

Grazing reduces bee abundance and diversity in saltmarshes by suppressing flowering of key plant species

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1	Grazing suppresses flowering of key species to reduce bee abundance and diversity on saltmarshes
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14 Running title: Saltmarsh grazing management for bees

15 Abstract

16 Global declines in pollinator populations and associated services make it imperative to identify and 17 sensitively manage valuable habitats. Coastal habitats such as saltmarshes can support extensive 18 flowering meadows, but their importance for pollinators, and how this varies with land-use intensity, 19 is poorly understood. We hypothesised that saltmarshes provide important bee foraging habitat, 20 and that livestock grazing either suppresses or enhances its value by reducing the abundance - or 21 increasing the diversity - of flowering plants. To test these hypotheses, we surveyed 11 saltmarshes 22 in Wales (UK) under varying grazing management (long-term ungrazed, extensively grazed, 23 intensively grazed) over three summers and investigated causal pathways linking grazing intensity 24 with bee abundance and diversity using a series of linear mixed models. We also compared observed 25 bee abundances to 11 common terrestrial habitats using national survey data. 26 Grazing reduced bee abundance and richness via reductions in the flower cover of the two key food 27 plants: sea aster Tripolium pannonicum and sea lavender Limonium spp. Grazing also increased 28 flowering plant richness, but the positive effects of flower richness did not compensate for the 29 negative effects of reduced flower cover on bees. Bee abundances were approximately halved in 30 extensively grazed marshes (relative to ungrazed) and halved again in intensively grazed marshes. 31 Saltmarsh flowers were primarily visited by honeybees Apis mellifera and bumblebees Bombus spp. 32 in mid and late summer. Compared to other broad habitat types in Wales, ungrazed saltmarshes 33 ranked highly for honeybees and bumblebees in July-August, but were relatively unimportant for 34 solitary bees. Intensively grazed saltmarshes were amongst the least valuable habitats for all bee 35 types. 36 Under appropriate grazing management, saltmarshes provide a valuable and previously overlooked 37 foraging habitat for bees. The strong effects of livestock grazing identified here are likely to extend

38 geographically given that both livestock grazing and key grazing-sensitive plants are widespread in

39 European saltmarshes. We recommend that long-term ungrazed saltmarshes are protected from

- 40 grazing, and that grazing is maintained at extensive levels on grazed marshes. In this way,
- 41 saltmarshes can provide forage for wild and managed bee populations and support ecosystem
- 42 services.
- 43
- 44
- 45 Keywords
- 46 Apis, Bombus, grassland management, livestock, pollinators

47 1. Introduction

48 Flower-visiting insects, particularly bees, provide a vital ecosystem service by pollinating crop plants and wild flowers (Gallai et al., 2009; Garibaldi et al., 2011; Hanley et al., 2015). However, pollinators 49 50 are under threat from habitat loss, agrochemicals, disease, invasive species and climate change 51 (Brown and Paxton 2009; Potts et al. 2010a), leading to long-term declines in wild and managed 52 pollinator populations (Potts et al. 2010a; Potts et al. 2010b; Powney et al. 2019). Agricultural 53 intensification is a major driver of bee declines (Le Féon et al. 2010; Potts et al. 2010a), but 54 appropriate grassland management can yield significant benefits for pollinators (Bruppacher et al., 55 2016; Garrido et al., 2019). However, the relationship between livestock grazing and pollinator 56 abundance and diversity is not clear or consistent, showing positive (Vulliamy et al., 2006), negative 57 (Kimoto et al., 2012; Kruess and Tscharntke, 2002) and non-linear relationships (Lázaro et al., 2016; 58 Mu et al., 2016). Difficulty in disentangling the various effects may originate from a lack of 59 understanding of the mechanisms by which grazers influence pollinator activities and abundances in 60 different habitats.

61 Saltmarshes are productive grasslands of halophytic herbs, grasses and shrubs that form in the 62 intertidal zone of sheltered coastal areas. Saltmarshes deliver important ecosystem services (Barbier 63 et al., 2011; McKinley et al., 2018), yet are rarely considered for their potential value as a pollinator 64 habitat (Rickert et al., 2018, 2012; van Klink et al., 2016). However, saltmarshes can be floristically 65 rich (Adam, 1990), harbouring many flowering plants visited by bees and other pollinators (Agassiz, 66 2000; Falk and Lewington, 2015). European saltmarshes are commonly grazed by livestock, with 67 consequences for their ecosystem properties and service provision (Davidson et al., 2017; Pagès et 68 al., 2018). Although European saltmarshes do not cover a large area - approximately 440,000 ha in 69 mainland Europe and the British Isles (McOwen et al., 2017) – they sit within a wider network of 70 semi-natural coastal habitats, and could act as a vital corridor, increasing ecosystem connectivity and 71 facilitating biological flow between crops and bee nesting and foraging areas (Viana et al., 2012). It is

therefore worthwhile to understand how valuable marshes are for pollinators, and how grazing
management affects their value.

74 Little is known about the effect of grazing on saltmarsh pollinator communities. Grazing increases 75 saltmarsh plant richness (Davidson et al., 2017) which often predicts increased pollinator abundance 76 and diversity (Lázaro et al., 2016; Potts et al., 2004; Vulliamy et al., 2006). However, in Wadden Sea 77 marshes, intensive grazing led to reductions in flower and pollinator abundance compared to less 78 intensive grazing (van Klink et al., 2016) and intensive sheep grazing disrupted moth-plant 79 associations (Rickert et al., 2018). Additionally, livestock alter saltmarsh soil properties and reduce 80 vegetation cover (Davidson et al., 2017) which may affect the suitability of the habitat as a nesting 81 site for bees (Vulliamy et al., 2006; Wuellner, 1999). To understand how and why livestock grazing 82 impacts pollinators, we must understand the nature and strength of these potentially opposing 83 effects.

84 Here, we investigate the effects of grazing on bee communities across multiple saltmarshes on the 85 south coast of Wales (UK). Marshes in this region hold plant communities typical of those in north 86 and western European sites, with a relatively high diversity of halophytic herbs (Adam 1990), and a 87 long history of livestock grazing. We combine field surveys of bee and plant communities to 88 investigate the causal pathways linking bee abundance and diversity with grazing. We hypothesised 89 that grazing affects bees via three pathways: (i) by altering the quantity of floral resource available, 90 (ii) by altering plant diversity, and (iii) by modifying substrate conditions and directly disturbing bees 91 or their nests; the net effect of grazing on bee communities depends on the balance of these 92 positive and negative pathways. We developed a conceptual model, incorporating causal pathways 93 and key covariates (weather, timing, landscape), before investigating the individual hypothesised 94 pathways. To scale up effects across the broader coastal landscape, we investigated the effect of 95 grazing on the β -diversity of bees. Finally, we assessed how saltmarsh bee abundances compare to 96 various terrestrial habitats, using pollinator survey data collected across Wales for the Glastir

Monitoring and Evaluation Programme (Emmett and the GMEP team, 2017). To the best of our
knowledge, this is the first study to compare bee communities in grazed and ungrazed marshes, and
to quantify the importance of saltmarshes as a bee foraging habitat, relative to terrestrial habitats.

100

101 2. Materials and methods

102 2.1 Field surveys

103 We surveyed 11 salt marshes in south Wales (UK) every summer from 2016-2018 (Fig. 1, see Table 104 A.1 for full site details, marsh 'LW' not surveyed in 2016). Sites were selected to cover a range of 105 grazing intensities (4 long-term ungrazed, 3 extensive, 4 intensive) and livestock species (cattle, 106 ponies, sheep), and to be large enough to allow sampling along four 200m transects covering 107 multiple inundation zones and vegetation communities. It was not possible to calculate accurate 108 grazing levels in livestock units per hectare (LUha⁻¹), because several of our study sites were part of 109 much larger unfenced grazing lands with extremely clustered livestock distribution. Grazing 110 categories (absent, extensive, intensive) were evaluated based on dung counts and visual 111 assessments performed at each transect on every visit, then averaged for the study site as a whole 112 (see Appendix A, Table A.2, Fig. A.1). Ungrazed marshes had not been grazed by livestock for a 113 minimum for 30 years. Extensively grazed marshes were characterised by having little damage to standing biomass and turf, and a relatively complex sward (estimated grazing density of 0.3-0.4 114 115 LUha⁻¹ during the summer grazing period). Intensively grazed marshes were characterised by 116 removal of much of the standing biomass, leaving a relatively short, uniform sward, and widespread 117 compaction or cutting up of the turf by animal trampling (estimated grazing density >0.8 LUha⁻¹). 118 Variation in sediment type, marsh geomorphology and surrounding landscape was distributed 119 evenly across the grazing categories (Table A.1).

We did not assess grazing levels of wild grazers such as hares, rabbits and wildfowl. There was littlevisible evidence of grazing by small mammals in the study marshes, and any impacts of these on

122 vegetation are likely to be small (He and Silliman, 2016). However, herbivorous geese are present 123 across the study area during winter months (Davidson and Griffin, 2018). Livestock grazing facilitates 124 goose grazing (Bos et al., 2002; Davidson et al., 2017; van der Graaf et al., 2002), so the study 125 marshes grazed by livestock are likely to also have higher levels of goose grazing, adding to the 126 impacts of livestock on the vegetation community. However, in the study marshes, herbivorous 127 geese are most abundant during the winter months, when plants are not in flower, and wildfowl 128 generally have a lower impact on saltmarsh vegetation than livestock (He and Silliman, 2016), so 129 geese are likely to have lower impacts on bee communities than livestock.

130 Each marsh was surveyed along four 200m fixed transects on seven days over three summers (with 131 the exception of marsh 'LW' which was surveyed on six days over two summers), covering the major 132 flowering period in these marshes. Marshes were surveyed in mid-summer (12th July – 10th August) 133 in 2016, and in early (9th - 29th June), mid (12th July – 10th August) and late (24th August – 19th 134 September) summer in 2017 and 2018. Surveys were conducted between 10am and 5pm, preferably on warm, calm, dry days (minimum temperature: 15°C, maximum wind speed: 7.5 m s⁻¹). Transects 135 136 were run parallel to the shore and distributed as evenly as possible across each marsh (dependent upon safe access and avoidance of major creeks), to represent the major vegetation communities 137 138 present.

139 Bee surveys were conducted using standardised pollinator transect methodologies (Pollard and 140 Yates, 1993). The surveyor walked each 200m transect at a slow, steady pace and noted any bee 141 visiting a flower within a 5x5m area extending either side and in front. The flower species was noted 142 and bees were identified to species level (with the exception of Bombus terrestris/lucorum workers, 143 which cannot be reliably separated morphologically) using Falk and Lewington (2015). Bees that 144 could not be identified in the field were captured in a net (a subsample of 5-10 individuals were 145 collected when that bee type was abundant), transferred to a plastic vial with ethyl acetate, and 146 subsequently identified under a x30 stereo microscope at Swansea University. Each transect was

147 walked twice, with a 10 minute gap between walks to allow bees to re-settle. We used the total 148 number of bees per marsh per survey visit (*i.e.* bees per 1.6 km of transect) in our regression models. 149 We assessed the vegetation within a 1x1m quadrat placed every 20m along each transect. For each 150 plant species, we took the mean number of quadrats in which it was present to obtain an average 151 transect occupancy for each marsh (potential range of 0-11). Species composition (present/absent in 152 quadrat) was recorded in mid-summer in 2016 and 2017. The mean for each marsh over these two 153 years was used as a predictor in regression models. Saltmarsh plant communities in south Wales, 154 and more widely, are relatively stable over time under consistent grazing management (Pauls, 2017; 155 Taubert and Murphy, 2012), therefore we expect these mean values to be a fair reflection of the 156 plant community across the three years. Percentage flower cover of each species and vegetation 157 canopy height were recorded on every survey visit. Limonium vulgare and Limonium humile are 158 grouped together in the analyses, as these species are difficult to distinguish morphologically and 159 can hybridise (Dawson and Ingrouille, 1995). We used the mean flower cover per species across all 160 44 quadrats in the marsh (11 quadrats x 4 transects per marsh per visit) in our regression models.

161

162 2.2 Data analysis

For our analyses, we were only interested in plants that provide pollen and nectar resources for pollinators. Hereafter, when we refer to plants or flower cover, we only include insect-pollinated (IP) plants. *Spartina* grasses are generally considered to be wind-pollinated, but we noted several bees visiting *S. anglica* during our surveys, so included it with the IP plants in our analyses. All statistical analyses were conducted in R Studio running R3.5.2. using packages as detailed in Appendix A.

168

169 2.2.1 Testing the effect of grazing on bee abundance and α -diversity

170 We used Linear Mixed Models (LMMs) to test the net effect of grazing on bee abundance, bee

171 species richness, and bee Shannon diversity. We tested the effect of grazing at the marsh-scale

172 rather than the transect-scale, as this is the relevant scale for managers. Each row in our data was a 173 single survey visit to a marsh (n=76). Each model also included year and season as predictors to 174 explore temporal patterns of bee foraging. We included wind speed, temperature and surrounding 175 landscape (proportion of natural habitat, see Appendix A for calculation) where their inclusion 176 improved model fit (reduced AIC by >2). Marsh was included as a random effect, to control for 177 repeated sampling within each marsh. Model assumptions were verified by examining residual plots 178 (scaled residuals versus predicted values and versus each covariate in the model) and testing 179 goodness of fit (Kologorov-Smirnov) of observed versus expected values. Response variables were 180 log-transformed where necessary to meet model assumptions (Ives, 2015). We used likelihood ratio 181 tests (LRTs) to test the significance of grazing, year and season. If significant, we compared different 182 levels of these factors using t-tests. Initial and final model terms are presented in the full statistical 183 results provided in the online Supplementary material.

184 To explore the mechanisms of grazing effects, we created a conceptual model incorporating the 185 three hypothesised pathways by which grazing may affect bee populations (Fig. 2), and tested the 186 proposed links using a series of LMMs . For each stage in the network, we built our initial model 187 containing all biologically relevant predictors, with marsh as a random effect (Table 1). We used AIC 188 to determine if fit was improved by log-transformation of continuous predictors. We used LRTs to 189 test: (1) if IP plant richness was affected by grazing; (2) if IP plant occupancy was affected by grazing; 190 (3) if flower cover was affected by grazing, controlling for the effect of IP plant occupancy; (4) if bee 191 abundance was affected by grazing, IP plant richness, and flower cover; (5) if bee richness was 192 affected by grazing, IP plant richness, and flower cover, controlling for the effect of bee abundance. 193 Two plants, sea aster Tripolium pannonicum (formerly Aster tripolium, hereafter 'Aster') and the sea 194 lavenders Limonium spp. (hereafter 'Limonium') received 95% of all bee visitations. To gain further 195 insight, we repeated models (2-5) above with IP plant occupancy and flower cover separated into a) 196 Aster, b) Limonium and c) other IP plants (see Fig. A.2 and online Supplementary material for full 197 model details). We repeated all models using Shannon's H' as our measure of diversity instead of

species richness, and with *Apis mellifera* excluded, to test if results are consistent for wild bees only(Table 1).

200 Plant diversity and plant occupancy were not measured in 2018, therefore models (1-2) test only 201 2016/7 data (when plant diversity and plant occupancy were used as predictors in models (3-5) we 202 used the average value from 2016/7 for each marsh). In south Wales, Aster blooms in late summer 203 and Limonium blooms in mid-summer. Therefore, the models to predict Aster flower cover (3a) and 204 Limonium flower cover (3b) only include late and mid-summer survey results respectively to avoid 205 zero-inflated distributions. Sub-setting our dataset in this way precluded analysis using a structural 206 equation modelling approach. Instead, we conducted separate LMMs for each stage of the network 207 and have presented the results for these in a single network diagram, to aid interpretation.

208

209 *2.2.2 Testing the effect of grazing on β-diversity*

We explored how grazing affected three components of β -diversity (Baselga, 2010) based on 210 211 respective distance matrices of bee composition across sites: total β -diversity (Sørensen index, β_{sor}), 212 the turnover component of β -diversity (Simpson index, β_{sim}) and the nestedness component of β -213 diversity ($\beta_{nes} = \beta_{sor} - \beta_{sim}$). Based on these matrices, we used Permutational Multivariate Analysis of 214 Variance (PERMANOVA, Anderson, 2001) to test whether grazing was a significant source of 215 variation in species composition. As the PERMANOVA test is sensitive to differences in group 216 dispersions, we also ran a permutation-based test for homogeneity of multivariate dispersions 217 (PERMDISP, Anderson, 2006). Both tests used the distance matrix as the dependent variable and 218 grazing level as the grouping variable.

219

220 2.2.3 Comparing saltmarshes with terrestrial habitats

We compared our saltmarsh transect counts with transect counts from other habitats by integrating
 our July-August saltmarsh survey data with pollinator survey data collected in July-August 2013-2016

223 in all terrestrial broad habitat types (classified as JNCC 2019) for the Welsh Government under the 224 Glastir Monitoring & Evaluation Programme (Emmett and the GMEP team, 2017). These data were 225 collected from 1km squares across Wales under a stratified random sampling design. Each 1km 226 square was visited in July and August during one year of the period 2013-2016 and surveyed for bees 227 along ten 200m transect sections (see Appendix A for full details). The surveys noted all bees present 228 on the transect, compared with only foraging bees in the saltmarsh surveys, therefore comparisons 229 are likely to be conservative towards saltmarsh abundances. We used negative binomial mixed 230 effects models to predict the number of honeybees, bumblebees, and solitary bees per 200m 231 transect in each of 14 habitat types (11 main terrestrial habitats, ungrazed, extensively, and 232 intensively grazed saltmarsh) while controlling for the fixed effects of wind and temperature and the 233 random effects of observer and transect nested in site. We tested whether habitat was a significant 234 predictor of bee counts using LRTs. We were unable to control for the effect of year in our models, 235 as year covaried with habitat type. However, each survey block (terrestrial, saltmarsh) spanned ≥ 3 236 years, which should minimise any effect of year.

237

238 **3. Results**

239 In total we recorded 1594 foraging bees across the 11 sites, averaging 13.1 ± 4.0 (S.E.) bees per km 240 of transect, and comprising 19 species across 10 genera (see online Supplementary material for bee 241 species data, flower cover and flower visitation data). Most individuals were either honeybees (52%) 242 or bumblebees Bombus spp. (47%). We observed bees foraging on just nine plant species, although 243 we recorded 17 species of insect-pollinated plants in the marshes. Two plants in particular, Aster 244 (Tripolium pannonicum) and Limonium (L. vulgare, L. humile), received the great majority of bee visits (52 and 43% of observed visits, respectively) and were disproportionately preferred relative to 245 246 their flower cover (33% and 30% of total flower cover).

248 3.1 Grazing, bee abundance and α -diversity

Grazing intensity had a significant effect on bee abundance and bee richness, but not on Shannon (H') diversity (Fig. 3*a-c*, Supplementary material). Intensively grazed marshes had significantly lower bee abundance and bee richness than ungrazed marshes, while extensively grazed marshes were intermediate and not significantly different from the other two categories. Bee abundance, richness and H' diversity were significantly higher in mid and late summer, compared to early summer (Fig. 3*d-f*) but were unaffected by survey year (Supplementary material).

255

Grazing affected bee communities via two pathways: negative effects on flower cover and positive effects on plant richness. When all plant species are combined (Fig. 4*a*, Supplementary material), intensive grazing reduced flower cover, which had negative effects on bee abundance, leading to reduced bee richness. However, this negative effect on bee richness was mitigated by a positive effect of extensive and intensive grazing on plant richness, and a positive effect of plant richness on bee richness.

262 Separating out key plant species (Fig. 4b, Supplementary material) highlights how grazing 263 predominantly affected the flower cover of Aster and Limonium (Fig. B.1), and these plants had the 264 strongest effects on bee abundance and therefore richness (Fig. B.2). Grazing reduced both the 265 occupancy (i.e. coverage across the marsh) and flower cover of Limonium. Grazing had no effect on 266 Aster occupancy, but increased grazing intensity directly reduced Aster flower cover. Grazing had no 267 effect on other plant occupancy or flower cover. Increasing both Limonium and Aster flower cover 268 strongly increased bee abundance. While flower cover of other plants had no significant effect, plant 269 richness had a positive effect on bee abundance. Bee richness increased with increasing bee 270 abundance, although there was a small negative effect of increased Aster flower cover on bee 271 richness. When analysed with key plant species separated, the positive effect of plant richness on 272 bee richness was no longer significant (P=0.056, Fig. B.2e). When honeybees were excluded from the models, the effect of Aster cover on bee richness became positive, but otherwise results for wild
bees did not differ from the models including honeybees (Supplementary material). When
Shannon's (H') index was used as the diversity measure instead of species richness, all trends
remained the same, although some predictors were no longer significant (Supplementary material
and Fig B.1, B.2).

278

279 3.2 Grazing and β-diversity

280 We observed 16 bee species in ungrazed marshes (eight of these being unique to ungrazed marshes,

Fig. 5), 10 species with extensive grazing (one unique), and six species with intensive grazing (one

unique). Total β-diversity (pairwise Sørensen dissimilarity) did not differ between grazing levels,

either in terms of centroid location in multivariate space (PERMANOVA), or in terms of within-group

284 dispersion (PERMDISP). However, when β -diversity was partitioned into turnover and nestedness

285 components, there were differences between grazing levels.

286 Grazing significantly affected nestedness-resultant dissimilarity (PERMANOVA F=4.5, P=0.042;

287 pairwise comparisons not significant) but had no effect on turnover-resultant dissimilarity

288 (Supplementary material), indicating that differences between bee communities at different grazing

levels were driven by nestedness, rather than turnover. The effect of grazing on nestedness was not

driven by differences in within-group dispersion of nestedness (PERMDISP F=1.7, P=0.232). Within-

291 group dispersion due to turnover was lower in intensively grazed marshes than for other grazing

292 levels (PERMDISP F=10.1, P<0.001; pairwise comparisons P<0.05), indicating there was little species

293 replacement across intensively-grazed marshes. These results did not change when only wild bees

were considered.

296 3.3 Comparing salt marshes with terrestrial habitats

297 In July and August, the contribution of honeybees, bumblebees and solitary bees were 48%, 51% and 298 <1% in saltmarshes, compared to 18%, 78% and 4% in terrestrial habitats. Habitat had a significant 299 effect on the abundances of all bee types in July-August (Supplementary material). When ranked 300 with other habitats (Fig. 6), ungrazed saltmarshes were the highest-ranked habitat for honeybee 301 abundances, and the fifth highest-ranked habitat for bumblebees, but were less important for 302 solitary bees. Grazed marshes were amongst the lowest-ranked habitats for wild bees, but 303 extensively grazed marshes were the third highest-ranked habitat for honeybees. However, there 304 was high variability within many habitat types, and habitat and weather predicted only a small 305 proportion of the observed variation in bee abundance (marginal R²=0.25, 0.06, 0.08 for honeybee, 306 bumblebee and solitary bee models).

307

308 4. Discussion

This study shows for the first time that saltmarshes provide important foraging grounds for high numbers of honeybees and bumblebees, and that just two flowering plants account for practically all of this habitat provisioning service: Aster *Tripolium pannonicum* and *Limonium* spp. Livestock grazing reduces bee abundance and alpha diversity, and the effects are strongest with intensive grazing. There is a pattern of high species loss and low species replacement as grazing intensity increases.

Grazing impacts on bees principally operated via changes to the cover of two flowering plants
(pathway i, Fig. 2). Grazing reduced Limonium flower cover both directly and indirectly *via* reduced
Limonium occupancy. Intensive grazing reduced Aster flower cover but did not affect Aster
occupancy. Aster's higher grazing tolerance may be partly due to its occurrence in lower, wetter
areas of the marsh (Adam, 1981) which are less used by livestock (Sharps et al., 2017). Additionally,
although Aster is highly palatable, Aster plants rarely die as a result of grazing (Nolte et al., 2013),

whereas Limonium is extremely susceptible to trampling and defoliation of young buds (Adnitt et al.,
2007; Boorman, 1967).

323 Limonium and Aster were the two plants with the highest flower cover (30 and 33% of total flower 324 cover, respectively) but were disproportionately preferred by bees, accounting for 95% of total bee 325 foraging visits. Both plants have high densities of flowers/florets, due to their dense clusters of small 326 flowers (Limonium) and composite flowers (Aster), making them a good food source (Kirk and 327 Howes, 2012). Bees prefer to visit only one or two flower types to maximise foraging efficiency, and 328 will target flowers that are abundant and have high food rewards (Free, 1963; Gegear and Laverty, 329 1998). Surprisingly, increasing Aster cover had a slight negative impact on bee richness. This is likely a result of controlling for bee abundance in our model: high Aster cover led to a large increase in bee 330 331 abundance (predominantly honeybees), without a corresponding increase in bee richness.

332 Grazing had a positive effect on plant richness (pathway ii, Fig. 2), which in turn had a positive effect 333 on bee abundance. However, combined 'other' flower cover had no effect on bee abundance, and 334 only supported 5% of all observed bee visits for 37% of total flower cover. This may be because 335 'other' flower cover was dominated by Armeria maritima, which is rarely visited by bees on 336 saltmarshes (Eisikowitch and Woodell, 1975), obscuring the effect of rarer flowering species. Our 337 plant-pollinator networks indicate that these rarer species become more important in grazed 338 marshes, where Aster and Limonium cover is reduced. Despite the benefits of increased plant 339 richness, the positive effect of plant richness on bee abundance did not compensate for the negative 340 effect of reduced flower cover. This result may be driven by the relatively limited floral and bee 341 community of a saltmarsh. We recommend similar investigation of the relative importance of flower 342 richness and flower cover in other habitats to explore the universality of this process, as this could 343 determine appropriate grazing management.

There was no evidence that grazed saltmarshes harbour distinct assemblages of bees. Beta diversity
 between grazing levels was driven by nestedness rather than turnover. Two of the observed species

(*B. humilis, B. muscorum*) are listed under the Environment (Wales) Act 2016 Section 7, which sets
priority species for biodiversity conservation. Priority species were present on three ungrazed
marshes, one extensively grazed, and no intensively grazed marshes. Due to the very low numbers of
individuals observed for most species, we cannot make predictions about how individual species
respond to grazing, but a general pattern of species loss with increased grazing is clear.

351 The number of bees foraging in saltmarshes in July/August was not systematically higher or lower 352 than numbers in terrestrial habitats, despite being surveyed in different years, covering a different 353 range of latitudes and altitudes, and having slightly different survey methodology (only foraging bees 354 recorded in saltmarshes vs all bees in terrestrial habitats). However, the relative ranking of 355 saltmarshes varied depending on grazing management and bee guild. Compared to terrestrial 356 habitats, ungrazed and extensively grazed marshes were well used by honeybees, with ungrazed 357 marshes ranking as the top habitat. The presence of honeybees is strongly reliant on the presence of 358 managed colonies in a location. Since coastal areas are more densely populated by humans than 359 inland areas, this may partly explain the dominance of a domesticated bee species in saltmarsh 360 habitats. Additionally, some beekeepers move hives around the landscape and may target 361 saltmarshes in late summer. Ungrazed marshes were in the top five habitats for bumblebees, but all 362 saltmarsh categories were in the lower half of habitats for solitary bees. The scarcity of solitary bees 363 on saltmarshes may be due to their shorter foraging range (Greenleaf et al., 2007), limiting them to 364 foraging areas close to their nest (which cannot be located on mid-low areas of a saltmarsh due to 365 tidal inundation).

The comparisons with terrestrial habitats were for July-August only, when Aster and Limonium are in bloom, but saltmarsh bee abundances were much lower in June. British bees are active from February to October (Falk and Lewington, 2015) and need forage throughout this period. However, forage for honeybees and bumblebees more generally is low in mid-late summer (Couvillon et al., 2014; Timberlake et al., 2019), so the floral resources on saltmarshes during this time may be particularly valuable to help fill this 'hunger gap'. The plant communities on British saltmarshes are
present across north-west Europe (Adam, 1990), therefore the patterns from this study are likely to
apply across temperate Europe. We have identified two consistently important plants for bees,
meaning that European saltmarshes can be rapidly assessed for their value to bees. American
marshes also contain *Limonium* spp. and Asian marshes harbour Aster and *Limonium* spp. (Adam,
1990), so the value of saltmarshes for pollinators is likely to extend more widely.

377

378 5. Conclusions

379 Pollinator declines are primarily driven by habitat loss and agricultural intensification (Potts et al. 380 2010a). We have demonstrated that saltmarshes can provide a vital resource for wild and managed 381 bees during the 'hunger gap' of mid-late summer, contingent on appropriate management. Grazing, 382 particularly intensive grazing, reduces the cover of key food plants, and the increase in plant 383 diversity does not compensate for these reductions. Sensitively-managed saltmarshes have the 384 potential to contribute an important foraging habitat in a coastal landscape, enhancing the levels 385 and reliability of pollination services (Garibaldi et al., 2011; Viana et al., 2012), and supporting wild 386 species conservation.

387 This research provides evidence for three key management recommendations. Firstly, that to 388 maximise pollinator presence saltmarshes should manage for extensive or no grazing. We do not 389 recommend abandonment of grazing, as this can lead to a homogenous grass-dominated habitat 390 (Adam, 1990). Therefore, grazed marshes should be maintained at - or reduced to - extensive levels, 391 to encourage increased flower cover of preferred species. Secondly, that grazing management 392 targeted towards high plant diversity does not necessarily benefit pollinators. Thirdly, that for both 393 local and landscape diversity of bees, and conservation of priority species, long-term ungrazed 394 marshes are optimal and intensively grazed marshes have little value.

396 Authors' contributions

KD and JG designed methodology; KD conducted the saltmarsh surveys and statistical analyses; KD
and JG led the writing of the manuscript; MB co-ordinated terrestrial surveys and JA curated the
terrestrial data for subsequent analysis. All authors contributed critically to the drafts and gave final
approval for publication.

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402

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559

- 561 Appendix A: Methods
- 562
- 563 <u>Contents</u>
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- 570 Table A.3. Simplification of broad habitat types
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574 Supplementary methods: Allocation of grazing levels quantitatively and qualitatively

Grazing levels were allocated both quantitatively and qualitatively to every transect on every visit, and
combined to obtain an overall relative grazing level for each marsh. The grazing level was assessed
quantitatively at each transect by counting the number of dung piles per grazer species lying 1m to either side
of the transect line. For each species (cattle, pony, sheep), we rescaled the dung counts on a scale of 0-1,
based on the maximum observed value across all surveys, and summed them to get a total for the transect
(potential range 0-3).

E 0 1	Desceled dung count -	no. cattle droppings	no. pony droppings	no. sheep droppings		
301	Rescaled dulig could =	max no. cattle droppings	max no. pony droppings	max no. sheep droppings		
582	We averaged these dung counts	across every transect	and visit to get a single c	lung count value for the		
583	surveyed areas of the marsh. Du	ie to tidal action, dung	may be washed off or de	eposited on the marsh,		
584	depending on the stage in the spring-neap tidal cycle. Therefore, we also made a qualitative assessment of the					
585	grazing level at each transect on	every visit (0: ungraze	d, 1: lightly, 2: moderate	ly, 3: heavily) based on visual		
586	indicators such as animal preser	nce, droppings, damage	e to ground and vegetati	on (Table A.2). We averaged the		
587	qualitative grazing levels across	every transect and visi	t to obtain a single quali	tative grazing level for the		
588	surveyed areas of the marsh (po	tential range 0-3).				
589	There was a strong positive corr	elation between the gr	azing level assessed dun	g counts and the grazing level		

assessed qualitatively (Kendall's tau correlation between the grazing level assessed dung counts and the grazing level sesses qualitatively (Kendall's tau correlation test, tau=0.88, p<.001). We allocated each marsh to one of three grazing categories (absent, extensive, intensive grazing) based on these scores (Fig. A.1). The allocated grazing levels are relative and not defined in terms of livestock units (LUs). Where LUs could be reasonably estimated for the entire marsh (*e.g.* on enclosed marsh areas) we have noted these in Table A.1. Intensively grazed marshes were characterised by having more damage to the ground, more visible droppings, and more areas of vegetation that had been closely and uniformly cropped by grazers: in the intensively grazed marshes at least a quarter of all quadrats (ranging 29-74% in the four marshes) had a sward height of <8cm, whereas

- fewer than a quarter of quadrats (15-24% per marsh) in extensively grazed marshes had such a short sward. In
 the four ungrazed marshes, the percentage of quadrats with this short sward ranged from 0-11%.
- 599

600 <u>Supplementary methods: Statistical packages</u>

601 LMMs were fitted using lme4 (Bates et al. 2015). We used ImerTest (Kuznetsova et al. 2017) to calculate t-test 602 P-values for comparison of different factor levels, and piecewiseSEM (Lefcheck 2016) to calculate R² values. 603 Negative binomial GLMMs were fitted using glmmTMB (Brooks et al. 2017) and sjsstats (Lüdecke 2019) was 604 used to calculate R² values. We used the DHARMa package (Hartig 2019) for residual checks and tests for 605 goodness of fit and zero-inflation. (G)LMM graphs were plotted using visreg (Breheny and Burchett 2017) and 606 ggplot2 (Wickham 2016) and 95% confidence intervals were estimated by parametric bootstrapping using the 607 bootpredictIme4 package (Duursma 2019) which implements the Ime4 bootMer function in visreg. For beta-608 diversity analyses, pairwise distance matrices were calculated from presence-absence species data using the 609 betapart package in R (Baselga and Orme 2012). PERMANOVA tests were conducted using the adonis 610 command in the vegan package (Oksanen et al. 2019) in R. Post-hoc tests for PERMANOVA were performed 611 using pairwise.perm.manova in RVAideMemoire (Hervé 2019) with fdr-adjusted P-values. PERMDISP tests 612 were conducted using betadisper and permutest in vegan. All permutational tests were performed with 9999 613 permutations.

614

615 Supplementary methods: Calculating surrounding landscape - proportion of natural habitat

Surrounding landscape can affect bee visitation rates and diversity, both responses declining with increasing distance from natural habitat (Ricketts et al 2008, Viana et al. 2012). Species sensitivity to land use is dependent on species traits such as foraging range and sociality (de palma et al 2015) and different guilds are affected by landscape context at different spatial scales (Steffan-Dewenter et al. 2002). To allow us to account for landscape effects in our models of bee abundance and bee diversity, we calculated the proportion of 621 natural habitat surrounding each transect at a range of scales. We used a 2015 land cover map (Rowland et al. 622 2017) which provides classification of UK land cover based on UK BAP broad habitat types at 25m resolution. We classified each broad habitat type as either semi-natural vegetated habitat (hereafter 'natural habitat') or 623 not, as defined in Table S3. We then calculated the proportion of surrounding landscape that is natural habitat 624 625 for each marsh at a range of radii from 250m to 3km (250, 500, 750, 1000, 1500, 2000, 3000m). Each radius 626 was tested individually in our LMMs, and assessed on the basis of Δ AIC compared with no landscape term. 627 Inclusion of the landscape variable did not improve any of our models. This may be due to the dominance of 628 honeybees and bumblebees in our data: multiple studies have shown that these guilds are less affected by 629 landscape context than non-Bombus wild bees (Bennett et al. 2014, Garibaldi et al. 2012, Murray et al. 2012, 630 Steffan-Dewenter et al. 2002).

All GIS analyses were conducted in ArcGIS 10.5.1.

632

633 Supplementary methods: Terrestrial surveys for GMEP

634 Pollinator surveys were conducted by the Centre for Ecology and Hydrology as part of the Glastir Monitoring & 635 Evaluation Programme (GMEP) for the Welsh Government (Emmett et al. 2017). GMEP included two pollinator 636 surveys - one in July and one in August - in each of 300 1km squares in Wales. Each square was visited only 637 once from 2013 to 2016, in the first round of a rolling environmental survey. Of the 300 squares, 150 638 comprised a stratified random sample to represent land classes across Wales, and 150 comprised a "targeted 639 component" and were selected based on various criteria associated with the Glastir agri-environment scheme. 640 Within each site, two 1km transects, divided into roughly 200m sections, were surveyed for bees between 641 10am and 4pm on warm, dry, calm days following the UK Wider Countryside Butterfly Survey (UKBMS 2019) 642 method. Transects were walked at an even pace, and all bees that were observed within a 5m box around the 643 observer were recorded and identified as honeybee, bumblebee or 'solitary bee' (*i.e.* non-Bombus wild bee). 644 Temperature and wind speed (Beaufort scale) were recorded for each transect. For more information on 645 square selection and survey methodology, see the GMEP reports and appendices (GMEP 2019).

646	A habitats survey was carried out in the GMEP squares during the same years as the pollinator surveys. Every
647	accessible land parcel in the square was assigned a broad habitat type according to UK Biodiversity Action
648	Plant broad habitat types (JNCC 2019). We extracted the underlying broad habitat throughout every ~200m
649	pollinator transect section by intersecting with habitat polygons in ArcGIS Desktop 10.6 (ESRI, Redlands,
650	California). The broad habitat which accounted for the greatest proportion of each 200m transect section was
651	allocated as the dominant underlying habitat. Transect sections were only included in these analyses if >100m
652	intersected the allocated habitat type. Furthermore, we only assessed habitats with >50 transect sections.
653	
654	Supplementary methods: References
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- 717 Appendix B: Supplementary figures
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719 <u>Contents</u>

- 720 Fig. B.1. Model predictions for plant responses to grazing
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724 TABLES

- 725
- 726 **Table 1.** The five core linear mixed models used to test the pathways presented in our conceptual model (Fig. 1).

727 Variables in brackets show where multiple iterations of the model were run using Shannon H diversity instead of species

- richness, wild bees instead of all bees, and with plant occupancy and flower cover separated into Aster, Limonium and
- 729 other species. In all cases, only insect-pollinated plants were included. To avoid overfitting models, weather and habitat
- variables were minimised where possible by assessment of Aikake information criteria (final models presented in
- 731 supplementary material).

	Dependent variable	Fixed effects	Random effect	Ν
1	Plant richness (Plant H diversity)	Grazing level Year	Marsh	21
2	Plant occupancy (Aster occupancy) (Limonium occupancy) (ΣOther plant occupancy)	Grazing level Year	Marsh	21
3	Flower cover (Aster flower cover) (Limonium flower cover) (ΣOther flower cover)	Grazing level Plant occupancy Year Season	Marsh	76
4	Bee abundance (Wild bee abundance)	Grazing level Plant richness Total flower cover (Aster flower cover + Limonium flower cover + Σ Other flower cover) Year Season Wind speed Temperature + Temperature ² Natural habitat (250-3000m)	Marsh	76
5	Bee richness (Wild bee richness) (Bee H diversity) (Wild bee H diversity)	Grazing level Plant richness Total flower cover (Aster flower cover + Limonium flower cover + ΣOther flower cover) Year Season Wind speed Temperature + Temperature ² Natural habitat (250-3000m)	Marsh	76

732 Table A.1. Study site details. Grazing management and environmental characteristics for the 11 study sites. Livestock 733 Units per hectare (LUha⁻¹) estimated for the entire marsh (not only the surveyed areas) during the main summer grazing 734 period, where possible, based on information from landowners or animal head counts. Cattle=1, ponies=0.5, sheep=0.12 735 LU (Welsh Government 2014). National Vegetation Classification (NVC, a systemic catalogue of the plant communities of 736 Great Britain, Rodwell 2006) based on 1998 NVC Survey data (GIS shapefile provided by Natural Resources Wales) and 737 confirmed by field observations. Marsh geomorphology was classified according to Allen (2000) and estuary position 738 according to Adam(1990). Duration of current grazing levels was obtained from land managers/owners, but several had 739 no knowledge of grazing management prior to their tenancy, therefore figures shown are a minimum. Sediment types 740 defined as L-CL (loam-clay) or S (sandy). Adjacent habitat is shown for surrounding 1km, calculated from a 2015 land 741 cover map (Rowland et al. 2017) and classified according to Table A.2: Ag=agricultural land, Bu=built-up areas, 742 Na=natural or semi-natural areas, Op=open water or littoral zone.

743

Marsh code	Latitude, longitude	Livestock grazing intensity	LUha ⁻¹	Livestock type (timing)	Average subjective grazing level per transect	Average normalised dung count	Quadrats with sward height <8cm (%)	Current grazing levels	Zones sampled	NVC plant community by zone	Area§ (ha)	Marsh geomorphology and estuary position	Sediment type	Adjacent habitat (%)
СВ	51.622, -3.852	Ungrazed	0	N/A	0.0	0.0	6	>30 years (possible light cattle grazing previously)	Low Mid Upper	SM14 SM13, 16 SM24	33	Estuarine back- barrier, Seaward zone	L-CL, S‡	Ag=10 Bu=15 Na=51 Op=25
РВ	51.674, -4.276	Ungrazed	0	N/A	0.0	0.0	4	>40 years (possible grazing previously)	Low Mid Upper	SM14 SM13, 16 SM16, 24	93	Estuarine back- barrier, Seaward zone	L-CL, S†	Ag=3 Bu=1 Na=76 Op=21
TG	51.723, -5.167	Ungrazed	0	N/A	0.0	0.0	11	>30 years (never known to be grazed)	Mid Upper	SM13, 14 SM16, 18	19	Estuarine back- barrier, Central zone	L-CL†	Ag=65 Bu=2 Na=21 Op=12
US	51.523, -2.977	Ungrazed	0	N/A	0.0	0.0	0	Never grazed by livestock (inaccessible)	Low Mid Upper	SM6 SM13 SM24	29	Estuarine fringing, Seaward zone	L-CL‡	Ag=0 Bu=10 Na=27 Op=63
LW*	51.662 <i>,</i> -4.124	Extensive	0.31	Cattle (Apr-Oct)	1.0	0.5	16	>10 years	Low Mid Upper	SM14 SM16 SM18	70	Estuarine fringing, Central zone	L-CL‡	Ag=0 Bu=7 Na=66 Op=27
MU	51.786, -4.634	Extensive	0.39	Cattle (Jan- Dec)	1.2	0.7	15	>50 years	Low Mid Upper	SM6 SM12, 13, 16, 18 SM16	38	Estuarine fringing, Central zone	L-CL†	Ag=39 Bu=1 Na=33 Op=28
WH	51.636 <i>,</i> -4.242	Extensive	0.31	Ponies Sheep (Jan-Dec)	1.5	0.4	24	>5 years (previously grazed but intensity unknown)	Low Mid Upper	SM10, 13 SM16 SM18	64	Estuarine back- barrier, Seaward zone	L-CL, S†	Ag=0 Bu=0 Na=60 Op=40
TR	51.792, -4.463	Intensive	1.69	Cattle Sheep (May-Oct)	1.9	1.0	29	>10 years	Low-mid Mid Upper	SM15 SM16 SM16	42	Estuarine fringing, Landward zone	L-CL†	Ag=58 Bu=2 Na=33 Op=8
PM*	51.721, -4.311	Intensive	0.84	Cattle (Apr-Oct)	2.1	0.9	31	>5 years (previously grazed but intensity unknown)	Low-mid Mid Upper	SM12 SM16 SM16	179	Estuarine back- barrier, Central zone	L-CL†	Ag=34 Bu=1 Na=64 Op=1
CR	51.625 <i>,</i> -4.158	Intensive	-	Ponies Sheep (Jan-Dec)	2.4	1.1	51	>40 years	Low-mid Mid Upper	SM10, 13 SM16 SM18	218	Estuarine fringing, Central zone	L-CL, S†	Ag=19 Bu=5 Na=67 Op=9

- 746 Table A.2. Visual indicators used to allocate qualitative grazing levels. Each descriptor is not absolute, but was used in
- 747 combination to allocate the best representative grazing level to the area immediately surrounding each transect (within a

748 few hundred metres, approx. 5 ha).

Indicator	0: Ungrazed	1: Lightly grazed	2: Moderately grazed	3: Heavily grazed
Animal presence	None	Area accessible to animals but no more than a few animals present	Small herd (e.g. 5-10 cattle/ponies, 15-30 sheep) present	Many animals (e.g. >20 cattle/ponies, >50 sheep) present
Droppings	None	Infrequently seen	Commonly seen	Abundant across area
Damage to ground	None	Hoofprints rarely seen. Very little bare ground.	Hoofprints/poaching commonly seen. Some bare ground.	Ground is badly poached or extremely compacted. Areas of bare ground common.
Sward height and damage to vegetation	Majority of sward longer than 15cm, complex structure, no visible cropping	Majority of sward longer than ~15cm, complex structure, little visible cropping	Some areas shortly cropped (<~10 cm) interspersed with longer, more tussocky areas	Majority of vegetation cropped to a short, uniform sward; only unpalatable species are above ~10cm

749

750 Table A.3. Simplification of broad habitat types.

Broad habitat type	Classification	Natural habitat
Broadleaved woodland	Natural or semi-natural vegetated habitat	\checkmark
Coniferous woodland	Natural or semi-natural vegetated habitat	\checkmark
Arable and horticulture	Agricultural land	-
Improved grassland	Agricultural land	-
Neutral grassland	Natural or semi-natural vegetated habitat	\checkmark
Calcareous grassland	Natural or semi-natural vegetated habitat	\checkmark
Acid grassland	Natural or semi-natural vegetated habitat	\checkmark
Fen, Marsh and Swamp	Natural or semi-natural vegetated habitat	\checkmark
Heather	Natural or semi-natural vegetated habitat	\checkmark
Heather grassland	Natural or semi-natural vegetated habitat	\checkmark
Bog	Natural or semi-natural vegetated habitat	\checkmark
Inland rock	Natural or semi-natural vegetated habitat	\checkmark
Saltwater	Open water or littoral zone	-
Freshwater	Open water or littoral zone	-
Supra-littoral rock	Natural or semi-natural vegetated habitat	-
Supra-littoral sediment	Natural or semi-natural vegetated habitat	-
Littoral rock	Open water or littoral zone	-
Littoral sediment	Open water or littoral zone	-
Saltmarsh	Natural or semi-natural vegetated habitat	\checkmark
Urban	Built-up areas	-
Suburban	Built-up areas	-
Wetland*	Natural or semi-natural vegetated habitat	\checkmark

751 *Land managed by RSPB Newport Wetlands was classified as Arable and Horticultural in the Land Cover 2015 map which

752 is incorrect. We renamed these areas as Wetland in our GIS maps, classified under Natural or semi-natural vegetated habitat.

753

754





Figure 1. Location of 11 study sites across south Wales, United Kingdom. See Table A.1 for details of each site. The
ungrazed marshes were more widely distributed geographically due to the rarity of long-term ungrazed sites. Three sites
(WH, LL, CR) are situated on a single contiguous area of saltmarsh ~10 km long: each site was separated by at least 2.5 km
and two major creek channels. However, two of these three marshes were under the same grazing management
(intensive). As this could be deemed pseudoreplication, we repeated our net grazing effect models (see section 2.2.1)
with each of these sites excluded, which did not alter results.



- Figure 2. Mechanisms by which grazing may affect bee communities.
- 769 *a*) Simplified system showing three hypothesised pathways: (i) changes to insect-pollinated (IP) plant flower cover; (ii)
- changes to IP plant diversity, (iii) direct disturbance of bees or their nests.
- b) Theoretical system to be tested using linear mixed models, allowing pathway (i) to operate *via* changes to IP plant
- cover (occupancy) and direct changes to flower cover *via* defoliation. Numbers indicate the five responses tested using
- T73 LMMs as described in section 2.2.1. Temporal and environmental variables in grey will be included in models to control
- for these effects.
- 775
- 776



Figure 3. Model predictions (lines) and partial residuals (points) for net grazing effects (*a-c*) and seasonal effects (*d-f*) on bees. Means are predicted for mid-summer, 2017 in (*a-c*) and for ungrazed marshes, 2017 in (*d-f*). Factor levels that are significantly different (t-test) are indicated by different letters. 95% confidence intervals (shaded boxes), calculated by bootstrapping. Abundance and richness values were calculated on the log scale, but have been back-transformed for presentation.

783



785 786

Figure 4. The mechanisms of grazing effects investigated via a series of LMMs for *a*) all insect-pollinated (IP) plant species combined and *b*) key plant species separated out. Significance was tested using likelihood ratio test (LRT): solid lines indicate significant positive effects, dashed lines indicate significant negative effects, grey lines indicate P>0.05. When grazing was significant by LRT, each grazing level was compared against absent grazing by t-test: a solid line represents a significant positive effect, a dashed line represents a significant negative effect, a dot-dashed line represents a negative effect (P>0.05). Line thickness for significant effects is weighted by standardised coefficient, which is also shown above the line (coefficients for grazing levels are relative to absent). Marginal R² values are for the full model, including the effect of time and weather variables, which have not been drawn: see online supplementary material for full results.

794



796 797 Figure 5. Plant-pollinator network at each grazing level. Green circles with solid outline are plant species (diameter 798 proportional to flower cover), blue circles with dashed outline are bee species (weight of connector proportional to the square root of bee visits). Al.of: Althea officinalis, Ar.ma: Armeria maritima, Aster: Tripolium pannonicum, Limon.: 799 800 Limonium spp., Oe.la: Oenanthe lachenalii, Sp.an: Spartina anglica, Sp.me: Spergularia media, Tr.re: Trifolium repens. 801 A.mel: Apis mellifera, B.cam: Bombus campestris, B.hum: B. humilis, B.jon: B. jonellus, B.lap: B. lapidarius, B.mus: B. 802 muscorum, B.pas: B. pascuorum, B.pra: B. pratorum, B.ter: B. terrestris/lucorum complex, B.ves: B. vestalis, Andre.: 803 Andrena sp., C.elo: Coelioxys elongata, C.fod: Colletes fodiens, C.mar: Colletes marginatus, H.rub: Halictus rubicundus, 804 L.cal: Lasioglossum calceatum, L.lat: L. lativentre, M.mar: Megachile maritima, M.leo: Melitta leoprina. 805



809 bumblebees and solitary bees in July-August in terrestrial (open circles) and saltmarsh (filled circles) habitats.

810



811

812 Figure A.1. Allocation of grazing levels based on dung counts and qualitative assessment.



814

815 Figure A.2. Network tested using LMMs with key plant species separated. We also repeated the tests using Shannon's H'

816 index as the measure of diversity and for wild bees only (i.e. *Apis mellifera* excluded). Weather (wind, temperature) and

817 landscape predictors were only included where AIC values indicated model improvement.



819 820 **Figure B.1. Model predictions for plant responses to grazing.** The effect of grazing on: insect-pollinated plant richness (a),

and H diversity (b); the occupancy of Aster (c), Limonium (d), and other plants (e); and the flower cover of Aster (f),

822 Limonium (g), and other plants (h). Significant predictors (likelihood-ratio test) are indicated with an asterisk. Factor levels

- 823 that are significantly different from each other (t-test) are indicated by different letters. 95% confidence intervals
- 824 calculated by bootstrapping. All predictions have been back-transformed to the original scale.
- 825



826
827GrazingPlant H diversity (marsh)Flower cover (%)Bee abundance (per km)*827Figure B.2. Model predictions for bee responses to grazing and vegetation. The effect of grazing (a), plant richness (b),828and flower cover (c) on bee abundance. The effect of grazing (d), plant richness (e), flower cover (f), and bee abundance829(g) on bee richness. The effect of grazing (h), plant Shannon diversity (i), flower cover (j) and bee abundance (k), on bee830Shannon diversity. Significant predictors (likelihood-ratio test) are indicated with an asterisk. 95% confidence intervals831calculated by bootstrapping using the bootMer function. All predictions have been back-transformed to the original scale.