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**The importance of canopy complexity in shaping seasonal spider and beetle assemblages in saltmarsh habitats**

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**Running title:** *Canopy complexity and invertebrates*

**Abstract.** 1. Habitat structure, including vegetation structural complexity, largely determines invertebrate assemblages in semi-natural grasslands. The importance of structural complexity to the saltmarsh invertebrate community, where the interplay between vegetation characteristics and tidal inundation is key, is less well known.

2. We hypothesised that canopy complexity would be a more important predictor of spider and beetle assemblages than simple vegetation attributes (e.g. height, community type) and environmental variables (e.g. elevation) alone; measured in two saltmarsh regions, south-east (Essex) and north-west (Morecambe Bay) UK. Canopy complexity (number of non-vegetated ‘gaps’ in canopy  $\geq 1$  mm wide) was assessed using side-on photography. Over 1,500 spiders and beetles were sampled via suction sampling, winter and summer combined.

3. In summer, saltmarshes with abundant spider and beetle populations were characterised by high scores for canopy complexity often associated with tussocky grass or shrub cover. Simple vegetation attributes (plant cover, height) accounted for 26 % of variation in spider abundance, 14 % in spider diversity; rising to 46 and 41 % respectively with the addition of canopy complexity score. Over-wintering spider assemblages were associated with elevation and vegetation biomass. Summer beetle abundance, in particular the predatory and zoophagous group, and diversity were best explained by elevation and plant species richness.

4. Summer canopy complexity was identified as a positive habitat feature for saltmarsh spider communities (ground-running hunters and sheet weavers) with significant 'added value' over more commonly measured attributes of vegetation structure.

**Key words.** CBESS, invertebrate, over-wintering, salt marsh, structural complexity, vegetation structure.

## **Introduction**

Small-scale vegetation structural complexity plays a key part in shaping grassland invertebrate assemblages (Morris, 2000). Habitat complexity is associated with features such as availability of foraging sites, shelter and over-wintering or nesting sites, indicating abundance of resources (prey, pollen or nectar) and suitable refuges from predators, intra-guild cannibalism and competitors (Halaj *et al.*, 2000; McNett & Rypstra, 2000; Langellotto & Denno, 2004; Finke & Denno, 2006). Habitat complexity might also be considered an explanatory factor in species-area relationships (Hart & Horwitz, 1991). Enhanced structural complexity may offer greater space-size heterogeneity, providing habitable space to organisms with a wide range of body sizes, thereby increasing species richness (Tokeshi & Arakaki, 2012; Pierre &

Kovalenko, 2014). To determine the vegetation characteristics that best describe the relationship between arthropod communities and the vegetation they inhabit, various methods have been used. These include fractal geometry, architectural or branching complexity, soil microhabitat complexity, multi-variable habitat heterogeneity and vegetation density (Anderson, 1978; Hatley & MacMahon, 1980; Dennis *et al.*, 1998; Halaj *et al.*, 2000; McNett & Rypstra, 2000; Dennis, *et al.* 2001; Whitehouse *et al.*, 2002; Woodcock *et al.*, 2007).

In contrast, other studies tend to focus on simple measurements, such as vegetation height or above-ground biomass, often in concert with livestock grazing intensity. In this study, we introduce a novel side-on photography technique to accurately record vegetation structural complexity, via the quantification of canopy gaps, at a scale relevant to invertebrate communities.

Certain invertebrate groups, specifically generalist predators and spiders, appear to prefer more complex habitats (McNett & Rypstra, 2000; Shrewsbury & Raupp, 2006), with spiders in particular negatively affected when habitat structure is simplified (Marshall & Rypstra, 1999; Langellotto & Denno, 2004; Wise, 2006). Ground-dwelling spider communities respond to commonly measured structural attributes such as height, above-ground biomass, vegetation tip height diversity and depth of plant litter layer (Uetz *et al.*, 1999; Bonte *et al.*, 2000; Bell *et al.*, 2001; Traut, 2005; Pétilion *et al.*, 2008), but do not exhibit strong host-plant associations. Both phytophagous and predatory beetle habitat preferences are associated with commonly measured attributes of vegetation structure (Lassau *et al.*, 2005; Hofmann & Mason, 2006; Woodcock *et al.*, 2007) and satellite-derived vegetation indices (Lafage *et al.*, 2014).

Plant species richness may also contribute to vegetation structural complexity, and affect the abundance and species richness of predatory arthropods such as spiders and predatory

beetles via bottom-up trophic effects (Scherber *et al.*, 2010). A species-rich plant community tends to support a large number of herbivorous arthropods which in turn boosts the predatory arthropod population (Borer *et al.*, 2012). The 'Enemies Hypothesis' (Root *et al.*, 1973), proposes a mechanism of top-down control in which diverse vegetation assemblages provide more refuges for predatory arthropods and more opportunity for stable prey availability than low plant diversity assemblages, leading to higher predator efficiency and the resultant link between plant species richness and predatory arthropod abundance (Russell, 1989). The habitat heterogeneity hypothesis (Dennis *et al.*, 1998) predicts an asymptotic relationship between increasing plant species richness and vegetation structural heterogeneity, with greater resources available for the coexistence of multiple species of arthropods of each trophic group in structurally complex vegetation.

Ground and canopy dwelling invertebrates are sensitive to seasonal changes in environmental characteristics, such as changes in vegetation structure due to natural die-back in winter, but seasonal invertebrate- vegetation structure relations are rarely quantified. Dense vegetation may be important in winter for different reasons than in the summer. For example, tussocky grasses and leaf litter provide over-wintering shelter from predators for ground-dwelling invertebrates including wolf spiders (Edgar & Loenen, 1974; Collins *et al.*, 2002; Lewis & Denno, 2009), whereas in spring and summer, prey availability is often crucial (Wise, 2006) encouraging individuals to explore more open habitat. Tall vegetation offers several benefits for invertebrates including protection from predation and shelter from extreme weather events. However, daytime temperatures are lower in tall vegetation, potentially hindering thermophilic invertebrates, inhibiting movement and hiding prey, especially in dense grass mats such as *Festuca rubra* (Linnaeus) swards (Van Klink *et al.*, 2014). Hence, vegetation that

is tall, but not dense may be optimal. This level of vegetation structural detail, e.g. canopy openness, is difficult to capture, and simple measurements of vegetation height or above-ground biomass will not portray intricacies such as canopy gap availability.

Saltmarshes provide an important habitat for invertebrates, plants and insectivorous birds (Milsom *et al.*, 2000; Chatters, 2004; Pétilion *et al.*, 2005). They are characterised by a suite of plant communities differing in structural complexity, ranging from grass to shrub or rush dominated, making saltmarshes an ideal habitat to study the interplay between vegetation structural complexity and invertebrate assemblages. The two invertebrate orders focused on in this study, Araneae and Coleoptera, were chosen as they are well studied, known to respond to habitat complexity and are often used as bio-indicators of ecosystem health (Pearce & Venier, 2006).

The relationship between ground and canopy dwelling invertebrate communities and plant canopy complexity was examined, via suction sampling, in two English saltmarsh regions, south-east (Essex) and north-west (Morecambe Bay), in summer and winter. We used a novel side-on photography technique to record canopy complexity, via the quantification of canopy gaps. We examined the following two hypotheses: i) Canopy complexity will be a more important predictor of spider and beetle assemblages than simple vegetation attributes (e.g. height, community type) and environmental variables (e.g. surface elevation) alone. As the measurement of canopy complexity allows us to access a level of vegetation structural detail not captured by more commonly measured vegetation characteristics; and ii) Winter canopy complexity will be positively associated with spider abundance due to the provision of shelter and ability to avoid over-wintering wolf spiders, prone to preying on both smaller spiders and to cannibalism. The impact of winter canopy complexity on beetles is largely unknown.

## Materials and methods

### *Site description and experimental design*

Three marshes from Essex (south-east England) and three from the greater Morecambe Bay area (north-west England) were selected to represent two distinct saltmarsh regions differing broadly in inundation frequency and dominant vegetation type. In Essex, Abbots Hall (AH; 51° 47'N, 0° 52'E), Fingringhoe Wick (FW; 51° 49'N, 0° 58'E) and Tillingham marsh (TM; 51° 41'N, 0° 56'E) were all lagomorph grazed with Abbots Hall and Fingringhoe Wick both heavily grazed by over-wintering Brent geese (*Branta bernicla* Linnaeus) (Austin *et al.*, 2014). In Morecambe Bay, Cartmel Sands (CS; 54° 10'N, 3° 0'W) and Warton Sands (WS; 54° 8'N, 2° 48'W) were intensively sheep grazed (~4 - 5 sheep ha<sup>-1</sup>) with pink-footed geese (*Anser brachyrhynchus* Baillon) grazing during the winter. In contrast, West Plain (WP; 54° 9'N, 2° 58'W), in Morecambe Bay, was lightly grazed (<2 sheep ha<sup>-1</sup>), with historical annual cattle grazing potentially leading to a legacy effect on vegetation structure.

All experimental sites were sampled in winter 2013 (January/February) and again in late summer 2013 (August/September). In each study site we selected an area of 20 to 100 ha in size, dependent upon saltmarsh length (parallel to shore) and width (perpendicular to shore), including part of the low, mid and high marsh zones. Twenty two 1 x 1 m quadrats were marked in each site, according to a stratified random pattern.

### *Standard vegetation characteristics*

Above-ground vegetation characteristics were measured from within each 1 x 1 m quadrat. Percentage cover of each plant species within each quadrat was estimated by eye. Shannon-Weiner index (S-W index (H')) was calculated for each quadrat as a measure of plant species

diversity. British National Vegetation Classification (NVC) plant community types were calculated for each quadrat using Tablefit v1.1 (Hill, 2011). All plant nomenclature follows Stace (2010). Above-ground dry vegetation biomass (60° C, 72 h) was determined by cutting plants to ground level from a 50 x 25 cm area within each quadrat. Vegetation height was recorded at 10 random positions within each quadrat using a direct measurement (hand slid down metre stick until vegetation detected then height in cm recorded). Mean height per quadrat was used in the analysis. The standard deviation of height within each quadrat was calculated as a potential proxy for combined vegetation structure and height complexity. Coefficient of variation (CoV; Standard Deviation /Mean x 100) in vegetation height (CoV<sup>1</sup>) was calculated from the 10 direct vegetation height measurements per quadrat.

#### *Vegetation structure: side-on photography method*

Digital photographs to determine vegetation structure were taken side-on within each quadrat through a 20 cm deep section of vegetation, against a 60 cm wide red back board (Fig. 1a) at a fixed distance from the camera using a FujiFilm Finepix XP30 digital camera at full 14MP resolution following the method of Möller (2006). Photographs were only taken at quadrat locations where vegetation height exceeded the height of the steel frame (25 mm), with vegetation clearly visible against the backboard. The Matlab Camera Calibration Toolbox (Bouguet n.d.) was used to correct and calibrate the images, ERdas Imagine software was used for image classification. Unsupervised classification of the 3 band images into 20 classes was followed by manual attribution and recoding of those classes to either 'vegetation' or 'non-vegetation' with visual reference to the original photograph. Variations in illumination, vegetation colour and proportions of vegetation and background between photographs



meant that fully unsupervised classification did not provide consistent results. Matlab was subsequently used to process thematic images (Fig. 1b; doi reference to be added).

Structural complexity was assessed via a canopy complexity score, calculated as number of non-vegetated 'gaps' in canopy  $\geq 1$  mm wide, standardised to number of gaps per metre. This standardisation was important as background images varied slightly in horizontal width but were always close to 60 cm (width of back board). Henceforth, this 'canopy complexity score' will be referred to as 'canopy complexity'. Mean, median and standard deviation in 'gap' area for each quadrat were also calculated, alongside maximum gap area (combined area of all gaps in one quadrat), but were not found to relate to the structuring of spider and beetle assemblages. They will not be discussed further in this manuscript. Vertical vegetation density (from now on 'vegetation density') was calculated from each quadrat image by the proportion of the image classed as vegetation normalised by the horizontal extent of the image – i.e.  $\text{mm}^2/\text{mm}$ . Vegetation tip height diversity ( $\text{CoV}^2$ ) was measured by the coefficient of variation.  $\text{CoV}^2$  was calculated from the highest vegetation point measured from ten random columns of pixels per quadrat photograph.

### *Physical characteristics*

Saltmarsh elevation and salinity were measured as these can determine the distribution of some saline sensitive saltmarsh invertebrates. Elevation and x, y coordinates of each quadrat were measured by a Leica GS08 GNSS Differential Global Positioning System (DGPS) with CRS = OSGB(36) accuracy of  $\leq \pm 0.05$  m. Elevation was recorded in metres relative to Ordnance Datum Newlyn (ODN), converted to Chart Datum (CD) and presented relative to Mean High Water Neap (MHWN) as a rough proxy for tidal inundation frequency. Soil salinity was measured by proxy of electrical conductivity (EC) in the lab. Soil samples, of  $\sim 10$  g (fresh mass)

from the top 10 cm, were taken from within each quadrat, diluted by 1:2.5 with deionised water and measured for EC ( $\text{mS cm}^{-1}$ ) and pH using a Jenway 4320 conductivity meter. Soil bulk density was calculated from bulk density ring (3.1 cm height, 7.5 cm diameter) samples taken vertically to roughly quantify the 0 – 10 cm depth zone. Samples were dried ( $105^{\circ}\text{C}$ , 72 h) prior to calculation of bulk density. Soil moisture content was also calculated.

#### *Araneae and Coleoptera – Suction sampling*

Ground and vegetation dwelling invertebrates were suction sampled from each 1 x 1m quadrat using a modified garden vacuum (McCulloch MAC GBV345 Petrol Leaf Blower Vac 25cc). Each sample consisted of four 20 second suctions at four regularly placed intervals within the quadrat with a 20 cm diameter circular tube containing a 500 micron mesh to trap invertebrates. Care was taken to place the sampler tube end over the top of vegetation where possible, whilst maintaining good contact with the ground surface to ensure efficiency of sampling. In *Atriplex portulacoides* (Aellen) bushes we squashed the vegetation down with the sampler end to enable sampling through the column of vegetation and the soil surface. Where vegetation was very long, for example in *Juncus maritimus* (Lam) swards of up to 70 cm high we were not able to do this and so focused on bottom 10 cm of vegetation and soil surface. Each sample was then preserved in 70% industrial methylated spirits. Araneae and Coleoptera were identified to lowest possible taxonomic level, which in most cases was species, but in some cases genus or subfamily with a Novex stereoscope. Early stage juveniles, predominantly Linyphiidae, were classified to family level for Araneae. The majority of later stage juvenile *Pardosa* were assumed to be the most common saltmarsh species *Pardosa purbeckensis* (Cambridge). Invertebrate nomenclature follows Duff (2012) for Coleoptera and the World Spider Catalog (2016) for Araneae. Spider feeding guilds of ground running hunters,

foliage running hunters, sit and wait hunters, sheet weavers, space web builders and orb web weavers were classified according to Uetz *et al.* (1999). Beetles were grouped into predatory, zoophagous (predatory and scavenging), phytophagous (herbivore or granivorous) or detritivore (feed on detritus and associated decomposer community of fungi and bacteria) using several sources listed in the footnotes to Table S4. Spider or beetle species confined to saline habitats were classified as 'coastal specialists' whereas species occurring in habitats other than saltmarshes (usually other wet habitats or sand dunes) were classified as 'non-coastal specialists' (Hänggi *et al.*, 1995; Van Klink, 2014).

### *Statistical analysis*

Relationships between environmental variables and the abundance and species richness of the different invertebrate groups were examined using a generalized linear model with a nested structure (random = ~ 1 region/site/quadrat) and a Poisson distribution suitable for invertebrate count data, tested for over-dispersion (if ratio between residuals<sup>2</sup> and residual degrees of freedom is >5 data is over-dispersed). Best fit models were selected on the basis of lowest Akaike information criterion (AIC) value for three analyses: 1. Standard environmental variables (Elevation above MHWN + Plant cover + Plant species richness + Height + Above-ground biomass); 2. Standard environmental variables plus canopy complexity score; 3. Standard environmental variables plus side-on photography variables (Density + Vegetation tip height diversity + canopy complexity score) allowing the 'value added' component of the side-on photography method to be assessed. Analysis was carried out on the following spider feeding guilds: ground running hunters; foliage running hunters; and sheet weavers. Space web builders, orb web weavers and sit and wait hunters were excluded due to very low abundance. Beetles were analysed in two broad groups: i) predatory

and zoophagous and ii) phytophagous and detritivores. Generalised linear models (as detailed above) were also used to analyse regional differences in invertebrate abundance.

Testing for significant differences in vegetation and physical characteristics between regions (Essex, Morecambe bay) and site (AH, FW, TM, CS, WP, WS) was carried out using ANOVA output of a linear model, variables were logged where appropriate to normalise data, and post hoc Tukey tests calculated (Hothorn *et al.*, 2008). The relationship between elevation above MHWN and EC (proxy for salinity) was determined by Spearman's rank correlation coefficient.

Nonmetric Multidimensional scaling (NMDS) was used to assess how environmental factors, vegetation structure and site characteristics, influenced individual spider and beetle species habitat preferences. NMDS, an un-constrained ordination technique using rank order of species abundances, was carried out with Bray-Curtis dissimilarity calculations (1000 permutations) using the 'vegan' package (Oksanen *et al.*, 2016). To be included within either the winter or summer NMDS analysis each spider or beetle species had to have  $\geq 10$  individuals in total across all quadrats, Essex and Morecambe Bay saltmarsh sites combined. For pairs or sets of closely related environmental variables (e.g. vegetation height, above-ground biomass) only one variable was retained in the analysis based on an  $r_s$  value of  $\geq 0.5$  (Spearman's rank correlation coefficient). All statistical analysis was carried out in R (R Core Team, 2015).

## Results

### *Standard vegetation characteristics*

Vegetation height and above-ground biomass were greater for Essex than Morecambe Bay saltmarshes in both summer and winter (Tables S1 & S2). Summer plant diversity (S-W index) was greater in Morecambe Bay than Essex. For plant community (NVC) type the Essex marshes, Abbots Hall and Fingringhoe Wick were dominated by *Puccinellia maritima* (Hudson) community (SM13), a common saltmarsh grass species. Tillingham, in contrast, was characterised by *A. portulacoides* community (SM14), a common open saltmarsh shrub. For Morecambe Bay, Cartmel sands was dominated by a short sward of *P. maritima* (SM13), West Plain and Warton sands by *Juncus gerardii* (Loisel, SM16) and *J. maritimus* (SM18) communities. *J. maritimus* communities are characterised by large tussocks of *J. maritimus*, a large rush up to 70 cm tall.

### *Vegetation structure: side-on photography method*

Canopy complexity was variable across sites, with Tillingham and West plain gaining the highest summer scores for Essex and Morecambe Bay respectively (Table S1 & S2). For information on vegetation diversity and vegetation tip height diversity see Tables S1 & S2.

### *Physical characteristics*

Elevation relative to MHWN was significantly greater for Morecambe Bay (~ 2.5 m) than Essex (~ 1 m) saltmarsh sites (Table S1 & S2) in both winter and summer, indicating that the Essex saltmarshes were tidally inundated more often (despite differences in tidal range). This was confirmed by soil EC, a proxy for salinity, and soil moisture content being appreciably greater in Essex (10-30 mS cm<sup>-1</sup>; 45 – 60 %) than Morecambe Bay (1-5 mS cm<sup>-1</sup>; 25-40 %) across both

winter and summer. Elevation relative to MHWN was significantly negatively associated with EC in both summer (SPEARMANS:  $r_s = -0.77$ ,  $p < 0.001$ ) and winter ( $r_s = -0.82$ ,  $p < 0.001$ ). Elevation was also a stronger predictor of spider and beetle assemblages than EC in all statistical models. For these reasons elevation relative to MHWN was used instead of EC in the final set of models presented in this study. For site means and further information see Tables S1 & S2.

#### *Regional differences: Araneae and Coleoptera*

Nearly 400 spiders were sampled in winter, 60 % from Essex. Over 1000 were sampled in the summer with 72 % from Essex, Tillingham supported the most with >400 individuals (Table S3). Summer spider abundance and species richness were significantly greater in Essex than Morecambe Bay (Table S5, S6). However, total Araneae species richness, across sites and seasons, between Essex and Morecambe Bay was equal with 23 species apiece. Only 24 beetles were found in winter across all six sites, 75 % from Morecambe Bay. Nearly 300 were sampled in summer with 58 % from Morecambe (Table S4). Summer Coleoptera abundance showed marked differences between saltmarsh sites with shrubby Tillingham and tussocky West Plain having particularly abundant populations (Table S4), but with no significant difference between the two regions (Table S5). Total Coleoptera species richness, across sites and seasons, was greater for Morecambe Bay (26) than Essex (21).

#### *Summer: Araneae*

Summer spider abundance was associated positively with plant cover, canopy complexity and plant density, negatively with elevation above MHWN (Table 1). The best fit model for spider abundance improved from 26 % of variation explained for standard environmental variables

alone to 46 % with the addition of canopy complexity. Ground running hunters were positively associated with plant cover, height and canopy complexity, negatively with elevation (Table 1). Foliage running hunters were aligned with elevation and either vegetation height or density (depending on model type). Sheet weavers (including juveniles) were significantly associated with canopy complexity (Table 1). When spiders were analysed by feeding guild the importance of canopy complexity in explaining variation in abundance was much reduced (0.01 or 1 % increase in  $r^2$  compared to standard variables alone) compared to when spiders were considered as a group (0.2 or 20 % increase in  $r^2$ ).

The summer NMDS analysis included 7 spider species, with five environmental variables associated with invertebrate habitat choice (Fig. 2), canopy complexity ( $p < 0.001$ ), vegetation height ( $p < 0.001$ ), plant cover ( $p < 0.001$ ), plant species richness ( $p < 0.01$ ) and elevation above MHWN ( $p < 0.001$ ). Despite the fact that elevation above MHWN and plant species richness appear closely correlated on the summer NDMS plot they are only partially correlated with an  $r_s$  value of 0.43.

Spider species richness was positively associated with plant cover, plant height and canopy complexity, and negatively associated with elevation above MHWN. The best fit model for spider species richness improved from 14 % of variation explained for standard environmental variables alone to 41 % with the addition of canopy complexity. Interestingly, spider abundance in Essex, including juveniles, was well predicted by shrubby *A. portulacoides* cover alone ( $t = 2.50$ ,  $p < 0.05$ ) although this relationship does not hold for spider diversity or when juveniles are removed. There was a significant positive relationship between canopy complexity and *A. portulacoides* cover (SPEARMANS:  $r_s = 0.6$ ,  $p < 0.001$ ) in Essex.

312 *Winter: Araneae*

313 Models using environmental predictors of spider assemblages in winter performed much  
314 poorer than summer models with typically only 2 – 19 % of variation in abundance explained  
315 (Table 2). For all spiders combined and ground-running hunters abundance was negatively  
316 associated with elevation above MHWN. For sheet weavers this relationship was reversed,  
317 with a positive link between abundance and elevation (Table 2). Winter NMDS analysis of 4  
318 over-wintering spider species indicated that elevation above MHWN ( $p < 0.001$ ) and  
319 vegetation biomass ( $p < 0.01$ ) both significantly influenced species habitat choice (Fig. 2).

320 *Summer: Coleoptera*

321 Beetle abundance and species richness were positively linked to plant cover and elevation  
322 above MHWN, with beetle abundance negatively associated with plant species richness  
323 (Table 1). The predatory and zoophagous beetle group responded in a similar way to beetles  
324 as a whole but the phytophagous and detritivore group showed no significant response to  
325 either elevation or any structural variables. Neither beetle abundance, or species richness,  
326 were significantly associated with canopy complexity. Beetle abundance in Essex, including  
327 juveniles, was positively correlated to *A. portulacoides* cover ( $t = 218$ ,  $p < 0.05$ ), but not  
328 explicitly to canopy complexity. The summer NMDS analysis was dominated by 7 common  
329 spider species but did include 3 beetle species (Fig. 2). Additional results can be seen in the  
330 Supporting Information (Tables S1-S6).

331 *Winter: Coleoptera*

332 Beetles were excluded from winter analysis due to extremely low numbers of over-wintering  
333 individuals sampled.



### 334 *Coastal specialists*

335 The abundance of coastal specialist species, spiders and beetles combined (as defined in:  
336 Table S3 & S4), was greater in the more saline Essex marshes in summer (ANOVA;  $F = 65.27$ ,  
337 d.f. = 1,  $p < 0.001$ ). Abundance of coastal specialists was correlated negatively with elevation  
338 above MHWN (Table 1; 2) in both summer and winter.

### 339 **Discussion**

340 Vegetation structural complexity is recognised as a key component determining the  
341 invertebrate communities of semi-natural grasslands (Morris, 2000). Here we showed that  
342 saltmarsh vegetation characterised by high complexity, regardless of region, exhibited the  
343 greatest abundance and species diversity of spiders and beetles. For Araneae specifically,  
344 canopy complexity explained close to twice as much of the variation in spider abundance and  
345 diversity than standard vegetation measurements (plant cover, height) and elevation  
346 combined. However, when spiders were grouped by feeding guild the importance of canopy  
347 complexity in explaining variation in abundance was much reduced. Environmental and  
348 standard vegetation characteristics were better at predicting predatory and zoophagous  
349 beetle abundance and diversity than canopy complexity *per se*. For over-wintering spiders  
350 surface elevation and above-ground plant biomass were more important indicators of  
351 abundance than canopy complexity.

### 352 *Spider and beetle assemblages*

353 Spiders responded positively to canopy complexity, with ground-running hunting spiders in  
354 particular more abundant in complex, tall vegetation, as in other grassland studies (McNett  
355 & Rypstra, 2000; Pétilon *et al.*, 2007; Van Klink & Van Schroyen Lantman, 2015). Beetles

356 did not respond as clearly or positively to canopy complexity as spiders, mirroring the mixed  
357 responses to vegetation height seen in the literature (Morris, 2000; Woodcock *et al.*, 2007;  
358 Ford *et al.*, 2013). Despite the different responses of Coleoptera and Araneae to canopy  
359 complexity, both were abundant in the 'gappy' shrub cover of *A. portulacoides*. This  
360 vegetation type is often characterised by an even shrub layer, ~25 cm in height, with many  
361 small gaps,  $\geq 1$  mm, present throughout the whole canopy layer, unlike grass swards which  
362 often have very few non-vegetated canopy gaps at ground level. We propose that the  
363 complex canopy of an *A. portulacoides* dominated plant community allows shelter from  
364 inundation, storms and predators coupled with freedom of movement, providing ideal living  
365 conditions for many ground-dwelling invertebrates (Langellotto & Denno, 2004; Finke &  
366 Denno 2006). Despite the strong link apparent between habitat complexity and overall  
367 abundance and diversity, certain groups preferred less complex habitats. For example,  
368 Linyphiidae, especially specialist thermophiles such as *Erigone* and *Oedothorax* species, were  
369 commonly found in shorter, less complex vegetation. *Erigone longipalpis* (Sundevall), a  
370 coastal specialist, was associated with more saline environments than *Oedothorax fuscus*  
371 (Blackwall), an open ground grassland generalist. It is likely that *O. fuscus*, an active aeronaut,  
372 disperses into open habitats, such as close-cropped saltmarsh, where competition from larger  
373 invertebrate predators is low (Gibson *et al.*, 1992; Bell *et al.*, 2001; Ford *et al.*, 2013).

374 Beetle species richness was positively associated with plant cover and surface elevation as in  
375 other saltmarshes (Irmiler *et al.*, 2002; Finch *et al.*, 2007). Coleoptera lack submersion  
376 resistance techniques (Rothenbücher & Schaefer, 2006), possibly explaining why they were  
377 more abundant in drier Morecambe Bay than wetter, more frequently inundated, Essex.  
378 Surprisingly, a strong negative link was apparent between beetle abundance and plant species

richness. This has been found in grassland studies (Koricheva *et al.*, 2000) and in shrubby forest (Zou *et al.*, 2013), but stands in contrast to the more commonly postulated Enemy Hypothesis which predicts a positive relationship between plant species richness and predatory arthropod diversity. It is possible that increased plant diversity and the assumed associated increase in phytophagous prey may lead to enhanced competition between predatory Coleoptera and other predatory arthropods, such as spiders, leading to an eventual reduction in beetle abundance, as suggested by Zou *et al.* (2013).

Spiders were much more likely to over-winter on the saltmarsh than beetles with three species *P. purbeckensis*, *Pachygnatha degeeri* (Sundevall) and *O. fuscus* proving the most abundant. The strong link observed between above-ground vegetation biomass and the over-wintering wolf spider, *P. purbeckensis* was also demonstrated in juveniles by Kessler & Slings (1980), possibly due to protection from predators, avoidance of cannibalism and warmth (Wise, 2006; Lewis & Denno, 2009). In contrast, the small ground running spider, *P. degeeri*, and the open grassland generalist Linyphiidae, *O. fuscus*, over-wintered in large numbers in the short-cropped Morecambe Bay saltmarshes. Linyphiidae juveniles over-wintered in all study saltmarshes, regardless of vegetation height or structure.

#### *Vegetation structure: side-on photography method*

In this study we used the side-on photography method, adapted from Möller (2006), to assess the relationship between vegetation structure and invertebrate assemblage patterns, specifically via measurements of vegetation tip height diversity, vegetation density and canopy complexity. Vegetation tip height diversity was not a significant explanatory variable. However, vegetation density and canopy complexity both ‘added value’ to best fit models of spider abundance, with twice as much variation in abundance explained as standard

environmental and vegetation measurements alone. Canopy complexity is of particular interest as a measurement of vegetation structural complexity. Previously, grassland canopy complexity has been assessed by vertical drop pins (Woodcock, *et al.*, 2007), with number of contacts between vegetation and pins used to calculate a complexity index. Our method is roughly analogous to this with canopy complexity calculated from number of canopy gaps  $\geq$  1 mm wide, but is likely to be less time consuming. Canopy complexity also seems to be partially responsible for the positive relationship seen between spider and beetle abundance and cover of the ‘gappy’ saltmarsh shrub *A. portulacoides*. The side-on photography method may be advantageous over standard vegetation measurements that may be either destructive (e.g. above-ground biomass) or prone to human error (e.g. direct measurement of vegetation height). We argue that the assessment of vegetation structure by side-on photography proves a useful and novel addition to standard vegetation methods. However, one issue limits its effectiveness in shorter swards with vegetation  $\leq$  25 mm high not appearing in images due to height of base, reducing its usefulness for assessing small scale structural complexity.

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## 427 **Supporting information**

428 Additional Supporting Information may be found in the online version of this article under the  
429 DOI reference: xxxxxxxx

430 **Table S1.** Site characteristics for east and west coast English saltmarshes, winter 2013. Means  
431 per site are shown  $\pm$  standard deviation. Italicised letters denote significant site differences,  
432 final column, regional differences between Essex (AH = Abbots Hall, FW = Fingringhoe Wick,  
433 TM = Tillingham marsh) and Morecambe Bay (CS = Cartmel sands, WP = West Plain, WS =  
434 Warton sands).

435 **Table S2.** Site characteristics for east and west coast English saltmarshes, summer 2013.  
436 Means per site are shown  $\pm$  standard deviation. Italicised letters denote significant site  
437 differences, final column regional differences between Essex (AH = Abbots Hall, FW =  
438 Fingringhoe Wick, TM = Tillingham marsh) and Morecambe Bay (CS = Cartmel sands, WP =  
439 West Plain, WS = Warton sands).

440 **Table S3.** Total counts of all Araneae sampled in winter and summer 2013 from Essex (AH =  
441 Abbots Hall, FW = Fingringhoe Wick, TM = Tillingham marsh) and Morecambe Bay (CS =  
442 Cartmel sands, WP = West Plain, WS = Warton sands) saltmarsh study sites. 'Group' column  
443 indicates prey capture method as all spiders are predatory; GRH = Ground running hunter,  
444 FRH = Foliage running hunter, SWB = Space web builder, ORB = Orb web weaver, SIT = Sit-  
445 and-wait, SW = Sheet weaver (Uetz *et al.* 1999). CS = Coastal specialist as defined by Van Klink  
446 (2014) and Hänggi *et al.* (1995), nomenclature follows World Spider Catalog (2016).

447 **Table S4.** Total counts of all Coleoptera sampled in winter and summer 2013 from Essex (AH  
448 = Abbots Hall, FW = Fingringhoe Wick, TM = Tillingham marsh) and Morecambe Bay (CS =  
449 Cartmel sands, WP = West Plain, WS = Warton sands) saltmarsh study sites. 'Group' column  
450 indicates functional group assignment; PRE = predatory, ZOO = Zoophagous, PHY =  
451 Phytophagous, DET = Detritivore. CS = Coastal specialist defined by Van Klink (2014),  
452 nomenclature follows Duff (2012).

453 **Table S5.** Summer comparison of invertebrate abundance and species richness. Quadrat  
454 means per region are shown  $\pm$  standard error.

455 **Table S6.** Winter comparison of invertebrate abundance and species richness. Quadrat means  
456 per region are shown  $\pm$  standard error.

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**Table 1.** Relationship between saltmarsh spider and beetle assemblages and environmental variables in summer, best model fit for standard and side-on photography variables using generalized linear models.

	Best fit models:	Elevation	Plant cover	Plant sp.	Height	Canopy complexity	Density	AIC	R <sup>2</sup>
<i>Spiders</i>									
All (including juveniles)	Standard	ns	z = 4.45 ***	ns	ns	-	-	749.1	0.26
	Standard + complexity	z = -6.36 ***	z = 3.73 ***	ns	ns	z = 5.62 ***	-	710.4	0.46
	Standard + photo	z = -6.10 ***	z = 3.26 **	ns	ns	z = 4.59 ***	z = 2.60 **	705.8	0.48
All (excluding juveniles)	Standard	z = -3.41 ***	z = 14.9 ***	ns	z = 16.1 ***	-	-	615.1	0.48
	Standard + complexity	z = -8.20 ***	z = 3.44 ***	ns	ns	z = 4.60 ***	-	600.7	0.50
	Standard + photo	z = -8.37 ***	z = 2.87 **	ns	ns	z = 3.31 ***	z = 4.22 ***	586.0	0.57
GRH (including juveniles)	Standard	z = -5.70 ***	z = 3.29 ***	ns	z = 2.72 **	-	-	489.4	0.52
	Standard + complexity	z = -6.74 ***	z = 2.67 **	ns	z = 2.72 **	z = 2.71 **	-	474.1	0.53
	Standard + photo	z = -7.71 ***	z = 2.89 **	ns	ns	z = 2.86 **	z = 3.01 **	472.5	0.54
GRH (excluding juveniles)	Standard	z = -3.86 ***	z = 2.47 *	ns	z = 2.45 *	-	-	448.5	0.43
	Standard + complexity	z = -6.18 ***	ns	ns	z = 2.72 **	z = 3.29 **	- (ns)	435.3	0.48
FRH	Standard	z = 2.62 **	ns	ns	z = 2.05 *	-	-	127.6	0.06
	Standard + photo	z = 2.88 **	ns	ns	ns	- (ns)	z = 2.43 *	126.1	0.07
SW (including juveniles)	Standard	ns	z = 2.86 **	ns	ns	-	-	654.4	0.10
	Standard + complexity	ns	ns	ns	ns	z = 3.54 ***	-	628.6	0.11
	Standard + photo	ns	ns	ns	ns	z = 2.45 *	z = 2.58 **	623.9	0.16
SW (excluding juveniles)	Standard	ns	ns	ns	z = 3.41 ***	- (ns)	- (ns)	467.6	0.09
Species richness	Standard	ns	z = 2.19 *	ns	z = 2.74 **	-	-	420.4	0.14
	Standard + complexity	z = -4.54 ***	z = 2.52 *	ns	z = 2.92 **	z = 2.80 **	-	399.2	0.41
	Standard + photo	z = -5.28 ***	z = 2.76 **	ns	ns	z = 2.95 **	z = 2.72 **	400.1	0.40
<i>Beetles</i>									
All (including juveniles)	Standard	z = 2.30 *	z = 2.76 **	z = -3.03 **	- (ns)	- (ns)	- (ns)	424.2	0.26
All (excluding juveniles)	Standard	z = 2.29 *	z = 2.02 *	z = -2.83 **	- (ns)	- (ns)	- (ns)	404.8	0.25
PRE and ZOO	Standard	z = 2.15 *	ns	z = -2.82 **	ns	- (ns)	- (ns)	247.7	0.21
PHY and DET	Standard	ns	ns	ns	- (ns)	- (ns)	- (ns)	-	-
Species richness	Standard	z = 2.34 *	z = 2.05 *	z = -2.20 *	- (ns)	- (ns)	- (ns)	316.0	0.24
<i>Spiders &amp; beetles</i>									
Coastal specialists	Standard	z = -4.93 ***	z = 2.33 *	ns	- (ns)	- (ns)	- (ns)	442.5	0.46

Best fit models were selected from: 1. Standard environmental variables (Elevation above MHWN + Plant cover + Plant species richness + Height + Above-ground biomass); 2. Standard environmental variables plus canopy complexity score; 3. Standard environmental variables plus side-on photography variables

(Canopy complexity score + Density + Vegetation tip height diversity). Only significant variables are shown: \* =  $p < 0.05$ , \*\* =  $p < 0.01$ , \*\*\* =  $p < 0.001$ .  $R^2$  refers to proportion of variation explained by model fixed effects. ‘-’ = variable not in model, ‘*ns*’ = variable not significant  $p > 0.05$ , ‘- (*ns*)’ = variable not in listed model and not significant for either ‘standard + complexity’ or ‘standard + photo models’. Spider feeding guilds: GRH = Ground running hunter; FRH = Foliage running hunter; SW = Sheet weaver. Beetle diets: PRE = predatory; ZOO = zoophagous; PHY = phytophagous; DET = detritivore.

**Table 2.** Relationship between saltmarsh spider and beetle assemblages and environmental variables in winter, best model fit for standard and side-on photography variables using generalized linear models.

	Best fit models:	Elevation	Plant cover	Plant sp.	Height	Canopy complexity	Density	AIC	$R^2$
<i>Spiders</i>									
All (including juveniles)	Standard	$z = -104.2$ ***	<i>ns</i>	<i>ns</i>	<i>ns</i>	- ( <i>ns</i> )	- ( <i>ns</i> )	480.1	0.02
All (excluding juveniles)	Standard	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	- ( <i>ns</i> )	- ( <i>ns</i> )	-	-
GRH (including juveniles)	Standard	$z = -3.51$ ***	<i>ns</i>	<i>ns</i>	<i>ns</i>	- ( <i>ns</i> )	- ( <i>ns</i> )	292.5	0.19
GRH (excluding juveniles)	Standard	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	- ( <i>ns</i> )	- ( <i>ns</i> )	-	-
SW (including juveniles)	Standard	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	- ( <i>ns</i> )	- ( <i>ns</i> )	-	-
SW (excluding juveniles)	Standard	$z = 2.67$ **	<i>ns</i>	<i>ns</i>	<i>ns</i>	-	-	294.2	0.08
Species richness	Standard	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	- ( <i>ns</i> )	- ( <i>ns</i> )	-	-
Coastal specialists	Standard	$z = -3.74$ ***	<i>ns</i>	<i>ns</i>	<i>ns</i>	- ( <i>ns</i> )	- ( <i>ns</i> )	244.4	0.26

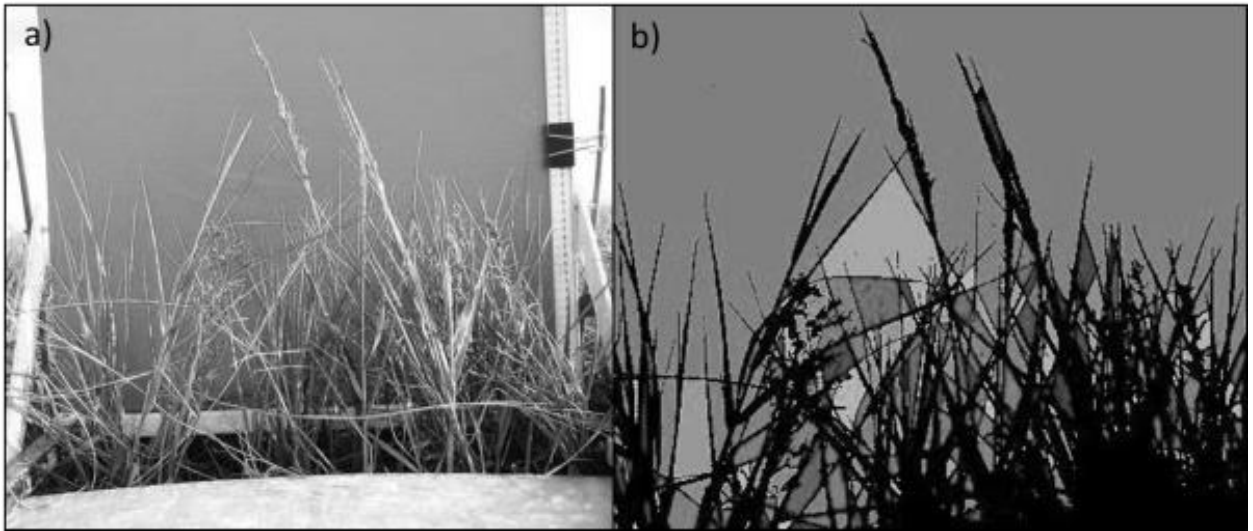
Best fit models were selected from: 1. Standard environmental variables (Elevation above MHWN + Plant cover + Plant species richness + Height + Above-ground biomass); 2. Standard environmental variables plus canopy complexity score; 3. Standard environmental variables plus side-on photography variables (Canopy complexity score + Density + Vegetation tip height diversity). Only significant variables are shown: \* =  $p < 0.05$ , \*\* =  $p < 0.01$ , \*\*\* =  $p < 0.001$ .  $R^2$  refers to proportion of variation explained by model fixed effects. ‘-’ = variable not in model, ‘*ns*’ = variable not significant  $p > 0.05$ , ‘- (*ns*)’ = variable not in listed model and not significant for either ‘standard + complexity’ or ‘standard + photo models’. Spider feeding guilds: GRH = Ground running hunter; SW = Sheet weaver. Beetles were excluded from winter analysis due to extremely low numbers of over-wintering individuals sampled.

## Figure list

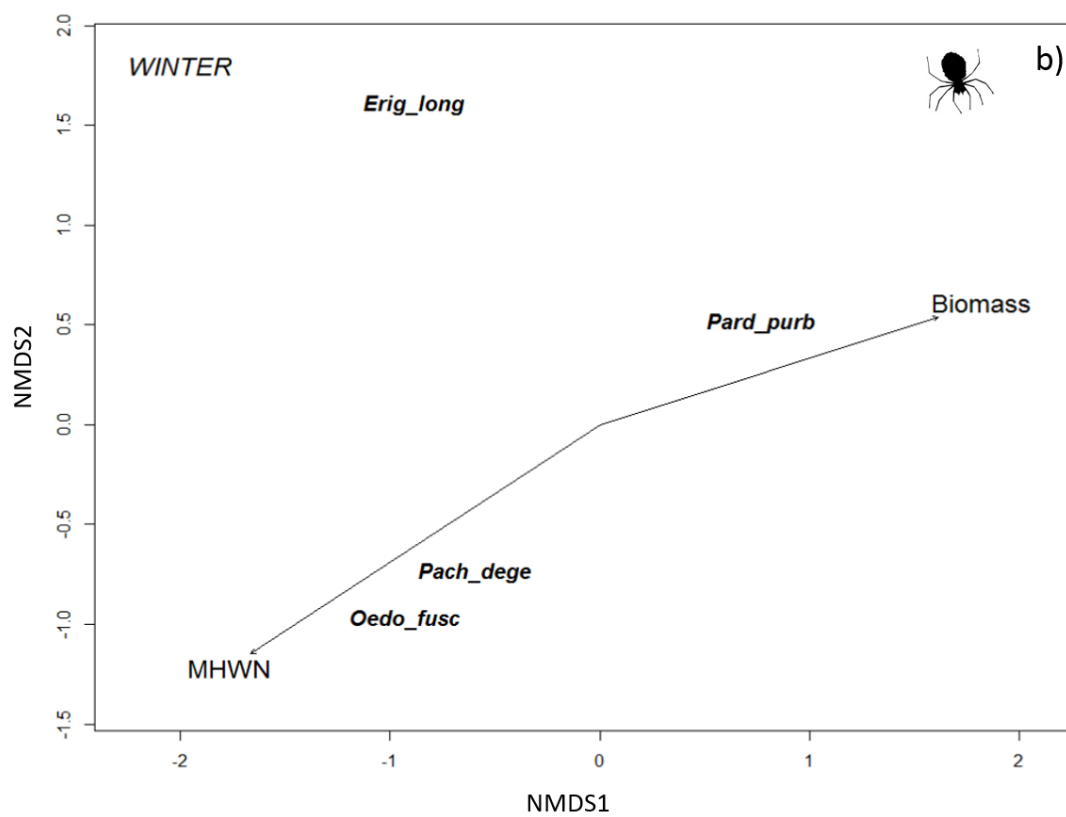
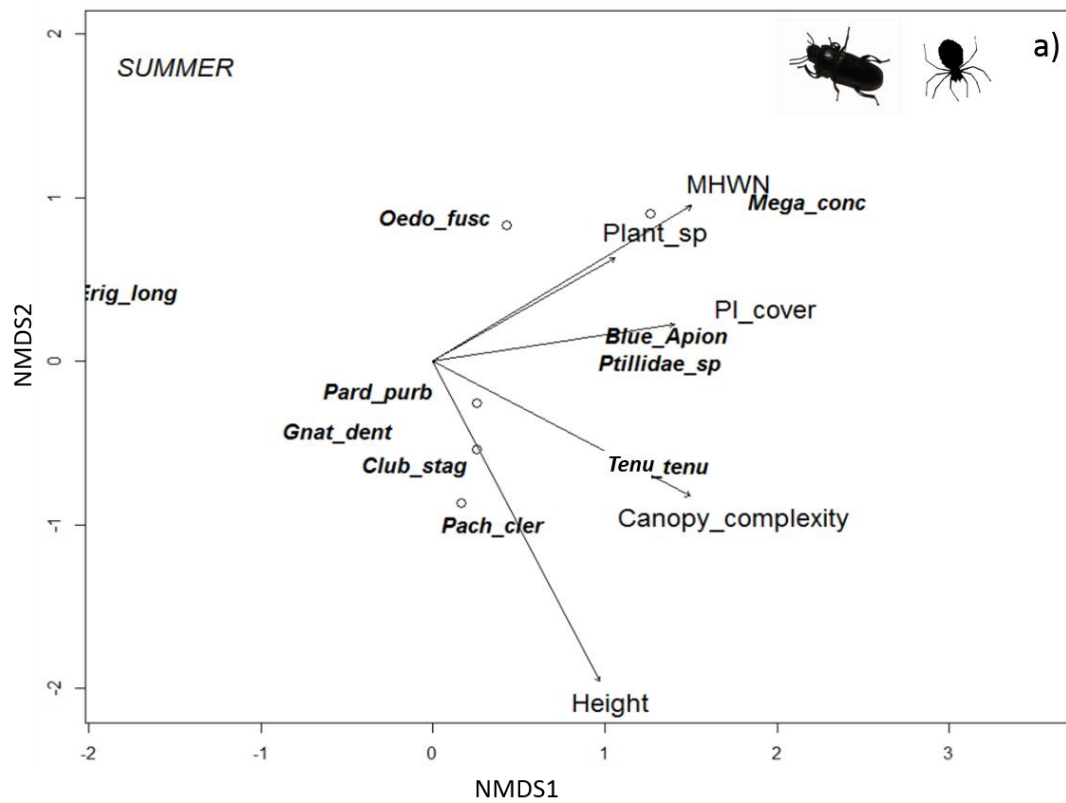
**Fig. 1.** Side-on photography method of determining vegetation structure with a) vegetation photographed in front of a contrasting red back-board and b) representation of canopy gaps identified from image analysis, from which vegetation canopy complexity score was derived.

**Fig. 2.** NMDS ordination plots for (a) 10 common summer spider and beetle species (b) 4 overwintering spider species across all saltmarsh sites from Essex and Morecambe Bay. Significant environmental predictors ( $p < 0.01$ ) of species abundance are shown alongside arrows. Non-significant environmental variables are not shown. Plant\_sp = Plant species richness  $m^2$ , Pl\_cover = Plant cover (%), MHWN = Elevation above mean high water neap, Biomass = Above-ground biomass, Canopy\_complexity = Canopy complexity score. Invertebrate species names have been shortened to first 4 letters of genus and species (e.g. Pard\_purb = *Pardosa purbeckensis*; full names in Tables S1 & S2).





**Fig. 1.**



**Fig. 2.**