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

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ABSTRACT

Global declines in pollinator populations and associated services make it imperative to identify and sensitively manage valuable habitats. Coastal habitats such as saltmarshes can support extensive flowering meadows, but their importance for pollinators, and how this varies with land-use intensity, is poorly understood. We hypothesised that saltmarshes provide important bee foraging habitat, and that livestock grazing either suppresses or enhances its value by reducing the abundance - or increasing the diversity - of flowering plants. To test these hypotheses, we surveyed 11 saltmarshes in Wales (UK) under varying grazing management (long-term ungrazed, extensively grazed, intensively grazed) over three summers and investigated causal pathways linking grazing intensity with bee abundance and diversity using a series of linear mixed models. We also compared observed bee abundances to 11 common terrestrial habitats using national survey data.

Grazing reduced bee abundance and richness *via* reductions in the flower cover of the two key food plants: sea aster *Tripolium pannonicum* and sea lavender *Limonium* spp. Grazing also increased flowering plant richness, but the positive effects of flower richness did not compensate for the negative effects of reduced flower cover on bees. Bee abundances were approximately halved in extensively grazed marshes (relative to ungrazed) and halved again in intensively grazed marshes. Saltmarsh flowers were primarily visited by honeybees *Apis mellifera* and bumblebees *Bombus* spp. in mid and late summer. Compared to other broad habitat types in Wales, ungrazed saltmarshes ranked highly for honeybees and bumblebees in July-August, but were relatively unimportant for solitary bees. Intensively grazed saltmarshes were amongst the least valuable habitats for all bee types.

Under appropriate grazing management, saltmarshes provide a valuable and previously overlooked foraging habitat for bees. The strong effects of livestock grazing identified here are likely to extend geographically given that both livestock grazing and key grazing-sensitive plants are widespread in European saltmarshes. We recommend that long-term ungrazed saltmarshes are protected from grazing, and that grazing is maintained at extensive levels on grazed marshes. In this way, saltmarshes can provide forage for wild and managed bee populations and support ecosystem services.

1. Introduction

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 are under threat from habitat loss, agrochemicals, disease, invasive species and climate change (Brown and Paxton, 2009; Potts et al., 2010a), leading to long-term declines in wild and managed pollinator populations (Potts et al., 2010a, b; Powney et al., 2019). Agricultural intensification is a major driver of bee declines (Le Féon et al., 2010; Potts et al., 2010a), but appropriate grassland management can yield significant benefits for pollinators (Bruppacher et al., 2016; Garrido et al., 2019). However, the relationship between livestock grazing and pollinator abundance and diversity is not clear or consistent, showing positive (Vulliamy et al., 2006), negative (Kimoto et al., 2012; Kruess and Tscharntke, 2002) and non-linear relationships (Lázaro et al., 2016;

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Mu et al., 2016). Difficulty in disentangling the various effects may originate from a lack of understanding of the mechanisms by which grazers influence pollinator activities and abundances in different habitats.

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

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

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

2. Materials and methods

2.1. Field surveys

We surveyed 11 salt marshes in south Wales (UK) every summer from 2016 to 2018 (Fig. 1, see Table A1 for full site details, marsh 'LW' not surveyed in 2016). Sites were selected to cover a range of grazing intensities (4 long-term ungrazed, 3 extensive, 4 intensive) and livestock species (cattle, ponies, sheep), and to be large enough to allow sampling along four 200 m transects covering multiple inundation zones and vegetation communities. It was not possible to calculate accurate grazing levels in livestock units per hectare (LUha^{-1}), because several of our study sites were part of much larger unfenced grazing lands with extremely clustered livestock distribution. Grazing categories (absent, extensive, intensive) were evaluated based on dung counts and visual assessments performed at each transect on every visit, then averaged for the study site as a whole (see Appendix A, Table A2, Fig. A1). Ungrazed marshes had not been grazed by livestock for a 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 LUha^{-1} during the summer grazing period). Intensively grazed marshes were characterised by removal of much of the standing biomass, leaving a relatively short, uniform sward, and widespread compaction or cutting up of the turf by animal trampling (estimated grazing density > 0.8 LUha^{-1}). Variation in sediment type, marsh geomorphology and surrounding landscape was distributed evenly across the grazing categories (Table A1).

We did not assess grazing levels of wild grazers such as hares, rabbits and wildfowl. There was little visible evidence of grazing by small mammals in the study marshes, and any impacts of these on vegetation are likely to be small (He and Silliman, 2016). However, herbivorous geese are present across the study area during winter months (Davidson and Griffin, 2018). Livestock grazing facilitates goose grazing (Bos et al., 2002; Davidson et al., 2017; van der Graaf et al., 2002), so the study marshes grazed by livestock are likely to also have higher levels of goose grazing, adding to the impacts of livestock on the vegetation community. However, in the study marshes, herbivorous geese are most abundant during the winter months, when plants are not in flower, and wildfowl generally have a lower impact on saltmarsh vegetation than livestock (He and Silliman, 2016), so geese are likely to have lower impacts on bee communities than livestock.

Each marsh was surveyed along four 200 m fixed transects on seven days over three summers (with the exception of marsh 'LW' which was surveyed on six days over two summers), covering the major flowering period in these marshes. Marshes were surveyed in mid-summer (12th July–10th August) in 2016, and in early (9th–29th June), mid (12th July–10th August) and late (24th August–19th 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 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 present.

Bee surveys were conducted using standardised pollinator transect methodologies (Pollard and Yates, 1993). The surveyor walked each 200 m transect at a slow, steady pace and noted any bee visiting a flower within a 5 × 5 m area extending either side and in front. The flower species was noted and bees were identified to species level (with the exception of *Bombus terrestris/lucorum* workers, which cannot be reliably separated morphologically) using Falk and Lewington (2015). Bees that could not be identified in the field were captured in a net (a subsample of 5–10 individuals were collected when that bee type was abundant), transferred to a plastic vial with ethyl acetate, and subsequently identified under a ×30 stereo microscope at Swansea University. Each transect was walked twice, with a 10 min gap between walks to allow bees to re-settle. We used the total number of bees per marsh per survey visit (*i.e.* bees per 1.6 km of transect) in our regression models.

We assessed the vegetation within a 1 × 1 m quadrat placed every 20 m along each transect. For each plant species, we took the mean number of quadrats in which it was present to obtain an average transect occupancy for each marsh (potential range of 0–11). Species

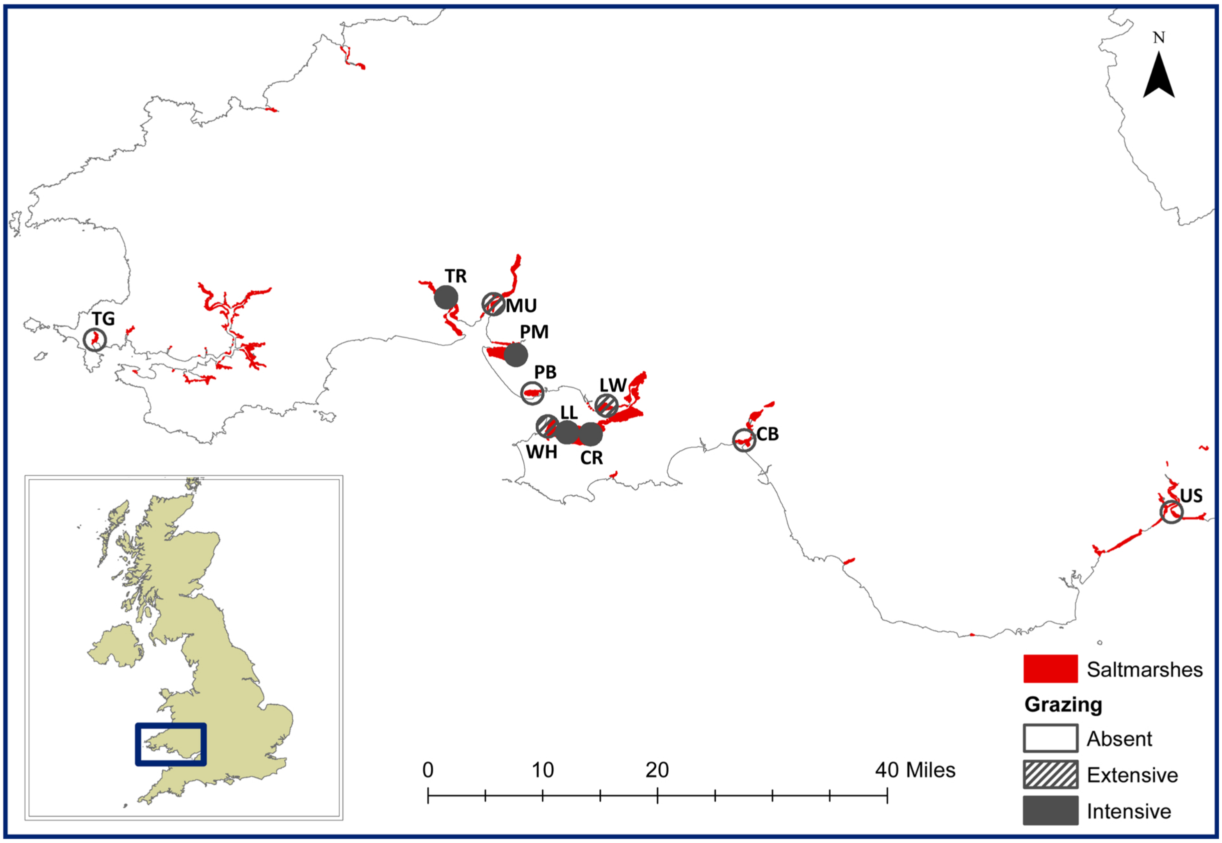

Fig. 1. Location of 11 study sites across south Wales, United Kingdom. See Table A1 for details of each site. The ungrazed marshes were more widely distributed geographically due to the rarity of long-term ungrazed sites. Three sites (WH, LL, CR) are situated on a single contiguous area of saltmarsh ~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 the significance of results.

composition (present/absent in quadrat) was recorded in mid-summer in 2016 and 2017. The mean for each marsh over these two years was used as a predictor in regression models. Saltmarsh plant communities in south Wales, and more widely, are relatively stable over time under consistent grazing management (Pauls, 2017; Taubert and Murphy, 2012), therefore we expect these mean values to be a fair reflection of the plant community across the three years. Percentage flower cover of each species and vegetation canopy height were recorded on every survey visit. *Limonium vulgare* and *Limonium humile* are grouped together in the analyses, as these species are difficult to distinguish morphologically and can hybridise (Dawson and Ingrouille, 1995). We used the mean flower cover per species across all 44 quadrats in the marsh (11 quadrats × 4 transects per marsh per visit) in our regression models.

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.

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

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

To explore the mechanisms of grazing effects, we created a conceptual model incorporating the three hypothesised pathways by which grazing may affect bee populations (Fig. 2), and tested the proposed links using a series of LMMs. For each stage in the network, we built our initial model containing all biologically relevant predictors, with marsh as a random effect (Table 1). We used AIC to determine if fit was improved by log-transformation of continuous predictors. We used LRTs to test: (1) if IP plant richness was affected by grazing; (2) if IP plant occupancy was affected by grazing; (3) if flower cover was affected by grazing, controlling for the effect of IP plant occupancy; (4) if bee abundance was affected by grazing, IP plant richness, and flower cover;

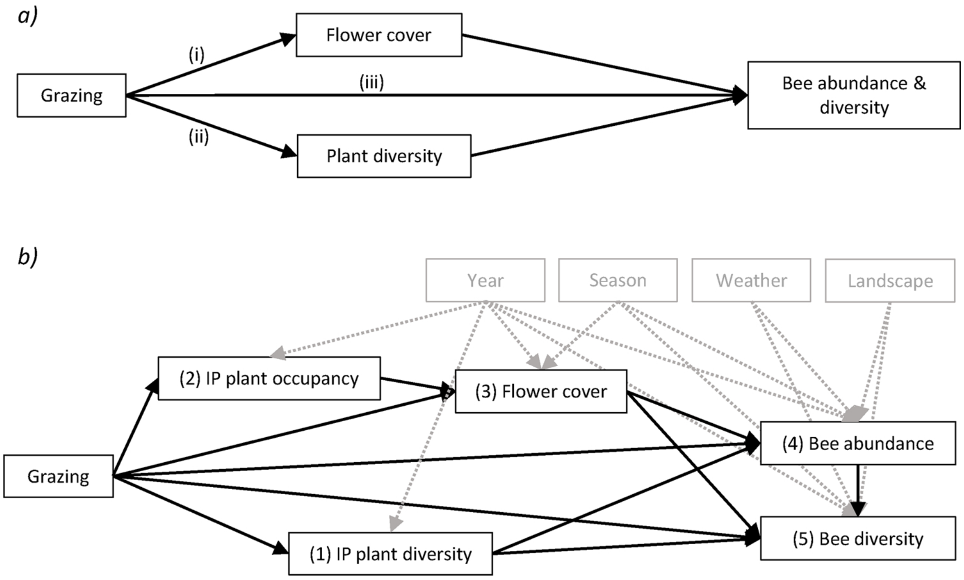

Fig. 2. Mechanisms by which grazing may affect bee communities.
a) Simplified system showing three hypothesised pathways: (i) changes to insect-pollinated (IP) plant flower cover; (ii) changes to IP plant diversity, (iii) direct disturbance of bees or their nests. *b*) Theoretical system to be tested 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 LMMs as described in Section 2.2.1. Temporal and environmental variables in grey will be included in models to control for these effects.

(5) if bee richness was affected by grazing, IP plant richness, and flower cover, controlling for the effect of bee abundance. Two plants, sea aster *Tripolium pannonicum* (formerly *Aster tripolium*, hereafter 'Aster') and the sea lavenders *Limonium* spp. (hereafter 'Limonium') received 95 % of all bee visitations. To gain further insight, we repeated models (2–5) above with IP plant occupancy and flower cover separated into a) Aster, b) Limonium and c) other IP plants (see Fig. A2 and Appendix C for full 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).

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

Table 1
The five core linear mixed models used to test the pathways presented in our conceptual model (Fig. 1). 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 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 Appendix C).

	Dependent variable	Fixed effects	Random effect	N
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 + ΣOther 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

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

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

3. Results

In total we recorded 1594 foraging bees across the 11 sites, averaging 13.1 ± 4.0 (S.E.) bees per km of transect, and comprising 19 species across 10 genera (see Appendix C for bee species data, flower cover and flower visitation data). Most individuals were either honeybees (52 %) or bumblebees *Bombus* spp. (47 %). We observed bees foraging on just nine plant species, although we recorded 17 species of insect-pollinated plants in the marshes. Two plants in particular, Aster (*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 their flower cover (33 % and 30 % of total flower cover).

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*, Appendix C). 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 (Appendix C).

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*, Appendix C), 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.

Separating out key plant species (Fig. 4*b*, Appendix C) highlights how grazing predominantly affected the flower cover of Aster and Limonium (Fig. B1), and these plants had the strongest effects on bee abundance and therefore richness (Fig. B2). Grazing reduced both the occupancy (*i.e.* coverage across the marsh) and flower cover of Limonium. Grazing had no effect on Aster occupancy, but increased grazing intensity directly reduced Aster flower cover. Grazing had no effect on other plant occupancy or flower cover. Increasing both Limonium and Aster flower cover strongly increased bee abundance. While flower cover of other plants had no significant effect, plant richness had a positive effect on bee abundance. Bee richness increased with increasing bee abundance, although there was a small negative effect of increased Aster flower cover on bee richness. When analysed with key plant species separated, the positive effect of plant richness on bee richness was no longer significant ($P = 0.056$, Fig. B2*e*). 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 (Appendix C). 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 (Appendix C and Fig. B1, B2).

3.2. Grazing and β-diversity

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 dispersion (PERMDISP). However, when β-diversity was partitioned into turnover and nestedness components, there were differences between grazing levels.

Grazing significantly affected nestedness-resultant dissimilarity (PERMANOVA $F = 4.5$, $P = 0.042$; pairwise comparisons not significant) but had no effect on turnover-resultant dissimilarity (Appendix C), 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-group dispersion due to turnover was lower in intensively grazed marshes than for other grazing levels (PERMDISP $F = 10.1$, $P < 0.001$; pairwise comparisons $P < 0.05$), indicating there was little species replacement across intensively-grazed marshes. These results did not change when only wild bees were considered (Appendix C).

3.3. Comparing salt marshes with terrestrial habitats

In July and August, the contribution of honeybees, bumblebees and solitary bees were 48 %, 51 % and < 1 % in saltmarshes, compared to 18 %, 78 % and 4 % in terrestrial habitats. Habitat had a significant effect on the abundances of all bee types in July-August (Appendix C). When ranked with other habitats (Fig. 6), ungrazed saltmarshes were the highest-ranked habitat for honeybee abundances, and the fifth highest-ranked habitat for bumblebees, but were less important for solitary bees. Grazed marshes were amongst the lowest-ranked habitats for wild bees, but extensively grazed marshes were the third highest-ranked habitat for honeybees. However, there was high variability within many habitat types, and habitat and weather predicted only a small proportion of the observed variation in bee abundance (marginal

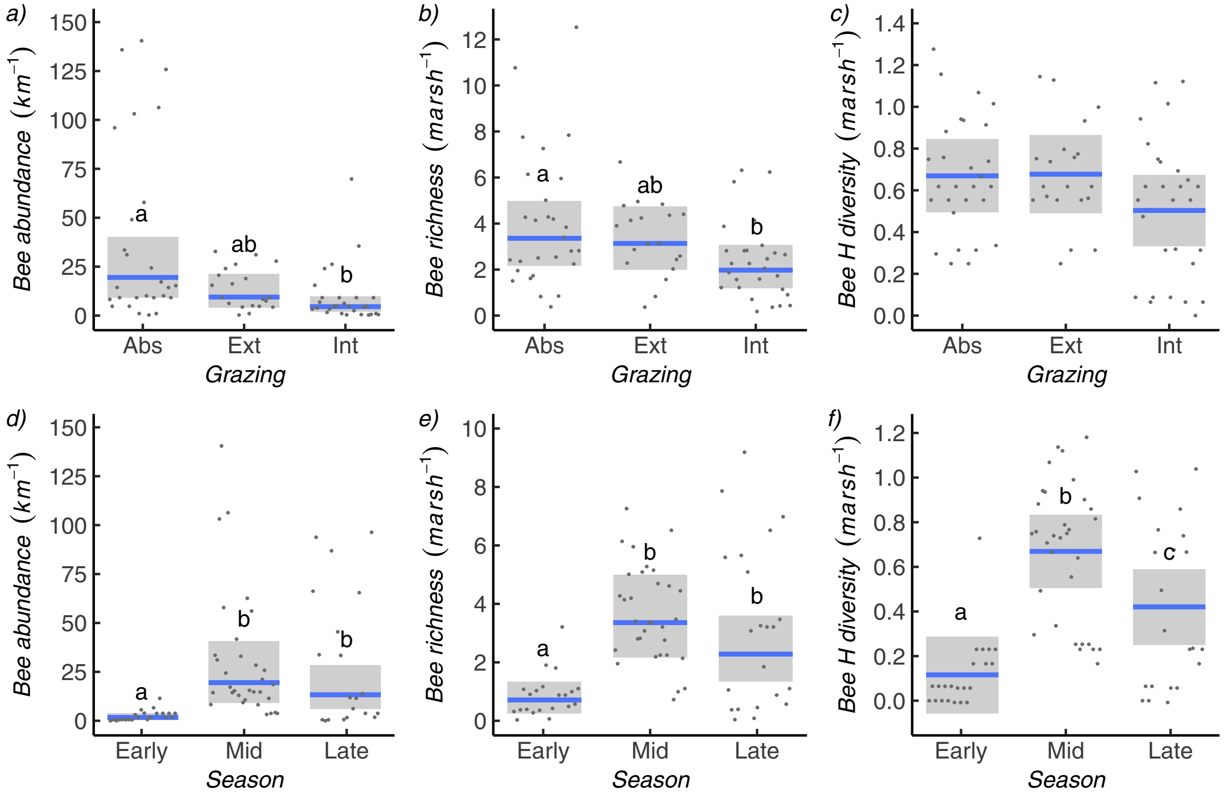

Fig. 3. Model predictions (lines) and partial residuals (points) for net grazing effects (*a-c*) and seasonal effects (*d-f*) on bees. Means are predicted for mid-summer, 2017 in. (*a-c*) and for ungrazed marshes, 2017 in.(*d-f*). Factor levels that are significantly different (*t*-test) are indicated 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.

R^2 = 0.25, 0.06, 0.08 for honeybee, bumblebee and solitary bee models).

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).

Limonium and Aster were the two plants with the highest flower cover (30 and 33 % of total flower cover, respectively) but were disproportionately preferred by bees, accounting for 95 % of total bee foraging visits. Both plants have high densities of flowers/florets, due to their dense clusters of small flowers (Limonium) and composite flowers (Aster), making them a good food source (Kirk and Howes, 2012). Bees prefer to visit only one or two flower types to maximise foraging efficiency, and will target flowers that are abundant and have high food rewards (Free, 1963; Gegear and Laverty, 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 abundance (predominantly honeybees), without a corresponding increase in bee richness.

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

The number of bees foraging in saltmarshes in July/August was not

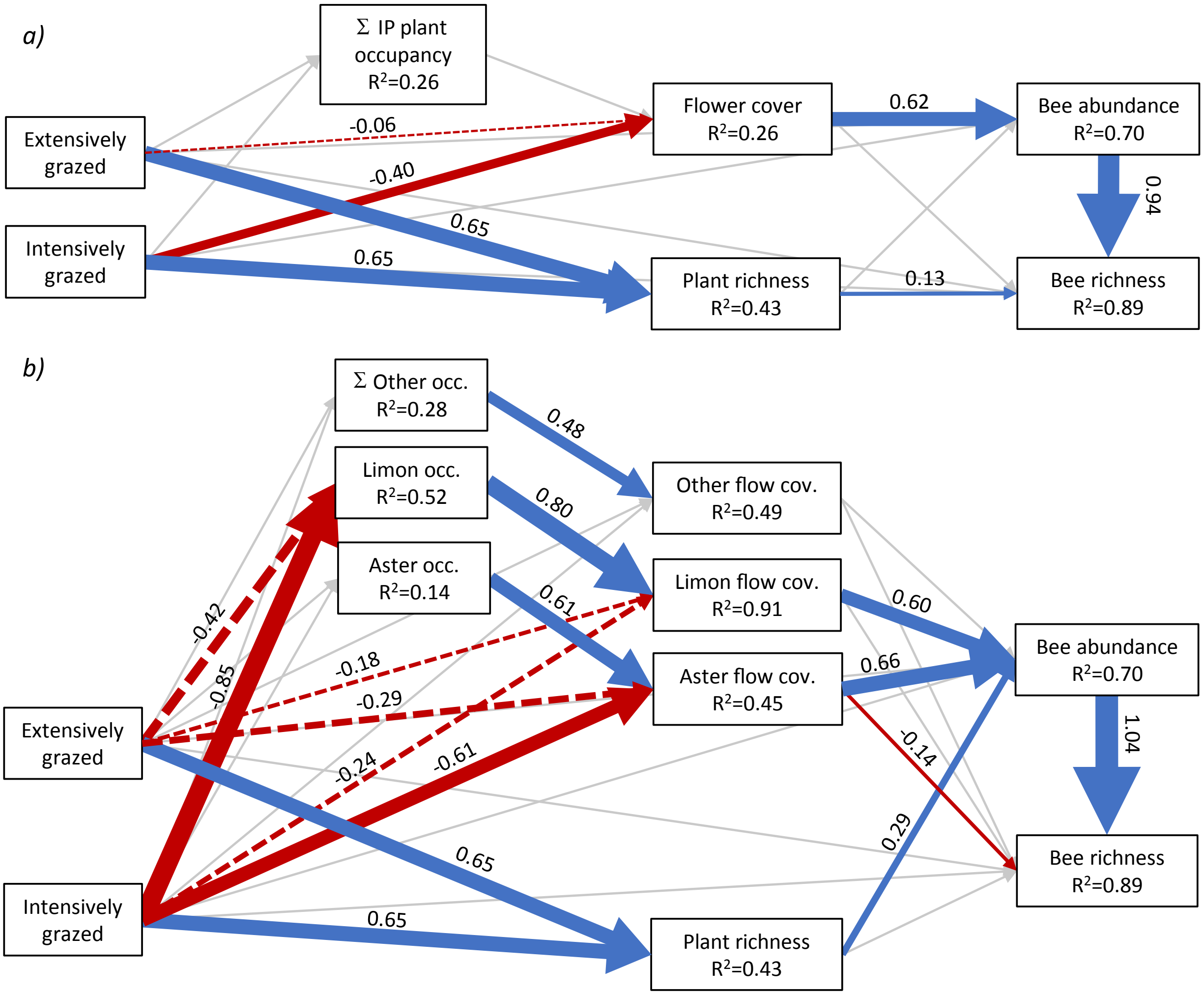

Fig. 4. The mechanisms of grazing effects investigated *via* a series of LMMs for *a*) all insect-pollinated (IP) plant species combined and *b*) key plant species separated out. Significance was tested using likelihood ratio test (LRT): blue lines indicate significant positive effects, red lines indicate 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 $P \leq 0.05$, a dashed line represents $P > 0.05$. 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 R^2 values are for the full model, including the effect of time and weather variables, which have not been drawn: see Appendix C for full results. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

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

5. Conclusions

Pollinator declines are primarily driven by habitat loss and agricultural intensification (Potts et al., 2010a). We have demonstrated that saltmarshes can provide a vital resource for wild and managed bees during the ‘hunger gap’ of mid-late summer, contingent on appropriate management. Grazing, particularly intensive grazing, reduces the cover

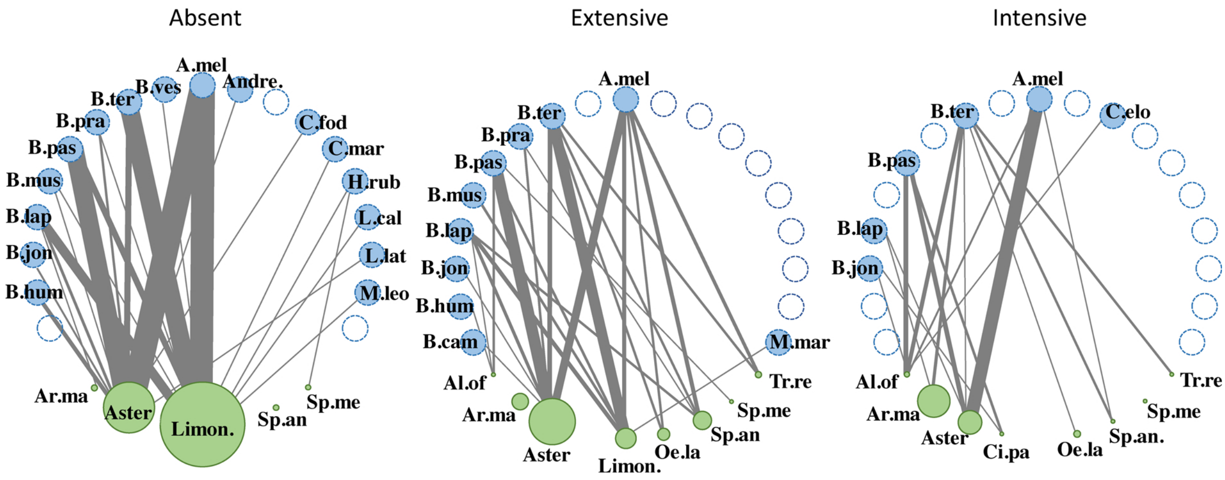

Fig. 5. Plant-pollinator network at each grazing level. Green circles with solid outline are plant species (diameter proportional to flower cover), blue circles with dashed outline are bee species (weight of connector proportional to the square root of bee visits). Al.of: *Althea officinalis*, Ar.ma: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

of key food plants, and the increase in plant diversity does not compensate for these reductions. Sensitively-managed saltmarshes have the potential to contribute an important foraging habitat in a coastal landscape, enhancing the levels and reliability of pollination services (Garibaldi et al., 2011; Viana et al., 2012), and supporting wild species conservation.

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

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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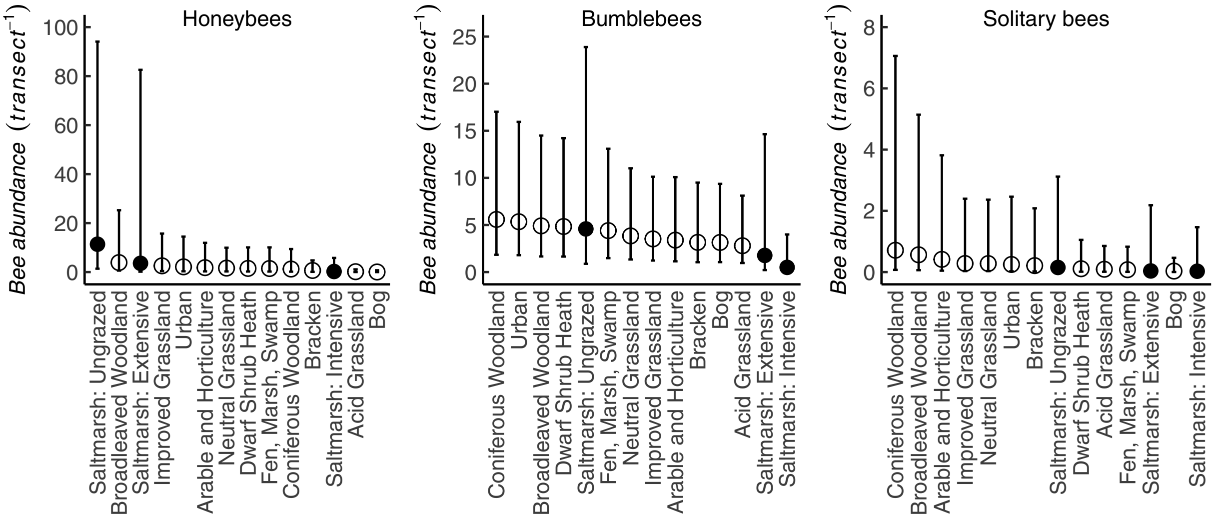

Fig. 6. Bee abundances in different habitats. Predicted abundance (per 200 m transect) and 95 % CIs of honeybees, bumblebees and solitary bees in July-August in terrestrial (open circles) and saltmarsh (filled circles) habitats.

Declaration of Competing Interest

None.

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Appendix A. Supplementary material

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