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CONTINENTAL-SCALE IMPACTS OF LIVESTOCK GRAZING ON ECOSYSTEM SUPPORTING AND REGULATING SERVICES

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ABSTRACT

Grazing by livestock supports millions of people worldwide, particularly in drylands, but has marked negative effects on ecosystem services and functions. In Australia, its effects on ecosystem services have not been fully quantified. We examined the extent to which grazing by livestock influenced supporting (productivity, habitat for organisms and biodiversity) and regulating (carbon cycling and hydrological function) services, using data from published and unpublished studies on livestock grazing from a large number of sites across Australia. Grazing reduced our measure of supporting services by about 20% and regulatory services by 8%. On average, grazing reduced plant productivity by 40%, habitat value by 20%, and biodiversity, hydrological function and carbon sequestration by about 10%. Habitat and productivity showed strong declines with increasing grazing intensity, and carbon showed strong declines at the lowest and highest contrasts. Hydrological function and biodiversity did not decline with increasing grazing intensity. Overall, the results indicate that livestock grazing leads to substantial degradation at a continental scale by reducing ecosystem services associated with habitat provision, biodiversity, and soil and water functions. Management of livestock grazing will be critical if we are to retain functional levels of ecosystem services into the next century.

KEY WORDS: grazing; ecosystem services; soil carbon; plant productivity; livestock; herbivory

INTRODUCTION

Rangelands, land used extensively by grazing animals, occupy about half of the land area of the globe and are important for sustaining wildlife and human populations (Friedel *et al.*, 2000). Rangelands provide essential products for humans such as water, timber, a source of medicinal plants and wild relatives of existing plants, as well as social, cultural and recreational opportunities. They also maintain important ecosystem services that are critical for supporting and regulating soil and ecological processes such as hydrological functions (water flow, infiltration and runoff), fixing atmospheric carbon (carbon sequestration), building healthy soils, and providing habitat for plants and animals (Lund, 2007; Petz *et al.,* 2014). Declines in the provision of these services are indicative of declines in the productive potential of the land and are therefore a proxy for land degradation. We define regulating services as those that result from the regulation of ecosystem processes (*sensu* Millennium Ecosystem Assessment (MEA), 2005) and include carbon sequestration and the maintenance of hydrological function. Supporting services are characterised as those required for the production of all ecosystem services, and include primary productivity, habitat for organisms, and the maintenance of a diverse plant and animal community. Globally, rangelands provide significant forage production for native and exotic herbivores, and in developing countries, sustain the grazing of livestock that provide traditional peoples with milk, meat and hide, fuel and fertiliser (dung), security, transportation and the potential to accumulate capital to millions of people (Campos *et al.,* 2016).

Overgrazing by livestock is perhaps the most pervasive and significant degrading processes in rangelands. Consequently, grazing has been referred to as the ‘long shadow’ (Steinfeld *et al.,* 2006). Grazing can be viewed as a combination of two separate but connected processes that relate to herbivore activity: (1) trophic-level effects associated with herbivory and (2) non-trophic, engineering effects associated with changes in the physical structure of plant communities or the soil surface. Livestock grazing reduces plant cover and biomass, and therefore alters plant community structure (Sala *et al.,* 1986). Grazing also has more persistent effects, by altering the structure and function of the soil surface (Cerdà & Lavee, 1999; Eldridge *et al.,* 2011a, 2011b). Trampling by livestock reduces the cover and connectivity of plant, litter and biocrust cover (Daryanto *et al.,* 2013), reduces soil porosity and therefore water flow (Eldridge *et al.,* 2015), and disaggregates soil particles, making the surface more susceptible to wind and water erosion (Tongway *et al.,* 2003; Aubault *et al.,* 2015). Indirect effects of grazing include, but are not limited to, reductions in organic matter decomposition and mineralization (Golluscio *et al.*, 2009), and shifts in structure and therefore habitat for plants and animals (Socher *et al.,* 2013).

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Rangelands face severe challenges, particularly into the next century, partly because of the stresses placed upon them by overgrazing, and these effects will undoubtedly be exacerbated by a changing climate. Increasing temperatures and reductions in the amount and reliability of rainfall will accelerate land degradation and desertification, reduce food and water security, and compromise the capacity of Earth's ecosystems to provide the essential services on which human populations depend (IPCC, 2013). Indeed, the effects of climate change are likely to be most strongly felt in rangelands, particularly drylands, where cultures rely heavily on livestock grazing for their livelihood. Declining levels of primary productivity under a drying climate will place additional stress on rural communities, forcing them into areas that are more marginal for grazing. Thus, understanding and quantifying the effects of livestock grazing on the many ecosystem services provided by rangelands are critical for formulating sustainable management and conservation policies under the influence of changing environments.

Despite the growing body of literature providing evidence that overgrazing compromises ecosystem functions and leads to resource degradation in terrestrial ecosystems, most studies have tended to focus on particular functions or services, generally at a small scale, or in a specific region (Golodets *et al.,* 2011; Hanke *et al.,* 2014; Irisarri *et al.,* 2016; but see Fleischner, 1994; Milchunas & Lauenroth, 1993). We lack, therefore, a synthesis of studies quantifying the simultaneous effects of livestock grazing on multiple supporting and regulating services at the continental scale, although see Petz *et al.* (2014) for a global assessment. This lack of knowledge limits our ability to include land use intensification in ecosystem simulation models, and impedes our ability to manage biotic attributes for the sustainable provision of services and functions on which societies depend.

Herein, we use a synthetic database, derived from published literature of livestock grazing studies across Australia, to quantify the extent to which different intensities of grazing by European livestock lead to a degradation of functions related to plant production, hydrology and the provision of habitat for biota. We use new data from a continental dataset described in Eldridge *et al.* (2016) to focus on the effects of differences in grazing intensity on regulating and supporting ecosystem services. Our aims in this study were twofold: first, to examine and quantify the overall effects of average levels of grazing by domestic (European) livestock on supporting and regulating ecosystem services, and second, to examine the effect of increasing grazing intensity on five specific services that are related to the health or condition of terrestrial ecosystems and therefore their degradation state (carbon sequestration, hydrological function, plant productivity, habitat and biodiversity). Consistent with previous studies focusing on single services at a local scale (Eldridge *et al.,* 2016; Irisarri *et al.,* 2016), we predicted that the magnitude of multiple supporting and regulating services would decline with increasing grazing intensity at a continental scale. Further, we expected that productivity would show the strongest decline with increased grazing intensity, given that the predominant effect of herbivore activity is the removal of plant material.

MATERIAL AND METHODS

Database Construction

We used the ISI Web of Knowledge (www.isiwebofknowledge.com) database (1945–2016 period) and the keywords 'grazing' and 'Australia' to extract data from published and unpublished reports, articles and reviews on the effects of European livestock grazing on plant, soil and animal variables for Australia only. We compiled a database of 7,621 records of an effect of grazing on 294 biotic and abiotic response variables from 224 studies nationwide (Eldridge *et al.,* 2016). Studies were only included if they reported quantitative results of experiments or trials, conducted under natural field conditions, for at least two levels of grazing (see succeeding details). We only included data on response variables that would be affected by livestock. Thus, for example, we did not include data relating to land clearing, agricultural intensification, fertilisation or other agricultural activities that might be associated with grazing enterprises. Data collection was limited to land used for grazing (rangelands) and excluded grazing land where the plant community had been improved or altered (i.e. improved pasture). Large areas of Australia's rangelands are also grazed by variable densities of macropods (kangaroos, *Macropus* spp.). Thus, any livestock grazing in rangelands also includes variable but generally low background populations of free-ranging kangaroos. Our results reported here consider livestock (sheep and cattle) grazing with these background levels.

Many studies reported results for more than one response variables (e.g. plant biomass, plant richness, soil carbon and shrub cover), or the experiment was conducted at more than one independent location. In these cases, for a given response variable or case study, each contrast between any two levels of grazing, provided us with a separate measure of grazing effect size, but each was labelled by the particular study in order to account for the non-independence of measures within a study (see section on Statistical Analyses). We retained all measures from any one study as separate observations in order to ensure that our results were as general as possible (Piñeiro *et al.,* 2013). This approach tends to reduce the overall heterogeneity when estimating effect sizes (see subsequently), excluding multiple results from one data source can underestimate such sizes (Gurevitch & Hedges, 1999). This approach has been applied widely in many previous ecological meta-analyses (Piñeiro *et al.,* 2013).

We partitioned ecosystem services into supporting (biodiversity, plant productivity and habitat for organisms) and regulating (carbon sequestration and hydrological function) services. The attributes comprising our biodiversity category represented ecosystem signatures relating to the number or variety of species within ecosystems. These attributes, which included diversity, richness and abundance of different biota (Table I), are known to be correlated and are

Table I. Attributes used to derive the five ecosystem services

Service		Attribute
Supporting	Biodiversity	Tree, shrub, forb, herb, grass, geophyte, therophyte, moss, lichen, hemicryptophyte richness and abundance;
		Ant, beetle, grasshopper, spider, termite, collembolan and mite richness
		Amphibian and reptile richness and abundance
		Bird, kangaroo and small mammal richness and abundance
	Habitat	Tree, shrub, forb, herb, grass, log, moss, lichen and litter cover
		Patch width, cover, area and complexity; log and coarse woody debris cover
		Shrub height, width and volume; stem diameter; tree hollow density
Regulating	Productivity	Shrub, forb, herb, grass, geophyte and litter biomass
	Carbon	Soil total, labile and organic carbon; microbial carbon; soil organic matter
	Hydrological function	Soil moisture, water holding capacity, infiltration, hydraulic conductivity, sorptivity, time to ponding and runoff, runoff,

The attribute ‘runoff’ was multiplied by −1 to bring it into the same scale as the other attributes.

widely used in studies investigating the impacts of livestock grazing (Landsberg *et al.,* 2003). Habitat variables included plant cover, patchiness, complexity, patch size and area relationships, which are useful predictors of the capacity of landscapes to capture and retain resources (Tongway, 1995; Ludwig *et al.,* 1999). These variables provide a measure of the structure that specific organisms require for habitat (habitat quality, van Klink *et al.,* 2014). The carbon category included total, labile and organic soil carbon, microbial carbon and soil organic matter, and hydrological function comprised measures of soil moisture and water holding capacity, infiltration capacity, and runoff. The log response ratio for runoff was multiplied by −1 to ensure that it was aligned in the same direction as the other hydrological variables, that is, declining runoff equates with greater service. The productivity category was largely a measure of the biomass of vascular plants, and the habitat category comprised measures of vascular and non-vascular plant cover, measures of patch size area and complexity, coarse woody debris and woody plant size.

An important consideration is that our analyses aimed to provide generalisable results that were applicable to different grazing contrasts (i.e. differences between any two different intensities or levels of grazing). We did not expect different variables within each of the specific services to respond similarly to grazing, and have demonstrated this previously (Eldridge *et al.,* 2016). Thus, for example, ant diversity might increase under moderate levels of grazing, whereas reptile diversity might decline under any levels of livestock grazing, and both were included under the category ‘biodiversity’. Thus, we focus on the overall response of each group of services, instead of focusing on one or several group of species that would not be representative of a natural ecosystem. Further, using a log response ratio allowed us to combine different taxa, for example, different biota, within the service biodiversity.

Quantifying Grazer Impacts

From each of the studies, we extracted quantitative and/or qualitative information on grazing intensity used in the study. This allowed us to place grazing intensity into four possible intensity categories: ungrazed, low, moderate or high grazing (see Eldridge *et al.,* 2016 for a more detailed treatment). We adopted the authors’ own assessment of grazing intensity provided in their study because we acknowledge that they were best placed to describe the level of grazing at their particular site. These qualitative judgments of grazing intensity were compared with 3,134 grazing records for which we had both qualitative information provided by the author (e.g. ungrazed, low, moderate or high) and quantitative data (i.e. actual data on the number of livestock grazing in an area, standardised to a common grazing unit; Supporting Information A).

For all of our attributes, we calculated an effect size for all the possible contrasts between the four levels of grazing intensity (ungrazed, low, moderate and high). This resulted in six possible grazing contrasts, that is, ungrazed versus low, ungrazed versus moderate, ungrazed versus high, low versus moderate, low versus high and moderate versus high. The effect size was estimated as the natural logarithm (ln) of the response ratio (RR), that is, $\ln RR = \ln\ (X_L/X_H)$ where X_L is the mean value of the response variable at the lower level of grazing and X_H is that value for the higher level. So, for example, if one study reported total soil carbon levels at ungrazed, low and high levels of grazing, we were able to calculate a log response ratio for total soil carbon for three independent grazing contrasts, that is, ungrazed versus low, ungrazed versus high and low versus high. The log response ratio is negative when the value of a given response variable is lower as a result of a greater level of grazing.

When the mean values of any record were zero (e.g. if the plant cover for an ungrazed record was 10% and that for a heavily grazed comparison 0%), we added to each of these values the minimum value that was likely to be detected with the sampling method used. Thus, the ungrazed record would become 11% and the heavily grazed value 1% (Poore *et al.*, 2012). This allowed us to improve our ability to detect useful effects of grazing on some response variables with infrequent or low values. Examination of funnel plots of effect sizes versus sample size did not indicate any publication biases that would be expected in cases of underreporting of non-significant results with low replication (Møller &

Jennions, 2001). Consistent with several recent meta-analyses (Mooney *et al.,* 2010; Eldridge *et al.,* 2016), we took the conservative approach of not weighting effect sizes by their variance.

Statistical Analyses

We used linear mixed models in R (*lme 4*, Bates *et al.,* 2014) with lnRR as the dependent variable, to examine the average effects of grazing on the two broad service categories (i.e. supporting *vs.* regulating) and on individual services (productivity, habitat, biodiversity, hydrological function and soil carbon), and their interactions. The significance of these models was tested with likelihood ratio tests. Estimates of lnRR were derived from restricted maximum likelihood and 95% confidence intervals for the estimates obtained from the likelihood profile.

We then tested the effects of increasing intensities of grazing on lnRR using low, moderate and heavy levels of grazing compared with ungrazed (six possible grazing contrasts) on the two broad service categories using linear mixed models with grazer contrasts as fixed factors and an individual study as a random factor. Thus, a greater grazing contrast corresponds to a larger difference in grazing intensity. Note that in plotting our results, we arranged the six grazing contrasts from the smallest contrast (ungrazed to low grazing) to the greatest contrast (ungrazed to heavy grazing) with intermediate contrasts (e.g. low to medium grazing) ordered in what we believe to be a logical sequence of increasing grazing (Eldridge *et al.,* 2016). Changing the order of these intermediate contrasts did not result in any substantial changes in the results shown here. Finally, for each of the five separate services, we examined the magnitude of potential grazing effects using linear mixed models with grazing contrast fixed and study a random factor.

RESULTS

Across all grazing contrasts, the log response ratios for both supporting and regulatory service categories were always < zero (Figure 1a). On average, the supporting service category was reduced by about 20% and the regulatory category by 8%. There were significant differences between the two service types ($F_{1,1464} = 57 \cdot 33$, $P < 0 \cdot 001$) and among the five individual services ($F_{4,1461} = 34 \cdot 22$, $P < 0 \cdot 001$). For these individual services, grazing resulted in a significant difference among the three supporting services, but there was little difference between the two regulating services. Thus, on average, grazing resulted in reductions of 40% for productivity, 20% for habitat, and 10% for biodiversity, water and carbon (Figure 1b).

When we examined the effects of increasing grazing pressure on the two supporting and regulatory service categories, two trends emerged: (1) a consistent decline in supporting services with increasing grazing contrast ($F_{5,1202} = 20 \cdot 71$, $P < 0 \cdot 001$; Figure 2a), and (2) a unimodal response by regulatory services that manifest itself as substantial declines at the lowest and highest contrasts, but no significant effect at intermediate grazing contrasts ($F_{5,255} = 5 \cdot 48$, $P = 0 \cdot 001$; Figure 2b). Examination of individual services revealed a range of responses. The provision of habitat and productivity showed strong declines with increasing grazing intensity, water and biodiversity did not decline, and carbon showed strong declines at the lowest and highest contrasts (Figure 3).

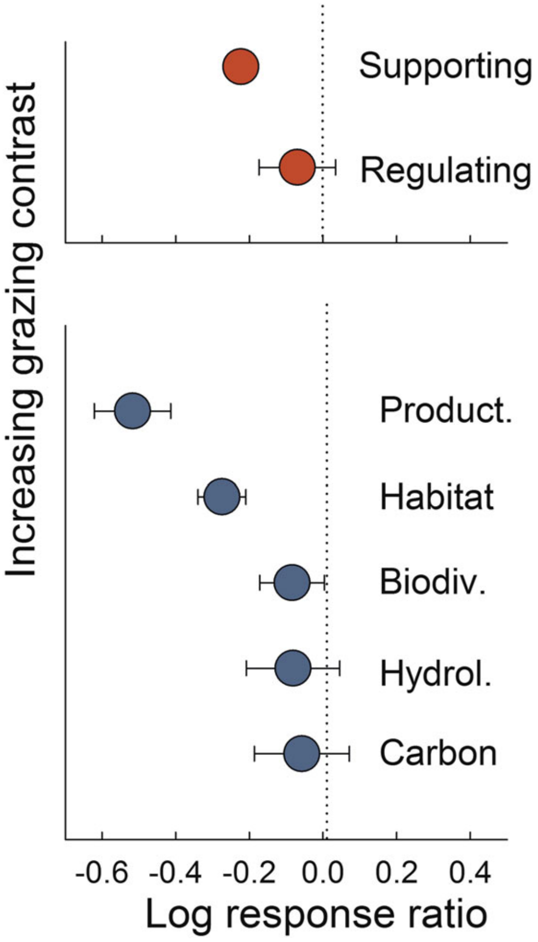

Figure 1. Estimates (±95% CI) of the log response ratio for (a) the two different types of services (Supporting: $n = 2{,}617$; Regulating: $n = 506$), and (b) productivity ($n = 365$), habitat ($n = 1{,}016$), biodiversity ($n = 1{,}236$), hydrology ($n = 365$) and carbon ($n = 203$). The number of independent observations are given in parentheses. [Colour figure can be viewed at wileyonlinelibrary.com]

DISCUSSION

Livestock Grazing Reduces Ecosystem Supporting and Regulating Services

Using a database of 7,621 records from across Australia, we provide strong evidence that, across a broad range of environments, climatic areas and plant communities, average levels of grazing reduce both regulatory and supporting services, which are critical for human well-being. In particular, we quantify for the first time, for a large area of Australia, the greater decline in supporting services (20%) than regulatory services (8%) for a continent with a short evolutionary history of grazing. This decline suggests to us that the

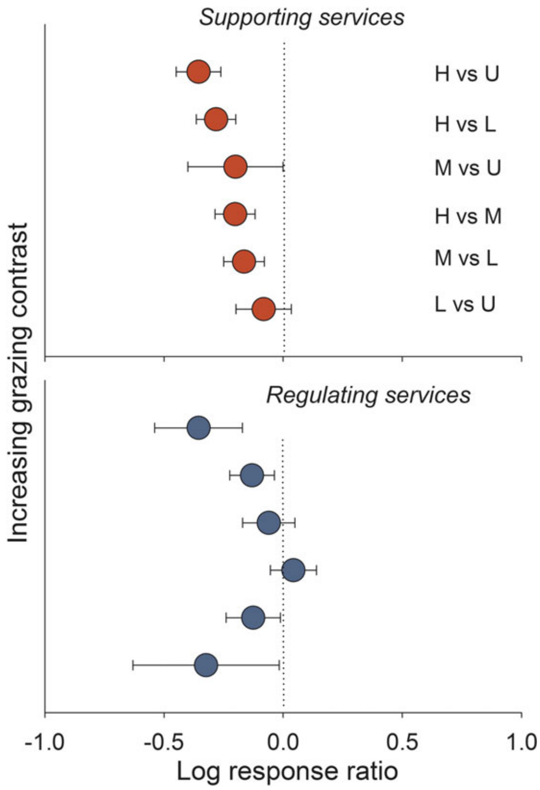

Figure 2. Estimates (±95% CI) of the log response ratio for (a) the three supporting services (productivity, habitat and biodiversity) and (b) the two regulating services (water and carbon) for each of the six grazing contrasts. Within a panel, the magnitude of the grazing contrast increases from L versus U (small contrast) to H versus U (large contrast). [Colour figure can be viewed at wileyonlinelibrary.com]

services provided by ecosystems and their ability to function are more susceptible to the effects of grazing by livestock than changes in ecosystem structure. This knowledge is of paramount importance for formulating sustainable management and conservation policies under changing environments.

The clearest outcome of our study was that two specific services, groundstorey plant productivity and the provision of habitat for organisms, were not only suppressed by grazing but also declined markedly with increasing grazing intensities at all but the lowest grazing contrasts. Consumption and removal of plant material is the most apparent impact of grazing (Lunt *et al.,* 2012; Irisarri *et al.,* 2016; Petz *et al.,* 2014), and the extent to which herbivores remove plant material varies greatly among herbivore type, plant community and season. In our study, 78% of the 365 comparisons of an effect of grazing on plant biomass were negative, consistent with the notion that grazing reduces plant productivity (Dorrough *et al.,* 2004) and with results of global meta-analyses (Milchunas & Lauenroth, 1993) and modelling (Petz *et al.,* 2014). The remaining 82 (22%) positive records were from studies across a wide range of rainfall classes; thus regional productivity cannot explain the negative log response ratios we detected (*sensu* Milchunas & Lauenroth, 1993; Lezama *et al.,* 2014). Similarly, community type varied across these sites, from

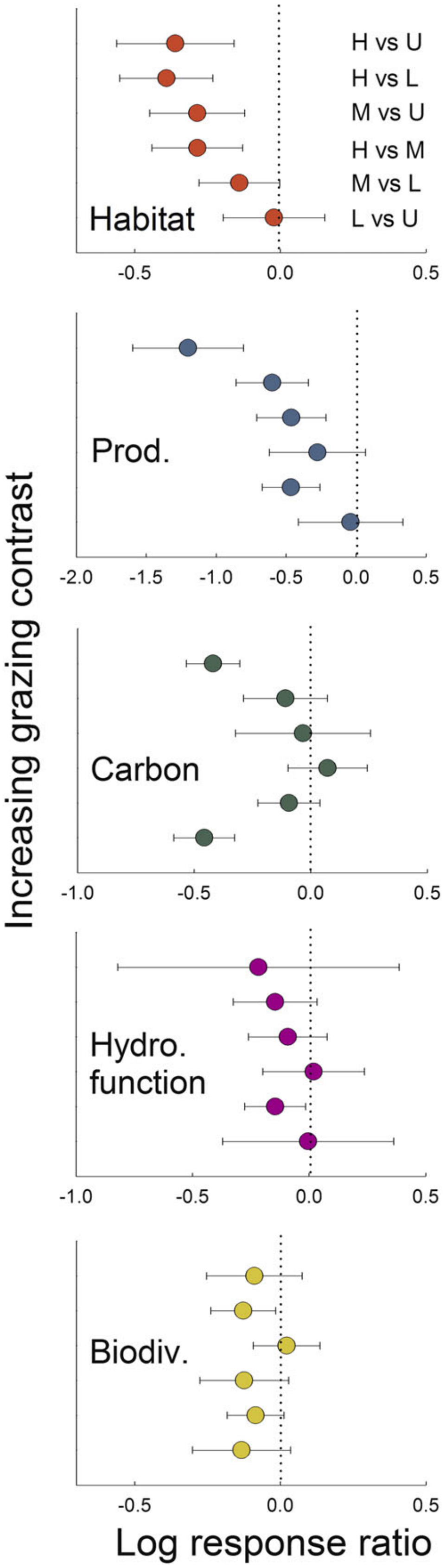

Figure 3. Estimates (±95% CI) of the log response ratio for habitat, productivity, carbon, hydrological function and biodiversity in relation to the six grazing contrasts. Within a panel, the magnitude of the grazing contrast increases from L versus U (small contrast) to H versus U (large contrast). [Colour figure can be viewed at wileyonlinelibrary.com]

perennial and annual grass dominant, to forbfields and shrublands. We cannot ascribe declines, therefore, to structural shifts from perennial grassland to annual forbs or shrubland (Williams, 1969; Eldridge *et al.,* 2011a).

Our records show that most studies used year-round grazing (set stocking), a management practice whereby livestock remain in fixed paddocks over long periods, thereby suppressing plant selectivity and resulting in substantial spatial differences in grazing. Changes in aboveground biomass in response to grazing will depend on plant functional type and plant species, seasonal and environmental conditions, so different grazing effects would be expected for a given level of grazing intensity. Despite this, the average effect of grazing was negative, and this effect was particularly apparent at the most extreme grazing contrast (Figure 3b). This apparent grazing threshold in aboveground biomass is not unexpected, and consistent with results for soil chemistry and plant productivity under very heavy levels of grazing close to livestock watering points in Australia (Andrew, 1988).

Livestock Grazing Effects on Individual Supporting Services: Productivity, Habitat and Biodiversity

Grazing reduced productivity by 40%, habitat by 20% and biodiversity by 10%. Consistent with the literature (Sliwinski & Koper, 2015), our data showed that the relationship between grazing contrast and productivity was closely aligned with that of habitat value (Figure 3). This is not unexpected, given that grazing reduces leaf area, and plant height, basal area (Sala *et al.,* 1986) and vigour (Clary & Leininger, 2000), attributes that provide food and shelter for a range of plant specialists such butterflies and grasshoppers (Kruess & Tscharntke, 2002; Ludwig *et al.,* 1999). Grazing is also associated with a change from erect to prostrate plant growth forms (Dumont *et al.,* 2007), which reduces surface heterogeneity (Sliwinski & Koper, 2015). Grazing has also been shown to reduce litter cover and depth (Fleischner, 1994) and soil surface roughness (Daryanto *et al.,* 2013), and therefore habitat for small mammals, ground-dwelling reptiles and macroinvertebrates (Read, 2002). Removal of shrubs by cattle has been shown to reduce bird diversity (Taylor, 1986), and increasing structure such as fallen branches, grass hummocks and shrubs has been shown to maintain or enhance reptile richness (Fischer *et al.,* 2004).

The log response ratios for our ‘habitat’ service were consistently negative across grazing contrasts, yet those for biodiversity were generally equivocal, questioning the notion that habitat is a good predictor of biodiversity. Our ‘biodiversity’ service included a range of taxa as diverse as Collembola, lichens, reptiles, plants and birds (Table I). Despite this, we still found, on average, a slight suppression of biodiversity (~10%) under grazing. Our inability to undertake separate analyses of specific groups of taxa (perennial grasses, ground-dwelling reptiles, grassland birds and beetles) due largely to insufficient data in the literature, likely accounts for the lack of a strong effect of increased grazing on our log response ratio, at least at low levels of grazing intensities. The effects of grazing on different taxa will vary, depending on their idiosyncratic habitat requirements, intensity of grazing and the specific ecosystem effects created by herbivores (e.g. herbivory effects cf. indirect, surface engineering/disturbance effects). Thus, any one configuration of habitat, structure or resource availability is unlikely to be optimal for every component of such a broad group.

Declines in some taxa, therefore, are likely to be compensated by increases in others, at least under low to moderate levels of grazing. For example, grazing-induced increases in dominant Dolichorine ants have been shown to buffer any reductions in grazing-sensitive species, resulting in no changes in richness (Nash *et al.,* 2004). Similarly, in chenopod shrublands, overgrazing leads to a loss of perennial shrubs (*Atriplex vesicaria*), but increases annuals, ephemerals and perennial grasses, with no net change in richness or diversity, but some declines in pastoral production (Wilson *et al.,* 1982). Largely for this reason, grazing-induced disturbance has been shown to be a poor predictor of biodiversity (Whitford *et al.,* 1999), particularly at low levels of grazing intensity (Petz *et al.,* 2014). Thus, declines in biodiversity with increased grazing intensity will only occur when the arrival of new taxa that are more suited to altered environmental conditions compensates for those taxa that are lost as a result of increased grazing. Extremely high levels of grazing reduce ecosystem structure and function, so we would expect the net effect of grazing to be strongly negative. That the log response ratio for the highest grazing contrast was not different from zero suggests that species replacement is still occurring, despite the high levels of grazing.

Livestock Grazing Effects on Carbon sequestration

Much has been written about the effects of grazing on soil carbon, and most studies have demonstrated either no effects (Shrestha & Stahl, 2008) or strong declines with grazing (Teague *et al.,* 2011; Steffens *et al.,* 2008). However, recent meta-analyses have shown that herbivore effects are highly context dependent, and likely to depend on precipitation, C_3/C_4 balance and soil texture (McSherry & Ritchie, 2013). Contrary to the linear decrease in ecosystem supporting services with increasing grazing intensity (from low to high), we found that the effect of increasing grazing on regulatory services was strongly unimodal, with strong negative effects at low and high grazing contrasts, but neutral effects at the three intermediate contrasts. There is some suggestion in our work that, compared with no grazing, moderate grazing intensity might improve regulatory services. For example, Stavi *et al.* (2015) showed that moderate levels of grazing led to increased water and entrained sediment retention at the patch scale, largely through the fragmentation of livestock trampling routes (tracks), thereby reducing runoff and resource loss. In our study, however, we found no effect of grazing on hydrological function, and the trend was due almost entirely to soil carbon. Furthermore, the strong negative values of the log response ratio for the low compared with ungrazed contrast came from five studies, across a range of rainfalls, aridity zones and management types. Our study emphasises the no linear relationship between grazing intensity and land degradation that is apparent in our results for soil organic carbon.

Declines in carbon at low grazing contrasts could be due to the breakdown and loss of volatile and labile forms of carbon, which are susceptible to soil disturbance at even very low levels of grazing. Microbial biomass and labile carbon respond more rapidly to changes in management than total soil carbon (Carter, 1986; Weil *et al.,* 2003) and are therefore likely to be more sensitive to management (Holt, 1997). For example, Holt (1997) showed that microbial biomass carbon, and enzymes associated with the mineralization of nitrogen, declined substantially from a functional system under very low grazing to heavily grazed, subtropical woodlands in northern Australia. Similarly, Northup *et al.* (1999) showed that organic carbon, soil organic matter and soil microbial biomass carbon were reduced at even very low levels of grazing. Combined with even low levels of kangaroo grazing, small increases in cattle grazing can have negative effects on plant and litter cover, and therefore reduce microbial activity (Northup *et al.,* 1999). Increasing levels of grazing could also increase soil carbon by increasing the proportion of net primary productivity allocated to the roots, which have a larger effect on soil carbon than aboveground tissue, particularly in semi-arid environments (Piñeiro *et al.,* 2010). With increasing grazing contrast, therefore, we expect that declines in labile carbon will be offset by increases in the contribution from dung and urine, as well as increases in root-derived carbon. Together, these effects likely partially compensate for the loss of more labile forms of carbon. At high levels of grazing, however, declines in ecosystem structure associated with the removal of vegetation cover, soil destabilisation and erosion are likely to lead to substantial reductions in total carbon.

Our results suggest that average levels of livestock grazing will lead to greater ecosystem degradation, because of reductions in both supporting and regulating services at a continental scale, particularly ecosystem productivity and habitat value. Furthermore, ecosystem services are likely to decline substantially as the level of grazing intensity increases beyond low to moderate. While we have not attempted to prescribe threshold levels of grazing that coincide with marked changes in services, our data suggest that carrying capacities above about 1, 5 and 6 dry sheep equivalents ha^{-1}, for arid/semi-arid, sub-humid and humid, respectively (Eldridge *et al.,* 2016), will lead to consistent steady declines in supporting services (i.e. habitat value and productivity), and to a lesser extent, in regulating services (i.e. carbon sequestration and hydrological function).

CONCLUSIONS

Balancing the management of a productive, cost-effective grazing enterprise with the need to maintain critical supporting and regulating functions is clearly a major challenge for land managers. While our results are applicable to other systems that have a relatively short evolutionary history of grazing, the implications may differ for systems with a longer history of ungulate grazing or where grazing has differential effects on processes such as shrub encroachment (Maestre *et al.,* 2009; Eldridge *et al.,* 2011a). Nevertheless, the effects of overgrazing are likely to be more far reaching than those outlined here. Overgrazing is likely to prolong and exacerbate the negative effects of climate change on carbon sequestration, productivity and hydrological function, with flow on effects to habitat value and biodiversity. Managing any changes resulting from overgrazing will be a challenge for governments if we are to sustain healthy, productive ecosystems with functioning biota and hydrological processes in the face of an ever drying environment.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web site:

Table S1. Dry sheep equivalent (DSE) values for different herbivores.

Figure S1. Relationship between the assessed grazing rate for those studies reporting both a categorical level of grazing (i.e. ungrazed, low, moderate or heavy) and a numerical rate e.g. sheep per hectare. The numerical grazing rate has been standardized to DSEs (dry sheep equivalents).