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

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

2　**in saltmarsh habitats**

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

13　**Abstract.** 1. Habitat structure, including vegetation structural complexity, largely determines

14　invertebrate assemblages in semi-natural grasslands. The importance of structural complexity

15　to the saltmarsh invertebrate community, where the interplay between vegetation

16　characteristics and tidal inundation is key, is less well known.

17　2. We hypothesised that canopy complexity would be a more important predictor of spider

18　and beetle assemblages than simple vegetation attributes (e.g. height, community type) and

19　environmental variables (e.g. elevation) alone; measured in two saltmarsh regions, south-east

20　(Essex) and north-west (Morecambe Bay) UK. Canopy complexity (number of non-vegetated

21　'gaps' in canopy ≥ 1 mm wide) was assessed using side-on photography. Over 1,500 spiders

22　and beetles were sampled via suction sampling, winter and summer combined.

23   3. In summer, saltmarshes with abundant spider and beetle populations were characterised

24   by high scores for canopy complexity often associated with tussocky grass or shrub cover.

25   Simple vegetation attributes (plant cover, height) accounted for 26 % of variation in spider

26   abundance, 14 % in spider diversity; rising to 46 and 41 % respectively with the addition of

27   canopy complexity score. Over-wintering spider assemblages were associated with elevation

28   and vegetation biomass. Summer beetle abundance, in particular the predatory and

29   zoophagous group, and diversity were best explained by elevation and plant species richness.

30   4. Summer canopy complexity was identified as a positive habitat feature for saltmarsh spider

31   communities (ground-running hunters and sheet weavers) with significant 'added value' over

32   more commonly measured attributes of vegetation structure.

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

34   structure.

35   **Introduction**

36   Small-scale vegetation structural complexity plays a key part in shaping grassland invertebrate

37   assemblages (Morris, 2000). Habitat complexity is associated with features such as availability

38   of foraging sites, shelter and over-wintering or nesting sites, indicating abundance of

39   resources (prey, pollen or nectar) and suitable refuges from predators, intra-guild cannibalism

40   and competitors (Halaj *et al*., 2000; McNett & Rypstra, 2000; Langellotto & Denno, 2004; Finke

41   & Denno, 2006). Habitat complexity might also be considered an explanatory factor in

42   species-area relationships (Hart & Horwitz, 1991). Enhanced structural complexity may offer

43   greater space-size heterogeneity, providing habitable space to organisms with a wide range

44   of body sizes, thereby increasing species richness (Tokeshi & Arakaki, 2012; Pierre &

45 Kovalenko, 2014). To determine the vegetation characteristics that best describe the

46 relationship between arthropod communities and the vegetation they inhabit, various

47 methods have been used. These include fractal geometry, architectural or branching

48 complexity, soil microhabitat complexity, multi-variable habitat heterogeneity and vegetation

49 density (Anderson, 1978; Hatley & MacMahon, 1980; Dennis *et al*., 1998; Halaj *et al*., 2000;

50 McNett & Rypstra, 2000; Dennis, *et al*. 2001; Whitehouse *et al*., 2002; Woodcock *et al*., 2007).

51 In contrast, other studies tend to focus on simple measurements, such as vegetation height

52 or above-ground biomass, often in concert with livestock grazing intensity. In this study, we

53 introduce a novel side-on photography technique to accurately record vegetation structural

54 complexity, via the quantification of canopy gaps, at a scale relevant to invertebrate

55 communities.

56 Certain invertebrate groups, specifically generalist predators and spiders, appear to prefer

57 more complex habitats (McNett & Rypstra, 2000; Shrewsbury & Raupp, 2006), with spiders in

58 particular negatively affected when habitat structure is simplified (Marshall & Rypstra, 1999;

59 Langellotto & Denno, 2004; Wise, 2006). Ground-dwelling spider communities respond to

60 commonly measured structural attributes such as height, above-ground biomass, vegetation

61 tip height diversity and depth of plant litter layer (Uetz *et al*., 1999; Bonte *et al*., 2000; Bell *et*

62 *al*., 2001; Traut, 2005; Pétillon *et al*., 2008), but do not exhibit strong host-plant associations.

63 Both phytophagous and predatory beetle habitat preferences are associated with commonly

64 measured attributes of vegetation structure (Lassau *et al*., 2005; Hofmann & Mason, 2006;

65 Woodcock *et al*., 2007) and satellite-derived vegetation indices (Lafage *et al*., 2014).

66 Plant species richness may also contribute to vegetation structural complexity, and affect the

67 abundance and species richness of predatory arthropods such as spiders and predatory

68 beetles via bottom-up trophic effects (Scherber *et al.*, 2010). A species-rich plant community

69 tends to support a large number of herbivorous arthropods which in turn boosts the

70 predatory arthropod population (Borer *et al.*, 2012). The 'Enemies Hypothesis' (Root *et al.*,

71 1973), proposes a mechanism of top-down control in which diverse vegetation assemblages

72 provide more refuges for predatory arthropods and more opportunity for stable prey

73 availability than low plant diversity assemblages, leading to higher predator efficiency and the

74 resultant link between plant species richness and predatory arthropod abundance (Russell,

75 1989). The habitat heterogeneity hypothesis (Dennis *et al.*, 1998) predicts an asymptotic

76 relationship between increasing plant species richness and vegetation structural

77 heterogeneity, with greater resources available for the coexistence of multiple species of

78 arthropods of each trophic group in structurally complex vegetation.

79 Ground and canopy dwelling invertebrates are sensitive to seasonal changes in environmental

80 characteristics, such as changes in vegetation structure due to natural die-back in winter, but

81 seasonal invertebrate- vegetation structure relations are rarely quantified. Dense vegetation

82 may be important in winter for different reasons than in the summer. For example, tussocky

83 grasses and leaf litter provide over-wintering shelter from predators for ground-dwelling

84 invertebrates including wolf spiders (Edgar & Loenen, 1974; Collins *et al.*, 2002; Lewis &

85 Denno, 2009), whereas in spring and summer, prey availability is often crucial (Wise, 2006)

86 encouraging individuals to explore more open habitat. Tall vegetation offers several benefits

87 for invertebrates including protection from predation and shelter from extreme weather

88 events. However, daytime temperatures are lower in tall vegetation, potentially hindering

89 thermophilic invertebrates, inhibiting movement and hiding prey, especially in dense grass

90 mats such as *Festuca rubra* (Linnaeus) swards (Van Klink *et al.*, 2014). Hence, vegetation that

91 is tall, but not dense may be optimal. This level of vegetation structural detail, e.g. canopy

92 openness, is difficult to capture, and simple measurements of vegetation height or above-

93 ground biomass will not portray intricacies such as canopy gap availability.

94 Saltmarshes provide an important habitat for invertebrates, plants and insectivorous birds

95 (Milsom *et al.*, 2000; Chatters, 2004; Pétillon *et al.*, 2005). They are characterised by a suite

96 of plant communities differing in structural complexity, ranging from grass to shrub or rush

97 dominated, making saltmarshes an ideal habitat to study the interplay between vegetation

98 structural complexity and invertebrate assemblages. The two invertebrate orders focused on

99 in this study, Araneae and Coleoptera, were chosen as they are well studied, known to

100 respond to habitat complexity and are often used as bio-indicators of ecosystem health

101 (Pearce & Venier, 2006).

102 The relationship between ground and canopy dwelling invertebrate communities and plant

103 canopy complexity was examined, via suction sampling, in two English saltmarsh regions,

104 south-east (Essex) and north-west (Morecambe Bay), in summer and winter. We used a novel

105 side-on photography technique to record canopy complexity, via the quantification of canopy

106 gaps. We examined the following two hypotheses: i) Canopy complexity will be a more

107 important predictor of spider and beetle assemblages than simple vegetation attributes (e.g.

108 height, community type) and environmental variables (e.g. surface elevation) alone. As the

109 measurement of canopy complexity allows us to access a level of vegetation structural detail

110 not captured by more commonly measured vegetation characteristics; and ii) Winter canopy

111 complexity will be positively associated with spider abundance due to the provision of shelter

112 and ability to avoid over-wintering wolf spiders, prone to preying on both smaller spiders and

113 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

136   diversity. British National Vegetation Classification (NVC) plant community types were

137   calculated for each quadrat using Tablefit v1.1 (Hill, 2011). All plant nomenclature follows

138   Stace (2010). Above-ground dry vegetation biomass (60° C, 72 h) was determined by cutting

139   plants to ground level from a 50 x 25 cm area within each quadrat. Vegetation height was

140   recorded at 10 random positions within each quadrat using a direct measurement (hand slid

141   down metre stick until vegetation detected then height in cm recorded). Mean height per

142   quadrat was used in the analysis. The standard deviation of height within each quadrat was

143   calculated as a potential proxy for combined vegetation structure and height complexity.

144   Coefficient of variation (CoV; Standard Deviation $/$ Mean x 100) in vegetation height (CoV^1)

145   was calculated from the 10 direct vegetation height measurements per quadrat.

Vegetation structure: side-on photography method

147   Digital photographs to determine vegetation structure were taken side-on within each

148   quadrat through a 20 cm deep section of vegetation, against a 60 cm wide red back board

149   (Fig. 1a) at a fixed distance from the camera using a FujiFilm Finepix XP30 digital camera at

150   full 14MP resolution following the method of Möller (2006). Photographs were only taken at

151   quadrat locations where vegetation height exceeded the height of the steel frame (25 mm),

152   with vegetation clearly visible against the backboard. The Matlab Camera Calibration Toolbox

153   (Bouguet n.d.) was used to correct and calibrate the images, ERdas Imagine software was

154   used for image classification. Unsupervised classification of the 3 band images into 20 classes

155   was followed by manual attribution and recoding of those classes to either 'vegetation' or

156   'non-vegetation' with visual reference to the original photograph. Variations in illumination,

157   vegetation colour and proportions of vegetation and background between photographs

158   meant that fully unsupervised classification did not provide consistent results. Matlab was

159   subsequently used to process thematic images (Fig. 1b; doi reference to be added).

160   Structural complexity was assessed via a canopy complexity score, calculated as number of

161   non-vegetated 'gaps' in canopy ≥ 1 mm wide, standardised to number of gaps per metre. This

162   standardisation was important as background images varied slightly in horizontal width but

163   were always close to 60 cm (width of back board). Henceforth, this 'canopy complexity score'

164   will be referred to as 'canopy complexity'. Mean, median and standard deviation in 'gap' area

165   for each quadrat were also calculated, alongside maximum gap area (combined area of all

166   gaps in one quadrat), but were not found to relate to the structuring of spider and beetle

167   assemblages. They will not be discussed further in this manuscript. Vertical vegetation density

168   (from now on 'vegetation density') was calculated from each quadrat image by the proportion

169   of the image classed as vegetation normalised by the horizontal extent of the image – i.e.

170   mm^2/mm. Vegetation tip height diversity (CoV^2) was measured by the coefficient of variation.

171   CoV^2 was calculated from the highest vegetation point measured from ten random columns

172   of pixels per quadrat photograph.

Physical characteristics

174   Saltmarsh elevation and salinity were measured as these can determine the distribution of

175   some saline sensitive saltmarsh invertebrates. Elevation and x, y coordinates of each quadrat

176   were measured by a Leica GS08 GNSS Differential Global Positioning System (DGPS) with CRS

177   = OSGB(36) accuracy of <± 0.05 m. Elevation was recorded in metres relative to Ordnance

178   Datum Newlyn (ODN), converted to Chart Datum (CD) and presented relative to Mean High

179   Water Neap (MHWN) as a rough proxy for tidal inundation frequency. Soil salinity was

180   measured by proxy of electrical conductivity (EC) in the lab. Soil samples, of ~10 g (fresh mass)

181 from the top 10 cm, were taken from within each quadrat, diluted by 1:2.5 with deionised

182 water and measured for EC (mS cm^{-1}) and pH using a Jenway 4320 conductivity meter. Soil

183 bulk density was calculated from bulk density ring (3.1 cm height, 7.5 cm diameter) samples

184 taken vertically to roughly quantify the 0 – 10 cm depth zone. Samples were dried (105°C, 72

185 h) prior to calculation of bulk density. Soil moisture content was also calculated.

Araneae and Coleoptera – Suction sampling

187 Ground and vegetation dwelling invertebrates were suction sampled from each 1 x 1m

188 quadrat using a modified garden vacuum (McCulloch MAC GBV345 Petrol Leaf Blower Vac

189 25cc). Each sample consisted of four 20 second suctions at four regularly placed intervals

190 within the quadrat with a 20 cm diameter circular tube containing a 500 micron mesh to trap

191 invertebrates. Care was taken to place the sampler tube end over the top of vegetation where

192 possible, whilst maintaining good contact with the ground surface to ensure efficiency of

193 sampling. In *Atriplex portulacoides* (Aellen) bushes we squashed the vegetation down with

194 the sampler end to enable sampling through the column of vegetation and the soil surface.

195 Where vegetation was very long, for example in *Juncus maritimus* (Lam) swards of up to 70

196 cm high we were not able to do this and so focused on bottom 10 cm of vegetation and soil

197 surface. Each sample was then preserved in 70% industrial methylated spirits. Araneae and

198 Coleoptera were identified to lowest possible taxonomic level, which in most cases was

199 species, but in some cases genus or subfamily with a Novex stereoscope. Early stage juveniles,

200 predominantly Linyphiidae, were classified to family level for Araneae. The majority of later

201 stage juvenile *Pardosa* were assumed to be the most common saltmarsh species *Pardosa*

202 *purbeckensis* (Cambridge). Invertebrate nomenclature follows Duff (2012) for Coleoptera and

203 the World Spider Catalog (2016) for Araneae. Spider feeding guilds of ground running hunters,

204 foliage running hunters, sit and wait hunters, sheet weavers, space web builders and orb web

205 weavers were classified according to Uetz *et al*. (1999). Beetles were grouped into predatory,

206 zoophagous (predatory and scavenging), phytophagous (herbivore or granivorous) or

207 detritivore (feed on detritus and associated decomposer community of fungi and bacteria)

208 using several sources listed in the footnotes to Table S4. Spider or beetle species confined to

209 saline habitats were classified as 'coastal specialists' whereas species occurring in habitats

210 other than saltmarshes (usually other wet habitats or sand dunes) were classified as 'non-

211 coastal specialists' (Hänggi *et al*., 1995; Van Klink, 2014).

212 *Statistical analysis*

213 Relationships between environmental variables and the abundance and species richness of

214 the different invertebrate groups were examined using a generalized linear model with a

215 nested structure (random = ~ 1 region/site/quadrat) and a Poisson distribution suitable for

216 invertebrate count data, tested for over-dispersion (if ratio between residuals^2 and residual

217 degrees of freedom is >5 data is over-dispersed). Best fit models were selected on the basis

218 of lowest Akaike information criterion (AIC) value for three analyses: 1. Standard

219 environmental variables (Elevation above MHWN + Plant cover + Plant species richness +

220 Height + Above-ground biomass); 2. Standard environmental variables plus canopy

221 complexity score; 3. Standard environmental variables plus side-on photography variables

222 (Density + Vegetation tip height diversity + canopy complexity score) allowing the 'value

223 added' component of the side-on photography method to be assessed. Analysis was carried

224 out on the following spider feeding guilds: ground running hunters; foliage running hunters;

225 and sheet weavers. Space web builders, orb web weavers and sit and wait hunters were

226 excluded due to very low abundance. Beetles were analysed in two broad groups: i) predatory

227 and zoophagous and ii) phytophagous and detritivores. Generalised linear models (as detailed

228 above) were also used to analyse regional differences in invertebrate abundance.

229 Testing for significant differences in vegetation and physical characteristics between regions

230 (Essex, Morecambe bay) and site (AH, FW, TM, CS, WP, WS) was carried out using ANOVA

231 output of a linear model, variables were logged where appropriate to normalise data, and

232 post hoc Tukey tests calculated (Hothorn *et al*., 2008). The relationship between elevation

233 above MHWN and EC (proxy for salinity) was determined by Spearman's rank correlation

234 coefficient.

235 Nonmetric Multidimensional scaling (NMDS) was used to assess how environmental factors,

236 vegetation structure and site characteristics, influenced individual spider and beetle species

237 habitat preferences. NMDS, an un-constrained ordination technique using rank order of

238 species abundances, was carried out with Bray-Curtis dissimilarity calculations (1000

239 permutations) using the 'vegan' package (Oksanen *et al*., 2016). To be included within either

240 the winter or summer NMDS analysis each spider or beetle species had to have ≥ 10

241 individuals in total across all quadrats, Essex and Morecambe Bay saltmarsh sites combined.

242 For pairs or sets of closely related environmental variables (e.g. vegetation height, above-

243 ground biomass) only one variable was retained in the analysis based on an r_s value of ≥ 0.5

244 (Spearman's rank correlation coefficient). All statistical analysis was carried out in R (R Core

245 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

12

268   winter and summer. Elevation relative to MHWN was significantly negatively associated with

269   EC in both summer (SPEARMANS: r_s = -0.77, p < 0.001) and winter (r_s = -0.82, p < 0.001).

270   Elevation was also a stronger predictor of spider and beetle assemblages than EC in all

271   statistical models. For these reasons elevation relative to MHWN was used instead of EC in

272   the final set of models presented in this study. For site means and further information see

273   Tables S1 & S2.

274   *Regional differences: Araneae and Coleoptera*

275   Nearly 400 spiders were sampled in winter, 60 % from Essex. Over 1000 were sampled in the

276   summer with 72 % from Essex, Tillingham supported the most with >400 individuals (Table

277   S3). Summer spider abundance and species richness were significantly greater in Essex than

278   Morecambe Bay (Table S5, S6). However, total Araneae species richness, across sites and

279   seasons, between Essex and Morecambe Bay was equal with 23 species apiece. Only 24

280   beetles were found in winter across all six sites, 75 % from Morecambe Bay. Nearly 300 were

281   sampled in summer with 58 % from Morecambe (Table S4). Summer Coleoptera abundance

282   showed marked differences between saltmarsh sites with shrubby Tillingham and tussocky

283   West Plain having particularly abundant populations (Table S4), but with no significant

284   difference between the two regions (Table S5). Total Coleoptera species richness, across sites

285   and seasons, was greater for Morecambe Bay (26) than Essex (21).

286   *Summer: Araneae*

287   Summer spider abundance was associated positively with plant cover, canopy complexity and

288   plant density, negatively with elevation above MHWN (Table 1). The best fit model for spider

289   abundance improved from 26 % of variation explained for standard environmental variables

13

290 alone to 46 % with the addition of canopy complexity. Ground running hunters were positively

291 associated with plant cover, height and canopy complexity, negatively with elevation (Table

292 1). Foliage running hunters were aligned with elevation and either vegetation height or

293 density (depending on model type). Sheet weavers (including juveniles) were significantly

294 associated with canopy complexity (Table 1). When spiders were analysed by feeding guild

295 the importance of canopy complexity in explaining variation in abundance was much reduced

296 (0.01 or 1 % increase in r^2 compared to standard variables alone) compared to when spiders

297 were considered as a group (0.2 or 20 % increase in r^2).

298 The summer NMDS analysis included 7 spider species, with five environmental variables

299 associated with invertebrate habitat choice (Fig. 2), canopy complexity ($p < 0.001$), vegetation

300 height ($p < 0.001$), plant cover ($p < 0.001$), plant species richness ($p < 0.01$) and elevation

301 above MHWN ($p < 0.001$). Despite the fact that elevation above MHWN and plant species

302 richness appear closely correlated on the summer NDMS plot they are only partially

303 correlated with an r_s value of 0.43.

304 Spider species richness was positively associated with plant cover, plant height and canopy

305 complexity, and negatively associated with elevation above MHWN. The best fit model for

306 spider species richness improved from 14 % of variation explained for standard environmental

307 variables alone to 41 % with the addition of canopy complexity. Interestingly, spider

308 abundance in Essex, including juveniles, was well predicted by shrubby *A. portulacoides* cover

309 alone ($t = 2.50$, $p < 0.05$) although this relationship does not hold for spider diversity or when

310 juveniles are removed. There was a significant positive relationship between canopy

311 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; Pétillon *et al.*, 2007; Van Klink & Van Schrojenstein 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, ≥ 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 (Irmler *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

379   richness. This has been found in grassland studies (Koricheva *et al.*, 2000) and in shrubby

380   forest (Zou *et al.*, 2013), but stands in contrast to the more commonly postulated Enemy

381   Hypothesis which predicts a positive relationship between plant species richness and

382   predatory arthropod diversity. It is possible that increased plant diversity and the assumed

383   associated increase in phytophagous prey may lead to enhanced competition between

384   predatory Coleoptera and other predatory arthropods, such as spiders, leading to an eventual

385   reduction in beetle abundance, as suggested by Zou *et al.* (2013).

386   Spiders were much more likely to over-winter on the saltmarsh than beetles with three

387   species *P. purbeckensis*, *Pachygnatha degeeri* (Sundevall) and *O. fuscus* proving the most

388   abundant. The strong link observed between above-ground vegetation biomass and the over-

389   wintering wolf spider, *P. purbeckensis* was also demonstrated in juveniles by Kessler & Slings

390   (1980), possibly due to protection from predators, avoidance of cannibalism and warmth

391   (Wise, 2006; Lewis & Denno, 2009). In contrast, the small ground running spider, *P. degeeri*,

392   and the open grassland generalist Linyphiidae, *O. fuscus,* over-wintered in large numbers in

393   the short-cropped Morecambe Bay saltmarshes. Linyphiidae juveniles over-wintered in all

394   study saltmarshes, regardless of vegetation height or structure.

395   *Vegetation structure: side-on photography method*

396   In this study we used the side-on photography method, adapted from Möller (2006), to assess

397   the relationship between vegetation structure and invertebrate assemblage patterns,

398   specifically via measurements of vegetation tip height diversity, vegetation density and

399   canopy complexity. Vegetation tip height diversity was not a significant explanatory variable.

400   However, vegetation density and canopy complexity both 'added value' to best fit models of

401   spider abundance, with twice as much variation in abundance explained as standard

402 environmental and vegetation measurements alone. Canopy complexity is of particular

403 interest as a measurement of vegetation structural complexity. Previously, grassland canopy

404 complexity has been assessed by vertical drop pins (Woodcock, *et al.*, 2007), with number of

405 contacts between vegetation and pins used to calculate a complexity index. Our method is

406 roughly analogous to this with canopy complexity calculated from number of canopy gaps ≥

407 1 mm wide, but is likely to be less time consuming. Canopy complexity also seems to be

408 partially responsible for the positive relationship seen between spider and beetle abundance

409 and cover of the 'gappy' saltmarsh shrub *A. portulacoides*. The side-on photography method

410 may be advantageous over standard vegetation measurements that may be either destructive

411 (e.g. above-ground biomass) or prone to human error (e.g. direct measurement of vegetation

412 height). We argue that the assessment of vegetation structure by side-on photography proves

413 a useful and novel addition to standard vegetation methods. However, one issue limits it

414 effectiveness in shorter swards with vegetation ≤ 25 mm high not appearing in images due to

415 height of base, reducing its usefulness for assessing small scale structural complexity.

427 **Supporting information**

428 Additional Supporting Information may be found in the online version of this article under the

429 DOI reference: xxxxxxx

430 **Table S1.** Site characteristics for east and west coast English saltmarshes, winter 2013. Means

431 per site are shown ± standard deviation. Italicised letters denote significant site differences,

432 final column, regional differences between Essex (AH = Abbotts 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 ± standard deviation. Italicised letters denote significant site

437 differences, final column regional differences between Essex (AH = Abbotts 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 Abbotts 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   = Abbotts 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 ± standard error.

455   **Table S6.** Winter comparison of invertebrate abundance and species richness. Quadrat means

456   per region are shown ± standard error.

References

457 **References**

458 Anderson, J.M. (1978) A method to quantify soil-microhabitat complexity and its application

459 to a study of soil animal species diversity. *Soil Biology and Biochemistry*, **10**, 77-78.

460 Bell, J.R., Wheater, P., & Cullen, W.R. (2001) The implications of grassland and heathland

461 management for the conservation of spider communities: a review. *Journal of Zoology*, **255**,

462 377‑387.

463 Bonte, D., Maelfait, J.-P., & Hoffman, M. (2000) The impact of grazing on spider communities

464 in a mesophytic calcareous dune grassland. *Journal of Coastal Conservation*, **6**, 135‑144.

465 Borer, E.T., Seabloom, E.W., Tilman, D. & Novotny, V. (2012) Plant diversity controls arthropod

466 biomass and temporal stability. *Ecology letters*, **15**, 1457–1464.

467 Bouguet, J.-Y. (n.d.) *Camera Calibration Toolbox for Matlab*. [WWW document]. URL

468 http://www.vision.caltech.edu/bouguetj/calib_doc/ [accessed on 16.03.16].

469 Chatters, C. (2004) Grazing domestic animals on British saltmarshes. *British Wildlife* **15**, 392‑

470 400.

471 Collins, K.L., Boatman, N.D., Wilcox, A., Holland, J.M. & Chaney, K. (2002) Influence of beetle

472 banks on cereal aphid predation in winter wheat. *Agriculture, Ecosystems and Environment*

473 **93**, 337-350.

474 Dennis, P., Young, M.R. & Gordon, I.J. (1998) Distribution and abundance of small insects and

475 arachnids in relation to structural heterogeneity of grazed, indigenous grasslands. *Ecological*

476 *Entomology*, **23**, 253-264.

477   Dennis, P., Young, M.R. & Bentley, C. (2001) The effects of varied grazing management on

478   epigeal spiders, harvestmen and pseudoscorpions of *Nardus stricta* grassland in upland

479   Scotland. *Agriculture, Ecosystems & Environment*, **86**, 39-57.

480   Duff, A.G. (2012) Checklist of beetles of the British Isles. [WWW document]. URL

481   http://www.coleopterist.org.uk/checklist2012.pdf [accessed on 6th April 2016].

482   Edgar, W. & Loenen, M. (1974) Aspects of the overwintering habitat of the wolf spider

483   *Pardosa lugubris*. *Journal of Zoology*, **172**, 383–388.

484   Finch, O.-D., Krumen, H., Plaisier, F. & Schultz, W. (2007) Zonation of spiders (Araneae) and

485   carabid beetles (Coleoptera: Carabidae) in island saltmarshes at the North Sea coast.

486   *Wetlands Ecology and Management*, **15**, 207‑228.

487   Finke, D.L. & Denno, R.F. (2006) Spatial refuge from intraguild predation: implications for prey

488   suppression and trophic cascades. *Oecologia*, **149**, 265-275.

489   Ford, H., Garbutt, A., Jones, L. & Jones, D.L. (2013) Grazing management in saltmarsh

490   ecosystems drives invertebrate diversity, abundance and functional group structure. *Insect*

491   *Conservation and Diversity*, **6**, 189-200.

492   Gibson, C.W.D., Hambler, C. & Brown, V.K. (1992) Changes in spider (Araneae) assemblages

493   in relation to succession and grazing management. *Journal of Applied Ecology* **29**, 132‑142.

494   Halaj, J., Ross, D.W. & Moldenke, A.R. (2000) Importance of habitat structure to the arthropod

495   food-web in Douglas-fir canopies. *Oikos*, **90**, 139-152.

496   Hänggi, A., Stöckli, E. & Nentwig, W. (1995) *Habitats of Central European Spiders*. Centre

497   Suisse do cartoghraphie de la faune, Neuchatel.

498   Hart D.D. & Horwitz R.J. (1991) Habitat diversity and the species-area relationship: alternative

499   models and tests. *Habitat Structure: the Physical Arrangement of Objects in Space* (ed. by S.S.

500   Bell, E.D. McCoy & H.R. Mushinsky), pp. 47–68. Chapman & Hall, London.

501   Hatley, C.L. & MacMahon, J.A. (1980) Spider community organization: seasonal variation and

502   the role of vegetation architecture. *Environmental Entomology*, **9**, 632-639.

503   Hill, M. (2011) *Tablefit: A program to identify types of vegetation by measuring goodness-of-*

504   *fit to association tables*. Version 1.1. URL http://www.ceh.ac.uk/services/tablefit-and-

505   tablcorn [accessed on 6th April 2016].

506   Hofmann, T.A. & Mason, C.F. (2006) Importance of management on the distribution and

507   abundance of Staphylinidae (Insecta: Coleoptera) on coastal grazing marshes. *Agriculture,*

508   *Ecosystems and Environment,* **114**, 397‑406.

509   Hothorn, T., Bretz, F. & Westfall, P. (2008) Simultaneous Inference in General Parametric

510   Models. *Biometrical Journal*, **50**, 346-363.

511   Irmler, U., Heller, K., Meyer, H. & Reinke, H.-D. (2002) Zonation of ground beetles (Coleoptera:

512   Carabidae) and spiders (Araneidae) in salt marshes at the North and the Baltic Sea and the

513   impact of the predicted sea level increase. *Biodiversity and Conservation*, **11**, 1129‑1147.

514   Kessler, A. & Slings, R. (1980) Microhabitat selection in adults and juveniles of *Pardosa*

515   *purbeckensis* F.O.P.-Cambridge (Araneae, Lycosidae). *Proceedings of the 8th International*

516   *Congress of Arachnology* (ed. by J. Gruber), pp. 151–154, Verlag H. Egermann, Wien.

517   Koricheva, J., Mulder, C.P.H., Schmid, B., Joshi, J. & Huss-Danell, K. (2000) Numerical

518   responses of different trophic groups of invertebrates to manipulations of plant diversity in

519   grasslands. *Oecologia*, **125**, 271–282.

520   Lafage, D., Secondi, J., Georges, A., Bouzillé, J.-B. & Pétillon, J. (2014) Satellite-derived

521   vegetation indices as surrogate of species richness and abundance of ground beetles in

522   temperate floodplains. *Insect Conservation and Diversity*, **7**, 327-333.

523   Langellotto, G.A. & Denno, R.F. (2004) Responses of invertebrate natural enemies to complex-

524   structured habitats: a meta-analytical synthesis. *Oecologia*, **139**, 1-10.

525   Lassau, S.A., Hochuli, D.F., Cassis, G. & Reid, C.A.M. (2005) Effects of habitat complexity on

526   forest beetle diversity: do functional groups respond consistently? *Diversity and Distributions*,

527   **11**, 73‑82.

528   Lewis, D. & Denno, R.F. (2009) A seasonal shift in habitat suitability enhances an annual

529   predator subsidy. *Journal of Animal Ecology*, **78**, 752-760.

530   Marshall, S.D. & Rypstra, A.L. (1999) Spider competition in structurally simple ecosystems.

531   *Journal of Arachnology*, **27**, 343-350.

532   McNett, B.J. & Rypstra, A.L. (2000) Habitat selection in a large orb-weaving spider:

533   vegetational complexity determines site selection and distribution. *Ecological Entomology*,

534   **25**, 423-432.

535   Milsom, T.P., Langton, S.D., Parkin, W.K., Peel, S., Bishop, J.D., Harts, J.D. & Moore, N.P. (2000)

536   Habitat models of bird species distribution: an aid to the management of coastal grazing

537   marshes. *Journal of Applied Ecology*, **37**, 706‑727.

538   Möller, I. (2006) Quantifying saltmarsh vegetation and its effect on wave height dissipation:

539   Results from a UK East coast saltmarsh. *Estuarine, Coastal and Shelf Science*, **69**, 337-351.

540   Morris, M.G. (2000) The effects of structure and its dynamics on the ecology and conservation

541   of arthropods in British grasslands. *Biological Conservation*, **95**, 129‑142.

542   Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, R.P., O'Hara, R.B., Simpson, G.L.,

543   Solymos, P., Stevens, M.H.M. & Wagner, H. (2016) *Community Ecology Package Version 2.3-*

544   *4*.   [WWW   document].   URL   https://cran.r-project.org/web/packages/vegan/vegan.pdf

545   [accessed on 6th April 2016].

546   Pearce, J.L. & Venier, L.A. (2006) The use of ground beetles (Coleoptera: Carabidae) and

547   spiders (Araneae) as bioindicators of sustainable forest management: a review. *Ecological*

548   *Indicators*, 6, 780-793.

549   Pétillon, J., Ysnel, F., Canard, A. & Lefeuvre, J.-C. (2005) Impact of an invasive plant (*Elymus*

550   *athericus*) on the conservation value of tidal salt marshes in western France and implications

551   for management: responses of spider populations. *Biological Conservation*, **126**, 103‑117.

552   Pétillon, J., George, A., Canard, A., Lefeuvre, J.-C., Bakker, J.P. & Ysnel, F. (2008) Influence of

553   abiotic factors on spider and ground beetle communities in different salt-marsh systems.

554   *Basic and Applied Ecology*, **9**, 743‑751.

555   Pétillon, J., George, A., Canard, A. & Ysnel, F. (2007) Impact of cutting and sheep grazing on

556   ground-active spiders and carabids in intertidal salt marshes (Western France). *Animal*

557   *Biodiversity and Conservation*, **30**, 201‑209.

558   Pierre, J.I. & Kovalenko, K.E. (2014) Effect of habitat complexity attributes on species richness.

559   *Ecosphere*, **5**(2), 22. http://dx.doi.org/10.1890/ES13-00323.1

560   R Core Team (2015) *R: A language and environment for statistical computing*. R Foundation

561   for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/

562   Root, R.B. (1973) Organization of a plant-arthropod association in simple and diverse habitats:

563   the fauna of collards (*Brassica oleracea*). *Ecological Monographs*, **43**, 95-124.

564   Rothenbücher, J. & Schaefer, M. (2006) Submersion tolerance in floodplain arthropod

565   communities. *Basic and Applied Ecology*, **7**, 398-408.

566   Russell, E.P. (1989) Enemies hypothesis: a review of the effect of vegetational diversity on

567   predatory insects and parasitoids. *Environmental Entomology*, **18**, 590-599.

568   Scherber, C., Eisenhauer, N., Weisser, W.W., Schmid, B., Voigt, W., et al. (2010) Bottom-up

569   effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature*,

570   **468**, 553–556.

571   Shrewsbury, P.M. & Raupp, M.J. (2006) Do top-down or bottom-up forces determine

572   *Stephanitis pyrioides* abundance in urban landscapes? *Ecological applications*, **16**, 262-272.

573   Stace, C. (2010) *New Flora of the British Isles, third edition*. Cambridge University Press,

574   Cambridge, UK.

575   Tokeshi, M. & Arakaki, S. (2012) Habitat complexity in aquatic systems: fractals and beyond.

576   *Hydrobiologia*, **685**, 27-47.

577   Traut, B.H. (2005) The role of coastal ecotones: a case study of the salt marsh ∕ upland

578   transition zone in California. *Journal of Ecology*, **93**, 279‑290.

579   Uetz, G.W., Halaj, J. & Cady, A.B. (1999) Guild structure of spiders in major crops. *Journal of*

580   *Arachnology*, **27**, 270‑280.

581   Van Klink, R. (2014) *Of Dwarves and Giants: How large herbivores shape arthropod*

582   *communities on salt marshes*. University of Groningen PhD thesis. ISBN: 978-90-367-7083-5

583   Van Klink, R., Van der Plas, F., Van Noordwijk, C.G.E., WallisDeVries, M.F. & Olff, H. (2014)

584   Effects of large herbivores on grassland arthropod diversity. *Biological reviews*,

585   doi:10.1111/brv.12113

586   Van Klink, R. & Van Schrojenstein Lantman, M. (2015) Effecten van kwelderbeweiding op

587   spinnen en insecten. *Entomologische berichten*, **75**, 188-199.

588   Wise, D.H. (2006) Cannibalism, Food limitation, Intraspecific Competition, and the Regulation

589   of Spider Populations. *Annual Review Entomology*, **51**, 441-465.

590   Whitehouse, M.E.A., Shochat, E., Shachak, M. & Lubin, Y. (2002) The influence of scale and

591   patchiness on spider diversity in a semi-arid environment. *Ecography*, **25**, 395-404.

592   Woodcock, B.A., Potts, S.G., Westbury, D.B., Ramsay, A.J., Lambert, M., Harris, S.J. & Brown,

593   V.K. (2007) The importance of sward architectural complexity in structuring predatory and

594   phytophagous invertebrate assemblages. *Ecological Entomology*, **32**, 302-311.

595   World Spider Catalog (2016) *World Spider Catalog*. Natural History Museum Bern. URL

596   http://wsc.nmbe.ch, version 17.0 [accessed on 17th March 2016].

597   Zou, Y., Sang, W., Bai, F. & Axmacher, J.C. (2013) Relationships between plant diversity and

598   the abundance and α-diversity of predatory ground beetles (Coleoptera: Carabidae) in a

599   mature Asian temperate forest ecosystem. *PLOSone*, **8**, e8279.

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	R²
Spiders									
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
Beetles									
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
Spiders & beetles									
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
Spiders									
All (including juveniles)	Standard	z = -104.2 ***	*ns*	*ns*	*ns*	- (*ns*)	- (*ns*)	480.1	0.02
All (excluding juveniles)	Standard	*ns*	*ns*	*ns*	*ns*	- (*ns*)	- (*ns*)	-	-
GRH (including juveniles)	Standard	z = -3.51 ***	*ns*	*ns*	*ns*	- (*ns*)	- (*ns*)	292.5	0.19
GRH (excluding juveniles)	Standard	*ns*	*ns*	*ns*	*ns*	- (*ns*)	- (*ns*)	-	-
SW (including juveniles)	Standard	*ns*	*ns*	*ns*	*ns*	- (*ns*)	- (*ns*)	-	-
SW (excluding juveniles)	Standard	z = 2.67 **	*ns*	*ns*	*ns*	-	-	294.2	0.08
Species richness	Standard	*ns*	*ns*	*ns*	*ns*	- (*ns*)	- (*ns*)	-	-
Coastal specialists	Standard	z = -3.74 ***	*ns*	*ns*	*ns*	- (*ns*)	- (*ns*)	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 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 richess 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).
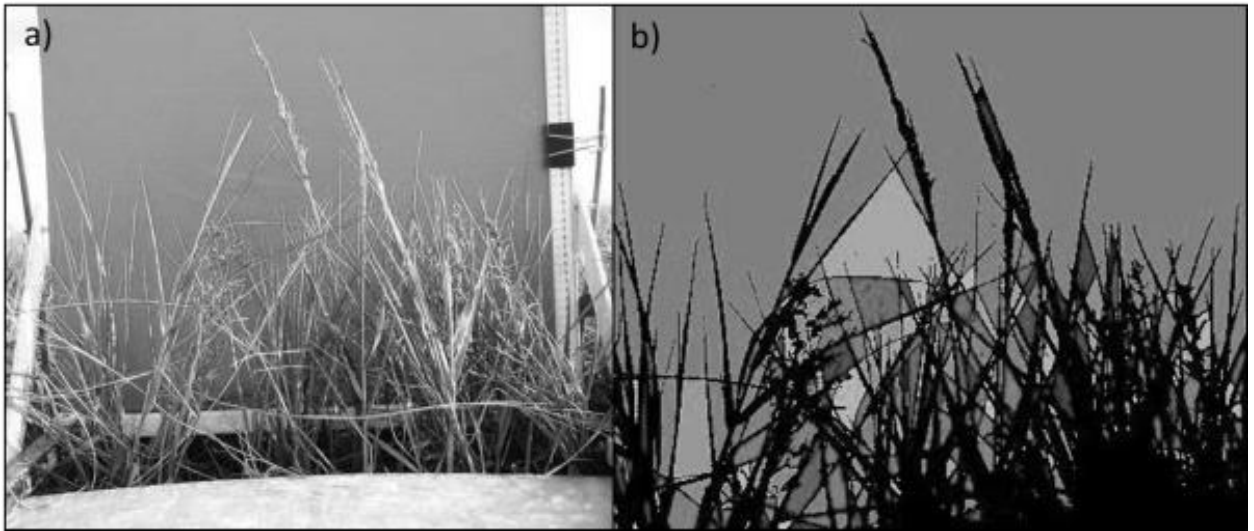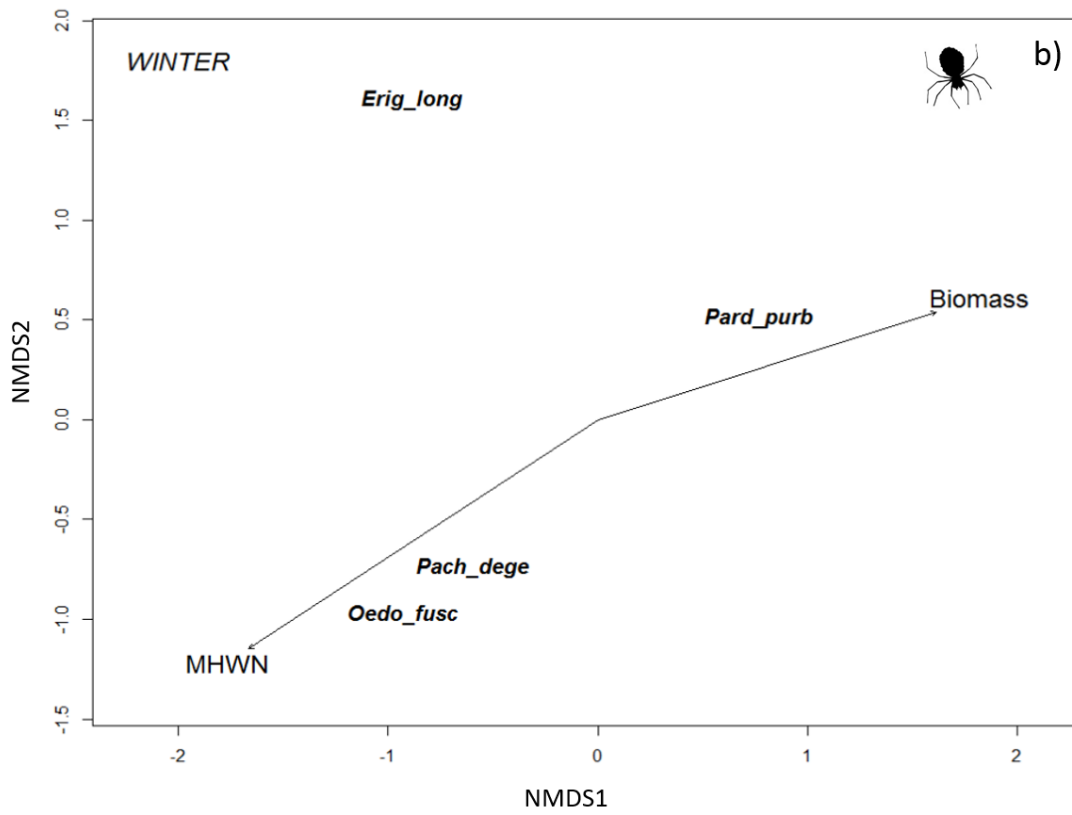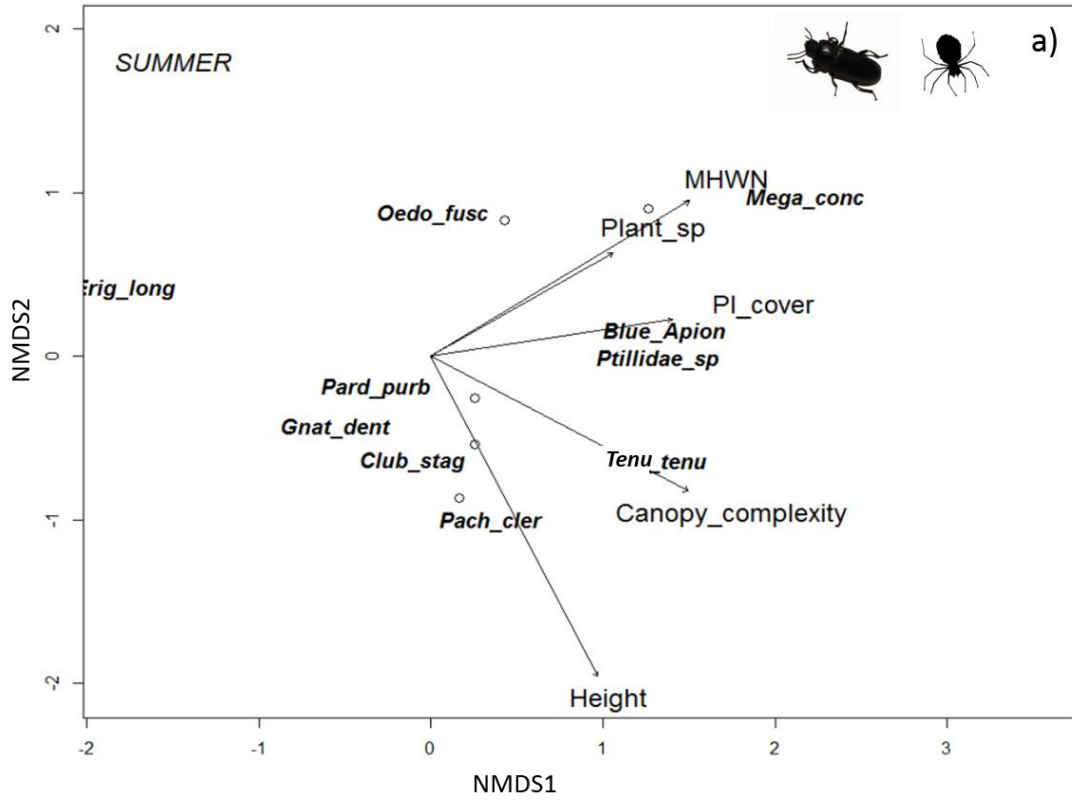
Fig. 1.

Fig. 2.