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Do grazing intensity and herbivore type affect soil health? Insights from a semi-arid productivity gradient

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Summary

1. Grazing is one of the most widespread forms of intensive management on Earth and is linked to reductions in soil health. However, little is known about the relative influence of herbivore type, herbivore intensity and site productivity on soil health. This lack of knowledge reduces our capacity to manage landscapes where grazing is a major land use.

2. We used structural equation modelling to assess the effects of recent (cattle, sheep, goats, kangaroos and rabbit dung) and historic (cattle, sheep/goat livestock tracks) herbivore activity on soil health at 451 sites across 0·5 M km^2 of eastern Australia. We assessed the direct and indirect effects of increasing herbivore intensity, using dung and livestock tracks, on 15 morphological, physical and chemical attributes that are indicative of soil health, and we used these attributes to derive three indices representing the capacity of the soil to maintain its structural integrity (stability), cycle nutrients (nutrients) and maintain water flow (infiltration).

3. Grazing had negative effects on the three soil health indices, but these effects varied with productivity. Grazing intensity was associated with strong reductions in the stability and nutrient indices under low productivity, but these effects diminished with increasing productivity. Herbivore effects on individual attributes varied in relation to productivity level and were strongly herbivore specific, with most due to cattle grazing, and to a lesser extent, sheep, goats and rabbits. Few effects due to kangaroos or historic grazing by livestock were observed.

4. *Synthesis and applications*. Our study shows that livestock and rabbits degrade soil health through grazing, and its effects are strongest under low or moderate productivity; however, kangaroo effects are benign. Our findings support calls for resource management agencies to consider site productivity, as well as herbivore type and intensity, when developing strategies to manage grazing by livestock, and feral and native herbivores.

Key-words: drylands, grazing, healthy soils, herbivore activity, kangaroo, livestock, productivity, rabbits, soil condition, soil nutrients

Introduction

Soil health is an essential component of human and environmental well-being and is defined as ‘the continued capacity of soil to function as a vital living system, within ecosystem and land-use boundaries, to sustain biological productivity, promote the quality of air and water environments, and maintain plant, animal, and human health’ (Pankhurst, Doube & Gupta 1997). Maintaining soil health is critical to support a growing global human population and the increased demand for food and fibre placed on a diminishing area of productive land (Lambin & Meyfroidt 2011). This is particularly true for drylands (i.e. arid, semi-arid and dry-subhumid ecosystems)

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because soils are generally shallow, contain low levels of nutrients and support generally sparse, patchily distributed vegetation that provides only limited protection against erosion (Ludwig *et al.* 2007). Drylands occupy 40% of the terrestrial land surface and sustain 38% of its human populations (Millennium Ecosystem Assessment (Program) 2005), so the loss of soil productive potential is likely to be one of the most pressing issues facing humans in these environments. Recent studies indicate that almost half of Earth's dryland soils are degraded due to overgrazing and deforestation, resulting in substantial wind and water erosion, soil structure decline, loss of topsoil and desertification (UNCCD 2015). This is likely to be exacerbated by the fact that drylands will be one of the biomes most susceptible to changing climates (Delgado-Baquerizo *et al.* 2013). The most recent climate forecasts indicate that the global extent of drylands may increase by up to 23% by the end of this century (Huang *et al.* 2016). Thus, understanding grazing-related mechanisms driving soil health in drylands is critically important for the sustainable management of ecosystem services on which human well-being depends.

Livestock grazing is known to reduce plant cover and biomass and to directly alter plant community structure by removing plant material (Jones 2000). We interpret 'grazing' as the synthesis of the two separate but related processes of (i) herbivory and (ii) trampling, which is associated with changes in the soil physical environment. Trampling by livestock reduces the cover and connectivity of plant, litter and biocrusts (Daryanto, Eldridge & Wang 2013); alters soil structure; and reduces function by reducing soil porosity and water flow (Eldridge, Beecham & Grace 2015), making the surface more susceptible to wind and water erosion (Tongway, Sparrow & Friedel 2003; Aubault *et al.* 2015). The physical effects of grazing have negative feedback effects on processes such as organic matter decomposition and mineralization, soil nutrient pools (Golluscio *et al.* 2009), and they have been shown to alter habitat for soil fauna, with major flow-on effects to plants (Whitford 1996). Despite the plethora of studies of the effects of grazing on soil health and ecosystem functioning (e.g. Neff *et al.* 2005; Cardoso *et al.* 2013), we still lack a comprehensive understanding of the main grazing drivers controlling soil health.

Herein, we evaluated the effects of recent grazing intensity by different herbivore types: cattle (*Bos taurus*), sheep/goats (*Ovis aries*/*Capra hircus*), kangaroos (*Macropus* spp.) and the European rabbit (*Oryctolagus cuniculus*) and historic grazing by cattle, and sheep/goats on soil health along a gradient in net primary productivity (NPP). Although the effects of livestock on soil health have been widely studied (e.g. Fleischner 1994; Jones 2000; Golluscio *et al.* 2009; Eldridge, Greene & Dean 2011), relatively little is known about how grazing by kangaroos or rabbits, the predominant free-ranging herbivores in eastern Australia, might influence specific measures of soil health (e.g. surface morphology) or indices derived from these measures. First, kangaroo effects on soils might be expected to be more benign than those of livestock because kangaroos graze in smaller groups, are not hard-hooved and therefore exert a lower pressure on the surface (Noble & Tongway 1986), are unconstrained by fencing, and importantly, unlike European livestock, have coevolved with vegetation and soils. We expected, therefore, that increasing intensity of livestock (cattle, sheep/goats) grazing would be associated with declines in measures of soil health, but that increased grazing by kangaroos would have minimal effects. Second, we predicted that rabbits would have marked negative effects on surface soils through their digging and removal of biocrust surface (Eldridge & Koen 2008). Third, we examined whether the grazing intensity effect was consistent across levels of NPP. Consistent with previous data (e.g. Lunt *et al.* 2007), we predicted that grazing intensity effects would be more pronounced under low than high productivity (e.g. Lezama *et al.* 2014).

To test our hypotheses, we examined the effect of increasing grazing intensity by livestock, kangaroos and rabbits, using the mass of dung and density of livestock tracks, on a suite of soil health attributes, and three derived indices, at 451 sites along a gradient in NPP. We used a systems-based approach to explore potential direct effects of grazing and the indirect effects, via plant cover and soil texture, on soil physical, chemical and morphological attributes, separately, and then used them to derive three indices of soil health based on the capacity of the soil to cycle nutrients, resist breakdown and therefore resist erosion, and maintain hydrological processes (Tongway 1995). These attributes and indices (e.g. soil surface condition index; Tongway 1995) are increasingly being used to assess changes in soil health in drylands (Tongway 1995; Ata Rezaei, Arzani & Tongway 2006; Maestre & Puche 2009). Our systems-based, *a priori* model (see Appendix S1, Supporting Information) also considered: (i) components unaffected by grazing but known to affect soil health (aridity, soil texture, NPP) and (ii) components that either directly or indirectly affect soil health (shrub cover, groundstorey cover). Understanding the effects of different herbivores on soil health is important if we are to improve our prediction of the effects of grazing on ecosystems and be able to develop protocols to use as early warning indicators of grazing-induced degradation.

Materials and methods

STUDY AREA

Our study was conducted at 451 sites across a large area (0·5 M km^2) of eastern Australia spanning about 900 km from east-central New South Wales (NSW) to southern and southwestern NSW. Our sites were selected to capture three markedly different vegetation communities classified as semi-arid woodland. The three communities are used extensively for livestock grazing, with smaller areas for conservation (national parks) and forestry.

Across this gradient, the climate is Mediterranean and typically semi-arid (Aridity Index, AI = 0·26–0·39; see Net primary productivity and aridity), with slightly more rainfall during the six warmer months in the east-central and during the cooler months in the south and southwest. Average rainfall (385–460 mm year^{-1}) and average temperatures (~18 °C) varied little across the sites.

The three different communities were dominated by blackbox (*Eucalyptus largiflorens* F.Muell.), white cypress pine (*Callitris glaucophylla* F.Muell.) or river red gum (*Eucalyptus camaldulensis* Dehnh.) and corresponded to low, moderate and high productivity, respectively. The least productive blackbox sites occurred on upper level floodplains that receive floodwater infrequently (10–40 years; Smith & Smith 2014). The soils are relatively deep, with a high proportion of fine sediments (silt + clay; Eldridge, Koen & Harrison 2007; Appendix S2). The soil surfaces support a moderate cover of biocrusts (biological soil crust) depending on disturbance history (Eldridge, Koen & Harrison 2007). Sites under high productivity (river red gum) occur as inland riverine forests on the lower terraces of major western river systems (Murray, Murrumbidgee and Lachlan Rivers). These systems receive supplementary moisture from floodwaters every 2–15 years, have very deep, relatively uniform soil profiles and have the highest levels of fine sediments along the gradient (Appendix S2). Sites at intermediate positions in the productivity gradient (cypress pine) occur on slightly undulating plains where moisture is derived entirely from rainfall. The soils have gradational soil profiles derived from Quaternary colluvium and aeolian material, with low levels of carbon (C), nitrogen (N) and phosphorus (P) restricted to the uppermost soil layers. Undisturbed soils are often support a dense cover of biocrusts.

SITE ESTABLISHMENT

For each community, we chose 150 sites (151 in cypress pine) based initially on distance from water as a stratification process. Distance from permanent water has been shown to be a useful surrogate of grazing intensity (Fensham & Fairfax 1988). Sites were first identified using Arc GIS and pre-inspected to ensure that they were more than 250 m from any track or road. In order to sample across a full spectrum of grazing intensities, we selected some low intensity and long ungrazed sites from conservation reserves, road verges with intermittent grazing, commercial forests, conservation reserves and long-term grazing exclosures. Only two sites were ungrazed by any herbivores (Appendix S3).

SITE ASSESSMENT AND GRAZING INTENSITY

Each site comprised a 200-m-long transect running perpendicular to the nearest livestock watering point, which was generally an earthen dam. Along this transect, we positioned five 25 m^2 (5 m × 5 m) plots every 50 m, within which we centrally located a smaller (0·5 m × 0·5 m) quadrat ('small quadrat'). We assessed the cover of groundstorey plants and shrubs at 100 points, located every 2 m along the 200-m transect using a point-intercept method.

We sampled a range of grazing intensities based on both recent (last 2–3 years) and historic (up to 20 years) grazing. To assess recent grazing intensity, we identified and counted the dung or pellets of all herbivores within the large (cattle, sheep/goat, kangaroo) and small (kangaroo, rabbit, sheep/goat) quadrats. Dung and pellet counts are used widely to estimate large herbivore abundance (Johnson & Jarman 1987; Marques *et al.* 2001). For cattle, we counted dung events rather than individual fragments, i.e. we considered a number of small fragments to have originated from one dung event, if the fragments were within an area of a few metres. At 10 sites, we counted, collected, dried and weighed the dung from 10 large quadrats to obtain a relationship between dung counts and dry mass for each herbivore. This relationship was then used to calculate the total oven-dried mass of dung per hectare per herbivore as our measure of recent grazing intensity. Where dung from the same herbivore was assessed in both the large and small quadrats, we derived an average mass per hectare based on both quadrats for that herbivore type. We were unable to discriminate between sheep, goat and, in very few cases, deer (*Cervus* spp.) dung or between European rabbit and European hare (*Lepus europaeus*) dung. To assess historic grazing intensity, we measured the width and depth of all livestock tracks crossing the 200-m transect to derive a total cross-sectional area of livestock tracks for each site (Pringle & Landsberg 2004). Kangaroo dung was found at almost all sites, but rabbit and sheep dung mainly in low and moderate productivity sites (Appendix S3). Cattle dung was recorded at 40–60% of sites across the gradient.

NET PRIMARY PRODUCTIVITY AND ARIDITY

One of our aims was to determine whether the effects of grazing on the three soil health indices (stability, infiltration and nutrient indices; Appendix S4) were consistent across different levels of productivity, and therefore, whether separate analyses for different communities were justified. NPP was calculated using MODIS satellite imagery data (http://neo.sci.gsfc.nasa.gov/) with a spatial resolution of 1 km. At a regional scale, these data provide a more realistic measure of the long-term productivity of a site than measures of above-ground biomass, which are seasonally and spatially highly variable. Despite some overlap, our three vegetation communities represented a gradient in NPP, expressed as a time rate of C production, from low (blackbox: 0·64 g C m^{-2} day^{-1}) to medium (cypress pine: 0·75 g C m^{-2} day^{-1}) to high (red gum: 1·03 g C m^{-2} day^{-1}; Appendix S2) productivity. We also used the FAO AI in our models because it has been shown to be a useful tool to account for spatial differences in the data among sites (Delgado-Baquerizo *et al.* 2013). Aridity was calculated as 1−AI, where AI = precipitation/potential evapotranspiration using FAO's global aridity map (http://ref.data.fao.org/map?entryId=221072ae-2090-48a1-be6f-5a88f061431a).

MEASURES OF SOIL HEALTH

We used rigorous, field-based protocols to assess the status and morphology of the soil surface within the small quadrats (Tongway 1995). Within these quadrats, we measured 11 attributes: surface roughness, crust resistance, crust brokenness, crust stability, surface integrity (cover of uneroded surface), cover of deposited material, biocrust cover, plant basal cover, litter cover, litter origin and the degree of litter incorporation (Appendix S4). The values of these attributes were used to calculate three indices of soil health that define the capacity of the soil to (i) resist disturbance (stability index), (ii) infiltrate water (infiltration index) and (iii) cycle nutrients (nutrient index; Tongway 1995). These indices have been shown to be highly correlated with ecosystem functions related to soil stability, nutrient cycling and infiltration (Maestre & Puche 2009; see Appendix S4 for specific analytical methods).

A sample of the top 5 cm of the soil was collected from the centre of the small quadrat, air dried, ground, and passed through a 2-mm sieve to remove any roots or organic debris. This was used to assess soil total C and N in the uppermost layers using high-intensity combustion (LECO CNS-2000; LECO Corporation, St. Joseph, MI, USA), available (Olsen) P (Colwell 1963), and particle size distribution (sand, silt and clay contents), using the hydrometer method (Bouyoucos 1962). In addition, we assessed the percentage of total surface litter that was made up of groundstorey litter, i.e. excluding litter from trees and shrubs.

STATISTICAL ANALYSES

We used structural equation modelling (SEM; Grace 2006) to analyse the effects of different grazing intensities (i.e. the mass of dung from different herbivores and density/size of livestock tracks) on soil health in two suites of models. In all models, we combined the effects of recent and historic grazing into a single composite variable ('grazing'). Increases in this composite variable corresponded to increasing grazing intensity. The use of composite variables does not alter the underlying SEM models but collapses the effects of multiple, conceptually related variables into a single combined effect, aiding the interpretation of model results (Grace 2006).

For the first set of analyses (hereafter 'regional analyses'), we examined the effects of grazing on the three soil health indices (stability, infiltration and nutrient indices). We first pooled data from all 451 sites to produce three models (one each for each index), then undertook separate analyses (an additional nine models) for each combination of the three productivity classes by three soil health indices (stability, infiltration and nutrients). In the second set of analyses (hereafter 'productivity-level analyses'), we examined potential effects of grazing intensity on nine of the 11 attributes used to assess stability, infiltration and nutrients described above, with separate models for each of the three levels of productivity (27 models). We excluded litter origin because it was almost constant across two of the three vegetation communities, and plant basal area, because it was highly correlated with surface roughness (Eldridge 1991). In addition, for these productivity-level analyses, we included soil C, N and P, the total depth of litter and the proportion of litter derived from groundstorey plants, as well as an additional index (hereafter 'combined health index') that was calculated as the mathematical mean, following standardization (z-transformation) of the 11 attributes used to assess the three measures of soil surface condition (additional 18 models; see Appendix S4). In total, therefore, we had 45 models (three productivity classes by 15 attributes).

Structural equation modelling is used to test the plausibility of a causal model, based on *a priori* information, in explaining the relationships among a group of variables of interest (Appendix S1). SEM allowed us to partition direct and indirect effects of one variable upon another and to estimate the strengths of these multiple effects. This is particularly important in grazing studies because grazing has both direct effects on soil health, for example, by disturbing surface soils through trampling, and indirectly, through removal of plant material (herbivory) and therefore decomposition processes.

For the SEM process, we first developed an *a priori* model using grazing, NPP, aridity, soil texture (% silt + clay), shrub cover and groundstorey plant cover across all 451 sites. In all regional and productivity-level analyses, we predicted that grazing intensity would have direct effects on our measures of soil health and that these effects would be mediated by soil texture, groundstorey cover and shrub cover (Appendix S1).

The *a priori* model was compared with the variance–covariance matrix of our data to enable an overall goodness-of-fit to be assessed, using the χ^2 statistic. The goodness-of-fit test estimates the likelihood of the observed data given the *a priori* model structure. Thus, high probability values indicate that these models are highly plausible causal structures underlying the observed correlations. Before fitting empirical data to our *a priori* models, we examined the univariate correlations among all variables and standardized (z-transformed) the predictor variables but not the soil health data. The stability of the resultant models was evaluated as described in Reisner *et al.* (2013). Analyses were performed using the AMOS 22 (IBM, Chicago, IL, USA) software. For each of our models, those with low χ^2, high goodness-of-fit index and high normal-fit index were interpreted as showing the best fit to our data (Appendix S1).

Results

DERIVED INDICES OF SOIL HEALTH

For the regional analyses, grazing intensity had direct, negative effects on all three soil health indices [path coefficient (PC) = −0·22 to −0·30; Fig. 1). Declines in the stability and infiltration indices were largely due to rabbit grazing intensity [standardized total effects (STE) = −0·29 and −0·15, respectively; Fig. 1d], whereas declines in the nutrient index were due mainly to grazing intensity by cattle (STE = −0·17; Fig. 1d). Aridity was associated with small declines in two of the three soil health indices (PC = −0·15 to −0·16; Fig. 1b,c) and was highly negatively correlated with productivity (PC = −0·60). Increasing productivity was associated with increasing values of the nutrient index (PC = 0·36; Fig. 1c) but declining values of stability (PC = −0·19; Fig. 1a).

For the separate, productivity-level models of soil health, grazing intensity was associated with declines in the stability index under low (PC = −0·20) and moderate (PC = −0·39) productivity, but the effects were not significant under high productivity (Fig. 2a–c). Different components of grazing intensity were linked to these effects, with cattle accounting for declines under low productivity (STE = −0·17), and both rabbits (STE = −0·27) and livestock tracks (STE = −0·28) under moderate productivity (Table 1). Effects on the infiltration index were apparent only under high productivity (PC = −0·22; Fig. 2f) and were largely due to cattle (STE = −0·18), while effects on the nutrient index were apparent only under low productivity (PC = −0·39), but also due to cattle grazing (STE = −0·36, Table 1). Grazing by cattle reduced the combined health index across all productivity levels (Table 2).

INDIVIDUAL SOIL HEALTH ATTRIBUTES

Overall, 35 of the 55 significant effects (Table 2) were due to livestock grazing (cattle, sheep/goats or livestock

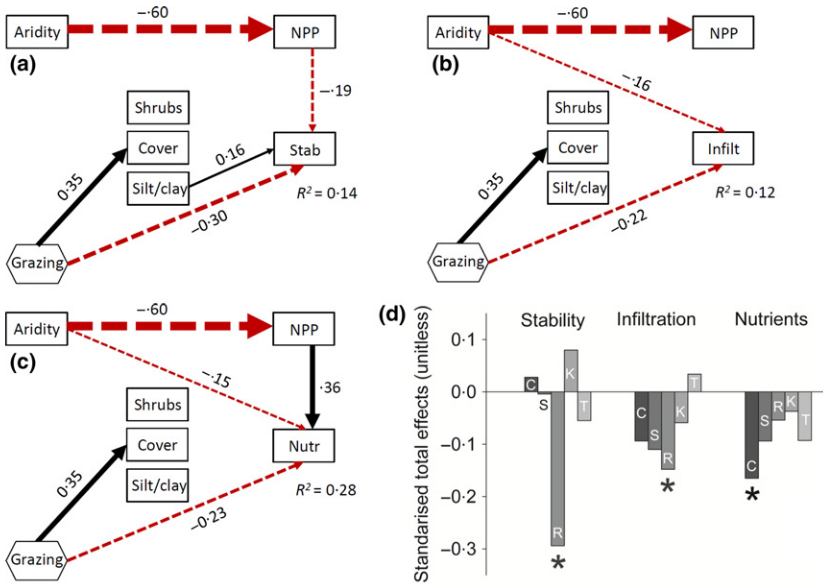

Fig. 1. Structural equation models of the direct and indirect effects of aridity, NPP, grazing, silt + clay content, and ground cover on indices of (a) stability (Stab), (b) infiltration (Infilt) and (c) nutrients (Nutr), and (d) the standardized total effects of livestock grazing (recent and historic livestock grazing) and recent wildlife grazing on the stability, infiltration and nutrient indices. Grazing is a composite variable comprising recent grazing by all herbivores and historic grazing by livestock. Only significant pathways are shown. Standardized path coefficients, adjacent to arrows, are analogous to partial correlation coefficients and indicative of the effect size of the relationship. Continuous and dashed arrows indicate positive and negative relationships, respectively. The width of arrows is proportional to the strength of path coefficients. The proportion of variance explained (R^2) appears above the three soil health response variables in the models. In panel (d), asterisks indicate a significant effects due to C = cattle, S = sheep and goat, R = rabbits, K = kangaroos or T = tracks. [Colour figure can be viewed at wileyonlinelibrary.com]

tracks). Of these, 26 represented substantial declines in soil health (26 negative effects). There were twice as many significant relationships between grazing intensity and individual soil indicators for moderate productivity sites (n = 28) than for low (n = 14) or high (n = 13) productivity sites. Two indices responded most significantly to grazing. Low surface integrity (extensive erosion) was related to livestock tracks and cattle, sheep/goat and rabbit dung. Surface roughness was related to all recent and historic measures of grazing.

For at least two of the three productivity levels, increased grazing intensity was associated with significant reductions in litter cover, surface integrity, increases in surface roughness and soil P (Table 2). We also recorded declines in crust resistance, crust stability, the cover of deposited materials, litter incorporation and litter depth with increased grazing intensity, but only at one productivity level. Kangaroo grazing was associated with weak reductions in soil N and P, and increases in roughness and biocrust cover under both high and low productivity. Overall, rabbit grazing was associated with substantial reductions in soil health, and increases in soil C, N and P, but only under moderate productivity.

Discussion

Our study provides clear evidence that, across a large area of eastern Australia, increased grazing intensity was associated with negative or benign effects on three indices of soil health related to the capacity of the soil to maintain its structural stability, cycle nutrients and sustain hydrological function. Importantly, we detected herbivore-specific effects on soil health, with effects on individual soil health attributes most due to livestock (cattle, sheep/goats, livestock tracks) or rabbit grazing. The results provide partial support for our first hypothesis of a strong livestock effect and benign effect of kangaroos and the second hypothesis of a substantial effect of rabbits. Grazing effects were more pronounced under moderate than either low or high productivities, providing only partial support for the third hypothesis. There was also a greater ability to predict soil health (greater R^2) under moderate productivity, possibly because moderate productivity sites span a greater range of aridity values than the other productivity classes.

GRAZING EFFECTS ON SOIL HEALTH VARY WITH PRODUCTIVITY AND HERBIVORE TYPE

The effect of increasing grazing intensity on soil health varied across the productivity gradient, consistent with our third hypothesis and studies of plant communities across productivity gradients (Bakker *et al.* 2006; Lezama *et al.* 2014). For example, we found negative relationships between grazing intensity and the stability index under low and moderate, but not high, productivity. Grazing effects under high productivity were idiosyncratic, with a slight suppressive effect on infiltration, but no effects on

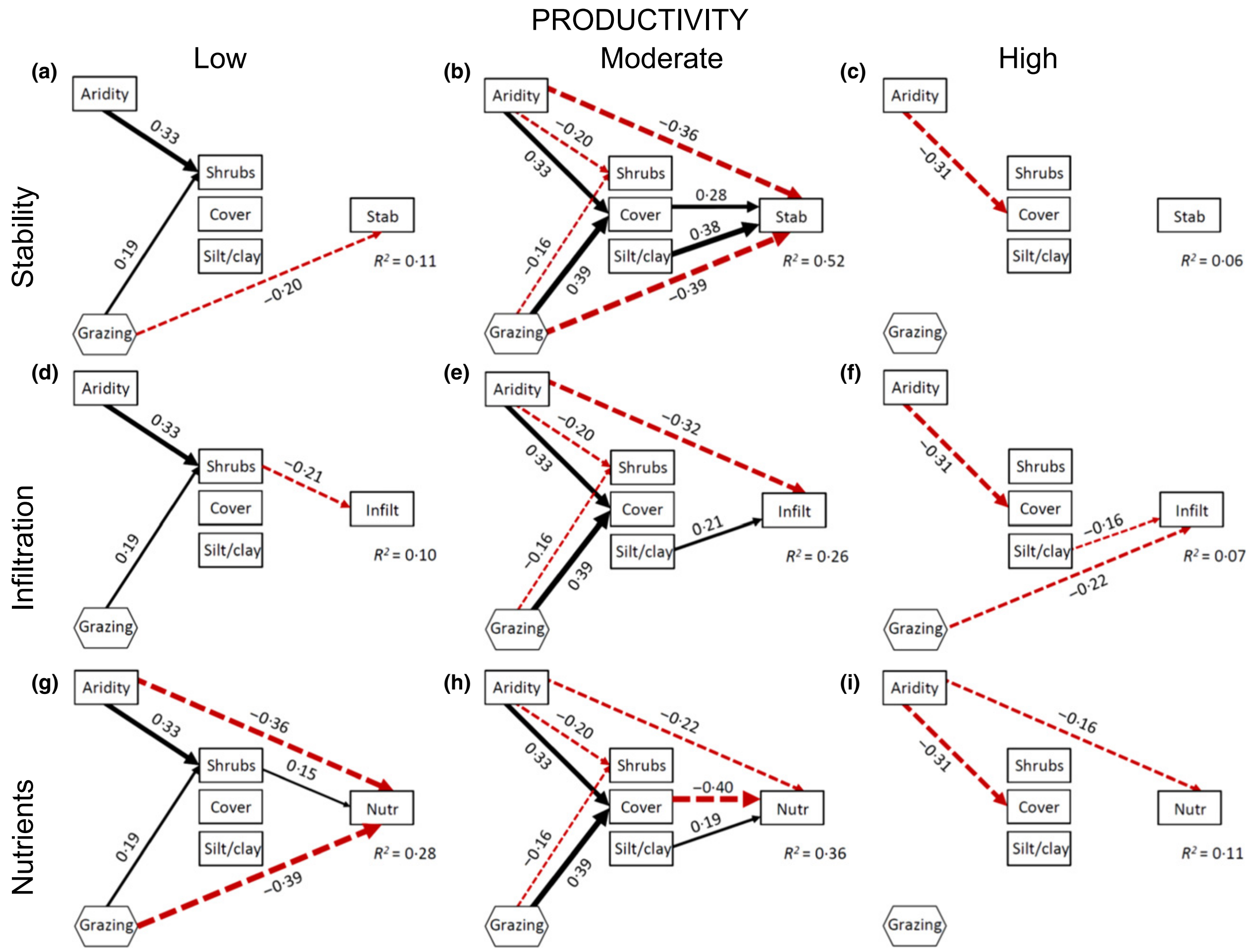

Fig. 2. Structural equation modelling of the direct and indirect effects of aridity, grazing, silt + clay content and ground cover on indices of stability (Stab; a–c), infiltration (Infilt; d–f) and nutrients (Nutr; g–i) under low, moderate and high productivity. Grazing is a composite variable comprising recent grazing by all herbivores and historic grazing by livestock. Standardized path coefficients, adjacent to arrows, are analogous to partial correlation coefficients and indicative of the effect size of the relationship. Continuous and dashed arrows indicate positive and negative relationships, respectively. The width of arrows is proportional to the strength of path coefficients. The proportion of variance explained (R^2) appears below the three soil health response variables in the models. [Colour figure can be viewed at wileyonlinelibrary.com]

Table 1. Standardized total effects (STE: sum of direct plus indirect effects) derived from the structural equation modelling) of aridity, grazing (cattle, sheep, rabbit, kangaroo, tracks), silt + clay content, shrub cover and groundstorey cover on the stability, infiltration and nutrient indices under different levels of productivity (NPP)

Attribute	NPP	Cattle	Sheep	Rabbit	Kangaroo	Track	PC	*P*-value
Stability	Low	**−0·17**	−0·05	−0·02	−0·01	−0·10	−0·20	0·015
	Moderate	0·03	0·01	**−0·27**	0·09	**−0·28**	−0·39	0·001
	High	–	–	–	–	–	−0·20	ns
Infiltration	Low	–	–	–	–	–	−0·04	ns
	Moderate	–	–	–	–	–	−0·20	ns
	High	**−0·18**	0·02	−0·06	0·01	0·11	−0·22	0·019
Nutrients	Low	**−0·36**	−0·12	0·00	−0·07	**−0·17**	−0·39	0·001
	Moderate	–	–	–	–	–	−0·26	ns
	High	–	–	–	–	–	−0·24	ns

Significant STEs are given in bold. The path coefficient (PC) from the composite variable ‘Grazing’ and the relevant *P*-value is presented. ns, not significant.

stability or nutrients. Soils might be expected to be more resistant to herbivore impacts under high productivity due to greater plant cover and richness, and therefore more stable soils (Loreau 2010). Conversely, low productivity sites would be more susceptible to livestock activity due to their sparser plant cover.

Table 2. Path coefficients derived from SEM of aridity, grazing, silt + clay content, shrub cover and groundstorey cover for individual indicators of grazing (cattle, sheep, rabbit, kangaroo, livestock tracks) in relation to individual soil surface attributes under three levels of productivity

Attribute	Productivity	Cattle	Sheep	Rabbit	Kangaroo	Tracks
Combined soil health index	Low	−0·16	–	–	–	–
	Moderate	−0·14	–	−0·24	–	–
	High	−0·16	–	–	–	–
Surface roughness	Low	0·16	–	–	0·15	0·27
	Moderate	−0·15	−0·32	−0·26	–	–
	High	0·16	–	–	0·15	0·27
Crust resistance	Low	–	–	–	–	–
	Moderate	−0·16	−0·25	–	–	–
	High	–	–	–	–	–
Crust brokenness	Low	−0·01	–	–	–	–
	Moderate	–	0·15	–	–	–
	High	–	–	–	–	–
Crust stability	Low	–	–	–	–	–
	Moderate	–	–	−0·14	–	–
	High	–	–	–	–	–
Surface integrity	Low	−0·62	−0·45	–	–	−0·41
	Moderate	−0·21	−0·28	−0·40	–	–
	High	−0·31	−0·22	–	–	−0·20
Deposited materials	Low	–	–	–	–	–
	Moderate	–	–	−0·43	–	–
	High	–	–	–	–	–
Biocrust cover	Low	–	–	–	0·30	–
	Moderate	−0·21	–	−0·26	–	−0·14
	High	–	–	–	0·30	–
Litter cover	Low	−0·20	–	–	–	−0·20
	Moderate	–	–	0·21	–	–
	High	−0·20	–	–	–	−0·20
Litter incorporation	Low	–	–	–	–	–
	Moderate	−0·22	−0·16	−0·10	–	–
	High	–	–	–	–	–
Litter depth	Low	–	–	–	–	–
	Moderate	−0·19	−0·15	–	–	–
	High	–	–	–	–	–
Ground litter	Low	–	–	–	–	–
	Moderate	0·21	–	0·17	–	–
	High	–	–	–	–	–
Soil C	Low	–	–	–	–	–
	Moderate	–	–	0·16	–	–
	High	–	–	–	–	–
Soil N	Low	–	–	–	−0·17	–
	Moderate	–	–	0·20	–	–
	High	–	–	–	−0·17	–
Soil P	Low	0·15	–	–	−0·14	–
	Moderate	0·14	–	0·53	–	–
	High	0·15	–	–	−0·14	–

Only significant ($P < 0{\cdot}05$) coefficients are shown. Ground litter is the proportion of all litter that is derived from groundstorey vegetation; combined soil health index = a composite index formed from 13 soil surface measurements.

Our findings provide evidence that site productivity is a significant biotic driver of herbivore effects on soil health, across even a moderately weak productivity gradient. Although grazing had the least effect under high productivity, increases in aridity are predicted to reduce the productivity of drylands globally by the end of the 21st century (Maestre *et al.* 2012; Dai 2013; Delgado-Baquerizo *et al.* 2013), thus increasing their vulnerability to livestock effects.

Soil health declined more with cattle grazing than other herbivores (e.g. combined soil health index, surface integrity; Table 2). Differences likely related to the larger body mass of cattle, and differences in hoof action and foraging behaviour. Cattle exert twice the static pressure on the soil as sheep, and three times that of kangaroos (Noble & Tongway 1986), and would be expected, therefore, to cause substantial soil compaction (Fleischner 1994). We attribute increased surface roughness under low and high productivity to deep hoof imprints in damp soil (pugging), which reduces soil porosity and hydraulic conductivity, causing considerable damage to plants (Drewry 2006). Areas trampled by livestock are highly susceptible to water erosion and wind erosion (Fleischner 1994; Drewry 2006), hence the marked declines in surface integrity under both cattle and sheep grazing across the entire gradient. Unlike cattle, the effects of sheep/goats were apparent only in sites of moderate productivity, reflecting their distribution across the study area (Appendix S3). Nevertheless, sheep/goat grazing was associated with reduced surface integrity, surface roughness, crust resistance, and litter depth and incorporation. Laboratory studies indicate that reductions in biocrust cover and a loss in surface micro-depressions, which contribute to surface roughness and integrity, are important mechanisms underlying increases in soil erodibility and sediment removal caused by sheep tramping (Eldridge 1998).

Of particular interest were the effects of residual herbivores, rabbits and kangaroos, on soil health. Consistent with prediction, rabbit grazing was associated with substantial reductions in biocrust cover, which contributes to surface roughness, crust stability, surface integrity and the combined health index, but increases in C, N and P. However, these effects were largely restricted to sites of moderate productivity. Soils under moderate productivity are likely less resilient than those under low or high, mainly because they support an extensive cover of biocrusts, which have been shown to be highly susceptible to livestock-induced soil disturbance (Eldridge 1998). Rabbits have two substantial effects on soils; they excavate small pits in the soil while foraging for roots and bulbs, effectively removing biocrusts, which are well developed in *Callitris glaucophylla* woodlands (Thompson, Eldridge & Bonser 2006). They also construct large burrow systems (warrens) with substantial soil excavation and inversion creating pockets of erodible soil, which ultimately influence plant germination (Eldridge & Koen 2008). To the best of our knowledge, there have been no studies of kangaroo effects on soil processes. Overall, kangaroo effects were equivocal and relatively benign, with some positive (increased roughness and biocrust cover), negative (reduced soil N) and neutral (reduced soil P) effects on soil health. Kangaroo dung was recorded at all but two of the 451 sites, and kangaroos are known to contribute to total grazing pressure by reducing plant biomass. Being largely unrestrained by fencing and therefore highly mobile compared with sheep and cattle, their effects on natural vegetation are likely less as long as biomass exceeds about $0{\cdot}25\ \mathrm{t\ ha^{-1}}$ (Short 1985).

The effects of grazing on soil nutrients were also herbivore specific. Phosphorus increased with cattle grazing across the gradient and declined with kangaroo grazing under low and high, but increased under moderate, productivity (Table 2). Phosphorus also increased with rabbit grazing under moderate productivity. Weak increases in P under cattle grazing, irrespective of productivity level, suggest a herbivore effect, as cattle dung is known to be a significant source of P (Cournane *et al.* 2011). Soil P levels were four times lower in the surface soils under moderate productivity, probably due to the lower clay and iron hydrous oxides levels in the soil and therefore a reduced capacity to adsorb P (Weaver, Ritchie & Anderson 1988). Despite this, rabbit grazing under moderate productivity was still associated with strong increases in soil P. The mechanism probably relates to substantial exposure of subsoil, which is a major source of ecosystem P (Delgado-Baquerizo *et al.* 2013) by rabbits during the construction of their extensive communal burrow systems.

Finally, the negative effects of increasing cattle grazing on the nutrient index but neutral effect on N or C might at first seem counterintuitive. However, a significant component of the nutrient index comprises attributes of litter (cover, origin and soil incorporation), which declined consistently under increasing cattle grazing. These litter attributes are surrogates of soil processes that are more indicative of the soil's potential to mineralize organic material rather than actual nutrient levels *per se*. Grazing could alter available C and N without changing total N, which would explain the lack of impact of grazing on total C or N, as has previously reported by some authors (e.g. McSherry & Ritchie 2013). The fact that grazing was significantly correlated with soil available P also supports this notion. The lack of a strong correlation could also be due to the relatively lower range of variation in our index and the fact that the strength of correlations varies with patch type and patch distribution (Maestre & Puche 2009).

CONCLUDING REMARKS AND IMPLICATIONS FOR WOODLAND MANAGEMENT

Overall, increased grazing intensity had negative effects on the stability and nutrient indices, but these effects varied with herbivore type and waned with increasing productivity. Increasing grazing intensity reduced surface integrity, biocrust cover, litter cover, depth and incorporation, and increased soil P, but had a variable effect on soil surface roughness. Surface integrity was the variable that showed the strongest and most consistent response across herbivores and productivity levels. Our study is timely because it provides governments with vital information on the likely effects of grazing on soil health and therefore the policies that best promote sustainable grazing practices.

Our results provide insights into the management of grazing in semi-arid woodlands. First, cattle were the herbivores most strongly associated with negative effects on soil health, particularly under moderate productivity where soils are mainly coarser textured. Strategies that reduce livestock densities or prevent the access of all livestock to sensitive areas such as riparian zones or sand hills may be the most effective way to mitigate declines in soil health. Second, rabbits were associated with substantially lower soil health, particularly on coarse-textured, moderately productive sites. Rabbit grazing not only destabilized surface soils but was also associated with increased soil P, potentially intensifying the likelihood of soil nutrient decoupling (Delgado-Baquerizo *et al.* 2013). Ongoing rabbit control should be a high priority of land managers, particularly in areas where rabbits occur with higher densities of livestock, thus leading to greater overall grazing pressure. Interestingly, the effects of kangaroos were largely benign, despite their widespread distribution and often high densities. This suggests that managing kangaroo densities is not a viable option for managing soil health.

Finally, the effects of aridity on soil health indices were of a similar magnitude and sign as any grazing effects, suggesting that predicted increases in aridity are likely to reduce soil health potentially as much as changes in grazing intensity. Thus, the cumulative effect of both grazing and aridity is likely to lead to significant reductions in soil health. Livestock densities will need to be managed, therefore, to mitigate potential declines in soil health resulting from increasing aridity. Our results indicate that land managers should consider productivity and herbivore type when developing strategies to manage grazing by livestock, and feral and native herbivores, particularly under drier climates.

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Data accessibility

Data on soil health and grazing are available from Dryad Digital Repository http://dx.doi.org/10.5061/dryad.k3p8n (Eldridge *et al.* 2016).

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Supporting Information

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

Appendix S1. Structural equation model procedures and the *a priori* model.

Appendix S2. Description of the three communities.

Appendix S3. Dung loads and herbivore occurrence.

Appendix S4. Description of attributes and their relevance for assessing soil health.