REVIEW

Livestock grazing alters multiple ecosystem properties and services in salt marshes: a meta-analysis

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Running title: Salt marsh grazing meta-analysis

Summary

1. The far-reaching impacts of livestock grazing in terrestrial grasslands are widely appreciated, but how livestock affect the structure and functions of sensitive coastal ecosystems has hitherto lacked synthesis. Grazing-induced changes in salt marshes have the potential to alter the provision of valuable ecosystem services, such as coastal protection, blue carbon and biodiversity conservation.

2. To investigate how livestock alter soil, vegetation and faunal properties in salt marshes, we conducted a global meta-analysis of ungulate grazer impacts on commonly measured ecosystem properties (498 individual responses from 89 studies). We also tested stocking density, grazing duration, grazer identity, and continent and vegetation type as potential modifiers of the grazing effect. The majority of studies were conducted in Europe (75) or the Americas (12), and investigated cattle (43) or sheep (22) grazing.

3. All measures of aboveground plant material (height, cover, aboveground biomass, litter) were decreased by grazing, potentially impairing coastal protection through diminished wave attenuation.

4. Soil carbon was reduced by grazing in American, but not European marshes, indicating a trade-off with climate regulation that varies geographically. Additionally, grazing increased soil bulk density, salinity and daytime temperature, and reduced redox potential.

5. Biodiversity responses depended on focal group, with positive effects of grazing on vegetation species richness, but negative effects on invertebrate richness. Grazing reduced the abundance of herbivorous invertebrates, which may affect fish and crustaceans that feed in the marsh. Overall vertebrate abundance was not affected, but there was provisional evidence for increases over a longer duration of grazing, possibly increasing birdwatching and wildfowling opportunities.

6. *Synthesis and applications.* Our results reveal that the use of salt marshes for livestock production affects multiple ecosystem properties, creating trade-offs and synergies with other ecosystem services. Grazing leads to reductions in blue carbon in the Americas but not in Europe. Grazing may compromise coastal protection and the provision of a nursery habitat for fish while creating provisioning and cultural benefits through increased wildfowl abundance. Meanwhile, increases in plant richness are offset by reductions in invertebrate richness. These findings can inform saltmarsh grazing management, based on local context and desired ecosystem services.

***Keywords*:** biodiversity, blue carbon, cattle, coastal protection, ecosystem service trade-offs, grasslands, horses, sheep, soil, vegetation

Introduction

Livestock are grazed in semi-wild rangelands throughout the world. In terrestrial systems, their impacts on biodiversity and ecosystem properties are now well-established (e.g. Tanentzap & Coomes 2012; Alkemade *et al.* 2013; Daskin & Pringle 2016), together with the determinants of these impacts such as grazer density, type and plant composition (O'Rourke & Kramm 2012; McSherry & Ritchie 2013). However, livestock are also widely grazed in salt marshes – halophytic grasslands distributed along the world's wave-sheltered temperate shorelines – which may respond differently due to their distinct soil properties (e.g. higher salinity, lower redox potential), environmental stressors (tidal flooding) and plant communities. Although many empirical studies have measured livestock impacts in salt marshes, a comprehensive synthesis of these studies is currently lacking. Salt marshes are widely recognised for the value of their Ecosystem Services (ES) (Costanza *et al.* 1997; Barbier *et al.* 2011), but have suffered large losses in extent and are subject to multiple anthropogenic threats (Gedan, Silliman & Bertness 2009). As such, it is vital that remaining areas of salt marsh are managed sensitively to maximise their ES value.

The Millennium Ecosystem Assessment categorises ES as provisioning, regulating, cultural and supporting services (MA 2005). Salt marshes yield several provisioning services by supplying pastureland for domestic livestock and habitat for wild foods such as *Salicornia*, wildfowl, fish and crustaceans (Jones *et al.* 2011). Salt marshes also supply regulating services that help mitigate climate change and other anthropogenic impacts: they supply long-term carbon storage known as 'blue carbon' (Mcleod *et al.* 2011), offer coastal protection from extreme weather events (Costanza *et al.* 2008) and filter nutrients and pollutants from terrestrial run-off (Ribeiro & Mucha 2011; Alldred & Baines 2016). The cultural services of salt marshes are many and varied: they attract bird-watchers and walkers, offer artistic inspiration, aesthetic beauty and educational opportunities (Jones *et al.* 2011). Supporting services such as primary production, nutrient cycling, soil formation and biodiversity underly the production of all other services, and the unique characteristics of the salt marsh environment can enhance these services. For example, salt marshes have high primary productivity as they are unshaded and nutrients are replenished through tidal flooding (Mitsch & Gosselink 2000), underpinning their value as grazing land. The anaerobic conditions in salt marsh soils results in less efficient decomposition, maximising their usefulness for long-term carbon storage (Chmura 2009). Additionally, salt marshes provide a unique habitat for wildlife, supporting abundant and diverse biota (BRIG 2008; Wiest *et al.* 2016), from which much of their cultural value is derived.

Livestock pasturage is the most common resource use of salt marshes (Gedan, Silliman & Bertness 2009). European marshes have been grazed by domestic ungulates since pre-historic times (Barr & Bell 2016) and are still widely grazed today (Dijkema 1990), with saltmarsh meat obtaining a higher market value than standard products (Jones *et al.* 2011). However, in some areas, management authorities have excluded livestock for conservation purposes (Bakker, Bos & De Vries 2003). In China, many marshes are intensively grazed (Greenberg *et al.* 2014), as are those in South America, although here too there is pressure to stop grazing within conservation areas (Costa, Iribarne & Farina 2009). In North America, saltmarsh grazing is less common (Yu & Chmura 2010), but at several sites there are concerns over the effects of uncontrolled grazing by feral horse populations (Turner 1988; Taggart 2008).

Large grazers alter the biophysical structures and processes of an environment (ecosystem properties, EPs) via trampling, removal of vegetation, and defecation. These alterations will drive changes in ecosystem functioning, with consequences for the provision of ecosystem services (Haines-Young & Potschin 2010). For example, direct removal of plant material, and direct and indirect effects on biogeochemical cycling can lead to reduced storage of carbon in soils, diminishing the service of climate regulation (Tanentzap & Coomes 2012). These cascading effects enable EPs to be used as indicators for ES provision in the absence of direct measurements of services (Van Oudenhoven *et al.* 2012). A recent synthesis showed livestock grazing affects saltmarsh vegetation properties (He & Silliman 2016). However, equivalent syntheses of grazer effects on belowground properties and faunal biodiversity in salt marshes are missing. To understand how salt marshes and their ES are affected by grazing, it is necessary to analyse a broad range of EPs, and explore how management decisions and other contextual variables will moderate these effects.

Research from terrestrial rangelands has demonstrated that the direction and strength of livestock effects on ecosystem properties is moderated by variables relating to grazing management, such as stocking density and grazer species (Rook *et al.* 2004; Stewart & Pullin 2008; Paz-Kagan *et al.* 2016). Other local contextual variables such as climate, soil type and vegetation can moderate the impact of herbivory (*e.g.* He & Silliman 2016). European and American marshes differ in their soil formation (mainly derived from mineral deposits *vs* mainly derived from organic material, respectively) and vegetation (high diversity *vs* low diversity) characteristics (Cattrijsse & Hampel 2006; Bakker *et al.* 2015), which may cause grazing responses to vary between these continents. European saltmarsh vegetation consists of taxa from diverse lineages, with attendant diversity of traits, which may drive differential responses to grazing, depending on the dominating species. For example, grasses are generally more tolerant of grazing than forbs, due to the location of their growing regions (Briske & Richards, 1995). Similarly, faunal responses may be moderated by trophic level and clade. Herbivorous invertebrates are likely to suffer most strongly from livestock grazing, as they are in direct competition for the plant biomass (Tscharntke 1997). Conversely, grazing wildfowl are likely to benefit, as they favour nutritious, young plant shoots (Lambert 2000).

Here, we conduct a global systematic review and meta-analysis of the effects of ungulate grazers on saltmarsh EPs. We analyse 498 responses from 89 studies to identify significant changes in a suite of soil, vegetation and faunal properties. We hypothesise that these responses are moderated by stocking density, grazing duration, grazer identity, continent, vegetation type and faunal functional group. We show that grazing alters 11 out of the 21 EPs tested, and that grazing effects are dependent upon the nature of grazing, geography and vegetation. We use the observed responses to predict how saltmarsh grazing impacts on ecosystem functioning and service provision.

Materials and methods

STUDY SELECTION AND DATA EXTRACTION

We comprehensively searched published literature using standard techniques (detailed in Supporting Information Appendix S1). For inclusion, studies must have measured an EP on a grazed and ungrazed area of salt marsh. Only ungulate grazers (hereafter 'livestock') were considered. Both observational and experimental studies were included, as were those that replicated the effects of livestock by clipping or trampling.

From the figures, tables and text of each study we extracted grazed and ungrazed means, sample sizes and measures of variance (standard deviation, SD; standard error, SE; 95% confidence intervals, CI) for each EP. The results sections were also scanned for descriptions of changes induced by grazing, even if no mean values were provided. Often, multiple EPs were measured per study, thereby generating multiple grazing outcomes (hereafter referred to as 'entries'). In total, 498 entries for 29 properties were extracted from the 89 included studies (Table S1).

Where possible, study-specific variables were extracted for each entry (detailed fully in Appendix S1). Potential moderating variables relating to grazing management were recorded: stocking density (converted to a common metric of livestock units per hectare, LSU/ha), grazer species and grazing duration (time in years since introduction/removal of grazers). The dominant vegetation in grazed and ungrazed plots was classified as *Spartina*, other graminoids or forbs. Marsh zone and sediment type were also noted, but were not tested as potential moderators due to a lack of data.

DATA ANALYSIS

The data were analysed using three different approaches. (1) A weighted meta-analysis, by inverse of variance (Hedges & Olkin 1985), was used to calculate an overall average effect of grazing for every EP that had mean and variance values from ≥3 separate publications. (2) A coded meta-analysis (Evans, Cherrett & Pemsl 2011) was used to visually summarise all extracted grazing responses, including those that reported only a qualitative description, or reported means without sample size and variances. While only semi-quantitative, due to its inclusiveness, this method provides a wider overview of all studies investigating grazer effects. (3) For all EPs with ≥10 entries, linear regression models were used to investigate potential moderators for their influence on the effect of grazing. To increase sample sizes, these meta-regressions were unweighted, allowing entries without a reported variance to be included.

1. Weighted meta-analysis

For each individual entry, the effect size of grazing treatment was quantified as the log Response Ratio (ln*RR*) of the mean of the grazed group ($\bar{X}_G$) against the mean of the ungrazed group ($\bar{X}_U$)

$$\ln RR = ln\frac{(\bar{X}_G)}{(\bar{X}_U)} \qquad \text{[Eqn. 1]}$$

The variance for each entry was then calculated as

$$Var = \frac{SD_G^2}{N_G\bar{X}_G^2} + \frac{SD_U^2}{N_U\bar{X}_U^2} \qquad \text{[Eqn. 2]}$$

Where SD_G= SD of grazed group, SD_U= SD of ungrazed group, N_G= sample size of grazed group, N_U= sample size of ungrazed group and $SD = \sqrt{N}\times SE$ or $= \sqrt{N}\times\frac{CI}{1.96}$.

When the SD could not be derived from the publication, the variance was estimated as

$$Var_{est.} = \left[\frac{N_G+N_U}{N_G N_U}\right] + \left[\frac{lnRR^2}{2(N_G+N_U)}\right] \text{ (Hedges \& Olkin 1985).} \qquad \text{[Eqn. 3]}$$

For each EP, a random-effects, multilevel linear model was used to combine individual effect sizes to estimate an overall mean effect with 95% CI. Models were fitted with a restricted maximum likelihood (REML) structure using the rma.mv function within the metafor package (Viechtbauer 2010) in R. Study (i.e. publication) nested within Site was included as a random factor to account for non-independence of multiple entries extracted from the same study, and multiple studies conducted at the same site. In addition, we examined funnel plots to assess publication bias (Sterne & Egger 2001).

2. Coded meta-analysis

Entries were coded by the direction and significance of the effect of grazing as causing a statistically significant ($P \leq 0.05$) increase in the EP, an increase, no change, a decrease, or a statistically significant decrease. Entries were coded as no change when the difference between the grazed and ungrazed means was not significant and <2%. *P*-values were not always reported, therefore some changes may be recorded as not significant while actually being statistically significant.

3. Regression analyses

To assess potential moderators of the grazing effect, linear, mixed-effect meta-regressions were conducted to test whether stocking density (LSU/ha), grazing duration (years), grazer identity (sheep; cattle, including water buffalo; mixed species; other), or continent (America;

Europe) had a significant effect on the ln*RR* of that EP. Within European studies only, vegetation type (graminoid-dominant; forb-dominant) was also tested. *Spartina* spp. were excluded from the graminoid category due to physiological differences (C_4 *vs* C_3 photosynthesis; Osborne *et al*. 2014) and habitat preference (*Spartina* are pioneer species found at the seaward edge of European marshes; Bakker *et al.* 2015). There were insufficient European *Spartina* replicates (3 studies) to treat it as a separate category, so this vegetation type was not analysed. Because grazing can alter the plant community composition (de Vlas *et al.* 2013), vegetation type was only included when it was consistent across grazed and ungrazed plots, to allow it to be treated as a predictor of grazing effects, rather than a response to grazing.

There were missing values for each moderator, and frequent collinearity of moderators; as such, each potential moderator was tested for significance in separate models and *P*-values were adjusted for multiple comparisons within that EP using the False Discovery Rate (FDR, Benjamini and Hochberg 1995). Unadjusted *P*-values were also examined, to gain insight into moderators that may potentially be important. All models had Study nested within Site as a random effect. For the EPs of invertebrate abundance and vertebrate abundance, functional group (benthos, detritivore, herbivore, predator; goose, passerine, wader, hare, fish respectively) was included as a random term in each model, to control for varying responses by each group. We also tested functional group as a fixed term in separate models. The majority of studies were conducted at stocking density 0-2.0 LSU/ha, but two studies were conducted at 7.5 and 12 LSU/ha respectively. Similarly, all studies had a duration of 0.1-100 years, except a single study reporting 210 years of grazing. In these cases, models were run with these outliers (>3 SD from the mean) included and excluded, to determine whether this changed the result. Predictions were only conducted using the models that excluded the outliers, so that these unusual observations did not exert undue influence on the outcomes.

Models were fitted with a REML structure using the lmer function within the lme4 package (Bates *et al.* 2015) in R. Visual checks of residual plots were used to confirm model residuals met assumptions of normality and heteroscedasticity (Pardoe 2012). Model predictions were made using the predictInterval command in the merTools package (Knowles & Frederick 2016) with 1000 simulations, for an unspecified Site and Study. This analysis resamples from the normal distribution of the fixed coefficients, incorporating residual variation to simulate new predictions, and returning a mean prediction and 95% prediction intervals (PI). All analyses were performed using R statistical software version 3.1.2 (R Core Team 2014).

Results

The majority of the 89 studies included were conducted in Europe and over 30% originated from a single country – the Netherlands (Fig. 1a). A variety of grazers were investigated: cattle, sheep, horses, deer and water buffalo, with cattle being most common (Fig. 1b). Several manipulative study designs were used (installation of exclosures/enclosures, artificial replication by clipping and trampling, before/after comparison, laboratory study), but over half of the studies were observational (Fig. 1c). The duration of grazing ranged from short-term 4-week exclosure experiments, to observational studies in marshes grazed for over 200 years.

1. WEIGHTED META-ANALYSIS FOR MEAN EFFECTS OF LIVESTOCK GRAZING

We found that livestock grazing affected 11 of the 21 EPs tested, spanning soil, vegetation and faunal response variables (Fig. 2, Table S2). Grazing significantly altered four of seven soil variables: increasing soil bulk density, salinity and daytime temperature, and decreasing redox potential. Mean accretion rate, soil carbon content and pH were all unaffected. Grazing also significantly affected five of seven vegetation responses: increasing species richness while reducing aboveground biomass (AGB), cover, canopy height and litter biomass. There was no effect on belowground biomass (BGB) or plant nitrogen content. Grazing was associated with a significant reduction in invertebrate richness, but did not affect vertebrate or total invertebrate abundance. However, when invertebrate abundance data were analysed by functional group, herbivore abundance was significantly reduced by grazing. The majority of the vertebrate data were extracted from studies on bird abundance (85% of entries) and goose abundance in particular (62%). When goose abundance was analysed separately, the mean effect was positive, but not significant.

The ability to detect reporting bias is limited with smaller sample sizes (Sedgwick 2013), but for most properties, no bias was evident from visual assessment of funnel plots (Fig. S1). The exceptions were redox potential, plant cover and plant richness, all of which indicated bias towards reporting of negative effects in smaller, less precise studies (those with a larger standard error). This indicates that the true effects on redox, cover and plant richness may be more positive than our calculated values. Exclusion of 'artificial replication' entries did not alter the direction or significance of the grazing effect for any EP.

2. CODED META-ANALYSIS OF ALL REPORTED OUTCOMES

Results from the coded meta-analysis demonstrate that most EPs have displayed both positive and negative responses to grazing in different studies (Fig. S2). Generally, the balance of responses support the results produced by the weighted meta-analysis. However, the weighted meta-analysis for accretion (5 entries) showed no significant effect of grazing, whereas the coded meta-analysis reveals that 11 out of a total 13 entries for accretion showed a negative effect of grazing. Additional patterns were revealed for EPs that could not be analysed statistically in the weighted meta-analysis. Grazing had predominantly negative effects on flowering (8 out of 8 entries) and fish richness/abundance (3 out of 3), but had positive effects on stem density (5 out of 6) and hare abundance (2 out of 2). Grazing had generally positive effects on wader abundance (8 out of 12) but negative effects on wader nest survival (3 out of 3).

3. WHAT MODERATES THE EFFECT OF GRAZING?

Regression analyses adjusted for multiple comparisons

Two moderators that significantly influenced the outcome of grazing were highlighted using linear regression analyses with adjusted *P*-values (Table 1). Continent moderated the effect of grazing on soil carbon: grazing is predicted to reduce soil carbon in American marshes but slightly (non-significantly) increase soil carbon in European marshes (Fig. 3a). Stocking density moderated the effect on canopy height: a higher density of livestock more strongly reduced canopy height (Fig. 3b).

Unadjusted analyses

Examination of unadjusted *P*-values allowed the identification of other, potentially important moderators (Table 1), although these results were considered less robust. The effect of grazing management (stocking density, duration and type of grazer) was significant for five EPs (Fig. S3). Increased stocking density reduced soil salinity and aboveground biomass. Increased grazing duration led to increased vertebrate abundance. Additionally, a positive effect of grazing on BGB was stronger for cattle relative to sheep or a mixture of domestic grazers. For the BGB subset of data, the cattle studies were conducted at a lower stocking density than the sheep or mixture studies, so this result could be an artefact of stocking density (although stocking density was not found to be a significant moderator for BGB when analysed directly). Within European studies, the dominant vegetation type was a significant moderator for two EPs (Fig. S4): areas dominated by forbs experienced larger reductions in percentage cover and species richness than areas dominated by graminoids.

Discussion

We have synthesised four decades of individual studies to highlight key saltmarsh properties affected by livestock grazing, including increased plant richness, reduced invertebrate richness and herbivorous invertebrate abundance, reductions in plant material and altered soil conditions. We have also identified previously unappreciated moderating variables that alter the strength or direction of these responses, including an effect of continent on soil carbon and, provisionally, an effect of grazing duration on vertebrate abundance. The findings are applicable to predicting how grazing affects ecosystem functioning and service provision in saltmarsh landscapes (see Fig. 4 for conceptual diagram).

FROM ECOSYSTEM PROPERTIES TO ECOSYSTEM SERVICES

Species richness, soil properties and supporting services

Biodiversity supports many services and high biodiversity appears to promote ecosystem stability and resilience (Seddon *et al.* 2016). Extensive grazing is often used as a management method to maintain grassland diversity, as the removal of plant biomass prevents highly competitive species from becoming dominant (WallisDeVries, Bakker & Van Wieren, 1998). Our results reveal that grazing is generally beneficial to saltmarsh plant richness (Fig. 2). However, biodiversity responses were inconsistent: provisional results indicate that increases in richness are only achieved in graminoid-dominated plots (Fig. S4b). Moreover, the overall increase in plant richness was offset by reductions in invertebrate richness and herbivorous invertebrate abundance (Fig. 2). These results confirm that responses to land management vary among taxa, and plant richness cannot be used as a broad indicator of biodiversity (Hess *et al*. 2006).

Altered soil conditions can drive changes to biotic communities and their functioning, affecting supporting services such as nutrient cycling (Wichern, Wichern & Joergensen 2006; Husson 2013). Soil bulk density, daytime temperature and salinity all increased with grazing, while redox potential decreased (Fig. 2). The increase in bulk density is expected as a direct effect of trampling by large herbivores (Southorn & Cattle 2004; Bell *et al.* 2011) and this leads to decreased oxygen diffusion and more reduced conditions (Husson 2013). An increase in soil temperature is widely reported from other grazed systems (*e.g.* van der Wal, van Lieshout & Loonen 2001) as a result of reduced shading, compacted soil and anaerobic respiration. Increased evaporation from warmer, unshaded soils will lead to the observed increase in salinity. Evidence of how these effects will manifest and interact in salt marshes is lacking, and direct measurements of ecosystem functioning are needed to disentangle their mechanisms. Some studies have begun to address grazer impacts on saltmarsh biogeochemical cycles (*e.g.* Olsen *et al.* 2011; Ford *et al.* 2012; Schrama *et al.* 2013), although there were insufficient data to combine in our meta-analysis.

Soil formation in a salt marsh occurs by accumulation of sediment and plant biomass, and allows marshes to accrete vertically in response to rising sea-levels (Bakker *et al.* 2016; Boyd & Sommerfield 2016). Our analyses revealed that grazers compact the sediment and reduce aboveground biomass, but this did not translate into a significant overall reduction in accretion rates (Fig. 2). This may be because grazer-driven compaction increases the strength of the soil, making it more resistant to erosion (Ghebreiyessus *et al.* 1994). There is also evidence from salt marshes that increased plant richness improves sediment stability (Ford *et al.* 2016). Therefore grazers may directly and indirectly stabilise the marsh surface and protect against lateral and horizontal erosion. However, accretion rates are highly context-dependent, driven by local factors such as sediment input (Bakker *et al.* 2016), which may mask the effects of grazing in some studies. In light of the results of our coded meta-analysis (11 out of 13 entries presented negative results for accretion), we recommend further research on the mechanisms and context-dependency of livestock-impacts, as reduced capacity for vertical accretion could lead to submergence under rising seas with concomitant loss in the provision of all services.

Soil carbon and climate regulation

In salt marshes, the majority of the carbon stock is stored as soil organic carbon (Murray *et al.* 2011), so reductions in aboveground biomass are of limited relevance when assessing this service. Overall, soil carbon content was not affected by livestock grazing. However, our analysis revealed that the impact of grazing varied geographically; grazing was found to reduce soil carbon in American marshes, with no consistent effect in the European studies which dominated the dataset (Fig. 3). A range of factors could be driving this geographical effect. Reductions in plant material are likely to have a stronger impact on soil quality in organogenic American marshes compared to minerogenic European marshes, where sediment supply will have a stronger effect (Bakker *et al.* 2015). Moreover, soils in American marshes may be more easily degraded by livestock due to more frequent flooding and a lower stem density compared to European marshes (Cattrijsse & Hampel 2006). American marshes tend to be dominated by *Spartina* spp., a favoured food plant of livestock (Furbish & Albano 1994), whereas European marshes have a higher floral diversity (Cattrijsse & Hampel 2006), which may confer an increased capacity for grazing resistance (Callaway *et al.* 2005). The aerial extent of American marshes is an order of magnitude higher than that of European marshes (Ouyang & Lee 2014). Therefore a negative impact of grazing on soil carbon has potential consequences for global storage of 'blue carbon'. Comparative studies in American and European *Spartina* marshes are needed to determine the variables and mechanisms driving grazer impacts on soil carbon.

Vegetation and coastal protection

Vegetated coastal regions reduce wave energy more effectively than bare mudflats (Möller *et al.* 1999; Shepard, Crain & Beck 2011), with tall, denser vegetation being most effective (Möller *et al.* 2014; Paul *et al.* 2016). Unsurprisingly, aboveground biomass, canopy height and cover were reduced in the presence of livestock, with a general trend of stronger effects at higher stocking density or duration of grazing (Fig. 3b, Fig. S3) and within forb-dominated plots (Fig. S4a). These alterations could lead to reduced wave attenuation in a grazed salt marsh. However, geomorphological characteristics, such as lateral expanse and slope, contribute significantly to wave height reduction (Shepard *et al.* 2011; van Loon-Steensma & Vellinga 2013). Therefore, the impact of grazing must be considered alongside these known determinants of wave attenuation. Considering the high value of the coastal protection service offered by salt marshes (Costanza *et al.* 2008), it is worthwhile addressing this grazer effects on wave attenuation through direct field measurements, laboratory study and modelling.

Species abundance and provisioning services

Provisional results show that vertebrate abundance (predominantly geese) increased with grazing duration (Fig. S3d), indicating that livestock grazing supports the provision of vertebrate prey for wildfowlers. The benefit of longer-term grazing is probably due to the site-fidelity exhibited by migratory birds (Hestbeck, Nichols, & Malecki 1991). However, there are indications of a trade-off with fish populations, as the three fish studies included in the coded meta-analysis presented negative outcomes of grazing. Decreased herbivorous invertebrate abundance (Fig. 2) reduces food resources for juvenile fish and crustaceans, while decreased cover (Fig. 2) reduces the shelter value of salt marshes (Levin *et al.* 2002;

Colclough *et al.* 2005; Kritzer *et al.* 2016). These effects are likely to be more important in North America than Europe, where marshes are larger and play a greater role as nursery habitat for commercially important fish and crustaceans (reviewed by Cattrijsse & Hampel 2006).

Cultural services

In ES research, cultural services are often undervalued or left out altogether, as they are difficult to quantify and are interlinked with both provisioning and regulating services (Chan *et al.* 2016). The present evidence on how grazing alters EPs nevertheless informs an assessment of cultural services. The provision of optimal wildfowl habitat will promote the conservation of charismatic species and attract birdwatchers (Green & Elmberg 2014). Not all cultural services are likely to benefit from grazing. The presence of livestock may impede access to the marsh, and could alter aesthetic appreciation through changes to floral diversity and abundance (Clay & Daniel 2000; Ryan 2011). Conversely, the livestock themselves can act as a tourist attraction and point of interest (van Zanten *et al.* 2016). Further interdisciplinary research is necessary to assess how appreciation and use of the saltmarsh environment may be enhanced or degraded by the presence of grazers.

EVIDENCE GAPS

These analyses were dominated by European studies. Only one EP (soil carbon) displayed a significantly different response in American marshes. However, there was limited power to detect effects across continents due to the small number of American studies. Additionally, no Australian studies and only one Chinese study were included in this review, despite these countries harbouring a large proportion of the global extent of salt marshes (Ouyang & Lee

2014). Addressing this evidence gap would lead to a more globally representative understanding of livestock grazing impacts in salt marshes.

Due to collinearity of some moderators, and incomplete reporting of study-specific information, we were unable to test for several potentially important moderators (e.g. marsh zone, soil type), nor could we test for interactions between moderators. We did not analyse the effect of plot scale, although this can influence species richness responses in salt marshes (Wanner *et al.* 2014). We were also unable to assess certain services, such as pollution control and water quality regulation - among the most important services provided by salt marshes (Environment Agency 2007) - and recommend that future work investigate how grazing affects bioremediation in salt marshes. We have used ecosystem properties to inform an assessment of livestock impacts on ES provision, but the links between properties, functions and services are not fully understood. Future research to gain a more mechanistic understanding would facilitate quantitative predictions of the impacts of livestock grazing on ES provision.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

We have conducted the first meta-analysis of the above- and below-ground effects of livestock grazing in a salt marsh, identifying key patterns that can be used to inform management and direct future research. Reductions in plant biomass, height and cover will diminish coastal defence through reduced wave attenuation, therefore grazing should be carefully managed in salt marshes fronting coastal structures at risk from storm surges. In general, European marshes can be grazed without compromising their blue carbon value. However, we have presented evidence that grazing may impair carbon storage in American marshes. Species richness responses varied by taxa, therefore managers should not use plant richness as a proxy for overall richness. Grazing management for conservation is particularly important as the biodiversity of a salt marsh underpins many services. Ultimately, considering the high value of saltmarsh ecosystem services, and the widespread use of these marshes for grazing purposes, further research into the nature of trade-offs and synergies between these services, especially in regions outside of Europe, is strongly recommended.

Authors' contributions

KD and JG conceived the ideas and designed methodology; KD collected and analysed the data; JG and MF provided statistical guidance; KD and JG led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Acknowledgements

Financial support was provided by an EU Marie Curie Career Integration Grant (FP7 MC CIG 61893) to JG., a Swansea University scholarship to KD, and the Welsh Government and HEFCW through the Sêr Cymru NRN-LCEE to MS, JG, and MF.

Data accessibility

The data used in this meta-analysis will be archived in figshare.

References

Alkemade, R., Reid, R.S., van den Berg, M., de Leeuw, J. & Jeuken, M. (2013) Assessing the impacts of livestock production on biodiversity in rangeland ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, **110**, 20900–20905.

Alldred, M. & Baines, S.B. (2016) Effects of wetland plants on denitrification rates: a meta-analysis. *Ecological Applications*, **26**, 676–685.

Bakker, J.P., Baas, A.C.W., Bartholdy, J., Jones, L., Ruessink, G. & Temmerman, S. (2016) Environmental Impacts – Coastal Ecosystems. In Quante, M. & Colijn, F. (Eds.), *North Sea Region Climate Change Assessment, Regional Climate Studies* (pp. 275-314). Springer, New York.

Bakker, J.P., Bos, D. & De Vries, Y. (2003) To graze or not to graze: that is the question. In K. Essink, M. van Leeuwe, A. Kellermann & W. Wolff (Eds.), *Proceedings of the 10th International Scientific Wadden Sea Symposium* (pp. 67–88). Ministry of Agriculture, Nature management and Fisheries, The Hague, and Department of Marine Biology, University of Groningen.

Bakker, J.P., Nielsen, K.J., Alberti, J., Chan, F., Hacker, S. D., Iribarne, O.O., Kuijper, D.P.J., Menge, B.A., Schrama, M. & Silliman, B.R. (2015) Bottom-up and top-down interactions in coastal interface systems. In T.C. Hanley & K.J. La Pierre (Eds.) *Trophic Ecology: Bottom-Up and Top-Down Interactions across Aquatic and Terrestrial Systems.* (pp. 157–200). Cambridge University Press, Cambridge.

Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C. & Silliman, B.R. (2011) The value of estuarine and coastal ecosystem services. *Ecological Monographs*, **81**, 169–193.

Barr, K., & Bell, M. (2016) Neolithic and Bronze Age ungulate footprint-tracks of the Severn Estuary: Species, age, identification and the interpretation of husbandry practices. *Environmental Archaeology*. Bates, D., Maechler, M., Bolker, B. & Waler, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, **67**, 1-48.

Bell, L.W., Kirkegaard, J.A., Swan, A., Hunt, J.R., Huth, N.I. & Fettell, N.A. (2011) Impacts of soil damage by grazing livestock on crop productivity. *Soil and Tillage Research*, **113**, 19–29.

Benjamini, Y. & Hochberg, Y. (1995) Controlling the False Discovery Rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B (Methodological)*, **57**, 289–300.

Boyd, B. M., & Sommerfield, C. K. (2016). Marsh accretion and sediment accumulation in a managed tidal wetland complex of Delaware Bay. *Ecological Engineering*, **92**, 37–46. http://doi.org/10.1016/j.ecoleng.2016.03.045

BRIG (ed. Ant Maddock) (2008) *UK Biodiversity Action Plan; Priority habitat descriptions*.

Briske, D.D., & Richards, J.H. (1995) Plant responses to defoliation: A physiological, morphological and demographic evaluation. In D.J. Bedunah & R.E. Sosebee (Eds.), *Wildland plants: Physiological ecology and developmental morphology* (pp. 635–710). Society for Range Management, Denver.Callaway, R.M., Kikodze, D., Chiboshvili, M., & Khetsuriani, L. (2005) Unpalatable plants protect neighbours from grazing and increase plant community diversity. *Ecology*, **86**, 1856–1862.

Cattrijsse, A. & Hampel, H. (2006) European intertidal marshes: A review of their habitat functioning and value for aquatic organisms. *Marine Ecology Progress Series*, **324**, 293–307.

Chan, K.M.A., Balvanera, P., Benessaiah, K., Chapman, M., Díaz, S., Gómez-Baggethun, E., Gould, R., Hannahs, N, Jaz, K., Klain, S., Luck, G.W., Martín-López, B., Muraca, B., Norton, B., Ott, K., Pascual, U., Satterfield, T., Tadaki, M., Taggart, J. & Turner, N. (2016) Opinion: Why protect nature? Rethinking values and the environment. *Proceedings of the National Academy of Sciences*, **113**, 1462–1465.

Chmura, G.L. (2009) Tidal salt marshes. In Laffoley, D. & Grimsditch, G. (Eds.) *The Management of Natural Coastal Carbon Sinks* (pp. 5-11). IUCN, Gland.

Clay, G.R. & Daniel, T.C. (2000) Scenic landscape assessment: the effects of land management jurisdiction on public perception of scenic beauty. *Landscape and Urban Planning*, **49**, 1–13.

Colclough, S., Fonseca, L., Astley, T., Thomas, K. & Watts, W. (2005) Fish utilisation of managed realignments. *Fisheries Management and Ecology*, **12**, 351–360.

Costa, C.S., Iribarne, O.O. & Farina, J.M. (2009) Human impacts and threats to the conservation of South American salt marshes. In B.R. Silliman, E. Grosholz, & M.D. Bertness (Eds.), *Human impacts on salt marshes: A global perspective* (pp. 337–360).University of California Press Ltd, Berkeley and Los Angeles.

Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P. & van den Belt, M. (1997) The value of the world's ecosystem services and natural capital. *Nature*, **387**, 253–260.

Costanza, R., Pérez-Maqueo, O., Martinez, M.L., Sutton, P., Anderson, S.J., & Mulder, K. (2008) The value of coastal wetlands for hurricane protection. *AMBIO: A Journal of the Human Environment*, **37**, 241–248. Daskin, J.H. & Pringle, R.M. (2016) Does primary productivity modulate the indirect effects of large herbivores? A global meta-analysis. *Journal of Animal Ecology*, **85**, 857–868.

de Vlas, J., Mandema, F., Nolte, S., van Klink, R. & Esselink, P. (2013). Nature conservation of salt marshes: The influence of grazing on biodiversity. It Fryske Gea, Olteterp.

Dijkema, K.S. (1990) Salt and brackish marshes around the Baltic Sea and adjacent parts of the North Sea: Their vegetation and management. *Biological Conservation*, **51**, 191–209.

Environment Agency (2007) *Saltmarsh management manual*. Environment Agency, Bristol. Retrieved from http://publications.environment-agency.gov.uk/PDF/SCHO0307BMKH-

E-E.pdf

Evans, L., Cherrett, N., & Pemsl, D. (2011) Assessing the impact of fisheries co-management interventions in developing countries: A meta-analysis. *Journal of Environmental Management*, **92**, 1938–1949.

Ford, H., Garbutt, A., Jones, L., & Jones, D.L. (2012) Methane, carbon dioxide and nitrous oxide fluxes from a temperate salt marsh: Grazing management does not alter Global Warming Potential. *Estuarine, Coastal and Shelf Science*, **113**, 182–191.

Ford, H., Garbutt, A., Ladd, C., Malarkey, J. & Skov, M.W. (2016) Erosion stabilisation linked to plant diversity and environmental context in coastal grasslands. *Journal of Vegetation Science*, doi:10.1111/jvs.12367..

Gedan, K.B., Silliman, B.R. & Bertness, M.D. (2009) Centuries of human-driven change in salt marsh ecosystems. *Annual Review of Marine Science*, **1**, 117–141.

Ghebreiyessus, Y.T., Gantzer, C.J., Alberts, E.E. & Lentz, R.W. (1994). Soil erosion by concentrated flow: shear stress and bulk density. *Transactions of the American Society of Agricultural and Biological Engineers*, **37**, 1791–1797.

Green, A.J. & Elmberg, J. (2014) Ecosystem services provided by waterbirds. *Biological Reviews*, **89**, 105–22.

Greenberg, R., Cardoni, A., Ens, B.J., Gan, X., Isacch, J.P., Koffijberg, K. & Loyn, R. (2014) The distribution and conservation of birds of coastal salt marshes. In B. Maslo & J.L. Lockwood (Eds.), *Coastal Conservation* (pp. 180–212). Cambridge University Press, Cambridge.Haines-Young, R. & Potschin, M. (2010) The links between biodiversity, ecosystem services and human well-being. In D. Raffaelli & C. Frid (Eds.), *Ecosystem Ecology: a new synthesis* (pp. 110–139). Cambridge University Press, Cambridge.

He, Q. & Silliman, B.R. (2016) Consumer control as a common driver of coastal vegetation worldwide. *Ecological Monographs*, **86**, 278–294.

Hedges, L.V. & Olkin, I. (1985) *Statistical methods for meta-analysis*. Academic Press, San Diego.

Hess, G. R., Bartel, R. A., Leidner, A. K., Rosenfeld, K. M., Rubino, M. J., Snider, S. B., & Ricketts, T. H. (2006). Effectiveness of biodiversity indicators varies with extent, grain, and region. *Biological Conservation*, **132**(4), 448–457. http://doi.org/10.1016/j.biocon.2006.04.037

Hestbeck, J.B., Nichols, J.D. & Malecki, R.A. (1991) Estimates of movement and site fidelity using mark-resight data of wintering Canada Geese. *Ecology*, **72**, 523–533.

Husson, O. (2013) Redox potential (Eh) and pH as drivers of soil/plant/microorganism systems: A transdisciplinary overview pointing to integrative opportunities for agronomy. *Plant and Soil*, **362**, 389–417.

Jones, L., Angus, S., Cooper, A., Doody, P., Everard, M., Garbutt, A., Gilchrist, P., Hansom, J., Nicholls, R., Pye, K., Ravenscroft, N., Rees, S., Rhind, P. & Whitehouse, A. (2011) Coastal Margins. In *UK National Ecosystem Assessment Technical Report* (pp. 411–458). UNEP-WCMC, Cambridge.

Knowles, J.E., & Frederick, C. (2016) merTools: Tools for analyzing mixed effect regression models 0.2.1. Retrieved from https://cran.r-project.org/web/packages/merTools/merTools.pdf

Kritzer, J.P., DeLucia, M.B., Greene, E., Shumway, C., Topolski, M.F., Thomas-Blate, J., Chiarella, L.A., Davy, K.B. & Smith, K. (2016) The importance of benthic habitats for coastal fisheries. *BioScience*, **66**, biw014.

Lambert, R. (2000) Practical management of grazed saltmarshes. In B.R. Sherwood, B.G. Gardiner & T. Harris (Eds.), *British Saltmarshes* (pp. 333–340). Forrest Text for The

Linnean Society of London, Ceredigion.

Levin, P.S., Ellis, J., Petrik, R. & Hay, M.E. (2002) Indirect effects of feral horses on estuarine communities. *Conservation Biology*, **16**, 1364–1371.

MA [Millenium Ecosystem Assessment] (2005) *Ecosystems and Human Well-being: Synthesis*. Island Press, Washington, DC.

Mcleod, E., Chmura, G.L., Bouillon, S., Salm, R., Bjork, M., Duarte, C.M., Lovelock, C.E., Schlesinger, W.H. & Silliman, B.R. (2011) A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO2. *Frontiers in Ecology and The Environment*, **9**, 552–560.

McSherry, M.E. & Ritchie, M. E. (2013) Effects of grazing on grassland soil carbon: a global review. *Global Change Biology*, **19**, 1347–1357.

Mitsch, W.J. & Gosselink, J.G. (2000) *Wetlands* (3rd Ed.). John Wiley & Sons, New York.

Möller, I., Kudella, M., Rupprecht, F., Spencer, T., Paul, M., van Wesenbeeck, B.K., Wolters, G., Jensen, K., Bouma, T.J., Miranda-Lange, M. & Schimmels, S. (2014) Wave attenuation over coastal salt marshes under storm surge conditions. *Nature Geoscience*, **7**, 727–731.

Möller, I., Spencer, T., French, J.R., Leggett, D.J. & Dixon, M. (1999) Wave transformation over salt marshes: A field and numerical modelling study from north Norfolk, England. *Estuarine, Coastal and Shelf Science*, **49**, 411–426.

Murray, B. C., Pendleton, L., Jenkins, W. A., & Sifleet, S. (2011). *Green payments for blue carbon: Economic incentives for protecting threatened coastal habitats*. Durham, North Carolina.

O’Rourke, E. & Kramm, N. (2012) High nature value (HNV) farming and the management of upland diversity: A review. *European Countryside*, **4**, 116–133.

Olsen, Y.S., Dausse, A., Garbutt, A., Ford, H., Thomas, D.N. & Jones, D.L. (2011) Cattle grazing drives nitrogen and carbon cycling in a temperate salt marsh. *Soil Biology and Biochemistry*, **43**, 531–541.

Osborne, C.P., Salomaa, A., Kluyver, T., Visser, V., Kellogg, E, Morrone, O., Vorontsova, M.S., Clayton, W.D. & Simpson, D. (2014) A global database of C4 photosynthesis in grasses. *New Phytologist*, **204**, 441–446.

Ouyang, X. & Lee, S.Y. (2014) Updated estimates of carbon accumulation rates in coastal marsh sediments. *Biogeosciences*, **11**, 5057–5071.

Pardoe, I. (2012) *Applied Regression Modeling* (2nd ed.). John Wiley & Sons Inc, New Jersey.

Paul, M., Rupprecht, F., Moller, I., Bouma, T.J., Spencer, T., Kudella, M., Wolters, G., van Wesenbeeck, B.K., Jensen, K., Miranda-Lange, M. & Schimmels, S. (2016) Plant stiffness and biomass as drivers for drag forces under extreme wave loading: A flume study on mimics. *Coastal Engineering*, **117**, 70–78.

Paz-Kagan, T., Ohana-Levi, N., Herrmann, I., Zaady, E., Henkin, Z. & Karnieli, A. (2016) Grazing intensity effects on soil quality: A spatial analysis of a Mediterranean grassland. *Catena*, **146**, 100-110.

R Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Retrieved from http://www.r-project.org/

Ribeiro, H. & Mucha, A. P. (2011) Hydrocarbon degradation potential of salt marsh plant–microorganisms associations. *Biodegradation*, **22**, 729–739.

Rook, A.J., Dumont, B., Isselstein, J., Osoro, K., WallisDeVries, M.F., Parente, G. & Mills, J. (2004) Matching type of livestock to desired biodiversity outcomes in pastures – a review. *Biological Conservation*, **119**, 137–150.

Ryan, J. (2011) Anthoethnography: Emerging research into the culture of flora, aesthetic experience of plants, and the wildflower tourism of the future. *New Scholar*, **1**, 28–40.

Schrama, M., Heijning, P., Bakker, J.P., van Wijnen, H.J., Berg, M.P. & Olff, H. (2013) Herbivore trampling as an alternative pathway for explaining differences in nitrogen mineralization in moist grasslands. *Oecologia*, **172,** 231–243.

Shepard, C.C., Crain, C.M. & Beck, M.W. (2011) The protective role of coastal marshes: a systematic review and meta-analysis. *PloS One*, **6**, e27374.

Southorn, N. & Cattle, S. (2004) The dynamics of soil quality in livestock grazing systems. In *SuperSoil 2004: 3rd Australian and New Zealand Soils Conference, 5-9 December 2004*. University of Sydney, Australia.

Sterne, J.A.C. & Egger, M. (2001) Funnel plots for detecting bias in meta-analysis: Guidelines on choice of axis. *Journal of Clinical Epidemiology*, **54**, 1046–1055. http://doi.org/10.1016/S0895-4356(01)00377-8

Stewart, G.B. & Pullin, A.S. (2008) The relative importance of grazing stock type and grazing intensity for conservation of mesotrophic “old meadow” pasture. *Journal for Nature Conservation*, **16**, 175–185. http://doi.org/10.1016/j.jnc.2008.09.005

Taggart, J.B. (2008) Management of feral horses at the North Carolina National Estuarine Research Reserve. *Natural Areas Journal*, **28**, 187–195.

Tanentzap, A.J. & Coomes, D.A. (2012) Carbon storage in terrestrial ecosystems: do browsing and grazing herbivores matter? *Biological Reviews of the Cambridge Philosophical Society*, **87**, 72–94.

Tscharntke, T. (1997) Vertebrate effects on plant-invertebrate food webs. In A.C. Gange & V.K. Brown (Eds.), *Multitrophic Interactions in Terrestrial Systems* (pp. 277–298). Backwell Science, Oxford.

Turner, M.G. (1988) Simulation and management implications of feral horse grazing on Cumberland Island, Georgia. *Journal of Range Management*, **41**, 441–447.

van der Wal, R., van Lieshout, S.M.J. & Loonen, M.J.J.E. (2001) Herbivore impact on moss depth, soil temperature and arctic plant growth. *Polar Biology*, **24**, 29–32. van Loon-Steensma, J.M. & Vellinga, P. (2013) Trade-offs between biodiversity and flood protection services of coastal salt marshes. *Current Opinion in Environmental Sustainability*, **5**, 320–326.

Van Oudenhoven, A.P.E., Petz, K., Alkemade, R., Hein, L. & De Groot, R.S. (2012) Framework for systematic indicator selection to assess effects of land management on ecosystem services. *Ecological Indicators*, **21**, 110–122.

van Zanten, B.T., Verburg, P.H., Scholte, S.S.K. & Tieskens, K.F. (2016) Using choice modeling to map aesthetic values at a landscape scale: Lessons from a Dutch case study. *Ecological Economics*, **130**, 221–231.

Viechtbauer, W. (2010) Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, **36**, 1–48. Retrieved from http://www.jstatsoft.org/v36/i03/

WallisDeVries, M.F., Bakker, J.P. & Van Wieren, S.E. (Eds.). (1998). *Grazing and conservation management*. Kluwer Academic Publishers, Dordrecht.

Wanner, A., Suchrow, S., Kiehl, K., Meyer, W., Pohlmann, N., Stock, M. & Jensen, K. (2014) Scale matters: Impact of management regime on plant species richness and vegetation type diversity in Wadden Sea salt marshes. *Agriculture, Ecosystems & Environment*, **182,** 69–79.

Wichern, J., Wichern, F. & Joergensen, R.G. (2006) Impact of salinity on soil microbial communities and the decomposition of maize in acidic soils. *Geoderma*, **137**, 100–108.

Wiest, W.A., Correll, M.D., Olsen, B.J., Elphick, C.S., Hodgman, T.P., Curson, D.R. &

Shriver, W.G. (2016) Population estimates for tidal marsh birds of high conservation concern in the northeastern USA from a design-based survey. *The Condor*, **118**, 274–288.

Yu, O.T. & Chmura, G.L. (2010) Soil carbon may be maintained under grazing in a St Lawrence Estuary tidal marsh. *Environmental Conservation*, **36**, 312–320.

Tables and Figures

Table 1. Moderators found to be significant (*P*<0.05) in regression analyses. n(N) = number of entries (number of studies); df, F and *P* show results of ANOVA; FDR-*P* = False Discovery Rate-adjusted *P* value; Marginal R^2 = proportion of variance explained by fixed moderator. FDR-*P* values < 0.05 are highlighted in bold. Moderators: stocking density ('LSU'; livestock units per hectare), duration of grazing at site ('Duration'; years), grazer identity ('Grazer'; artificial, cow, sheep, mixed, other), location of study ('Continent'; America, Europe), dominant vegetation type in European studies ('Vegetation'; forbs, graminoids). Functional group ('FG') was also tested for invertebrate abundance (benthic invertebrate, herbivore, predator, detritivore) and vertebrate abundance (goose, wader). The following EPs were tested but had no significant moderators: bulk density*, redox*†‡, litter biomass*, nitrogen content*†‡, invertebrate abundance* and invertebrate richness. Full results of regression analyses, including conditional R^2 values, model intercepts, estimates and standard errors are given in Table S3

Ecosystem Property	**Moderator**	**n(N)**	**df**	**F**	***P***	**FDR-*P***	**Marginal R^2**
Soil carbon*	Continent	27(16)	1,14.8	9.06	0.009	**0.036**	0.33
Salinity*	LSU	14(7)	1,11.0	5.84	0.034	0.136	0.33
AGB	LSU	18(10)	1,15.4	7.76	0.014	0.070	0.32
BGB*‡	Grazer	14(9)	2,5.9	6.25	0.035	0.105	0.59
Vegetation cover	Vegetation	10(7)	1,3.3	9.87	0.045	0.225	0.21
Canopy height‡	LSU	32(16)	1,22.4	12.91	0.002	**0.008**	0.28
	Duration	24(12)	1,6.6	6.28	0.043	0.086	0.22
Vegetation richness	Vegetation	23(14)	1,21.0	5.05	0.036	0.180	0.19
Vertebrate abundance*	Duration	13(7)	1,6.5	5.79	0.050	0.250	0.22

* Vegetation not tested due to lack of data
† LSU not tested
‡ Continent not tested

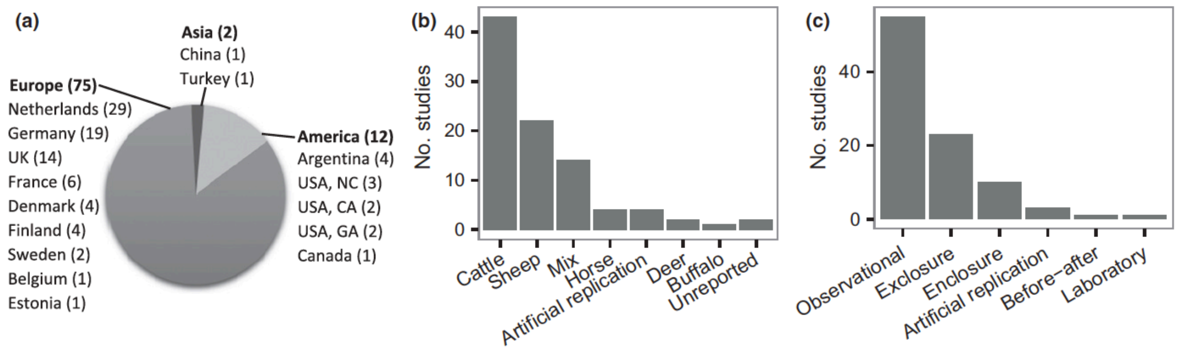

Fig. 1 Breakdown of the 89 studies by a) Continent and country (number of studies in brackets, some European studies encompassed >1 country); b) type of grazer; c) study design.

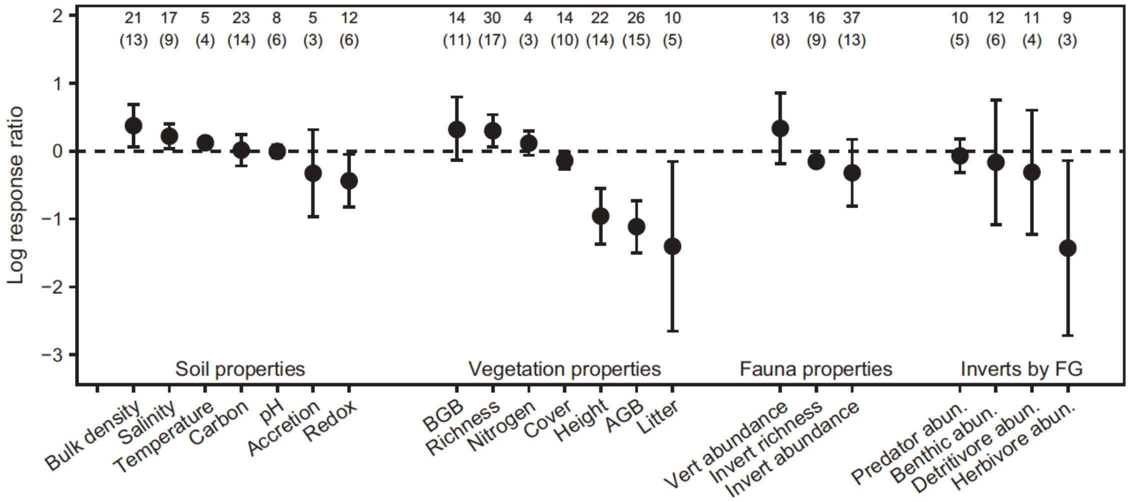

Fig. 2 Weighted meta-analysis. Weighted mean effects (Log Response Ratio, ln*RR*) ±95% confidence intervals of livestock grazing on saltmarsh properties. An ln*RR* >0 indicates a positive effect of grazing on that property, while an ln*RR* <0 indicates a negative effect of grazing. Effects are significant (*P*≤0.05) where confidence intervals do not intercept 0. Numbers above points represent number of entries (number of studies). See Table S2 for statistics.

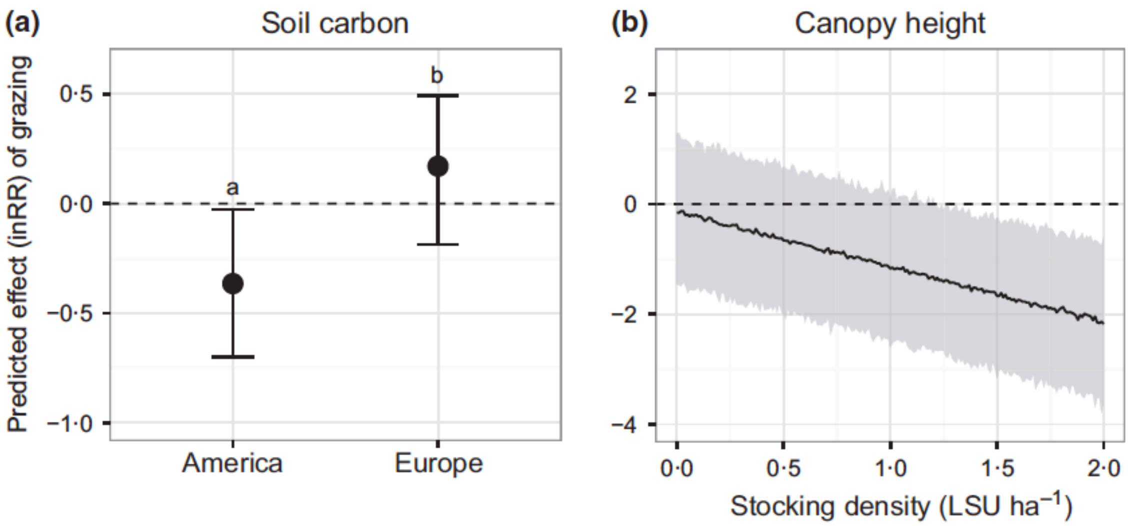

Fig. 3. Regression analyses. Effects of moderators found to be significant in FDR-corrected analyses. Predicted effects of a) Continent and b) stocking density on grazing outcomes, with 95% Prediction Intervals. Different letters indicate categories are significantly different from each other. LSU/ha = livestock units per hectare (see Appendix S1 for calculation).

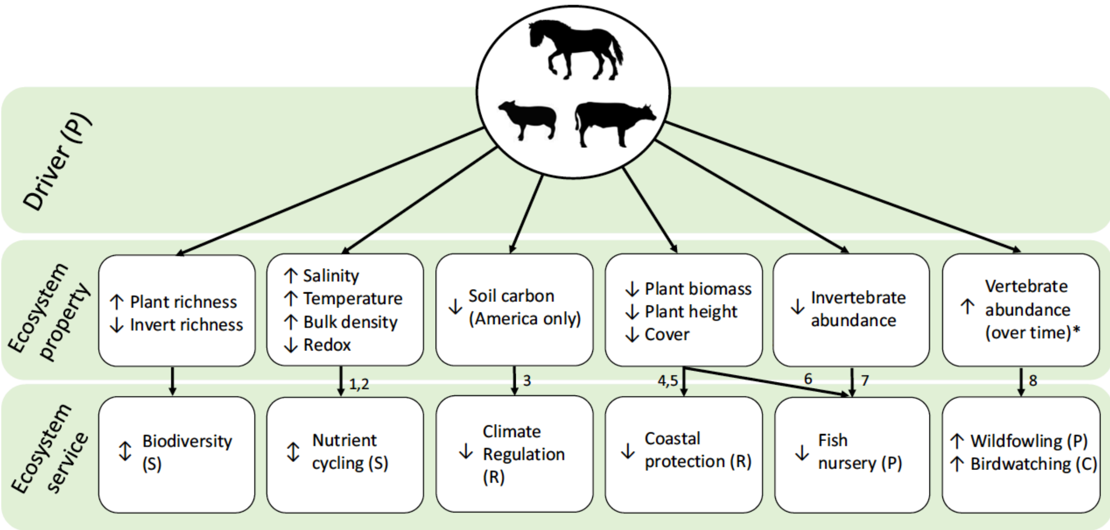

Fig. 4 Conceptual diagram of how changes in ecosystem properties predict ecosystem service provision. Services categorised as supporting (S), regulating (R), provisioning (P) and cultural (C). Examples of studies demonstrating ecosystem property – service link are shown as: [1]Husson 2013; [2]Wichern, Wichern & Joergensen 2006; [3]Mcleod *et al.* 2011; [4]Möller *et al.* 2014; [5]Paul *et al.* 2016; [6]Levin *et al.* 2002; [7]Cattrijsse & Hampel 2006; [8]Green & Elmberg 2014. *This result was not significant after correction for multiple comparisons.