The importance of canopy complexity in shaping seasonal spider and beetle assemblages in saltmarsh habitats
Ford, Hilary; Evans, Ben; van Klink, Roel; Skov, Martin; Garbutt, Angus

Ecological Entomology

DOI:
10.1111/een.12373

Published: 01/04/2017

Peer reviewed version

Cystwlit i’r cyhoeddiad / Link to publication

Dyfnyiad o’r fersiwn a gyhoeddwyd / Citation for published version (APA):

Hawliau Cyffredinol / General rights
Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

Take down policy
If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

04. Aug. 2019
The importance of canopy complexity in shaping seasonal spider and beetle assemblages in saltmarsh habitats

HILARY FORD,1,4 BEN EVANS,2 ROEL VAN KLINK,3 MARTIN W. SKOV,1 and ANGUS GARBU TT4

1School of Ocean Sciences, Bangor University, Anglesey, LL59 5AB, UK, 2Cambridge Coastal Research Unit, Department of Geography, University of Cambridge, Downing Place, Cambridge CB2 3EN, UK, 3Institute of Botany, Czech Academy of Sciences, Dukelská 135, 37982, Třeboň, Czech Republic, 4Centre for Ecology and Hydrology, Environment Centre Wales, Bangor, LL57 2UW, UK.

Correspondence: Hilary Ford, School of Environment, Natural Resources and Geography, Thoday buildings, Bangor University, LL57 2DG, UK. Telephone: +44(0)1248 382443. E-mail: hilary.ford@bangor.ac.uk

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 ≥ 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.

**Keywords.** 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; Pétillon 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; Pétillon 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, Abbotts 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 Abbotts 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⁻¹) 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⁻¹), 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 slide 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^1) 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, ERdias 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 ≥ 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. mm²/mm. Vegetation tip height diversity (CoV²) was measured by the coefficient of variation. CoV² 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 <± 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 ~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 (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\(^\circ\) 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 residuals² 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 ≥ 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 ≥ 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⁻¹; 45 – 60 %) than Morecambe Bay (1-5 mS cm⁻¹; 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.
Winter: Araneae

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

Summer: Coleoptera

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

Winter: Coleoptera

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

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

Discussion

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

Spider and beetle assemblages

Spiders responded positively to canopy complexity, with ground-running hunting spiders in particular more abundant in complex, tall vegetation, as in other grassland studies (McNett & Rypstra, 2000; Pétillon et al., 2007; Van Klink & Van Schrojenstein Lantman, 2015). Beetles
did not respond as clearly or positively to canopy complexity as spiders, mirroring the mixed
responses to vegetation height seen in the literature (Morris, 2000; Woodcock et al., 2007;
Ford et al., 2013). Despite the different responses of Coleoptera and Araneae to canopy
complexity, both were abundant in the ‘gappy’ shrub cover of A. portulacoides. This
vegetation type is often characterised by an even shrub layer, ~25 cm in height, with many
small gaps, ≥ 1 mm, present throughout the whole canopy layer, unlike grass swards which
often have very few non-vegetated canopy gaps at ground level. We propose that the
complex canopy of an A. portulacoides dominated plant community allows shelter from
inundation, storms and predators coupled with freedom of movement, providing ideal living
conditions for many ground-dwelling invertebrates (Langellotto & Denno, 2004; Finke &
Denno 2006). Despite the strong link apparent between habitat complexity and overall
abundance and diversity, certain groups preferred less complex habitats. For example,
Linyphiidae, especially specialist thermophiles such as Erigone and Oedothorax species, were
commonly found in shorter, less complex vegetation. Erigone longipalpis (Sundevall), a
coastal specialist, was associated with more saline environments than Oedothorax fuscus
(Blackwall), an open ground grassland generalist. It is likely that O. fuscus, an active aeronaught,
disperses into open habitats, such as close-cropped saltmarsh, where competition from larger
invertebrate predators is low (Gibson et al., 1992; Bell et al., 2001; Ford et al., 2013).
Beetle species richness was positively associated with plant cover and surface elevation as in
other saltmarshes (Irmler et al., 2002; Finch et al., 2007). Coleoptera lack submersion
resistance techniques (Rothenbücher & Schaefer, 2006), possibly explaining why they were
more abundant in drier Morecambe Bay than wetter, more frequently inundated, Essex.
Surprisingly, a strong negative link was apparent between beetle abundance and plant species
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 ≥ 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 it effectiveness in shorter swards with vegetation ≤ 25 mm high not appearing in images due to height of base, reducing its usefulness for assessing small scale structural complexity.

Acknowledgements

This study presents data collected as part of the Coastal Biodiversity and Ecosystem Service Sustainability project (CBESS: NE/J015644/1), part of the BESS programme; a six-year programme (2011-2017) funded by the Natural Environment Research Council (Bangor University grant reference: NE/J015350/1) and the Biotechnology and Biological Sciences Research Council (BBSRC) as part of the UK’s Living with Environmental Change (LWEC) programme. The views expressed are those of the authors and do not reflect the views of BESS Directorate or NERC. A.G. and M.W.S. acknowledge financial support from the Welsh Government and Higher Education Funding Council for Wales through the Sêr Cymru National

Supporting information

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

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

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

Table S3. Total counts of all Araneae sampled in winter and summer 2013 from Essex (AH = Abbotts Hall, FW = Fingringhoe Wick, TM = Tillingham marsh) and Morecambe Bay (CS = Cartmel sands, WP = West Plain, WS = Warton sands) saltmarsh study sites. ‘Group’ column indicates prey capture method as all spiders are predatory; GRH = Ground running hunter, FRH = Foliage running hunter, SWB = Space web builder, ORB = Orb web weaver, SIT = Sit-and-wait, SW = Sheet weaver (Uetz et al. 1999). CS = Coastal specialist as defined by Van Klink (2014) and Hänggi et al. (1995), nomenclature follows World Spider Catalog (2016).
Table S4. Total counts of all Coleoptera sampled in winter and summer 2013 from Essex (AH = Abbotts Hall, FW = Fingringhoe Wick, TM = Tillingham marsh) and Morecambe Bay (CS = Cartmel sands, WP = West Plain, WS = Warton sands) saltmarsh study sites. ‘Group’ column indicates functional group assignment; PRE = predatory, ZOO = Zoophagous, PHY = Phytophagous, DET = Detritivore. CS = Coastal specialist defined by Van Klink (2014), nomenclature follows Duff (2012).

Table S5. Summer comparison of invertebrate abundance and species richness. Quadrat means per region are shown ± standard error.

Table S6. Winter comparison of invertebrate abundance and species richness. Quadrat means per region are shown ± standard error.
References


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.

<table>
<thead>
<tr>
<th>Spiders</th>
<th>Best fit models:</th>
<th>Elevation</th>
<th>Plant cover</th>
<th>Plant sp.</th>
<th>Height</th>
<th>Canopy complexity</th>
<th>Density</th>
<th>AIC</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>All (including juveniles)</td>
<td>Standard</td>
<td>ns</td>
<td>z = 4.45 ***</td>
<td>ns</td>
<td>ns</td>
<td>-</td>
<td>-</td>
<td>749.1</td>
<td>0.26</td>
</tr>
<tr>
<td></td>
<td>Standard + complexity</td>
<td>z = -6.36 ***</td>
<td>z = 3.73 ***</td>
<td>ns</td>
<td>ns</td>
<td>z = 5.62 ***</td>
<td>-</td>
<td>710.4</td>
<td>0.46</td>
</tr>
<tr>
<td></td>
<td>Standard + photo</td>
<td>z = -6.10 ***</td>
<td>z = 3.26 **</td>
<td>ns</td>
<td>ns</td>
<td>z = 4.59 ***</td>
<td>z = 2.60 **</td>
<td>705.8</td>
<td>0.48</td>
</tr>
<tr>
<td>All (excluding juveniles)</td>
<td>Standard</td>
<td>z = -3.41 ***</td>
<td>z = 14.9 ***</td>
<td>ns</td>
<td>z = 16.1 ***</td>
<td>-</td>
<td>-</td>
<td>615.1</td>
<td>0.48</td>
</tr>
<tr>
<td></td>
<td>Standard + complexity</td>
<td>z = -8.20 ***</td>
<td>z = 3.44 ***</td>
<td>ns</td>
<td>ns</td>
<td>z = 4.60 ***</td>
<td>-</td>
<td>600.7</td>
<td>0.50</td>
</tr>
<tr>
<td></td>
<td>Standard + photo</td>
<td>z = -8.37 ***</td>
<td>z = 2.87 **</td>
<td>ns</td>
<td>ns</td>
<td>z = 3.31 ***</td>
<td>z = 4.22 ***</td>
<td>586.0</td>
<td>0.57</td>
</tr>
<tr>
<td>GRH (including juveniles)</td>
<td>Standard</td>
<td>z = -5.70 ***</td>
<td>z = 3.29 ***</td>
<td>ns</td>
<td>z = 2.72 **</td>
<td>-</td>
<td>-</td>
<td>489.4</td>
<td>0.52</td>
</tr>
<tr>
<td></td>
<td>Standard + complexity</td>
<td>z = -6.74 ***</td>
<td>z = 2.67 **</td>
<td>ns</td>
<td>z = 2.72 **</td>
<td>z = 2.71 **</td>
<td>-</td>
<td>474.1</td>
<td>0.53</td>
</tr>
<tr>
<td></td>
<td>Standard + photo</td>
<td>z = -7.71 ***</td>
<td>z = 2.89 **</td>
<td>ns</td>
<td>ns</td>
<td>z = 2.86 **</td>
<td>z = 3.01 **</td>
<td>472.5</td>
<td>0.54</td>
</tr>
<tr>
<td>GRH (excluding juveniles)</td>
<td>Standard</td>
<td>z = -3.86 ***</td>
<td>z = 2.47 *</td>
<td>ns</td>
<td>z = 2.45 *</td>
<td>-</td>
<td>-</td>
<td>448.5</td>
<td>0.43</td>
</tr>
<tr>
<td></td>
<td>Standard + complexity</td>
<td>z = -6.18 ***</td>
<td>ns</td>
<td>ns</td>
<td>z = 2.72 **</td>
<td>z = 3.29 **</td>
<td>- (ns)</td>
<td>435.3</td>
<td>0.48</td>
</tr>
<tr>
<td>FRH</td>
<td>Standard</td>
<td>z = 2.62 **</td>
<td>ns</td>
<td>ns</td>
<td>z = 2.05 *</td>
<td>-</td>
<td>-</td>
<td>127.6</td>
<td>0.06</td>
</tr>
<tr>
<td></td>
<td>Standard + photo</td>
<td>z = 2.88 **</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>(ns)</td>
<td>z = 2.43 *</td>
<td>126.1</td>
<td>0.07</td>
</tr>
<tr>
<td>SW (including juveniles)</td>
<td>Standard</td>
<td>ns</td>
<td>z = 2.86 **</td>
<td>ns</td>
<td>ns</td>
<td>-</td>
<td>-</td>
<td>654.4</td>
<td>0.10</td>
</tr>
<tr>
<td></td>
<td>Standard + complexity</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>z = 3.54 ***</td>
<td>-</td>
<td>628.6</td>
<td>0.11</td>
</tr>
<tr>
<td></td>
<td>Standard + photo</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>z = 2.45 *</td>
<td>z = 2.58 **</td>
<td>623.9</td>
<td>0.16</td>
</tr>
<tr>
<td>SW (excluding juveniles)</td>
<td>Standard</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>z = 3.41 ***</td>
<td>- (ns)</td>
<td>- (ns)</td>
<td>467.6</td>
<td>0.09</td>
</tr>
<tr>
<td></td>
<td>Standard + complexity</td>
<td>z = -4.54 ***</td>
<td>z = 2.52 **</td>
<td>ns</td>
<td>z = 2.92 **</td>
<td>z = 2.80 **</td>
<td>-</td>
<td>399.2</td>
<td>0.41</td>
</tr>
<tr>
<td></td>
<td>Standard + photo</td>
<td>z = -5.28 ***</td>
<td>z = 2.76 **</td>
<td>ns</td>
<td>ns</td>
<td>z = 2.95 **</td>
<td>z = 2.72 **</td>
<td>400.1</td>
<td>0.40</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Beetles</th>
<th>Best fit models:</th>
<th>Elevation</th>
<th>Plant cover</th>
<th>Plant sp.</th>
<th>Height</th>
<th>Canopy complexity</th>
<th>Density</th>
<th>AIC</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>All (including juveniles)</td>
<td>Standard</td>
<td>z = 2.30 *</td>
<td>z = 2.76 **</td>
<td>z = -3.03 **</td>
<td>- (ns)</td>
<td>- (ns)</td>
<td>- (ns)</td>
<td>424.2</td>
<td>0.26</td>
</tr>
<tr>
<td>All (excluding juveniles)</td>
<td>Standard</td>
<td>z = 2.29 *</td>
<td>z = 2.02 *</td>
<td>z = -2.83 **</td>
<td>- (ns)</td>
<td>- (ns)</td>
<td>- (ns)</td>
<td>404.8</td>
<td>0.25</td>
</tr>
<tr>
<td>PRE and ZOO</td>
<td>Standard</td>
<td>z = 2.15 *</td>
<td>ns</td>
<td>z = -2.82 **</td>
<td>ns</td>
<td>(ns)</td>
<td>(ns)</td>
<td>247.7</td>
<td>0.21</td>
</tr>
<tr>
<td>PHY and DET</td>
<td>Standard</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>- (ns)</td>
<td>- (ns)</td>
<td>- (ns)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Species richness</td>
<td>Standard</td>
<td>z = 2.34 *</td>
<td>z = 2.05 *</td>
<td>z = -2.20 *</td>
<td>- (ns)</td>
<td>- (ns)</td>
<td>- (ns)</td>
<td>316.0</td>
<td>0.24</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Spiders &amp; beetles</th>
<th>Best fit models:</th>
<th>Elevation</th>
<th>Plant cover</th>
<th>Plant sp.</th>
<th>Height</th>
<th>Canopy complexity</th>
<th>Density</th>
<th>AIC</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coastal specialists</td>
<td>Standard</td>
<td>z = -4.93 ***</td>
<td>z = 2.33 *</td>
<td>ns</td>
<td>- (ns)</td>
<td>- (ns)</td>
<td>- (ns)</td>
<td>442.5</td>
<td>0.46</td>
</tr>
</tbody>
</table>

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.

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

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 over-wintering 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. 2.