversity (Decaëns, 2010). The extent to which disturbances may alter local environmental conditions therefore is crucial to understand how much disturbance could influence local species diversity.

In this study, we analyze how the diversity and biomass of soil fauna communities change in the presence of two distinct types of stressors in a salt marsh: sea water inundation (physical stress) creating an abiotic stress gradient in terms of inundation periodicity and salinity, and cattle grazing (abiotic and biotic stress) creating differences in vegetation and leaf litter biomass, available soil pore space and redox potential of the soil (Schrama et al., 2012). Along the stress gradient in a salt marsh, intermediate disturbance is likely to be found spatially in between highly stressed sites that are very frequently inundated with salt water, such as every day or every week, and in less frequently inundated sites with low stress levels, such as inundated once every year due to very high tides (Hacker and Bertness, 1999). Salt marshes have distinct vegetation zones due to this variation in periodic inundation (Olff et al., 1997), and they are also characterized by the presence of numerous soil fauna species varying in their density along the inundation gradient (Hacker and Gaines, 1997; Schram et al., 2012).

The soil fauna living in the sub-surface of the soil in salt marshes face regular abiotic stresses in terms of salinity and anoxic conditions by the periodic sea water inundation (Hacker and Gaines, 1997; Pennings and Bertness, 2001). Regular inundation can increase the mortality of some species (Evin and Talley, 2002), whereas other species are adapted to salinity and survive inundation for some duration (Witteveen and Joosse, 1987). For example, salinity-intolerant soil fauna are higher in density in more elevated parts of the salt marsh where inundation frequency is low (Pennings and Bertness, 2001; Ellers et al., 2010), while salinity-tolerant species are often absent at high elevation parts because they are outcompeted by intolerant species as salinity and anoxia tolerance comes at a cost. Essentially, due to differences in adaptation, diversity of soil fauna has been suggested to vary with the frequency of sea water inundation in salt marshes (Hacker and Gaines, 1997; Pennings and Bertness, 2001).

Cattle grazing in some salt marshes has historically been introduced as a management practice to improve livestock health, such as in the salt marshes of the Wadden Sea in the Netherlands (Bakker, 1985), and as a nature conservation approach to reduce the presence of the grass species Elytrigia athericus. The parts of salt marshes that are grazed by cattle have a short vegetation height and low leaf litter biomass (Andresen et al., 1990; Bos et al., 2002; Wu et al., 2009). It is therefore likely that litter-feeding soil fauna have low densities in grazed sites due to reduced aboveground resource inputs (Andresen et al., 1990). Moreover, soil fauna in grazed sites is more exposed to light, with usually lower soil moisture content, higher temperatures, and stronger diurnal fluctuations in microclimate compared to ungrazed sites due to short vegetation (Andresen et al., 1990). Cattle grazing also changes soil

characteristics that increase the susceptibility of nutrient losses through water erosion (Neff and Reynolds, 2005), and trampling of fine-textured soil by cattle results in significant soil compaction, reduction in soil porosity and locally anoxic conditions (Schrama et al., 2012). All these effects of grazing together might result in lower soil fauna biomass in grazed sites compared to ungrazed sites (Andresen et al., 1990; Schrama et al., 2012). Moreover, grazed and ungrazed sites may differ in the composition of feeding guilds in the soil. For example, ungrazed sites have been found to be dominated by litter feeding macro-detritivores, whereas invertebrate herbivores are generally higher in density in the grazed sites of salt marshes (Andresen et al., 1990; Schrama et al., 2013).

According to the intermediate disturbance hypothesis, we hypothesize soil fauna diversity to peak at the sites with an intermediate sea water inundation frequency, i.e. every month, which is intermediate between annual and daily/weekly flooding at the high and low elevation end of the gradient, respectively (hypothesis 1). Further, we hypothesize that cattle grazing will overrule the effects of inundation frequency on soil fauna diversity due to its large effects on the habitat of soil fauna (hypothesis 2). We also test the community biomass-diversity relationship for soil fauna at both cattle grazed and ungrazed sites along the inundation gradient and show that this relation may help explain patterns observed for the disturbance–diversity relation. We finally illustrate total biomass of soil fauna of key feeding guilds on the inundation gradient and in response to cattle grazing to highlight soil fauna responses to stresses and subsequent effects on soil fauna diversity.

2. Material and methods

2.1. Study sites

The study area was located on the salt marsh of Schiermonnikoog, a barrier island in the Wadden Sea, the Netherlands (53°28′43N, 6°14′06 E). The field study was carried out from October to November 2011. Seven sites were selected based on inundation frequency, in an area with and without cattle grazing (Table 1, see also Comor et al., 2014). We selected sites that were characterized by daily inundation, weekly inundation, monthly inundation and yearly inundation, representing the low, lower-middle, upper-middle and elevated parts of the salt marsh, respectively (Hacker and Bertness, 1999). The exact locations of the sites were based on the thickness of the clay layer, as clay depth indicates inundation frequency in this salt marsh and separates intertidal zones (Olff et al., 1997; Schrama et al., 2012). Except for the daily inundated site, we selected at each inundation frequency two sites with similar thickness of the clay layer: one with and one without cattle grazing (grazing intensity: 1.6 animals/ha, Bakker, 1985). In the area that inundated daily no cattle were allowed. The ungrazed sites were separated from the grazed sites by an electric fence.

2.2. Soil fauna collection

We collected soil mesofauna and macrofauna species, two dominant groups on this salt marsh (Schrama et al., 2012; Comor et al., 2014). The selection of these two soil fauna groups represents a large proportion of soil animals in terms of their feeding interactions and body size variation (Decaëns, 2010). The mean body sizes of the soil macrofauna, comprising invertebrates such as Coleoptera and Mollusca, ranged from 2 mm to 20 mm, whereas mesofauna, such as Collembola, ranged from 100 μm to 2 mm (Decaëns, 2010). For the mesofauna, we only included Collembola, which is the most dominant mesofauna group in the study area (Schrama et al., 2012). We studied soil mesofauna and macrofauna

Table 1
Key characteristics of the seven selected sampling sites. The highlighted text indicate dominant species.

Sites	Inundation frequency	Grazing	Intertidal zone	Clay depth (in cm)	Salinity (EC in dS/m)[a]	Plant species (% soil cover)
1G	Yearly	Present	High	5	3.62	*Festuca rubra* (90%), *Carex distans* (5%), *Plantago coronopus* (2%), *Armeria maritima* (2%), *Agrostis stolonifra* (1%)
1U	Yearly	Absent	High	5	1.42	*Elytrigia atherica* (100%)
2G	Monthly	Present	Upper-middle	10−15	7.50	*Festuca rubra* (90%), *Carex distans* (2%), *Armeria maritima* (2%), *Salicornia procumbens* (2%), *Limonium vulgare* (2%), *Plantago coronopus* (2%)
2U	Monthly	Absent	Upper-middle	10−15	6.09	*Elytrigia atherica* (99%), *Atriplex portulacoides* (1%)
3G	Weekly	Present	Lower-middle	15−20	6.60	*Puccinellia maritima* (95%), *Limonium vulgare* (2%), *Atriplex portulacoides* (3%)
3U	Weekly	Absent	Lower-middle	15−20	8.25	*Elytrigia atherica* (95%), *Atriplex portulacoides* (5%)
4	Daily	Absent	Low	>20	13.56	*Atriplex portulacoides* (70%), *Limonium vulgare* (5%), *Salicornia procumbens* (15%)

[a] EC stands for electrical conductivity and dS/m stands for decisiemens per meter.

species because some of the captured macrofauna species predate on Collembola (a direct interaction), whereas other macrofauna species alter soil conditions (an indirect interaction). Due to these direct and indirect interactions, disturbance-induced effects on one group of taxa (for instance macrofauna) may directly or indirectly affect others (for instance Collembola).

Soil surface active macrofauna was collected using enclosed pitfall traps and identified in the laboratory using established keys. The pitfall traps were 10.5 cm wide and 12 cm deep. The traps were placed in the four corners of each 50 cm × 50 cm plot, enclosed with Perspex plates to enable density estimates of each species. The Perspex plates were forced into the ground to prevent soil organisms to escape. In total, we sampled four 50 cm × 50 cm plots in each of the seven sites, resulting in a total of 112 pitfall traps. The animals were collected from the pitfall traps every 24 h for 7 days, assuming most of the species within the 50 cm × 50 cm plots to be collected (Schrama et al., 2013). We used a detergent on the walls of pitfall traps (that makes wall smooth) every 24 h to prevent the escape of animals. Trapped animals were stored in 70% ethanol, and identified to at least family level, sometimes to genus levels and a few species to the species level except for spiders (Supplementary material Table S1). Spiders were separated into two groups: large and small individuals. All the individuals from the pitfall traps were dried in an oven at 105 °C for 24 h and later their dry body mass was measured (to the nearest g).

We extracted Collembola species from soil cores (10 cm diameter, 5 cm depth, taken with an auger) using Tullgren funnels, in which soil cores were kept upside-down for three weeks (Van Straalen and Rijninks, 1982), and we identified them to the genus or species level using the key from Hopkin (2007). The sampling depth of 1−5 cm is where the Collembola community is most abundant in the studied salt marsh (Schrama et al., 2012). Four samples per site from the 50 cm × 50 cm plots were taken for Collembola extractions (in total 28 samples in 7 sites). The limited number of samples was due to time and budget constraints although our sampling effort was consistent with previous experiments in this salt marsh for studying soil fauna (Schrama et al., 2012, 2013; Comor et al., 2014). The dry body mass of Collembola species were calculated using allometric relationships from Caballero et al. (2004), where species-specific body length and exponent values are provided for individual biomass estimation of the major body forms.

All species were assigned to one of the following five feeding guilds: meso-detritivores (all Collembola species), macro-detritivores, predators, herbivores, and omnivores (Supplementary material Table S2). The total biomass for each feeding guilds are provided in Supplementary material Table S3. Taxa richness was measured as the number of taxa per plot. The

Shannon−Wiener diversity index per plot was calculated using McCune and Grace (2002): $H' = -\sum p_i \times \ln p_i$, where p_i is the proportion of the ith taxon. Pielou's evenness index per plot was calculated using McCune and Grace (2002): $J = H'/\log S$, where S is the total number of taxa. We added the Shannon−Wiener diversity index and Pielou's evenness index to better understand the observed relationship between disturbance and taxa richness.

2.3. Measurement of environmental variables

We measured abiotic variables to characterize soil conditions relevant to soil invertebrates in the salt marsh: elevation above sea level, soil salinity and soil C: N ratio. The elevation of each 50 cm × 50 cm plot was measured using a leveling instrument (Lietz/Sokkisha B2A automatic level, Tokyo, Japan). An electrical conductivity meter was used to measure soil salinity. The soil samples for the salinity measurements were extracted from the top 10 cm of the soil using an auger (2 cm diameter) at each of the seven sites. Soil C and N contents were measured using a CHN−O analyzer (Fisons Instruments EA 1108, CE Instruments, Milan, Italy).

Further, we also measured biotic variables that might determine the soil fauna community composition: vegetation biomass, leaf litter dry mass and litter C: N ratio. Aboveground vegetation biomass and soil surface leaf litter were hand-sorted at each of the seven sites using quadrate sampling (50 cm × 50 cm) adjacent to the plots used for animal extraction (to avoid disturbance) and dried in the oven at 70 °C for 48 h. The dried biomass was expressed as g m^{-2}. Litter C and N concentrations were estimated using a CHN−O analyzer (Fisons Instruments EA 1108, CE Instruments, Milan, Italy). For each site, we also determined the vegetation composition by measuring the cover of the dominant plant species that were present during the experimental period, using random quadrate sampling of 50 cm × 50 cm plots nearby the plots where we collected soil animals.

2.4. Statistical analysis

First, principal component analysis (PCA, unconstrained ordination) was used to characterize the seven sites in terms of (a) the abundances of animal taxa (Supplementary material, Table S1) and (b) their feeding guilds (Supplementary material, Table S2), and we correlated the axes with the environmental variables. Both abundances of animal taxa and feeding guilds were expressed as number of ind. m^{-2}. In two separate PCAs, taxa abundance and feeding guilds were used as "species" and in both cases, the same set of environmental variables was used. The PCAs were done in Canoco 4.5 (Ter Braak and Smilauer, 2002), in which species were centered and log-transformed.

We then carried out a Two-way ANOVA to test differences between taxa richness, the Shannon—Wiener diversity index and Pielou's evenness index between the inundation (4 levels: daily, weekly, monthly and yearly) and grazing treatments (2 levels: with and without grazing) and their interaction (hypotheses 1 and 2). We used LSD post-hoc multiple comparison tests for hypothesis 1 (unimodal relationship suggested by IDH), else we used the more conservative Tukey post-hoc multiple comparison tests. LSD post-hoc multiple comparisons are less conservative than Tukey tests and are often used with a clear prior expectation such as for IDH (Saville, 1990). Two-way ANOVA and subsequent Tukey post-hoc multiple comparisons were carried out for testing differences in total biomass of feeding guilds of soil fauna among inundation frequency and between cattle grazed and ungrazed sites and the interactions between inundation frequency and cattle grazing. Finally, we used linear regression to analyze the relationship between faunal community biomass and taxa diversity and the differences in this relationship between the grazed and ungrazed sites. When needed, we ln-transformed dependent variables to meet the requirements of normally distributed residuals and homogeneity of variances. Statistical analyses were carried out in SPSS (version 16; Two way-ANOVA and multiple comparisons) and R statistical software version 2.15.2 (R Development Core Team, 2012; linear regressions).

3. Results

3.1. Soil fauna distribution

In total we identified 34 soil fauna taxa. The first axis of the PCA for soil fauna taxa composition explained almost 71% of the total variation in the faunal distribution across sites, whereas the second axis explained nearly 22% of the total variation (Fig. 1a). The first axis was negatively correlated with soil and animal C: N ratio, and positively correlated with shoot and leaf litter biomass, whereas the second axis was negatively correlated with all the remaining environmental variables. The grazed site in the high elevated area (i.e. annually inundation; site 1G) was characterized by the presence of many taxa of which a large proportion belonged to Collembola. The abundances of Collembola species were lower at the

Table 2
ANOVA results for the three different measurements of species diversity along the inundation gradient and between grazed and un-grazed sites.

Diversity index	Factors	df	F-value	p-value	Adj-R^2
Species richness	Inundation	3	41.694	<0.001	0.83
	Grazing	1	12.530	0.002	
	Inundation × Grazing	2	5.769	0.010	
Shannon—Wiener diversity index	Inundation	3	8.978	0.001	0.68
	Grazing	1	7.396	0.013	
	Inundation × Grazing	2	16.729	<0.001	
Pielou's evenness	Inundation	3	15.835	<0.001	0.79
	Grazing	1	2.503	0.129	
	Inundation × Grazing	2	21.810	<0.001	

ungrazed sites of the upper-middle and lower-middle salt marsh (sites 2U and 3U), where inundation occurs monthly and weekly, respectively. By contrast, macro-detritivores, such as the amphipod *Orchestia gammarellus* and mollusk *Ovatella* sp. had higher abundances at these sites (Fig. 1a, Table S1).

The PCA for feeding guilds showed that macro-detritivores and predator taxa were more abundant in the ungrazed upper-middle and lower-middle salt marsh (sites 2U and 3U) (Fig. 1b). The upper salt marsh (sites 1G and 1U) was characterized by the presence of meso-detritivores and herbivores. In the lower marsh (site 4U), the abundance of omnivores was highest. The first PCA axis explained 61% of the total variation in feeding guilds, and was negatively correlated with soil C: N ratio and leaf litter biomass, whereas the second axis explained 38.9% of the total variance and was negatively associated to litter biomass, litter C: N ratio and shoot biomass.

3.2. Taxa diversity

Inundation, cattle grazing and the interaction between the two factors significantly explained the variation in taxa richness, the Shannon—Wiener diversity index and Pielou's evenness index, except cattle grazing did not explain Pielou's evenness (Table 2). Post-hoc multiple comparisons showed that the Shannon—Wiener diversity index was highest at ungrazed, annually inundated sites, whereas taxa richness was highest at ungrazed, annually and
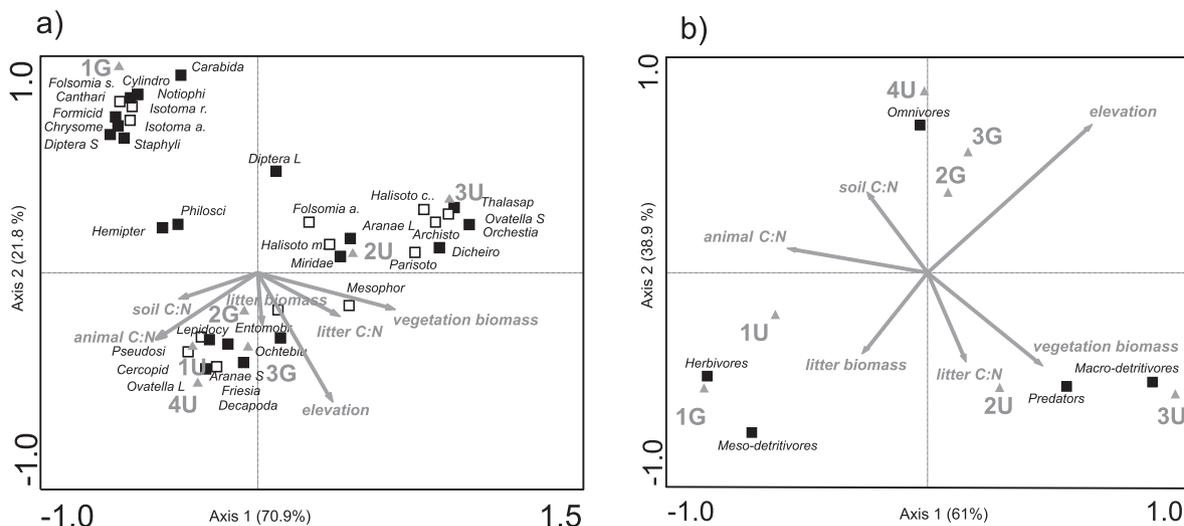

Fig. 1. PCA ordination diagram for a) soil fauna species and environmental variables at the seven sites, b) feeding guilds of soil fauna and environmental variables. The numbers in the figure (gray closed triangle) represent the sites, details of which are provided in Table 1. The closed rectangles in panel (a) indicate macro-fauna density and open rectangles indicate Collembola density; closed rectangles in panel (b) indicate feeding guild density. The full names of taxa are provided in the supplementary material (Supplementary material Table S1). Arrows in both panels show environmental variables (in gray text).
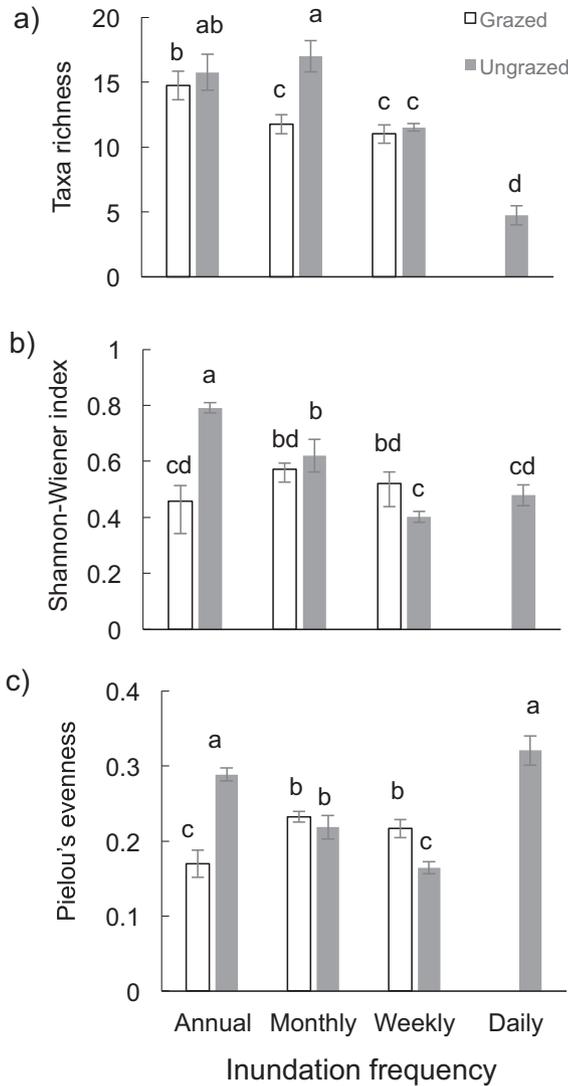
Fig. 2. Mean (±SE) of a) taxa richness, b) Shannon–Wiener diversity index and c) Pielou's evenness index for seven sites across the inundation gradient and with and without cattle grazing. The letters indicate significant differences based on the LSD post-hoc multiple comparison test.

Fig. 3. Relationships between community biomass and a) taxa richness, b) Shannon–Wiener diversity index, and c) Pielou's evenness index for grazed and ungrazed sites. For each relationship, the adjusted R^2 is given. Asterisk indicates that the slope of the relationship deviates from zero with $p < 0.05$.

monthly inundated sites (Fig. 2). Pielou's evenness was also highest at ungrazed annually inundated and daily inundated sites.

3.3. Community biomass and total biomass of feeding guilds

We found a significant negative relationship between community biomass and both the Shannon–Wiener diversity index ($b = -0.022$, $t = -2.564$, p-value = 0.022) and Pielou's evenness index ($b = -0.010$, $t = -2.972$, p-value = 0.010) for the ungrazed sites (and not for taxa richness: b = -0.45, $t = -0.149$, p-value = 0.884), but no significant relationship between all three measures for taxa diversity and community biomass for the grazed sites (taxa richness: b = -1.552, $t = -1.465$, p-value = 0.174, Shannon–Wiener index: b = 0.018, $t = 0.334$, p-value = 0.745, and Pielou's evenness index: b = 0.016, $t = 0.752$, p-value = 0.469) (Fig. 3).

Feeding guild biomass varied across the inundation gradient and also with grazing (Table 3, Fig. 4). Sites with annual inundation frequency and cattle grazing had the highest biomass of meso-detritivores (Fig. 4a). The total biomass of the macro-detritivorous
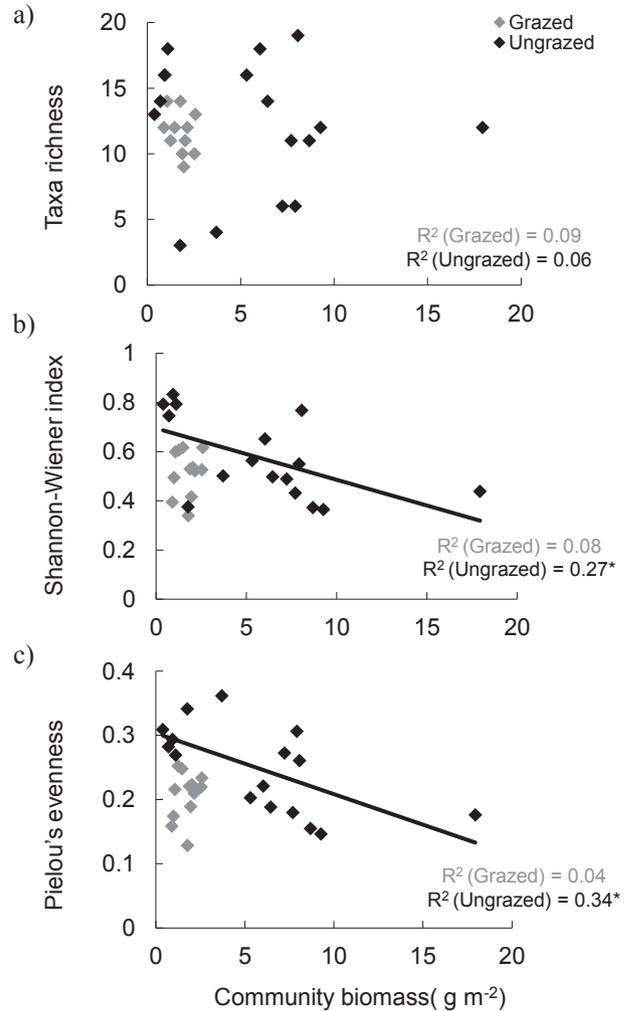
guild was highest at the monthly and weekly inundated sites compared to the annual and daily inundated sites, mainly at the ungrazed parts (Fig. 4b). The total biomass of predators was rather consistent across the inundation gradient, except for the high

Table 3
ANOVA results for differences in total biomass along the inundation gradient and between grazed and un-grazed sites for the five feeding guilds: a) meso-detritivores (ln-transformed), b) macro-detritivores, c) predators, d) herbivores and e) omnivores (ln-transformed).

| Feeding guilds	Factors	Df	*F*-value	*p*-value	Adj-R^2
Meso-detritivores	Inundation	3	24.080	<0.001	0.74
	Grazing	1	0.138	0.714	
	Inundation × Grazing	2	2.577	0.100	
Macro-detritivores	Inundation	3	21.448	<0.001	0.78
	Grazing	1	32.732	<0.001	
	Inundation × Grazing	2	9.079	0.001	
Predators	Inundation	3	5.458	0.006	0.44
	Grazing	1	0.014	0.906	
	Inundation × Grazing	2	5.048	0.016	
Herbivores	Inundation	3	5.794	0.005	0.33
	Grazing	1	0.059	0.810	
	Inundation × Grazing	2	0.727	0.495	
Omnivores	Inundation	3	12.551	<0.001	0.72
	Grazing	1	6.391	0.020	
	Inundation × Grazing	2	4.677	0.022	
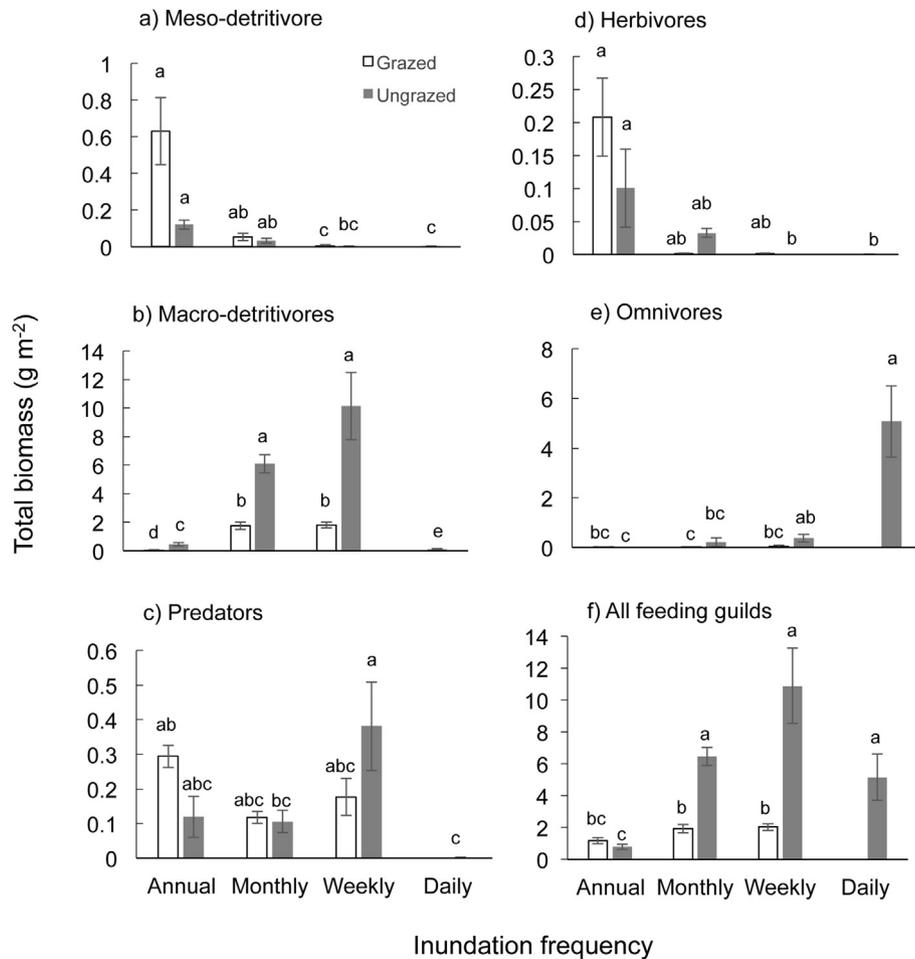
Fig. 4. Mean (±SE) of the community biomass of soil fauna for the five feeding guilds: a) meso-detritivores, b) macro-detritivores, c) predators, d) herbivores and e) omnivores. The letters indicated differences based on the Tukey's HSD post-hoc multiple comparison test.

biomass at the weekly inundated ungrazed sites (Fig. 4c). The total biomass of herbivores decreased with increasing inundation frequency (Fig. 4d), whereas the total biomass of omnivores was highest at the daily inundated sites (Fig. 4e). The total biomass of all feeding guilds was highest at the weekly inundated ungrazed sites, however, it was not significantly different from the monthly (ungrazed) and daily inundated sites (Fig. 4f).

4. Discussion

We did not find the expected peak of faunal diversity at the monthly inundated salt marsh, i.e. where the inundation frequency with sea water was intermediate between daily/weekly and annual inundation, hence contradicting our hypothesis 1. We observed two other kinds of disturbance–diversity relations: a negative relationship between disturbance and diversity at the ungrazed sites and no relationship at the grazed sites. At the ungrazed sites, both the Shannon–Wiener diversity index and Pielou's evenness index decreased with increasing inundation frequency except at the daily inundated site. As the thickness of the clay layer was used as proxy of inundation frequency, our results show that faunal diversity declined with increasing clay layer thickness (increasing inundation frequency) except for the daily inundated sites. We found significant interaction effects between inundation frequency and grazing on faunal diversity indicating that the presence of soil fauna taxa at a particular site is driven by both grazing effects, such as mediated by litter availability and soil compaction, as well as

inundation effects such as salinity. Moreover, the observed negative effects of inundation frequency on soil fauna diversity at the ungrazed sites was modified with cattle grazing, hence supporting our hypothesis 2 about stronger cattle grazing effects on faunal diversity than inundation frequency effects.

We found a significant negative relationship between community biomass and faunal diversity at the ungrazed sites, whereas no relationship was observed between community biomass and faunal diversity in the presence of cattle grazing. Community biomass was lower at the grazed sites than at the ungrazed ones. The negative relationship between community biomass and faunal diversity (Shannon–Wiener diversity index and Pielou's evenness index) suggests negative effects of competition on faunal diversity by higher community biomass (Guo, 2003), and some taxa dominated at high community biomass as indicated by the decrease of Pielou's evenness index with community biomass. Due to higher community biomass at the intermediately inundated sites, we can expect increased competition and dominance of few species, thus leading to a decline in faunal diversity. In the following, we will discuss what may have caused variations in faunal community biomass by highlighting patterns observed for the biomass of the five focal feeding guilds of the studied soil fauna.

Comparing the biomass of the different feeding guilds, we found that macro-detritivores dominated the ungrazed upper-middle and the lower-middle salt marsh (intermediately inundated sites). High biomass of macro-detritivores in the absence of large grazers has been reported to be due to a higher availability of litter mass

(Andresen et al., 1990; Schrama et al., 2013). The biomass of macro-detritivores was dominated by the amphipod *O. gammarellus* which has been reported to exhibit superior competitive ability in low quality litter (Kneib, 1984; Friend, 1986). *Orchestia gammarellus* is not only tolerant to salinity but can substantially alter the soil structure by acting as an ecosystem engineer (Schrama et al., 2012). Its profound effect on the local soil environment, such as by burrowing, may exert negative effects on other groups of soil fauna (Schrama et al., 2012). Moreover, *Orchestia* feeds on the microbial biofilm growing on the surface of leaf litter and is therefore a potential competitor of Collembola that also feed on litter fungi. We found Collembola species (meso-detritivores) to gradually decline towards the sites with increased frequency of inundation (Fig. 4 a), which could be due to species-specific intolerance to salinity, but also due to habitat unsuitability and competition caused by higher dominance of *O. gammarellus*. The PCA diagram (Fig. 1b) confirms that macro-detritivores were negatively associated with omnivores and meso-detritivores, whereas predators were positively related with macro-detritivores. Possibly *O. gammarellus* represents an important prey for many soil predators in the studied salt marsh (Dias and Sprung, 2003; Schrama et al., 2013). We argue that both the habitat unsuitability due to the frequent inundation as well as the negative effects of higher biomass of *O. gammarellus* on the other guilds were major determinants of the decline in soil faunal diversity along the inundation gradient.

The intermediate-disturbance hypothesis assumes that if the disturbance or stress is frequent, colonizing species are expected to dominate the ecosystem, whereas in ecosystems with low frequency of disturbances, competitive species dominate (Cadotte, 2007). In this study, on the contrary, we found that the monthly and weekly inundation frequency supported the competitively superior *O. gammarellus*, whereas colonizer species, such as the Collembola *Isotoma anglicana* (Dunger et al., 2004), dominated sites where inundation frequency was low. Regular inundation and high litter biomass of *Elytrigia atherica* at the ungrazed sites favored specialized groups of species, such as those with traits for salinity tolerance as well as the ability for exploiting low quality litter (Schrama et al., 2012). Such a pattern indicates that inferior colonizers (or superior competitors) can also increase in density at regularly disturbed sites mainly due to their disturbance-specific tolerance traits. The higher dominance of Collembola species at annually inundated sites indicates that these sites were high in litter quality and microbial biomass (Sabais et al., 2011; Szanser et al., 2011), and more so at the grazed sites with the presence of grass species such as *Festuca rubra* and *Carex distans* compared to nutrient-poor *Elytrigia atherica* litters (Kooijman and Besse, 2002). Collembola species, such as *Mesaphorura macrochaeta*, found at the frequently inundated sites have been reported to exhibit high tolerance to stress, such as salinity in this study, as well as surviving on low quality litter (Niklasson et al., 2000), meaning that only specialized groups of species and predators were able to co-exist with *O. gammarellus* at the monthly and weekly inundated sites of the ungrazed areas.

In conclusion, the observed disturbance–diversity relationship did not confirm the expected unimodal relationship and likely depended on the observed patterns of community biomass of soil fauna as has been suggested for plant communities (Gough and Grace, 1994; Guo et al., 1998). It could be possible that diversity patterns may have slightly differed if some studied taxa were identified to the species level (for instance spiders). The variations in community biomass were related to variations in the biomass of different feeding guilds that form the faunal community structure. Moreover, one dominant species behaved like an ecosystem engineer, with strong effects on soil structure and redox potential (Schrama et al., 2012), which might alter the unimodal relationship

between disturbance and diversity. In our studied salt marsh, where sea water inundation and cattle grazing occur together, we obtained two types of disturbance–diversity relationships: no relationship at the grazed sites and a negative relationship at the ungrazed sites. Our results highlight that disturbance–diversity relationships for soil fauna are context-dependent, for instance caused by distinct functional shifts, i.e. increase in total biomass of macro-detritivores, along the disturbance gradient.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2014.06.021.

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