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Grazing management in saltmarsh ecosystems drives invertebrate diversity, abundance and functional group structure

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1 Abstract

1. Saltmarsh conservation management often involves livestock grazing to maximise plant diversity and provide suitable breeding habitat for over-wintering coastal birds. The effect of grazing on invertebrates is rarely quantified, but results from limited studies of terrestrial and coastal grasslands demonstrate greater abundance and species richness in un-grazed grassland.

2. The impact of short sward (< 8 cm) cattle grazing on the ground dwelling invertebrate community was assessed on an English inter-tidal upper salt marsh using pitfall traps. Abundance, species richness, functional group structure, abundance of coastal specialists, environmental factors that influence invertebrate habitat choice and food web composition were compared for grazed and un-grazed marsh.

3. In total, 90000 invertebrates were sampled. Predatory, zoophagus and detritivorous Coleoptera were significantly more abundant on the un-grazed marsh.

In contrast, predatory Hemiptera and Araneae were significantly more abundant on the grazed marsh. Sheet weaver spiders were significantly more abundant on the grazed marsh, foliage running hunters and space web builders more abundant on the un-grazed marsh. Most inter-tidal coastal specialist species exhibited clear habitat preference for the grazed marsh. Total species richness was not significantly different between grazing treatments.

4. RDA analysis showed that two environmental variables influenced by grazing intensity, soil temperature and vegetation height, significantly explained the composition of invertebrate functional groups. Larger bodied invertebrates dominated the un-grazed food web.

5. We conclude that both short sward cattle grazed and un-grazed saltmarsh habitat should be maintained to maximise invertebrate abundance and diversity and provide suitable habitat for coastal specialists.

Key words Araneae, biodiversity, body size, Coleoptera, Hemiptera, food web, insects, pitfall, prey capture method, spiders.

2 Introduction

European salt marshes are highly productive and were traditionally managed as agricultural livestock grazing land (Bouchard *et al.*, 2003; Doody, 2008). Grazing is still common place within the salt marshes of North West Europe and is often maintained with the twin conservation aims of maximising plant and bird diversity (Chatters, 2004; Milsom *et al*., 2000). It is well known that intermediate grazing pressure maximises plant diversity on Northern European marshes (Adam, 1990; Bakker *et al*., 1993). Birds, however, show a variable response to grazing intensity as each species exhibits a particular habitat preference (Daan *et al.*, 2002; Bouchard *et al.*, 2003). Salt marshes are also an important coastal habitat for both highly specialised inter-tidal invertebrates (Pétillon *et al.*, 2005), certain Red Data Book (RDB) listed or Biodiversity Action Plan (BAP) species (Alexander *et al*., 2005; Webb *et al.*, 2010) and other invertebrates common to grasslands.

The effects of saltmarsh grazing management on invertebrate diversity and abundance are poorly understood. Previous saltmarsh invertebrate studies have tended to focus on the zonation of particular groups, especially carabid beetles and spiders, with marsh elevation. Irmler *et al.* (2002) and Finch *et al.* (2007) both found that species richness of carabid beetles and Araneae increased with distance above mean high tide. British carabid and Staphylinidae saltmarsh communities have also been well documented (Hammond, 2000; Luff & Eyre, 2000). Most studies report higher invertebrate species richness and abundance in un-grazed systems for both salt marshes and other grasslands (Bakker *et al.*, 1993; Gibson *et al.*, 1992a; Morris, 2000; Kruess & Tscharntke, 2002). Pétillon *et al.* (2007) found that although this was true for spiders, for Coleoptera species richness was higher on grazed marsh. Short sward, livestock grazed marshes provide a suitable habitat for inter-tidal coastal specialist species (Andresen *et al.*, 1990).

We define invertebrate coastal specialists as those species that are only found in inter-tidal or estuarine habitats. These species are habitually or physiologically adapted to cope with tidal inundation and variable salinity. Some species, such as the saltmarsh spider *Pardosa purbeckensis* avoid flooding by moving vertically in tall vegetation, but if submerged in saline water they survive longer than related terrestrial wolf spiders (Pétillon *et al.,* 2011). Another saltmarsh spider, *Arctosa fulvolineata*, withstands submersion by entering a hypoxic coma (Pétillon *et al.,* 2009). Some invertebrate species can osmoregulate in saline environments, controlling the water balance within their bodies (Williams & Hamm, 2002). Other marine invertebrates take advantage of plastron respiration (Flynn & Bush, 2008). Terrestrial invertebrates that occur in habitats likely to flood are often opportunists able to migrate horizontally to higher ground, enter a dormant stage underwater or reproduce rapidly to take advantage of flood free periods (Adis & Junk, 2002).

Livestock grazing reduces above-ground biomass and vegetation height, causes a rapid turnover of plant material via the production of fresh leaves, reduces plant litter build up and has direct effects on plant species composition and structure via preference or avoidance of particular plant species by livestock (Adam, 1990; Bos, 2002). Sheep provide a uniform short sward whereas cattle, as more selective feeders, often produce a more ‘tussocky’ sward (Adam, 1990; Lambert, 2000). With high stocking density cattle can however produce a short, even sward of high quality forage, attractive for feeding geese, or provide variable structure, suitable for breeding birds (Bakker, 1989; Bos, 2002). In contrast, either in historically un-grazed or abandoned upper salt marshes tall unpalatable grasses, such as *Elytrigia athericus* dominate (Bakker *et al*., 1993; Van Wijnen & Bakker, 1997; Bakker *et al*., 2002). Livestock grazing also impacts upon abiotic marsh characteristics. Short grazed vegetation leads to greater and more variable soil temperatures than un-grazed grassland (Curry, 1994). Cattle disturbance generally results in a topographically variable soil surface whereas sheep evenly compact it, but both can lead to waterlogged ground with high soil salinity (Lambert, 2000). Grazing herbivores also return nutrients to the soil via dung input (Bakker *et al*., 1993).

Abundance and diversity of terrestrial invertebrate fauna is greatest on un-grazed marshes, with a food web dominated by detritivores, as tall vegetation and increased litter layer depth increase available niches, food provision and provide cover from predators (Adam, 1990; Curry, 1994). The grazed marsh invertebrate food web is dominated by warmth seeking inter-tidal coastal specialists and phytophagus individuals dependent upon particular plant species (Andresen *et al.*, 1990; Bakker *et al.*, 1993). If grazing intensity is very high phytophagus invertebrates also decline (Meyer *et al.,* 1995). The marsh invertebrate food web can be characterised using functional groups (Blondel, 2003), in our study different trophic categories. ‘Bottom-up’ processes such as resource limitation or ‘top-down’ processes such as population limitation by predators can be studied using a functional group approach (Chen & Wise, 1999). Few studies have looked at the response of saltmarsh invertebrate functional groups to grazing. Meyer *et al*. (1995) described how the European saltmarsh invertebrate food web differed with sheep grazing intensity but most studies focus on either the macro-invertebrate community of the lower marsh (Salgado *et al*., 2007) or American saltmarsh food webs (Zimmer *et al*. 2004). As the marshes of North America differ from European marshes in terms of productivity, dominant plant species, effect of livestock grazing upon plant species richness and invertebrate community (Bazely & Jeffries, 1986; Adam, 1990; Ford & Grace, 1998;

Garbutt & Boorman, 2009), it is difficult to relate North American food web studies to European marshes.

Coleoptera communities are affected by moisture, temperature, salinity, vegetation height, trampling and soil compaction (Lassau *et al.*, 2005; Pétillon *et al.*, 2008; Hofmann & Mason, 2006; Morris, 2000). Spider species assemblages are particularly sensitive to moisture, vegetation height and vegetation structure (Bonte *et al.*, 2000; Uetz *et al.*, 1999; Bell *et al.*, 2001; Pétillon *et al.*, 2008). In a Californian saltmarsh a positive relationship was found between plant species richness, vegetation tip height diversity and spider family richness due to increased potential of nesting and web building sites (Traut, 2005). Hemiptera, phytophagus Auchenorrhyncha leafhoppers in particular, increase in abundance and diversity with greater plant diversity, vegetation height and structural complexity (Biedermann *et al*., 2005). *E. atherica* invasion of salt marshes, characteristic of un-grazed marshes, correlates to an increase in non coastal spider species leading to an overall increase in biodiversity but a decrease in abundance of coastal specialist species (Pétillon *et al.*, 2005; Pétillon *et al.*, 2010). Spider coastal specialists may decline as *E. atherica* stands tend to create drier more terrestrial conditions than other saltmarsh vegetation. Un-grazed inland salt meadows also exhibited a lower abundance of coastal specialist spider species than grazed meadows (Zulka *et al*., 1997).

The existing evidence suggests that un-grazed marshes may provide suitable habitat for a diverse invertebrate community, but that cattle grazed marshes with a uniform short sward may support a narrower range of saltmarsh specialist species. Prey selection within food webs may be influenced by body size of invertebrates; however, no published work has been carried out relating saltmarsh food web structure to body size of invertebrates. This study aims to assess the impact of grazing on abundance, diversity and functional group structure of the entire ground dwelling invertebrate community using pitfall sampling. Specifically addressing how grazing influences: abundance, species richness and functional group structure of Coleoptera, Hemiptera and Araneae; abundance and functional group structure of all other invertebrates; abundance of invertebrate coastal specialists; environmental factors that influence invertebrate habitat choice; and saltmarsh food web in relation to functional group and body size. The three main orders focused on within this study, Coleoptera, Hemiptera and Araneae, were chosen as they are well studied, easy to identify to species level, include important predators, often include larger bodied individuals and are used as bio-indicators of grassland ecosystem health (Biedermann *et al*., 2005; Pearce & Venier, 2006).

3 Methods

3.1 Site description

The salt marshes of the Ribble estuary cover around 2000 ha in total. The study area, Crossens Marsh (53^{o} 41' 15" N, 2^{o} 57' 4" W), is located on the southern edge of the Ribble estuary in North-West England and is part of the Sefton Coast Special Protection Area managed by Natural England, the statutory conservation body. The marsh was historically un-grazed but was split into two management types over 40 years ago, un-grazed and cattle grazed (Figure 1). The grazed marsh is characterised by predominantly *Festuca rubra* saltmarsh NVC community (SM16d) and the un-grazed marsh by *Elytrigia repens* saltmarsh (SM28; Rodwell, 2000). *E. repens* replaces *E. atherica* on UK west coast. The grazed part of the marsh covers 517 ha and is uniformly grazed by around 100 bullocks from late May to early October, approximately 0.2 cattle per hectare, and provides a consistent short sward (< 8 cm) for overwintering pink-footed geese (*Anser brachyrhynchus*) to feed. Small herbivores such as field voles are also present, particularly on the un-grazed marsh.

Figure 1 Crossens Marsh field site with fence line marking boundary between un-grazed vegetation on the left, dominated by a tall sward (20 – 30 cm) of *Elytrigia repens*, and consistently short cattle grazed vegetation on the right (< 8 cm).

3.2 Experimental design

All experimental units were selected within the high marsh zone where numerous creeks are present but tidal inundations are relatively rare, limited to around eight events a year on high equinox tides. A paired experimental design was used with six experimental units of approximately 10 m x 10 m set up on each side of a 600 m long section of the fence line, 100-150 m apart, in a 'mirror image' formation, giving six grazed (G1-G6) and six un-grazed (U1-U6) units (Figure 2). Each experimental unit was located between 20 m and 50 m from the fence line to ensure an adequate buffer zone and checked for standard elevation within ±10 cm. All measurements were carried out within these experimental units.

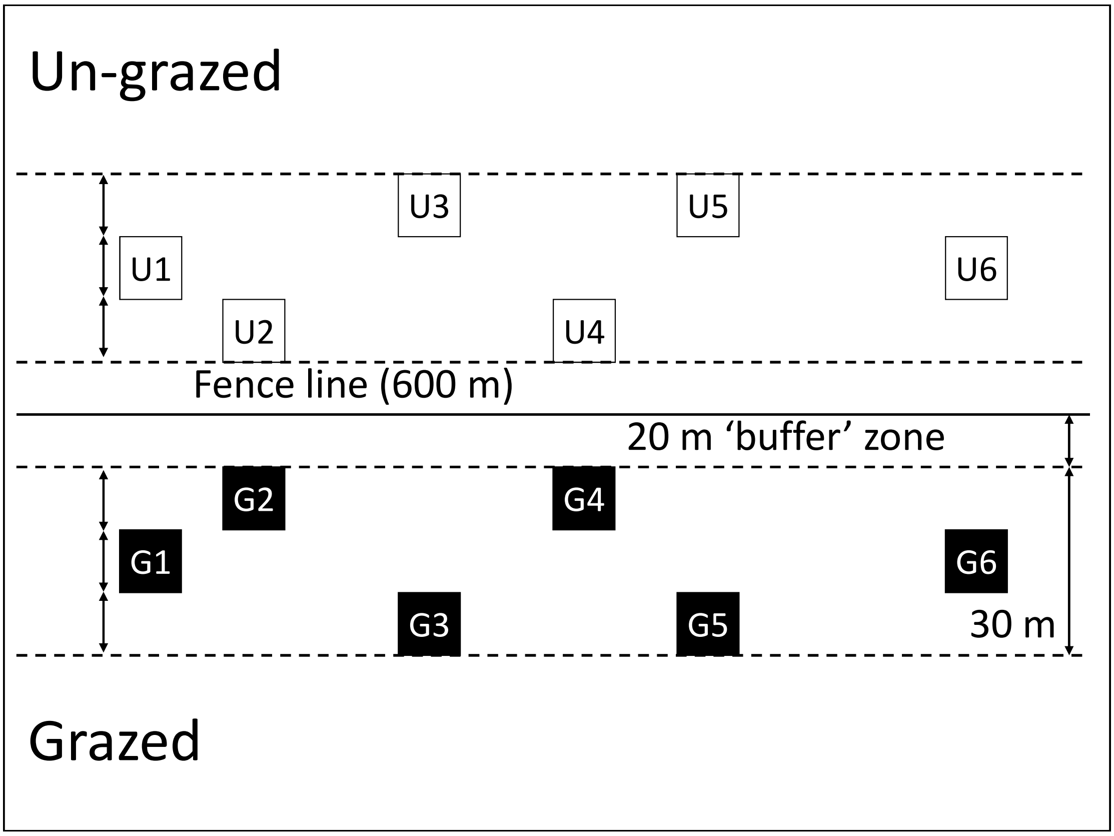


Figure 2 Experimental design at Crossens Marsh, G1–G6 were grazed experimental units, U1-U6 were un-grazed units.

3.3 Soil and vegetation characteristics

Soil samples were collected during September 2009 from the top 15 cm of soil to measure salinity and pH. Soil was sieved to 2 mm and a sub sample of 10 g was taken from each sample and shaken with 25 ml of deionised water (1:2.5 dilution factor). A *Hanna* pH209 pH meter was used to measure pH and a *Jenway* 4520 Conductivity meter to measure electrical conductivity (mS cm^{-1}) as a proxy for salinity (Douaik, Van Meirvenne & Tóth, 2007). Samples to determine bulk density and soil organic matter content were collected during September 2009 using intact soil cores of 3.8 cm diameter and 15 cm depth. Cores were dried at 105 ^{o}C for 72 hours and the dry mass divided by the volume of the core to calculate bulk density. Loss-on-ignition was used to estimate organic matter content (Ball, 1964). Soil moisture content and temperature were recorded at six locations within each experimental unit during September. Soil conductivity was measured in direct volts using a *Delta T* Theta Meter HH1 (four probes of 6 cm) and converted to percentage soil moisture content using a calibration suitable for organic soils. Soil temperature was measured using a digital thermometer (single 11 cm probe).

Plant species richness and percentage cover were estimated by eye during July 2009 in five 1 m x 1 m quadrats placed 3 m apart within each experimental unit. Within each quadrat a 25 cm x 50 cm corner was allocated and above-ground living vegetation collected. Plant litter was collected separately from the same area. One root core of 5 cm diameter and 10 cm depth was also taken per quadrat and washed to remove all soil. Above-ground vegetation, litter and roots were all dried at 80 °C for 24 hours and weighed to give indicators of above-ground live plant biomass, litter biomass and below-ground root biomass respectively. Vegetation height was measured in May and September at ten random positions within 1 m of each pitfall trap with a custom made drop disc of 20 cm diameter, 10 g mass. Vegetation height diversity was also calculated. All plant nomenclature follows Stace (2010).

3.4 Ground dwelling invertebrates - pitfall traps

Pitfall traps were used to sample ground dwelling invertebrates in spring and autumn. The traps were put in place for 28 days from 5th May to 2nd June 2009 and for 30 days between 4th September and 9th October 2009 (excluding 5 days where traps were removed due to high tides). Six pitfall traps per experimental unit were set up in two lines of three, 5 m apart. Each trap consisted of a plastic cup (80 mm diameter x 105 mm deep) a third full with a 50/50 mix of ethylene glycol and water, recommended for preservation of invertebrates (Schmidt *et al*., 2006), with a drop of washing up liquid to break the surface tension. Each trap was pushed into a hole made by a soil auger until they were flush with the soil surface. A rain hat was placed over each trap and set at 3 cm from the ground. A wire basket of 5 cm mesh size was also placed over each rain hat and pegged down to prevent interference by cattle. Pitfalls were emptied and replaced with new ethylene glycol mixture half way through the spring and autumn sampling periods to aid preservation of invertebrates. The contents of the pitfalls were preserved in 70 % Industrial strength methylated spirits (IMS).

3.5 Invertebrate classification - functional groups & coastal specialists

All invertebrates caught in the pitfall traps from Coleoptera, Hemiptera and Araneae were identified to species level, all other invertebrates were identified to family or order level. All invertebrates were also classified according to the following functional groups: predatory, zoophagus (predatory and scavenging), phytophagus (herbivore or granivorous), detritivore (feed on detritus and associated decomposer community of fungi and bacteria) (Kreeger & Newell, 2000), or an additional category 'not assigned' on the basis of species, family or order level information (Table A1). Invertebrate species authorities listed in Table A1. Spiderlings were excluded from the analysis as they were only counted in September. Larvae belonging to all other groups were assigned a functional group where possible. Araneae are all predators but were further grouped by prey capture method as proposed by Uetz *et al.* (1999).

Coastal specialist carabid beetles were defined by Luff (1998), Araneae by Harvey *et al.* (2002). Nationally scarce invertebrates associated with coastal saltmarsh were defined by Buglife – The Invertebrate Conservation Trust (Alexander *et al.* 2005), these species are not necessarily coastal specialists but are nationally scarce invertebrates only found in particular habitats. The UK distribution of coastal specialist species were also checked using the National Biodiversity Network interactive map (http://data.nbn.org.uk/imt, 2011). Invertebrate nomenclature follows Duff (2008) for Coleoptera and Fauna Europea (2004) for Araneae, Hemiptera and all other groups.

3.6 Statistical Analysis – soil and vegetation characteristics

Differences between grazing treatments for soil and vegetation characteristics were analysed using linear mixed effects models (lme) analysed by ANOVA using R v.2.12.1 (2010 As lme (salinity ~ grazing, random = ~1|block/grazing). This approach was used to enable the raw data to be analysed accounting for replication at the level of the experimental unit or block (n=6). Vegetation height diversity for the grazed and un-grazed marsh was calculated from the Coefficent of variance (CoV; Standard Deviation/Mean*100) of each set of ten heights from around each pitfall.

3.7 Statistical Analysis – ground dwelling invertebrates

For each of the twelve experimental units, the contents of the six pitfalls within each unit were pooled to give a total invertebrate count per unit. As trends in invertebrate community composition appeared similar between the May and September sampling periods the data were combined to give one measure of abundance to represent the year 2009. At the level of the experimental unit (n=6) differences in functional group abundance and species richness, within Coleoptera, Hemiptera, Araneae and all other invertebrate groups, between grazed and un-grazed treatments were tested for statistical significance using Wilcoxon matched pairs test, Genstat v.10 (Payne *et al.*, 2007). Box plots were produced using Minitab v.15 Statistical Software (2007).

3.8 Statistical Analysis – relationship between environmental variables and functional group occurrence

Linear direct gradient analysis (RDA) was carried out to examine the relationship between all environmental variables listed in Table 1 (mean at unit level), and the distribution of pitfall functional groups and prey capture methods from the six grazed and six un-grazed experimental units of the salt marsh. ‘Species’ data were entered into the analysis in the form log transformed count data (total for experimental unit) of functional groups or Araneae prey capture methods, RDA scaling was focused on inter-species correlations and centred by species, grazing treatment of each unit was included in the final RDA triplot but was not used to influence the analysis. The significance of environmental variables was tested using automatic forward selection (Monte Carlo test, 500 permutations). All multivariate analysis was carried out in Canoco v.4.5 (Ter Braak and Šmilauer, 2003).

3.9 Food web analysis

The most abundant groups of invertebrates on the grazed or un-grazed marsh (≥ 1% of total abundance on one marsh type) were used to create a food web for the salt marsh based on taxonomy, functional group, body size and prey selection preferences. Body size was divided into three size classes based on body length, large (≤ 30 mm), medium (≤ 20 mm) and small (≤ 10 mm). Body size was determined for Coleoptera (Unwin, 1988), Hemiptera (Burrows, 2009; Bantock & Botting, 2010), Araneae (Jones-Walters, 1989) and other invertebrates (Chinery, 1986; Tilling, 1987). Food web prey preferences, both for particular invertebrate groups and body size, were based on Lövei & Sunderland (1996), Clough *et al*. (2007), Rickers (2005) and Landis & Werf (1997) for predatory beetles and Hemiptera; Nyffeler (1999), Jones-Walters (1989) and Enders (1975) for spiders; Dias & Hassal (2005) for woodlice and sand hoppers.

4 Results

4.1 Soil properties and vegetation characteristics

Soil bulk density, percentage moisture content and temperature were all significantly higher on the grazed marsh; soil pH was significantly higher on the un-grazed marsh (Table 1). Plant species richness; percentage cover of *Agrostis stolonifera*, *Glaux maritima*, *Puccinellia maritima* and *Triglochin maritima*; and below-ground plant biomass were all significantly greater on the grazed marsh. Percentage cover of *Elytrigia repens*, above-ground plant biomass, litter biomass, vegetation height in May and September were all significantly higher on the un-grazed marsh. Soil salinity, soil organic matter content, percentage cover of *Festuca rubra* and vegetation height diversity were not significantly different between grazing treatments.

4.2 Invertebrate summary

This study captured nearly 90,000 ground dwelling invertebrates, around two thirds on the un-grazed marsh. Predators were one and a half times more abundant on the grazed than the un-grazed marsh, but not significantly so, 19 % and 9 % respectively of the total invertebrate count per grazing treatment. Zoophagus invertebrates were three times more abundant on the un-grazed marsh (Wilcoxon; $w = 0$, d.f. = 5, $p < 0.05$) and phytophagus individuals were equal between treatments, both groups only accounted for 1 - 3 % of total count per treatment. There were twice as many detritivores on the un-grazed than the grazed marsh, 78 % compared to 55 % of the total. There were twice as many not assigned invertebrates on the grazed marsh, 23 % to 9 % on the un-grazed. Coleoptera accounted for 6 %, Hemiptera 1 % and Araneae 9% of the total invertebrate count. For Coleoptera, Hemiptera and Araneae combined species richness was not significantly different between grazing treatments.

4.3 Abundance, species richness and functional group structure of Coleoptera

Coleoptera were around three times more abundant and significantly more species rich (Wilcoxon; $w = 0$, d.f. = 5, $p < 0.05$, Table 2) on the un-grazed marsh. Predatory, Zoophagus and Detritivorous Coleoptera were all significantly more abundant on the un-grazed marsh (Test statistics for each: Wilcoxon; $w = 0$, d.f. = 5, $p < 0.05$; Figure 3a). The most abundant species on the un-grazed marsh were zoophagus *Bembidion iricolor* (14 % of total Coleoptera), predatory *Cantharis rufa* (14 %) and predatory *Cordalia obscura* (11 %). The most abundant species on the grazed marsh were zoophagus *Bembidion aeneum (20 %)*, not assigned *Brundia marina* (14 %) and *C. rufa* (14 %).

Table 1 Soil properties and vegetation characteristics measured from the grazed and un-grazed marsh. Sampling depths are presented alongside treatment means ± standard errors, ANOVA results (n = 6), number of replicate samples per experimental unit and month sampled. For vegetation height, for each of the 6 replicates per treatment the mean of 10 measurements was used in the analysis. For vegetation height diversity, CoV = coefficient of variance.

	Depth (cm)	Grazed	Un-grazed		Reps	Month
Soil						
Salinity (mS cm^{-1})	0-15	4.2 ± 0.4	3.4 ± 0.3	*ns*	3	Sept.
pH	0-15	7.6 ± 0.1	7.9 ± 0.1	*	3	Sept.
Bulk density (g cm^{-3})	0-15	0.8 ± 0.0	0.7 ± 0.0	*	3	Sept.
Organic matter content (%)	0-15	7.4 ± 0.7	6.3 ± 0.4	*ns*	3	Sept.
Moisture content (%)	0-6	52.6 ± 0.1	44.5 ± 1.2	*	6	Sept.
Temperature (^{o}C)	0-11	14.9 ± 0.1	14.2 ± 0.0	*	6	Sept.
Vegetation						
Plant species richness (species m^{-2})	n/a	6.6 ± 0.3	3.7 ± 0.2	*	5	July
% cover						
Agrostis stolonifera L.	n/a	20.0 ± 5.3	0.0 ± 0.0	*	5	July
Elytrigia repens L.	n/a	0.7 ± 0.5	58.0 ± 6.0	**	5	July
Festuca rubra L.	n/a	25.4 ± 4.7	31.2 ± 5.4	*ns*	5	July
Glaux maritima L.	n/a	6.0 ± 1.4	0.0 ± 0.0	**	5	July
Puccinellia maritima Parl.	n/a	28.3 ± 5.7	0.0 ± 0.0	*	5	July
Triglochin maritima L.	n/a	11.3 ± 2.4	3.2 ± 2.8	*	5	July
Above ground biomass (kg dwt m^{-2})	n/a	0.3 ± 0.0	0.7 ± 0.1	*	5	July
Litter biomass (kg dwt m^{-2})	n/a	0.0 ± 0.0	0.3 ± 0.0	*	5	July
Below ground biomass (kg dwt m^{-2})	0-10	3.4 ± 0.2	1.0 ± 0.1	***	5	July
Vegetation height (cm)	n/a	8.1 ± 0.5	29.2 ± 0.8	***	6	May
Vegetation height (cm)	n/a	8.2 ± 0.4	19.2 ± 0.7	***	6	Sept.
Vegetation height diversity (CoV) (%)	n/a	31.5 ± 4.6	29.9 ± 3.2	*ns*	6	May
Vegetation height diversity (CoV) (%)	n/a	29.1 ± 3.7	32.6 ± 3.8	*ns*	6	Sept.

Significant differences between grazing treatments indicated by *($p < 0.05$), **($p < 0.01$) and ***($p < 0.001$). Non significant results recorded as *ns* ($p > 0.05$).

4.4 Abundance, species richness and functional group structure of Hemiptera

Hemiptera were around five times more abundant on the grazed than the un-grazed marsh but total species richness did not differ (Table 2). Predatory Hemiptera were significantly more abundant on the grazed marsh (Wilcoxon; w = 0, $p < 0.05$, Figure 3b), phytophagus Hemiptera did not differ with grazing. On the grazed marsh the predatory shore bug *Salda littoralis* accounted for 67 % of total Hemipteran abundance. Phytophagus aphids accounted for 18 % of total abundance on the grazed marsh, 61 % on the un-grazed marsh.

Table 2 Invertebrate species richness comparison between grazed and un-grazed marsh; Coleoptera, Hemiptera and Araneae combined, separated into orders and at a functional group or prey capture method level. Species richness data are shown by treatment medians ± inter-quartile range, n = 6 in all cases.

Invertebrate group	Functional group / prey capture method	Grazed	Un-grazed	
Coleoptera, Hemiptera, Araneae	All	51.0 ± 6.8	60.5 ± 7.3	*ns*
Coleoptera	All	28.0 ± 6.5	37.0 ± 1.5	*
Coleoptera	Predatory	10.0 ± 3.5	13.0 ± 1.5	*ns*
Coleoptera	Zoophagus	8.0 ± 0.8	9.0 ± 0.8	*ns*
Coleoptera	Phytophagus	5.0 ± 1.5	5.0 ± 1.5	*ns*
Coleoptera	Detritivore	3.0 ± 0.8	7.0 ± 2.8	*ns*
Coleoptera	Not assigned	2.0 ± 0.0	2.0 ± 0.0	*ns*
Hemiptera	All	6.0 ± 1.5	5.5 ± 2.5	*ns*
Hemiptera	Predatory	2.0 ± 0.0	1.0 ± 0.8	*ns*
Hemiptera	Phytophagus	4.5 ± 1.8	4.0 ± 1.5	*ns*
Araneae	All / Predatory	17.5 ± 1.8	20.0 ± 2.3	*ns*
Araneae	Foliage running hunter	0.5 ± 0.0	1.0 ± 0.0	*ns*
Araneae	Ground running hunter	4.5 ± 1.0	6.0 ± 0.8	*ns*
Araneae	Space web builder	0.0 ± 0.0	1.0 ± 0.0	*
Araneae	Sheet weavers	12.7 ± 0.5	12.0 ± 0.8	*ns*

Significant differences between grazing treatments indicated by *(p < 0.05), non significant results as *ns* (p > 0.05), Wilcoxon Matched-Pairs test.

4.5 Abundance, species richness and prey capture methods of Araneae

As an entirely predatory group Araneae were significantly more abundant on the grazed marsh (Wilcoxon; w = 0, d.f. = 5, p < 0.05, Figure 4a) but species richness did not differ (Table 2). Foliage running hunters were significantly more abundant on the un-grazed marsh (Wilcoxon; w = 0, d.f. = 5, p < 0.05, Figure 4b). Ground running hunter abundance was not significantly different between the grazed and un-grazed marsh. Space web builders were more abundant on the un-grazed marsh (Wilcoxon; w = 0, d.f. = 5, p < 0.05). Sheet weavers were significantly more abundant (Wilcoxon; w = 0, d.f. = 5, p < 0.05) but not more species rich on the grazed marsh. The grazed marsh was numerically dominated by two sheet weaver Linyphiidae species, *Erigone longipalpis* (42 % of total Araneae for grazing treatment) and *Oedothorax fuscus* (21 %). The wolf spider *P. purbeckensis* (9 %) were also common on the grazed marsh. The un-grazed marsh was characterised by the Linyphiidae *Allomengea scopigera* (39 %) and *P. purbeckensis* (20 %).

4.6 Abundance and functional group structure of other invertebrates

For all other invertebrates total abundance was twice as high on the un-grazed marsh. Zoophagus invertebrates, all harvestmen, were significantly more abundant on the un-grazed marsh (Wilcoxon; $w = 0$, d.f. = 5, $p < 0.05$, Figure 5a). Predatory (all parasitoid wasps), phytophagus, detritivore and not assigned functional groups did not differ significantly with grazing treatment (Figure 5a, 5b). Even though the abundance of all detritivores did not differ between grazing treatments their composition did. On the un-grazed marsh *Orchestia gammerella* (68 %) and woodlice (23 %) were most abundant. On the grazed marsh Collembola (69 %) and *O. gamerella* (30 %) were common. Of particular interest within the not assigned category are the Tipulidae, these were caught fifty times more frequently on the grazed marsh.

4.7 Abundance of coastal specialist species

Coastal specialist ground beetles, *Bembidion minimum* and *Dicheirotrichus gustavii*, rove beetle *B. marina* and nationally scarce saltmarsh shore bug *Saluda opacula* were found predominantly on the grazed side of the marsh (Table A1). As were Araneae coastal specialist species *Silometopus ambiguus* and *E. longipalpis.* The coastal spider *P. purbeckensis* was found almost equally on both the grazed and the un-grazed marsh. The carabid *B. iricolor* was recorded mainly on the un-grazed side. Even though *D. gustavii* and *S. opacula* show clear habitat preferences they are only found in low numbers compared to the other coastal specialist species listed. Three species, *B. marina*, *S. ambiguus* and *E. longipalpis* were sampled in greater abundances in G5, the most saline experimental unit, than any of the other units.

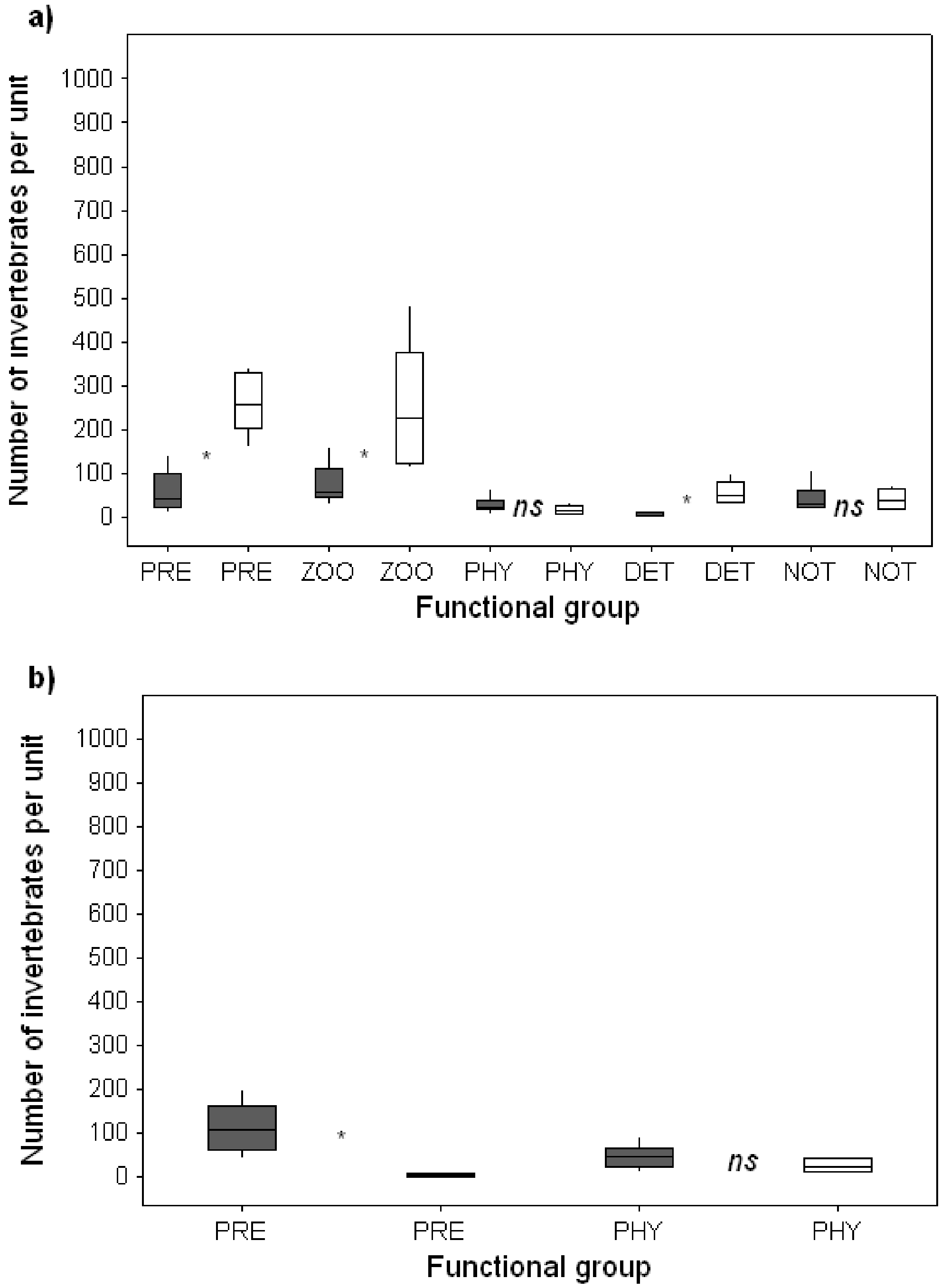


Figure 3 Coleoptera (a) and Hemiptera (b) abundance from grazed (grey bars) and un-grazed (white bars) salt marsh characterised by functional group: PRE = predatory; ZOO = zoophagus; PHY = phytophagus; DET = detritivore; NOT = not assigned. Significant differences between grazing treatment indicated by *(p < 0.05), non significant results as *ns* (p > 0.05), Wilcoxon matched pairs test.

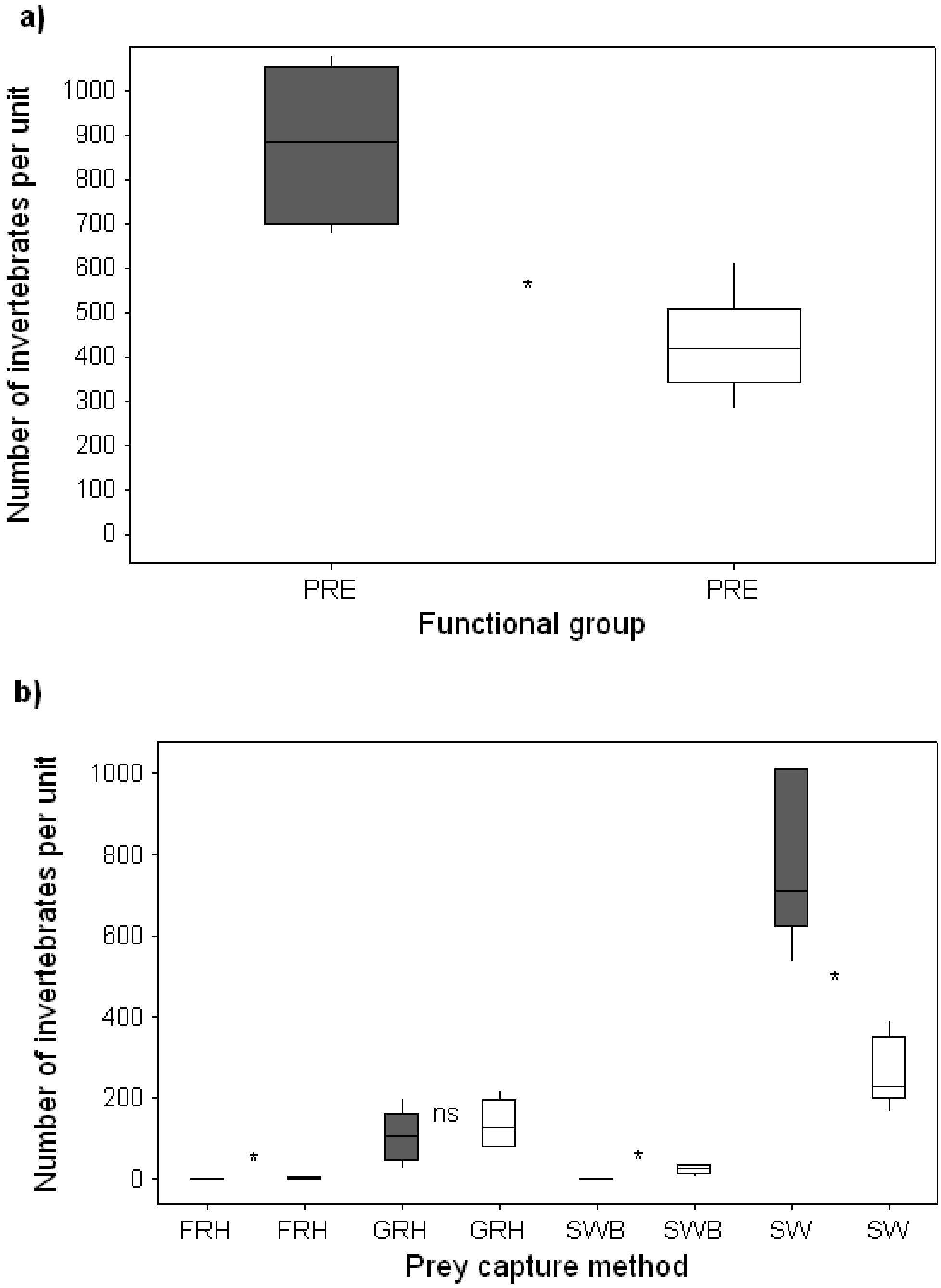
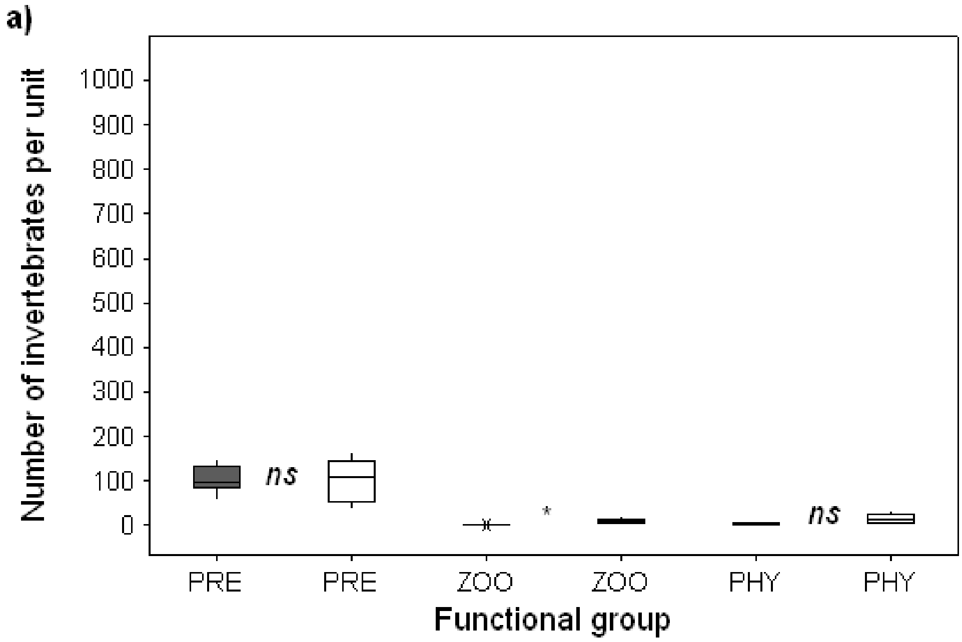


Figure 4 Araneae abundance from grazed (grey bars) and un-grazed (white bars) salt marsh characterised by functional group (a): PRE = predatory and further classified by prey capture method (b): FRH = foliage running hunter; GRH = ground running hunter; SWB = space web builder; SW = sheet weaver. Significant differences between grazing treatment indicated by *($p < 0.05$), non significant results as *ns* ($p > 0.05$), Wilcoxon matched pairs test.



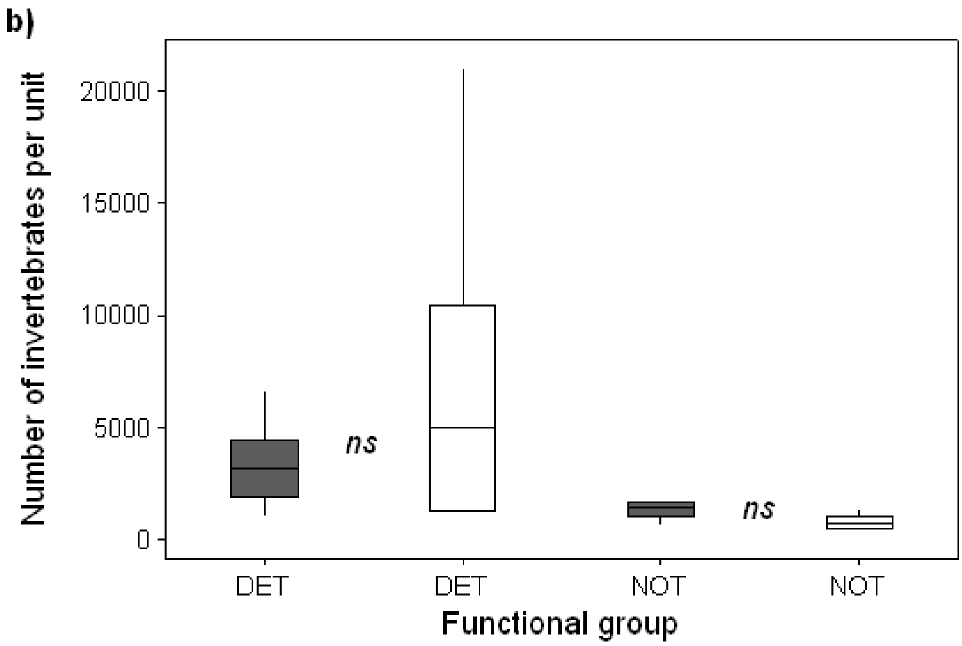


Figure 5 All other invertebrates (not Coleoptera, Hemiptera or Araneae) abundance from grazed (grey bars) and un-grazed (white bars) salt marsh characterised by functional group: a) PRE = predatory; ZOO = zoophagus & PHY = phytophagus; b) DET = detritivore & NOT = not assigned. Significant differences between grazing treatment indicated by *(p < 0.05), non significant results as *ns* (p > 0.05), Wilcoxon matched pairs test.

4.8 Environmental factors that influence invertebrate habitat choice

The RDA triplot (Figure 6) shows a visual interpretation of the relationship between eight environmental variables, selected by Monte Carlo forward selection, and the distribution of functional groups or prey capture methods. Axis 1 explained 79 % of the variation in functional group or prey capture method occurrence, axis 1 and 2 combined explained 89 % of the variation. The Monte Carlo test for all axes was significant for three environmental variables; temperature (positively correlated with axis 1: F-ratio = 23.73, $P < 0.01$), vegetation height (negatively correlated with axis 2: F-ratio = 3.59, $P < 0.05$) and salinity (positively correlated with axis 2: F-ratio = 2.38, $P < 0.05$), all other environmental variables either correlated with these three or did not describe a significant proportion of the variation in functional group occurrence. Grazing intensity was clearly separated out by axis 1, with all grazed experimental units positively associated with and all un-grazed units negatively associated with axis 1. Predatory, zoophagus, and detritivorous Coleoptera were all negatively associated with axis 1, as were foliage running hunters, space web builders and zoophagus and phytophagus other invertebrates. Predatory Hemiptera and sheet weaving spiders were positively associated with axis 1. Phytophagus Hemiptera and ground running hunter spiders were negatively associated with axis 2, not assigned Coleoptera and other detritivores were positively associated with axis 2.

4.9 Food web analysis

Large detritivores, mainly Orchestia and woodlice, accounted for 71 % of all the invertebrates sampled on the un-grazed marsh, 17 % on the grazed marsh (Figure 7). Small detritivores, predominantly collembola, accounted for only 6 % on the un-grazed marsh compared to 38 % on the grazed marsh. Large crane flies were more numerous on the grazed marsh (7 %). Small flies and mites were abundant in both grazing treatments. Large and medium predatory beetles accounted for 6 % of all invertebrates on the un-grazed marsh, 2 % on the grazed marsh. Medium hunting spiders were present in equal proportions on both marsh types (2 %). Small Linyphiidae were much more abundant, both in total and proportional abundance, on the grazed marsh (13 %) compared to the un-grazed marsh (3 %). Predatory shore bugs were only present on the grazed marsh (2 %).

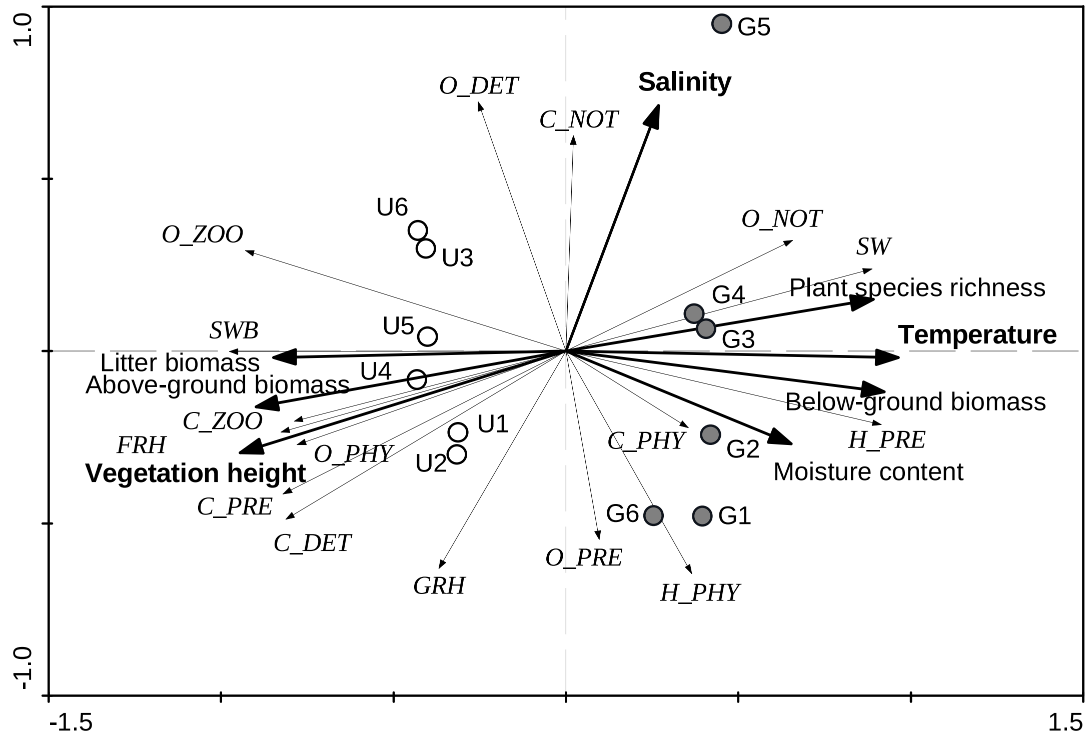


Figure 6 RDA triplot showing the relationship between eight environmental variables and the distribution of sixteen functional groups and prey capture methods. Environmental variables were selected by forward selection (Canoco v.4.5; Monte Carlo test, 500 permutations); the three significant ones, temperature, vegetation height and salinity are shown in bold. Grazed experimental units (G1-G6) are displayed as grey circles, un-grazed units (U1-U6) as white circles.

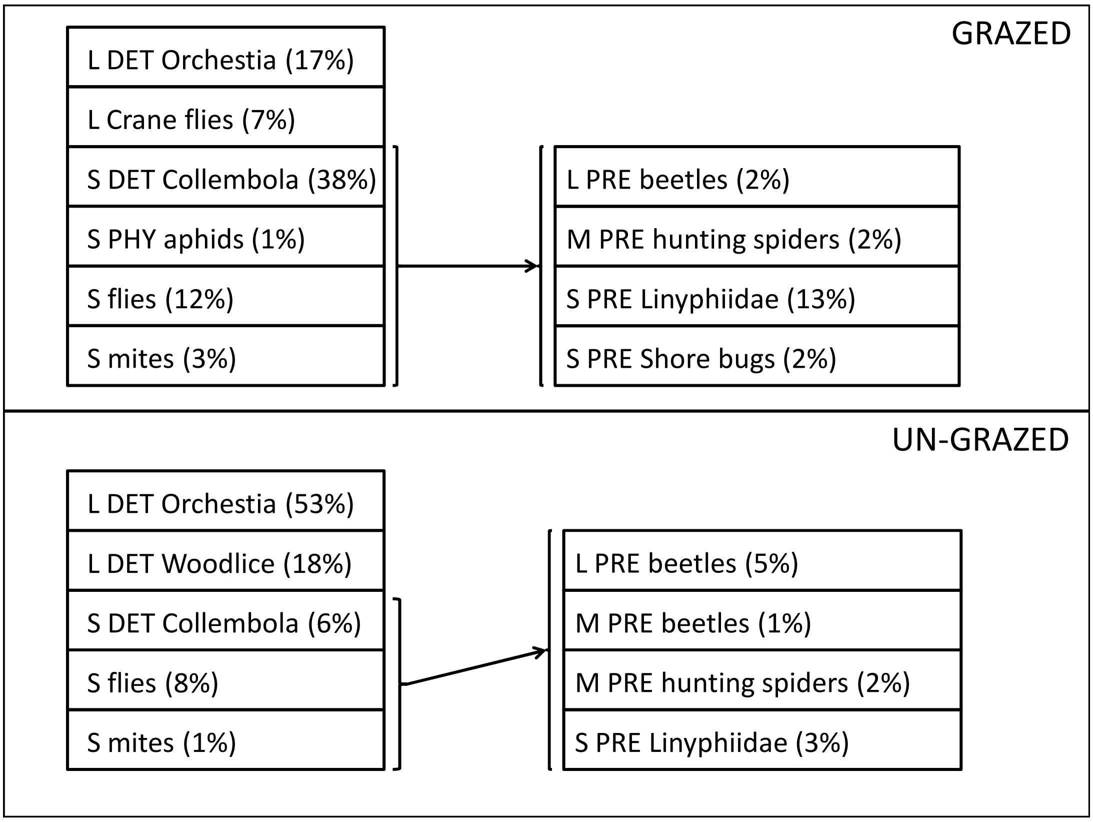


Figure 7 Ground dwelling invertebrate food web for cattle grazed and un-grazed salt marsh. Body length of invertebrates: L (large ≤ 30 mm), M (medium ≤ 20 mm), S (small ≤ 10 mm). Functional group of invertebrates: DET = detritivore, PHY = phytophagus, PRE = predatory (L PRE beetles also include zoophagus beetles). Invertebrate abundance is expressed as percentage of total invertebrates per grazing treatment.

5 Discussion

5.1 Overview

This study focused on the impact of cattle grazing on the abundance, diversity and functional group structure of the entire ground dwelling saltmarsh invertebrate community. Our results indicate that overall invertebrate abundance was greater on the un-grazed marsh. This finding is in line with evidence from other grassland and saltmarsh systems (Andresen *et al.* 1990; Bakker et al. 1993; Morris 2000). Coastal specialist abundance was greatest on the uniformly short sward cattle grazed salt marsh. European saltmarsh conservation often involves livestock grazing to improve plant diversity and provide a suitable habitat for over-wintering breeding birds and invertebrate coastal specialists. Here we argue that un-grazed areas of marsh also have a conservation value in their own right. As well as higher invertebrate abundance the functional structure of the un-grazed marsh is also different from the grazed marsh, with many large predators and detritivores present. The grazed marsh was characterised by high plant species richness, short vegetation, limited plant litter and warm compact soil prone to water-logging. The un-grazed marsh was dominated by *E. repens*, leading to a deep plant litter layer and drier less compact soil than the grazed marsh. Vegetation height diversity did not differ between grazing treatments.

5.2 Coleoptera, Hemiptera & Araneae

Coleoptera abundance and species richness was much higher on the un-grazed marsh. This may be due to reduced physical disturbance of the habitat. Duffey (1975) showed that even moderate trampling by humans of five treads a month, to simulate cattle treading, reduced Coleoptera abundance by 82 % after a year compared to an un-trampled control. Coleoptera also lack submersion resistance (Rothenbücher & Schaefer, 2006), relevant as un-grazed marshes are drier habitats than grazed marshes due to plant litter build up and reduced waterlogging. Large and medium sized predatory, zoophagus and detritivorous beetles were very abundant on the tall un-grazed marsh, in contrast small predatory Hemiptera preferred the short, moist vegetation of the grazed marsh. Large invertebrates favour the un-grazed marsh as birds select larger invertebrates when feeding so tall vegetation is likely to provide cover from this type of predation, small predatory invertebrates prefer the grazed marsh due to reduced competition from larger invertebrate predators (Enders, 1975; Lassau *et al*., 2005). Detritivorous beetles are associated with the un-grazed marsh due to the availability of greater amounts of plant detritus than the grazed marsh.

Overall spider abundance was greater on the grazed marsh due to the predominance of small sheet weaving Linyphiidae spiders. Foliage running hunters and space web builders were more abundant on the un-grazed marsh. Ground running hunters were slightly more abundant on the un-grazed marsh. These differences can largely be explained by structural differences between the two marsh types. *Erigone atra*, *Oedothorax fuscus*, *Oedothorax retusus* and *Savignya frontata*, all active Linyphiidae aeronauts, are found in much greater numbers on the grazed marsh than the un-grazed marsh, partly due to their ability to disperse into open or disturbed habitats, such as grazed land, where competition from larger invertebrate predators is low (Bell *et al*., 2001; Gibson *et al*., 1992b). Prey availability and preference for wetter habitats may also explain why Linyphiidae prefer the grazed marsh. Erigonine Linyphiidae, around half the sheet weavers sampled from the grazed marsh, are less than 2 mm long and feed on Collembola and small flies, an abundant food source on the grazed marsh (Enders, 1975; Figure 6). Another sheet weaver, *Hypomma bituberculatum*, was very abundant on the grazed marsh, it survives submersion in fresh water (Harvey *et al.*, 2002) and can therefore compete with other spider species in waterlogged plots. The comb spider *Robertus lividus*, a space web builder, was found only on the un-grazed marsh where litter levels were greatest as in Harvey *et al.* (2002). The foliage running hunter, *Clubiona stagnatilis,* was more abundant on tall un-grazed marsh. The most common ground running hunter species, *P. purbeckensis*, did not show a clear habitat preference but two other Lycosids, *Pardosa pullata* and *Pirata piraticus* were more abundant on the un-grazed marsh. It is worth noting that the use of pitfall traps to sample ground dwelling invertebrates will lead to under representation of certain spider groups, such as orb weavers, dependent upon the vertical structure of upper foliage layers.

5.3 Other invertebrates

Previously mentioned predatory groups, Coleoptera, Hemiptera and Araneae were often closely associated with a particular marsh type. In contrast, all other predatory invertebrates, parasitoid wasps, were equally abundant between grazing treatments. Parasitoid wasps are a diverse group providing a key ecosystem service in the regulation of insect populations (Fraser *et al.,* 2008), as active fliers this group was less influenced by ground level environmental variables. Zoophagus invertebrates were significantly more abundant on the un-grazed marsh. Dennis *et al.* (2001) found that in upland grasslands most harvestmen tended to prefer un-grazed or sheep grazed to cattle grazed swards. The crane flies, Tipulidae, were much more abundant on the grazed marsh, in line with Cole *et al*.'s findings (2010) from grazed uplands.

Large detritivores such as woodlice and the sand hopper, *O. gammerella,* were much more abundant on the un-grazed marsh due to the high level of plant detritus available as combined food source and shelter. Small detritivores such as Collembola were most abundant on the grazed marsh as in Meyer *et al*. (1995). They are able to proliferate here as they can survive anoxia in water-logged habitats by utilising passive drifting, a dormant egg stage and plastron respiration (Marx *et al*., 2009).

5.4 Abundance of coastal specialist species

For carabid inter-tidal coastal specialists *B. minimum* and *D. gustavii* the grazed marsh provided a more suitable habitat than the un-grazed marsh, as in Pétillon *et al.* (2007; 2008). The rove beetle *B. marina* also preferred the grazed marsh. In contrast, *B. iricolor* was more abundant on the un-grazed marsh. The Hemipteran nationally scarce invertebrate *Saldula opacula* was only present on the grazed marsh. For Araneae, coastal Linyphiidae specialists, *E. longipalpis* and *S. ambiguuus*, were much more abundant on the grazed marsh, as in Pétillon *et al.* (2005; 2007).

6 Conclusion

Soil temperature, bulk density and moisture content were higher on the grazed marsh. Plant species richness and below-ground root biomass were greater on the grazed marsh. Percentage cover of *E. repens*, above-ground plant biomass and litter biomass, were all significantly higher on the un-grazed marsh. Management of salt marshes for the conservation of invertebrates should aim to strike a balance between preserving maximum invertebrate diversity and abundance and maintaining a habitat suitable for coastal specialists. Un-grazed salt marshes provide a suitable habitat for an abundant and diverse invertebrate community, but cattle grazed marshes with short swards support a greater abundance and diversity of nationally scarce saltmarsh or inter-tidal coastal specialist species. The saltmarsh food web also differs markedly with grazing intensity. The un-grazed marsh is dominated by large detritivores and predatory beetles; the grazed marsh by smaller detritivores and Linyphiidae spiders adapted to open or disturbed habitats. Grazing intensity influences two key drivers of invertebrate habitat choice, vegetation height and soil temperature, via vegetation removal and soil compaction. Particular species, functional groups or coastal specialists respond differently to these variables. Therefore, the provision of both un-grazed and short sward cattle grazed habitat is important to salt marsh invertebrate conservation management.

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9 Appendix (Supplementary Material)

Table A1. Total counts of all invertebrates sampled from grazed 'G' and un-grazed 'U' marsh. Order, family, species, species authority and common name are listed alongside functional group, prey capture method and coastal specialist information in the 'Group' column (evidence for functional group assignment from list of superscript numbers). Order: COL = Coleoptera, HET = Heteroptera, HOM = Homoptera (Heteroptera and Homoptera both sub-orders of Hemiptera), ARA = Araneae, HYM = Hymenoptera, OPI = Opilones, PUL = Pulmonata, LEP = Lepidoptera, HAP = Haplotaxida, COLL = Collembola, ISO = Isopoda, AMP = Amphipoda, ACA = Acarina, DIP = Diptera, + includes larvae, L = larvae only. Group: PRE = predatory, ZOO = zoophagus, PHY = phytophagus, DET = Detritivore (DET (S) = scavenging, DET (F) = fungivorous), NOT = not assigned, FRH = foliage running hunter, GRH = ground running hunter, SWB = Space web builder, SW = Sheet weaver, CS = coastal specialist, N = notable species associated with salt marsh. Invertebrate nomenclature follows Duff (2008) for Coleoptera and Fauna Europea (2011) for all other invertebrates.

Order	Family	Species	Species authority	Common name	Group	G	U
COL	Staphylinidae	*Tachinus rufipes*	Linnaeus,1758	Rove beetle	PRE[1*]	0	30
COL	Staphylinidae	*Tachyporus nitidulus*	Fabricius, 1781	Rove beetle	PRE[1]	0	2
COL	Staphylinidae	*Tachyporus pusillus*	Gravenhorst, 1806	Rove beetle	PRE[1]	0	5
COL	Staphylinidae	*Amischa analis*	Gravenhorst, 1802	Rove beetle	PRE[1]	0	3
COL	Staphylinidae	*Cordalia obscura*	Gravenhorst, 1802	Rove beetle	PRE[1]	14	394
COL	Staphylinidae	*Oxypoda brachyptera*	Stephens, 1832	Rove beetle	PRE[1*]	33	56
COL	Staphylinidae	*Oxypoda procerula*	Mannerheim, 1830	Rove beetle	PRE[1*]	2	3
COL	Staphylinidae	*Stenus palustris*	Erichson, 1839	Rove beetle	PRE[1*]	2	0
COL	Staphylinidae	*Stenus fulvicornis*	Stephens, 1833	Rove beetle	PRE[1]	0	1
COL	Staphylinidae	*Stenus bimaculatus*	Gyllenhal, 1810	Rove beetle	PRE[1]	0	1
COL	Staphylinidae	*Stenus canaliculatus*	Gyllenhal, 1827	Rove beetle	PRE[1]	1	1
COL	Staphylinidae	*Stenus clavicornis*	Scopoli, 1763	Rove beetle	PRE	0	5
COL	Staphylinidae	*Stenus juno*	Paukull, 1789	Rove beetle	PRE[1]	2	7
COL	Staphylinidae	*Stenus brunnipes*	Stephens, 1833	Rove beetle	PRE[1*]	3	54
COL	Staphylinidae	*Lathrobium fulvipenne*	Gravenhorst, 1806	Rove beetle	PRE[1]	9	173
COL	Staphylinidae	*Lathrobium geminum*	Kraatz, 1857	Rove beetle	PRE[1*]	5	125
COL	Staphylinidae	*Sunius propinquus*	Brisout, 1867	Rove beetle	PRE[1*]	0	1
COL	Staphylinidae	*Othius laeviusculus*	Stephens, 1833	Rove beetle	PRE[1*]	4	0
COL	Staphylinidae	*Gabrius osseticus*	Kolenati, 1846	Rove beetle	PRE[1]	0	1
COL	Staphylinidae	*Philonthus carbonarius*	Gravenhorst, 1802	Rove beetle	PRE[1]	13	0
COL	Staphylinidae	*Philonthus cognatus*	Stephens, 1832	Rove beetle	PRE[1]	2	4
COL	Staphylinidae	*Philonthus umbratilis*	Gravenhorst, 1802	Rove beetle	PRE[1]	2	0
COL	Staphylinidae	*Quedius fuliginosus*	Gravenhorst, 1802	Rove beetle	PRE[1]	0	1
COL	Staphylinidae	*Quedius levicollis*	Brullé, 1832	Rove beetle	PRE[1*]	45	45
COL	Staphylinidae	*Quedius semiaeneus*	Stephens, 1833	Rove beetle	PRE[1*]	0	1
COL	Staphylinidae	*Ocypus aenocephalus*	De Geer, 1774	Rove beetle	PRE[1*]	0	1
COL	Staphylinidae	*Xantholinus linearis*	Olivier, 1795	Rove beetle	PRE[1]	4	1

COL	Staphylinidae	*Xantholinus longiventris*	Heer, 1839	Rove beetle	PRE[1]	7	89
COL	Coccinellidae	*Anisosticta novemdecimpunctata*	Linnaeus,1758	Lady bird	PRE[2]	2	0
COL	Coccinellidae	*Coccinella undecimpunctata*	Linnaeus,1758	Lady bird	PRE[2]	16	0
COL	Staphylinidae	*Tasgius globulifer*	Geoffroy, 1785	Rove beetle	PRE[3*]	1	26
COL	Staphylinidae	*Tasgius ater*	Gravenhorst, 1802	Rove beetle	PRE[3*]	0	1
COL	Cantharidae+	*Cantharis rufa*	Linnaeus,1758	Soldier beetle	PRE[2]	176	533
COL	Carabidae	*Loricera pilicornis*	Fabricius, 1775	Ground beetle	ZOO[4]	25	4
COL	Carabidae	*Clivina fossor*	Linnaeus,1758	Ground beetle	ZOO[4]	0	4
COL	Carabidae	*Dyschirius globosus*	Herbst, 1784	Ground beetle	ZOO[4]	0	2
COL	Carabidae	*Trechus quadristriatus*	Schrank, 1781	Ground beetle	ZOO[4]	0	1
COL	Carabidae	*Bembidion lampros*	Herbst, 1784	Ground beetle	ZOO[4]	0	1
COL	Carabidae	*Bembidion varium*	Olivier, 1795	Ground beetle	ZOO[4*]	20	3
COL	Carabidae	*Bembidion assimile*	Gyllenhal, 1810	Ground beetle	ZOO[4*]	17	269
COL	Carabidae	*Bembidion minimum*	Fabricius, 1792	Ground beetle	ZOO[4*] (CS)	64	4
COL	Carabidae	*Bembidion aeneum*	Germar, 1842	Ground beetle	ZOO[4]	246	267
COL	Carabidae	*Bembidion iricolor*	Bedel, 1879	Ground beetle	ZOO[4*] (CS)	13	517
COL	Carabidae	*Pterostichus niger*	Schaller, 1783	Ground beetle	ZOO[4]	3	162
COL	Carabidae	*Pterostichus minor*	Gyllenhal, 1827	Ground beetle	ZOO[4*]	20	148
COL	Carabidae	*Pterostichus nigrita*	Paykull, 1790	Ground beetle	ZOO[4]	0	2
COL	Carabidae	*Pterostichus diligens*	Sturm, 1824	Ground beetle	ZOO[4]	0	126
COL	Carabidae	*Olisthopus rotundatus*	Paykull, 1790	Ground beetle	ZOO[4]	9	5
COL	Carabidae	*Agonum marginatum*	Linnaeus,1758	Ground beetle	ZOO[4]	2	0
COL	Carabidae	*Agonum viduum*	Panzer, 1796	Ground beetle	ZOO[4]	0	1
COL	Carabidae	*Dicheirotrichus gustavii*	Crotch, 1871	Ground beetle	ZOO[5] (CS)	32	1
COL	Carabidae	*Demetrias atricapillus*	Linnaeus, 1758	Ground beetle	ZOO[4]	1	0
COL	Carabidae	*Amara communis*	Panzer, 1797	Ground beetle	PHY[4]	0	18
COL	Carabidae	*Harpalus rufipes*	De Geer, 1774	Ground beetle	PHY[4]	0	5
COL	Carabidae	*Harpalus affinis*	Schrank, 1781	Ground beetle	PHY[4]	1	0
COL	Staphylinidae	*Carpelimus corticinus*	Gravenhorst, 1806	Rove beetle	PHY[1]	0	1
COL	Chrysomelidae	*Chrysolina staphylaea*	Linnaeus, 1758	Leaf eater	PHY[2]	1	15
COL	Chrysomelidae	*Phaedon armoraciae*	Linnaeus, 1758	Leaf eater	PHY[2]	0	2
COL	Chrysomelidae L			Leaf eater	PHY[2]	3	10
COL	Apionidae	*Protapion fulvipes*	Geoffroy, 1785	Weevil	PHY[6]	4	0
COL	Erirhinidae	*Notaris scirpi*	Fabricius, 1793	Weevil	PHY[7]	8	6
COL	Helophoridae	*Helophorus brevipalpis*	Bedel, 1881	Water beetle	PHY[8]	64	18
COL	Hydraenidae	*Ochthebius dilatatus*	Stephens, 1829	Aquatic beetle	PHY[9]	72	24
COL	Byturidae	*Byturus ochraceus*	Scriba, 1790	Fruit beetle	PHY[10]	12	5

COL	Staphylinidae	*Omalium caesum*	Gravenhorst, 1806	Rove beetle	DET[1]	0	3
COL	Staphylinidae	*Micropeplus staphylinoides*	Marsham, 1802	Rove beetle	DET (F)[1]	0	3
COL	Staphylinidae	*Ischnosoma splendidum*	Gravenhorst, 1806	Rove beetle	DET (F)[1]	5	39
COL	Staphylinidae	*Sepedophilus marshami*	Stephens, 1832	Rove beetle	DET (F)[1]	0	71
COL	Staphylinidae	*Atheta graminicola*	Gravenhorst, 1806	Rove beetle	DET (F)[1]	1	0
COL	Staphylinidae	*Atheta triangulum*	Kraatz, 1856	Rove beetle	DET (F)[1]	2	0
COL	Staphylinidae	*Atheta* (other)		Rove beetle	DET (F)[1]	3	15
COL	Staphylinidae	*Anotylus rugosus*	Fabricius, 1775	Rove beetle	DET[1]	2	3
COL	Leiodidae	*Catops morio*	Fabricius, 1787	Fungus beetle	DET (S)[6]	0	8
COL	Cryptophagidae	*Atomaria atricapilla*	Stephens, 1830	Fungus beetle	DET (F)[11]	0	1
COL	Cryptophagidae	*Atomaria fuscata*	Schöenherr, 1808	Fungus beetle	DET (F)[11]	0	1
COL	Lathridiidae	*Corticaria punctulata*	Marsham, 1802	Mould beetle	DET[11]	1	7
COL	Lathridiidae	*Corticarina minuta*	Fabricius, 1792	Mould beetle	DET[11]	0	2
COL	Staphylinidae	*Lesteva sicula heeri*	Fauvel, 1871	Rove beetle	DET (S)[12]	0	5
COL	Staphylinidae	*Lesteva longoelytrata*	Goeze, 1777	Rove beetle	DET (S)[12]	1	0
COL	Hydrophilidae	*Cercyon impressus*	Fabricius, 1775	Water beetle	DET[13]	0	2
COL	Hydrophilidae	*Megasternum concinnum*	Marsham, 1802	Water beetle	DET[13]	17	111
COL	Hydrophilidae	*Sphaeridium scarabaeoides*	Linnaeus,1758	Water beetle	DET[13]	1	0
COL	Ptiliidae	*Ptenidium Sp.*		Feather beetle	DET (F)[13]	0	1
COL	Ptiliidae	*Acrotrichis Sp.*		Feather beetle	DET (F)[13]	2	67
COL	Staphylinidae	*Brundinia marina*	Mulsant & Rey, 1853	Rove beetle	NOT (CS)	172	111
COL	Staphylinidae	*Mocyta fungi*	Gravenhorst, 1806	Rove beetle	NOT	58	25
COL	Carabidae L				NOT	32	3
COL	Staphylinidae L				NOT	0	108
HET	Nabidae	*Stalia major*	Costa, 1841	Damsel bug	PRE[14]	0	1
HET	Nabidae	*Nabis lineatus*	Dahlbom, 1851	Damsel bug	PRE[14]	0	3
HET	Dipsocoridae	*Ceratocombus coleoptratus*	Zetterstedt, 1819		PRE[11]	0	13
HET	Saldidae	*Saldula opacula*	Zetterstadt, 1838	Shore bug	PRE[15*] (N)	28	0
HET	Saldidae	*Saldula pallipes*	Fabricius, 1794	Shore bug	PRE[15*]	4	0
HET	Saldidae+	*Salda littoralis*	Linnaeus, 1758	Shore bug	PRE[16]	638	2
HOM	Cicadellidae	*Aphrodes albifrons*	Linnaeus, 1758	Leaf hopper	PHY[17]	0	1
HOM	Cicadellidae	*Aphrodes bicinctus*	Schrank, 1776	Leaf hopper	PHY[17]	1	5
HOM	Cicadellidae	*Arthaldeus pascuellus*	Fallen, 1826	Leaf hopper	PHY[17]	5	1
HOM	Cicadellidae	*Psammotettix putoni*	Then, 1898	Leaf hopper	PHY[17]	12	0
HOM	Cicadellidae	*Conosanus obsoletus*	Kirshbaum, 1858	Leaf hopper	PHY[17]	6	3
HOM	Cicadellidae	*Streptanus sordidus*	Zetterstedt, 1828	Leaf hopper	PHY[17]	7	0
HOM	Cicadellidae	*Macrosteles viridigriseus*	Edwards, 1922	Leaf hopper	PHY[17]	5	0
HOM	Delphacidae	*Javesella dubia*	Kirschbaum, 1868	Leaf hopper	PHY[17]	1	2
HOM	Delphacidae+	*Javesella pellucida*	Fabricius, 1794	Leaf hopper	PHY[17]	0	29
HOM	Stenorrhyncha			Aphids only	PHY[17]	173	102
HET	Miridae	*Megaloceraera recticornis*	Geoffroy, 1785	Mirid bug	PHY[15]	0	1
HOM	Cicadellidae L	Cicadellidae larvae			PHY[17]	66	5
ARA	Clubionidae	*Clubiona stagnatilis*	Kulczynski, 1897	Foliage spider	PRE (FRH)[18]	3	25
ARA	Gnaphosidae	*Micaria pulicaria*	Sundevall, 1831	Ground spider	PRE (GRH)[18]	0	15

ARA	Lycosidae	*Trochosa ruricola*	De Geer, 1778	Wolf spider	PRE (GRH)[18]	12	49
ARA	Lycosidae	*Pardosa purbeckensis*	Cambridge, 1895	Wolf spider	PRE (GRH) [18] (CS)	454	515
ARA	Lycosidae	*Pardosa pullata*	Clerck, 1757	Wolf spider	PRE (GRH)[18]	2	22
ARA	Lycosidae	*Pirata piraticus*	Clerck, 1757	Wolf spider	PRE (GRH)[18]	5	73
ARA	Tetragnathidae	*Pachygnatha clercki*	Sundevall, 1823	-	PRE (GRH)[21]	73	153
ARA	Tetragnathidae	*Pachygnatha degeeri*	Sundevall, 1830	-	PRE (GRH)[21]	106	1
ARA	Theridiidae	*Robertus lividus*	Blackwall, 1836	Comb spider	PRE (SWB)[18]	0	153
ARA	Linyphiidae	*Walckenaeria nudipalpis*	Westring, 1851	Money spider	PRE (SW)[18]	0	1
ARA	Linyphiidae	*Walckenaeria vigilax*	Blackwall, 1853	Money spider	PRE (SW)[18]	33	9
ARA	Linyphiidae	*Walckenaeria incisa*	Cambridge, 1871	Money spider	PRE (SW)[18]	1	0
ARA	Linyphiidae	*Walckenaeria kochi*	Cambridge, 1873	Money spider	PRE (SW)[18]	21	37
ARA	Linyphiidae	*Walckenaeria acuminata*	Blackwall, 1833	Money spider	PRE (SW)[18]	0	83
ARA	Linyphiidae	*Hypomma bituberculatum*	Wider, 1834	Money spider	PRE (SW)[18]	243	58
ARA	Linyphiidae	*Oedothorax fuscus*	Blackwall, 1834	Money spider	PRE (SW)[18]	1086	13
ARA	Linyphiidae	*Oedothorax retusus*	Westring, 1851	Money spider	PRE (SW)[18]	156	9
ARA	Linyphiidae	*Silometopus ambiguus*	Cambridge, 1905	Money spider	PRE (SW)[18](CS)	273	15
ARA	Linyphiidae	*Savignia frontata*	Blackwall, 1833	Money spider	PRE (SW)[18]	242	104
ARA	Linyphiidae	*Araeoncus humilis*	Blackwall, 1841	Money spider	PRE (SW)[18]	1	0
ARA	Linyphiidae	*Erigone dentipalpis*	Wider, 1834	Money spider	PRE (SW)[18]	1	0
ARA	Linyphiidae	*Erigone atra*	Blackwall, 1833	Money spider	PRE (SW)[18]	177	1
ARA	Linyphiidae	*Erigone longipalpis*	Sundevall, 1830	Money spider	PRE (SW)[18] (CS)	2213	9
ARA	Linyphiidae	*Leptorhoptrum robustum*	Westring, 1851	Money spider	PRE (SW)[18]	10	4
ARA	Linyphiidae	*Centromerita concinna*	Thorell, 1875	Money spider	PRE (SW)[18]	0	26
ARA	Linyphiidae	*Bathyphantes approximatus*	Cambridge, 1871	Money spider	PRE (SW)[18]	6	9
ARA	Linyphiidae	*Bathyphantes gracilis*	Blackwall, 1841	Money spider	PRE (SW)[18]	70	27
ARA	Linyphiidae	*Bathyphantes parvulus*	Westring, 1851	Money spider	PRE (SW)[18]	0	7
ARA	Linyphiidae	*Tenuiphantes tenuis*	Blackwall, 1852	Money spider	PRE (SW)[18]	67	143
ARA	Linyphiidae	*Palliduphantes tenuis*	Cambridge, 1871	Money spider	PRE (SW)[18]	0	1
ARA	Linyphiidae	*Allomengea scopigera*	Grube, 1859	Money spider	PRE (SW)[18]	25	1010
HYM	Parasitic Hymenoptera			Parasitoid wasp	PRE[19]	623	615
OPI				Harvestmen	ZOO[19]	1	68
PUL				Snail	PHY[19]	7	78
LEP				Moth larvae	PHY[19]	21	22
HAP	Enchytraeidae			Pot worm	DET[20]	147	0
COLL				Springtail	DET[19]	13857	3391
ISO				Woodlice	DET (S)[19]	76	9539

AMP	Talitridae	*Orchestia gammarella*	Pallas, 1766	Sandhopper	DET (S)[19]	6133	27773
ACA				Mite	NOT	1168	563
HYM	Formicidae			Ant	NOT	18	4
DIP	Tipulidae+			Crane fly	NOT	2461	56
DIP	Other Diptera				NOT	4078	4087
DIP	Limoniidae L				NOT	29	0
DIP	Stratiomyidae L				NOT	48	3
DIP	Ephaedridae L				NOT	29	0
DIP	Scatophagidae L				NOT	48	0
DIP	Other fly larvae				NOT	281	37

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* refers to functional group assigned on the basis of conspecifics.

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