Contrasting effects of aridity and grazing intensity on multiple ecosystem functions and services in Australian woodlands

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Running header: Contrasting effects of aridity and grazing on functions and services

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23 **ABSTRACT**

24

25 Global change is expected to reduce the provision of multiple ecosystem services in drylands,

26 the largest biome on Earth. Understanding the relative importance of climate change and

27 overgrazing on ecosystems services is critical for predicting the effects of global change on

28 ecosystem well-being. We generated a system-level understanding of the effects of climate

29 (aridity intensity) and land use intensification (herbivore grazing intensity) on four regulating

30 ecosystem services (C-storage, and N- and P-availability, organic matter decomposition) and

31 one provisioning service (plant production) in wooded drylands from eastern Australia.

32 Climate change and grazing intensity had different effects on multiple ecosystem services.

33 Increasing aridity from 0.19 (Dry subhumid) to 0.63 (Arid) had consistent suppressive effects

34 on C-storage, N-availability, decomposition and plant biomass services, but not on P-

35 availability. The magnitude of these suppressive effects was greater than any effects due to

36 grazing. All sites showed evidence of kangaroo grazing, but the heaviest grazing was due to

37 cattle (dung: range 0 - 4545 kg ha^{-1}; mean 142 kg ha^{-1}). Any effects of grazing on ecosystem

38 services were herbivore specific, and ranged from positive to neutral or negative. Sheep, and

39 to a lesser extent cattle, were associated with greater N-availability. Rabbits, however, had a

40 greater effect on P-availability than aridity. Our study suggests that increases in livestock

41 grazing may fail to sustain ecosystem services because of the generally stronger negative

42 effect of increasing aridity on most ecosystem services in our model dryland. These services

43 are likely therefore to decline with global increases in aridity.

44

45 **Key words:** ecosystem services, nutrient cycling, climate change, dryland, grazing

46

47 **INTRODUCTION**

48

49 One of the terrestrial systems most at risk of environmental degradation is drylands, which

50 occupy about 45% of Earth's land mass (Prăvălie, 2016) and support about 38% of its people

51 (Reynolds *et al*., 2007). Drylands occur disproportionately in developing countries (Prăvălie,

52 2016), are agriculturally marginal, and support many socially disadvantaged groups that rely

53 heavily on grazing and farming for their livelihoods (Powell *et al*., 2004). Two of the most

54 important drivers of ecosystem function in drylands are overgrazing and increased aridity

55 (Maestre *et al*., 2016). Understanding the roles of land use intensification (overgrazing) and

56   climate change (increasing aridity) is of paramount importance if we are up to predict how

57   ecosystem services might change in the face of a drying climate and what this means for

58   societal well-being.

59

60   Overgrazing by livestock is emerging as one of the greatest threats to global biodiversity

61   conservation and ecosystem sustainability (Fleischner, 1994; Vázquez & Simberloff, 2003).

62   Over the past three centuries the total global area of land dedicated to grazing has increased

63   more than sixfold, from 524 to 3451 million ha, largely as a result of population growth and

64   colonization (Goldewijk, 2001, 2005). Consequently, almost a quarter of the global terrestrial

65   land mass is now under grazing by domestic livestock (Asner *et al*., 2004). About 60% of

66   land dedicated to grazing is considered drylands, where evapotranspiration exceeds rainfall

67   (Maestre *et al*., 2012; Prăvălie, 2016) and where the effects of human-induced changes such

68   as overgrazing are likely to have the largest effect on the provision of ecosystem services

69   (Eldridge & Delgado-Baquerizo, 2016). Carbon storage and N-availability in plant biomass

70   and forage supply may be greatest in moderately grazed drylands (Oñatibia *et al*., 2015).

71   However, overgrazing reduces vegetation cover and biomass (Jones, 2000), leading to a

72   decline in the spatial heterogeneity of litter cover (Daryanto *et al*., 2013b). Reduced litter

73   cover can lead to reduced decomposition and therefore smaller pools of soil C and N.

74

75   The effects of overgrazing on ecosystem functions and services may differ, however, across

76   different climatic conditions. For example, Rabbi *et al.* (2015) found that land management

77   did not influence the capacity of Australian drylands to soil carbon storage, a key ecosystem

78   service, due to the strong limitations in water availability, the main limiting factor in these

79   ecosystems. Because of this, the effect of overgrazing cannot be evaluated in isolation and

80   needs to consider the relative effects of multiple environmental factors, which are likely to

81   influence how ecosystem services respond to changing land use intensity. This has not been

82   widely reported in current literature.

83

84   The second driver, aridity, has negative effects on a large number of ecosystem functions and

85   services *via* multiple pathways. Increased aridity reduces the diversity and abundance of soil

86   microbial communities that carry out multiple soil functions (Maestre *et al*., 2012, 2015;

87   Delgado-Baquerizo *et al*., 2016b), reduces C-storage and N-availability by suppressing plant

88   production and therefore nutrient inputs into the soil, and may alter the concentration of some

89   soil enzymes, which control nutrient production processes (Li & Sarah, 2003; Delgado-

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90   Baquerizo *et al*., 2013a, 2013b). However, the suppressive effect of aridity on ecosystem

91   functions and services is highly dependent on the specific service. Increasing aridity, for

92   example, has been shown to enhance soil P, largely by increasing the exposure of P-rich

93   parent material and enhancing the amount of P bound to soil carbonates, which are abundant

94   under the most arid conditions (Delgado-Baquerizo *et al*., 2013b). This may also have

95   feedback effects on plant community composition by promoting plants that can grow in soil

96   with lower N:P ratios (Güsewell & Bollens, 2003), thereby reducing ecosystem resilience.

97   Single functions, therefore, should not be seen in isolation because overall ecosystem

98   functioning will depend on a range of functions or services operating together

99   (multifunctionality *sensu* Gamfeldt *et al*., 2008). In drylands, resilience of ecosystems to

100   ongoing global environmental change such as increased aridity and/or drought is enhanced by

101   increasing plant taxonomic and functional diversity and woody plant cover (Gaitan *et al*.,

102   2014; Valencia *et al*., 2015), or by maintaining a diverse and abundant soil microbial

103   community (Maestre *et al*., 2015). The maintenance of high levels of diversity in drylands is

104   critical in order to maximise the provision of a range of ecosystem services on which a range

105   of biota, including humans, depend (Naidoo *et al*., 2008; Bellard *et al*., 2012).

106

107   We know relatively little about the relative strengths of the two main drivers, grazing and

108   aridity, on ecosystem services in drylands (though see Ibáñez *et al.,* 2014 for a modelling

109   approach). This lack of knowledge hampers our capacity to manage change in drylands (e.g.

110   Prăvălie, 2016) or to determine the interactive effects of continued grazing at current levels

111   under a regime of reduced rainfall. We developed an *a priori model*, based upon the known

112   relationships among the various predictor and response variables (Fig. 1a; Table 1), and

113   included in our model woody plant cover and soil health. Soil health was included because it

114   is an essential component of human and environmental well-being (Pankhurst *et al.,* 1997). It

115   is also particularly important in drylands because the soils tend to be shallow and low in

116   available nutrients and are often sparsely vegetated and susceptible to wind and water

117   erosion. Both woody cover and soil health have been shown to mediate the effects of both

118   aridity and grazing on the provision of ecosystem services and functions (e.g. Maestre *et al*.,

119   2016). We predicted that increasing aridity (Path 3) would have negative effects on

120   ecosystem functions associated with C-storage, N-availability and plant production (Maestre

121   *et al*., 2012, 2016; Delgado-Baquerizo *et al*., 2016a; Zhang *et al*., 2016), but that P-

122   availability would be advantaged by increased aridity due to the re-distribution of P-rich

123   sediments resulting from increased degradation (Delgado-Baquerizo *et al.,* 2013b;

124   Hypothesis 1). Secondly, we expected to detect substantial herbivore-specific effects on

125   services and functions (Path 4). Specifically, kangaroos (i.e. native species) were predicted to

126   have few effects on functions and services because they have different grazing patterns from

127   livestock and have coevolved with plants and soils (Hypothesis 2). Conversely, we expected

128   to detect substantial increases in soil P-availability with increased grazing by rabbits or

129   livestock because rabbits create substantial soil disturbance, which exposes P-rich subsoil

130   (Hypothesis 3), and high levels of livestock grazing results in the concentration of P-rich

131   dung (Duncan *et al.,* 2008; Hypothesis 4). Finally, we predicted that increased livestock

132   grazing would be associated with substantial reductions in plant production (Hypothesis 5).

133

134   **METHODS**

135

136   *Study area*

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138   The study was undertaken in south-eastern Australia (Fig. 2). Landforms in the study area are

139   predominantly plains of coarse colluvium, and low ridges and valleys and slopes to 3%. The

140   soils are dominated by well-drained gradational red loams and red-brown duplex soils with

141   neutral to slightly acidic surfaces (pH 5–7; Thompson & Eldridge, 2005). The climate across

142   the area is Mediterranean and typically semi-arid (Table 2). Mean annual rainfall varies from

143   385 to 460 mm, and ranges from being evenly distributed throughout the year in the east and

144   central parts of the study area to 20% more rainfall during the six cooler months in the south

145   and south-west. Average temperature in the study area ranges from 9°C to 12°C for May to

146   September and from 18°C to 24°C for October to April, and the mean annual temperature

147   between 15°C and 18°C.

148

149   *Site selection, woody cover, grazing intensity and aridity*

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151   Between September and November 2013 we surveyed 151 sites that were characterised by

152   the community dominant *Callitrus glaucophylla* Joy Thomps. & L.A.S. Johnson (Fig. 2). The

153   study sites were first identified using Arc GIS and pre-inspected to ensure that they were

154   more than 250 m from any road. In order to sample across a full spectrum of grazing

155   intensities, we selected some low intensity and long ungrazed sites from conservation

156   reserves, road verges with intermittent grazing, commercial forests, conservation reserves and

157   long-term grazing exclosures as well as high intensity grazed sites (Table 2). At each site we

158 positioned a 200 m long transect within which were placed five 25 m^2 (5 m x 5 m) plots

159 (hereafter 'large quadrat') every 50 m (i.e. 0 m, 50 m, 100 m, 150 m and 200 m). A smaller

160 (0.5 m x 0.5 m) quadrat (hereafter: 'small quadrat') was located in the centre of the large

161 quadrat. Along the line transect, the projected cover of trees (> 3 m tall) and shrubs (0.5-3 m)

162 was recorded at 100 points every 2 m to provide a measure of woody (tree + shrub) cover.

163 We also measured the width and depth of all livestock tracks crossing the 200 m transect. We

164 used the total cross-sectional area, averaged to a 100 m transect (cm^2/100 m) of stock tracks

165 as a proxy of historic (long-term) grazing.

166

167 In order to assess recent grazing intensity at the sites, dung/pellets were identified and

168 counted in both of the small and large plots separately by herbivore type. Kangaroo

169 (*Macropus* spp.), rabbit (i.e. rabbits and hares; *Oryctolagus cuniculus* L. and *Lepus*

170 *europaeus* Pallas) and sheep (which included sheep *Ovis aries* L., and goats *Capra hircus* L.)

171 dung/pellets were counted in the small quadrats, and cattle dung (*Bos taurus* L.), sheep and

172 kangaroo dung/pellets counted in the large quadrats. For cattle, we counted dung events

173 rather than individual fragments, i.e. we considered a number of small fragments to have

174 originated from one dung event, if the fragments were within an area of a few metres. Dung

175 and pellet samples of each type were collected, oven dried at 40°C for 24 hours, and weighed

176 to estimate the mass of individual pellets, or in the case of cattle, dung events. Average mass

177 of dung was then used to calculate the total mass of each type of dung per hectare. We used

178 algorithms, developed previously for the study area (see Eldridge *et al*., 2016) to calculate the

179 total oven-dried mass of dung per hectare per herbivore based on the number of pellets

180 recorded in the field. This total oven dried mass of dung was used as our measure of recent

181 grazing intensity for each herbivore (Eldridge *et al*., 2016). Where dung from the same

182 herbivore was assessed in both the large and small quadrats, we derived an average mass per

183 hectare based on the large quadrat for that herbivore type. We used dung as a measure of

184 recent grazing because dung persists for about 3 years in the field before it is decomposed.

185 Thus it is a useful proxy of short-term grazing by herbivores. Stock tracks provide a long-

186 term integrated history of continued use by livestock.

187

188 Aridity was calculated as 1-AI, where AI = precipitation/potential evapotranspiration using

189 FAO's global aridity map (http://ref.data.fao.org/map). Subtracting AI from 1 changes the

190 direction of the index such that larger values are more arid.

191

Assessment of soil health and plant production (biomass)

We assessed the status and morphology of the soil surface within the small quadrats using rigorous, field-based protocols (Tongway, 1995). Within the small quadrats we measured 11 soil surface attributes: surface roughness, crust resistance, crust brokenness, crust stability, surface integrity (cover of uneroded surface), cover of deposited material (e.g. sand), biocrust cover, plant basal cover, litter cover, litter origin, and the degree of litter incorporation (see Supplementary Material Table S1). From these data we calculated a soil health index as the mathematical mean of the 11 attributes following standardization (*z*-transformation).

To estimate plant production, we took oblique photographs of all small quadrats, then clipped, oven-dried (45° C for 24 h) and weighed all above-ground material rooted within the small quadrats at the 50 m mark along the transect. Biomass values for all small quadrats were then estimated and calibrated against the 151 actual biomass values using the photostandards. Using this double-sampling approach, the predictive power, based on a second-order polynomial was $R^2 = 0.69$.

Soil sampling and analyses

During the field survey we collected about 500 g of soil, from the surface 5 cm, from the centre of each small quadrat. A total of 755 soil samples were analysed in this study, from 151 sites. The soil samples were air dried, passed through a 2 mm sieve to remove roots, organic debris and stones prior to chemical analyes. Total C and N were assessed using high intensity combustion (LECO CNS-2000; LECO Corporation, St. Joseph, MI, USA), available (Olsen) P according to Colwell (1963). Labile carbon was assessed by measuring the change in absorbance when slightly alkaline $KMnO_4$ reacts with the most readily oxidizable (active) forms of soil C to convert Mn (VII) to Mn (II; Weil *et al*., 2003). Ammonium and nitrate concentrations were measured using Flow Injection Analysis (Quick-Chem8500-LACHAT) following the extraction with 0.5M K_2SO_4. For the activity of the enzyme β-glucosidase (BG), a mixture of 1 g of air-dried soil and 33 ml of sodium acetate buffer (pH <7.5) was shaken at 200 rpm on an orbital shaker for 30 minutes and 800 μl soil slurry was sampled and 200 μl substrate of 4-Methylumbelliferyl β-D glucopyranoside solution were added to the slurry. The 1000 μl (1 ml) of solution was incubated at 25 °C for 3 hours and the activity (nmol activity g^{-1} dry $soil^{-1}$ h^{-1}) was measured at the 365 nm excitation wavelength and 450

226 nm of emission wavelength in a microplate reader. The same procedure was used, but with

227 different substrate solutions, for an additional three enzymes. Thus 4–Methylumbelliferyl β-

228 D-cellobioside was used for cellobiosidase (CB), 4-Methylumbelliferyl N β-D-glucosaminide

229 for N-acetyl-β-glucosaminidase (NAG) and 4-Methylumbelliferyl phosphatase for

230 phosphatase (PHOS) activity (Bell *et al*., 2013).

231

232 *Ecosystem services scoring*

233

234 In this study we used the term "ecosystem function" to define the 11 individual functions that

235 we measured. The term "ecosystem service" or service refers to an assemblage of functions

236 grouped according to similar functions that they perform, e.g. N-availability. The eleven

237 separate functions were grouped into five services as follow: C-storage (total C and labile C),

238 N-availability (total N, ammonia and nitrate), P-availability (Colwell P only), decomposition

239 (extracellular enzyme activities of β-glucosidase, cellobiosidase and β –N-

240 acetythexosaminidase and phosphatase) and plant biomass (plant biomass only).

241 Decomposition, C-storage, and N- and P-availability are regulating services, and biomass is a

242 provisioning service (MEA, 2005). Carbon storage and N- and P-availability are proxies of

243 ecosystem processes such as C sequestration and N and P mineralization. In the case of

244 available P, note that while total P is considered a soil property (mainly provided by

245 bedrock), available P is the result of P mineralization and solubilisation of soil organic matter

246 and minerals in the bedrock, a process conducted by plant roots and microbial communities.

247 The index of each service was calculated by averaging the standardised (*z*-transformed) value

248 of each function for each site into a single metric (multifunctionality *sensu* Maestre *et al*.,

249 2012; Soliveres *et al*., 2014; Delgado-Baquerizo *et al*., 2016a, 2016b; Zhang *et al*., 2016).

250 This allowed us to transform all services to a common scale of standard deviation units

251 (Maestre *et al*., 2012). Integrating or averaging the standardized multiple functions into a

252 single metric for overall ecosystem enables compensation of the decrease in one or several

253 function by the increase of one or several functions (Gamfeldt *et al*., 2008; Quero *et al*.,

254 2013), therefore it is highly informative quantitative measure of the overall ecosystem

255 performance.

256

257 *Statistical analyses and modelling*

258

259   Structural Equation Modelling (SEM) was used to build a system-level understanding on the

260   effects of grazing and aridity on the ecosystem services. An *a priori* model (Fig. 1a; Table 1)

261   was applied to the five ecosystem service indices. In the model, grazing and aridity were

262   included as the main factors on the ecosystem services, directly and indirectly *via* soil health

263   and tree cover. In our models, the effects of recent and historic grazing were combined into a

264   single composite variable ('grazing'). Increases in this composite variable corresponded to

265   increasing grazing intensity. The use of composite variables does not alter the underlying

266   SEM models, but collapses the effects of multiple, conceptually-related variables into a single

267   combined effect, aiding the interpretation of model results (Grace, 2006). The SEM allowed

268   us to partition direct and indirect effects of one variable upon another and to estimate the

269   strengths of these multiple effects.

270

271   We included woody cover, aridity, soil health and grazing in our models because we

272   considered them to be the most informative predictors of ecosystem services out of a suite of

273   many potential predictors. We are aware, however, that other variables not considered here,

274   could have been included, such as trampling by cattle or the number of pits dug by rabbits.

275   These may have provided additional insights into the mechanisms underlying grazing effects

276   on ecosystem services. To improve normality, values for soil health, woody cover, aridity and

277   grazing were standardized (*z*-transformed) prior to analyses. Overall goodness of fit

278   probability tests were performed to determine the absolute fit of the best models. The

279   goodness of fit test estimates the long-term probability of the observed data given the *a priori*

280   model structure. Thus high probability values indicate that these models are highly plausible

281   causal structures underlying the observed correlations. All SEM analysis was conducted

282   using AMOS Software Version 20. The stability of these models was evaluated as described

283   in Reisner *et al.* (2013).

284

285   **RESULTS**

286

287   Aridity (1-Aridity Index) at our study sites ranged from 0.19 (Dry subhumid) to 0.63 (Arid),

288   with a mean value of 0.36 (Semi-arid; Table 2). Average soil health index and woody cover

289   values were 44.1% and 41.9%, respectively. Recent grazing intensity data, as measured by

290   the mass of herbivore dung, varied markedly, from no grazing at some sites to more than 4.5 t

291   ha^{-1} of dung at one site grazed by cattle. Kangaroos were the only herbivore to be recorded at

292   all 151 sites. Plant biomass varied markedly (0.19 to 3.16 t ha^{-1}) with a mean of 1.14 t ha^{-1},

293   typical of these semi-arid woodlands. Soil enzyme concentrations ranged from 63 nmol g^{-1} h^{-1}

294   (cellobiosidase) to 112.9 (phosphatase). Total N (0.15%) and C (2.08%) reflected typically

295   low values found for eastern Australian rangelands.

296

297   *Effects of grazing on multiple ecosystem services*

298

299   Grazing had moderate to strong direct and positive effects on all services (Figs. 1b-f), but

300   also strong, indirect negative effects on N-availability, C-storage and plant biomass, *via* a

301   suppression of the positive effects of soil health on these three services (Figs. 1b-c, e).

302   Conversely, the indirect effect of grazing was positive on P-availability *via* reductions in soil

303   health (Fig. 1d). The standardised total effects from the SEM, i.e. the sum of all direct and

304   indirect effects, indicated a general positive effect of grazing on N-availability, which was

305   due mainly to sheep and cattle (Fig. 3a), but an overall neutral effect on C-storage (Fig. 3b).

306   Grazing had an overall positive effect on P-availability, due mainly to rabbit grazing (Fig.

307   3c). Conversely, for plant biomass, the overall effect of grazing was negative, though there

308   was evidence of an increase in plant biomass resulting from increased rabbit grazing (Fig.

309   3d). The overall positive effects of grazing on decomposition resulted from increases in

310   historic grazing (track; Fig. 3e). Overall, grazing effects were positive for C-storage, and N-

311   and P-availability but negative for plant biomass and neutral for decomposition.

312

313   *Effects of aridity on multiple ecosystem services*

314

315   Increasing aridity was associated with reduced soil health and lower cover of woody plants,

316   but its effects on various services were mixed (Fig. 1). There were significant negative and

317   direct effects of aridity on N-availability and C-storage (Figs. 1b, c) and decomposition (Fig.

318   1f). Increasing aridity suppressed the positive effect of soil health for N-availability and C-

319   storage (Figs. 1b-c) and plant biomass (Fig. 1e). However, increasing aridity had indirect

320   positive effects on P-availability *via* reductions in woody plants and soil health (Fig. 1d). In

321   general, the sum of all direct and indirect effects or the standardised total effect of aridity was

322   negative for four of the five services and the only positive effect was observed for P-

323   availability (Fig. 3).

324

325   **DISCUSSION**

326

327   Our results indicate that aridity had a strong suppressive effect on all functions and services,

328   except P-availability, whereas the effects of grazing ranged from positive, to negative or

329   neutral. The effect of aridity was strong, despite the relatively short gradient in our study

330   (0.19 to 0.63). Further, different herbivores had different effects on specific services, with

331   livestock associated with greater N-availability and decomposition, and rabbits with greater

332   P-availability and plant biomass. Management of critical services and functions associated

333   with plant production and C-storage, and N- and P-availability need to consider not only the

334   effects of grazing by different herbivores, but the effects of changing climates on these

335   attributes.

336

337   *Grazing effects on plant biomass*

338

339   Plant production is the attribute most strongly influenced by livestock grazing (herbivory:

340   Milchunas & Lauenroth, 1989; Charles *et al*., 2016; Eldridge *et al*., 2016), so reductions in

341   biomass with increasing grazing are expected. The standardised total effects indicated that the

342   overall effects of kangaroo grazing on plant biomass were largely neutral (Fig. 3d), consistent

343   with studies of kangaroo effects on soil health (Eldridge *et al*., 2016). Livestock grazing

344   resulted in reductions in plant biomass, but increasing rabbit grazing was associated with

345   increased plant biomass. This might at first seem counterintuitive, but rabbit grazing has been

346   shown to suppress small forbs and grasses at the expense of large, high biomass

347   Mediterranean weeds (Myers & Pool, 1963). Examination of sites in our study with a high

348   intensity of rabbit grazing (i.e. sites with a mass of rabbit dung > 100 kg ha^{-1}) showed that

349   they were dominated by annual or biennial weedy plants of high biomass and cover such as

350   *Echium plantagineum* L*., Stipa scabra* Lindl*., Hordeum leporinum* Link and *Arctotheca*

351   *calendula* Levyns, typically exotic plants (Table 3). Most importantly, as discussed more

352   fully below, rabbits had a positive effect on the amount of available P in the soil (Fig. 3). Soil

353   P is the main limiting soil nutrient in the largely weathered old soils from Australia (Lambers

354   *et al*., 2008), thus, by bringing back soil available P to the surface, rabbits may promote the

355   productivity of these sites.

356

357   *Grazing and aridity effects on C-storage*

358

359   Grazing and aridity had direct and contrasting effects on C-storage, with positive effects of

360   grazing and negative effects of increasing aridity (Fig. 1c). We also found strong, indirect

11

361 negative effect of grazing and aridity *via* the suppression of the positive effects of soil health

362 on this service. The standardised total effects for C-storage indicated that there is an overall

363 neutral effect of grazing, but a substantial negative effect of aridity on C-storage (Fig. 3b),

364 consistent with other studies (Delgado-Baquerizo *et al*., 2013b; Rabbi *et al*., 2015). Studies of

365 grazing exclosures have shown few differences in total C-storage after 15 years between

366 ungrazed and grazed sites (Nosetto *et al*., 2006). Similarly, Rabbi *et al*. (2015) showed that

367 land use in drylands in eastern Australia had a relatively neutral effect on C-storage,

368 explained only 1.4% of the total variation in C-storage. This contrasted with aridity, which,

369 along with soil clay content, explained 64% of the variation in C-content. Ecosystem services

370 other than C-storage, however, are likely to be more strongly influenced by differences in

371 land management.

372

373 *Grazing and aridity effects on N-availability*

374

375 Overall, grazing had a positive effect on N-availability, i.e. increased nitrate, ammonium and

376 total N; and this was due mainly to sheep/goat and cattle grazing (Fig. 3a). Increased grazing

377 intensity was associated with direct positive effects on N-availability, but indirect suppressive

378 effects, *via* reductions in soil health (Fig. 1b). The addition of nitrate and ammonium from

379 urine and dung, particularly at livestock resting camps, could partly account for the direct

380 effects of grazing on N-availability. Although much of the nitrate is lost *via* volatilization

381 (Powell *et al*., 1998), addition of dung and urine (i.e. ammonia) provides a source of readily

382 available nutrients for plants and microbes (Augustine *et al*., 2003; Schrama *et al*., 2013). In

383 support of this, we found that grazing intensity increased the $NH_4:NO_3$ ratio (Fig. S1), though

384 the strength of the relationship was weak ($R^2 = 0.08$). The mechanism underpinning the

385 indirect suppressive effect of grazing on N-availability may relate to reductions in soil

386 surface roughness and integrity, biocrust cover, the depth and incorporation of the litter layer

387 (Eldridge *et al*., 2016). Biocrusts are essential components of soil health, and cyanolichens

388 and cyanobacteria in biocrusts are known to fix atmospheric C and N, accounting for the

389 strong effect of increased soil health on both C-storage and N-availability, particularly in arid

390 and semiarid systems (Delgado-Baquerizo *et al*., 2014, 2016a). In our study, increases in this

391 ratio were linked to increases in the intensity of kangaroo grazing but reductions in cattle

392 grazing.

393

394 *Grazing effects on P-availability*

395

Phosphorus cycling was one of the ecosystem services less affected by increasing aridity and

grazing intensity. Unlike C and N, P is an abiotically-derived element, and its availability has

been shown to increase when P-rich parent material is exposed, often *via* soil erosion

(Delgado-Baquerizo *et al*., 2013b). Interestingly, rabbit grazing had the strongest stimulatory

effect on P-availability (Fig. 3c). Production of phosphatase is extremely costly in terms of N

and C. Thus, microbes and plants only produce phosphatase when it is really needed. If

rabbits are providing a directly available form of P, such as PO_3^- to plant and microbes by, for

example, exposing bedrock or dung, then it is likely that phosphatase production will be

inhibited. Indeed, P is a relatively large component of rabbit dung, with five-times more P in

rabbit than sheep or cattle dung (http://www.crossroadsrabbitry.com/rabbit-manure-info/).

This explains the decoupling of phosphatase from inorganic P-availability.

Kangaroo dung is known to contribute relatively high levels of total P to floodplain systems

(Kobayashi *et al*., 2011), but in our study, kangaroo effects on P-availability were neutral.

This may be due to slow breakdown of pellets in our system compared with floodplains, due

to low levels of soil moisture (Davis & Coulson, 2016). Thus, increased P could have resulted

from the concentration of rabbit dung, such as occurs in rabbit latrines (Dixon & Hambler,

1993), or the localisation of dense patches of dung in litter dams on sloping surfaces

following overland flow (Mitchell & Humphreys, 1987). The most parsimonious explanation,

however, is that P-rich subsoil is exposed during the construction of the extensive communal

burrow systems of rabbits. The relatively low to neutral pH values of these soils would have

made P more available because there is little soil calcium to bind onto the P (Lajtha &

Bloomer, 1988). Overall, therefore, increases in rabbit grazing are likely to lead to increases

in P, with resulting changes in the stoichiometry of P and N in some local areas from

Australia (Delgado-Baquerizo *et al*., 2013b; Fig. S2).

Organic matter decomposition

We detected small declines in decomposition, our measure of enzyme activity, with

increasing aridity and grazing. Aridity suppressed, and grazing slightly increased, all enzyme

functions except phosphatase (Fig. 4). Previous studies have shown that overgrazing reduces

phosphatase and beta-glucosidase, but that effects likely depend on the patch type in which

measurements are made (Zhang *et al*., 2016). In our study the decomposition service, and the

429   four individual enzymatic functions, were associated with livestock tracks, our measure of

430   historic grazing. Grazing is typically associated with declines in enzyme activity (e.g. Prieto

431   *et al*., 2011; Olivera *et al*., 2014) so it is somewhat counterintuitive that increased grazing in

432   our study was associated with increased enzyme activity. The standardised total effects

433   indicated that historic grazing (i.e. livestock tracks), rather than recent grazing (i.e. dung from

434   livestock), was linked to increases in the decomposition function (Fig. 3e). Our measure of

435   historic grazing could be a proxy for increasing soil texture given that livestock tracks would

436   be more pronounced in finer soils. Equally plausible is that increased historic grazing is

437   linked to larger pools of herbivore urine and dung and therefore greater levels of

438   decomposition. Also, herbivores break down organic matters such as plant litter through hoof

439   action, and this may enhances the decomposition process. Overall, however, grazing-linked

440   increases in decomposition were matched by declines due to increasing aridity, which would

441   reduce decomposition rates and therefore nutrient cycling functions (Maestre *et al*., 2015;

442   Delgado-Baquerizo *et al*., 2016b).

443

444   *Stronger negative effects of aridity on services than grazing*

445

446   Aridity levels are predicted to increase into the next century and lead to substantial shifts in

447   plant and microbial processes in drylands (Delgado-Baquerizo *et al*., 2014; Maestre *et al*.,

448   2016). This will likely reduce Earth's capacity to support essential ecosystem functions and

449   services associated with the storage and availability of C and N, and the production of forage

450   for livestock (Maestre *et al*., 2016). In our study, increasing aridity was associated with an

451   increase in P-availability, but reductions in the other four functions, with the greatest

452   reduction in C-storage (STE = -0.54; Fig. 3b) and N-availability (STE = -0.31; Fig. 3a).

453   Increasing aridity was also associated with indirect suppression of N-availability, C-storage

454   and plant biomass *via* reductions in soil health (Figs. 1b-c, e). Declines in N-availability with

455   aridity were matched by strong increases due to grazing. Predicted reductions in grazing

456   capacity with increased aridity are therefore likely to lead to global reductions in N-

457   availability. The shift from free-range grazing to feedlots will likely lead to reductions in C

458   emissions and may also reduce farm-level N deposition, but the positive effects of reduced N-

459   availability will likely be more apparent under less arid conditions (Giese *et al*., 2011). The

460   effect of aridity was also to suppress the negative effects of woody plants on plant biomass.

461   This could occur by removing competition for light or soil moisture, allelopathic effects that

462   exist in some *Eucalyptus* species (Zhang & Fu, 2009), or suppression resulting from below-

14

ground resource competition from *Callitrus glaucophylla* (Harris *et al*., 2003). Changes in land management may not lead to increased levels of ecosystem services due to the strong negative effect of aridity on most services. Thus services are likely to decline over the next century as aridity increases.

CONCLUDING RESULTS

The effects of grazing on ecosystem services are herbivore specific and vary from positive to neutral or negative. Critical functions associated with decomposition and nutrients cycling declined with increasing aridity, and these effects were of a greater magnitude than any effects due to grazing. Our study suggests that changes in land management may fail to compensate for the negative effects of aridity on all functions other than P-availability. Thus strategies to manage ongoing climate change are likely to be a priority of governments as we move towards a drier world.

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787   Table 1. Hypothesized mechanisms underlying the grazing *a priori* meta-model shown in
788   Figure 1a.
789

Path	Hypothesized mechanism
1	(-) Increasing aridity reduces woody cover in semiarid landscapes (Westerband *et al.*, 2015).
2	(+/-) Ecosystem multifunctionality peaks at 41-60% of relative woody covers (RWC), but aridity alters the effect of RWC on multifunctionality. The RCW and multifunctionality relationship was linear positive in dry-subhumid sites, but it shifted into hump-shaped and ended a negative relationship in most arid conditions (Soliveres *et al.*, 2014).
3	(-) Aridity has negative effects on ecosystem multi-functions or services (Maestre *et al.*, 2012; Delgado-Baquerizo *et al.*, 2016a), because it reduces soil microbial diversity and abundance that promote ecosystem multifunctions (Maestre *et al.*, 2015; Delgado-Baquerizo *et al.*, 2016b) and it reduces organic C, total N and enzyme activities such as phosphatase activity (Li & Sarah, 200; Delgado-Baquerizo *et al.*, 2013a, 2013b); (+) but aridity increases total P (Delgado-Baquerizo *et al.*, 2013b).
4	(-) Grazing has significant negative impact on overall ecosystem multifunction and multiservices (Zhang *et al.*, 2016) by dampening positive effect of shrubs (Eldridge *et al.*, 2013, 2015). It reduces plant biomass and litter cover (Eldridge *et al.*, 2016), therefore soil organic C (Daryanto *et al.*, 2013a) and increases bare soil (Daryanto *et al.*, 2012). (+/-) Under high intensity of grazing microbial biomass-C, phosphatase and dehydrogenase activities increases due to herbivore urine and dung at inter canopy, but reduces β-glucosidase activity, organic C and total N at under plant canopy soil (Prieto *et al.*, 2011; Olivera *et al.*, 2014).
5	(-) Soil organisms that is one of the soil health indicators are very sensitive to climate (Doran & Zeiss, 2000); Negative correlation between aridity and plant cover may enable soil erosion (Delgado-Baquerizo *et al.*, 2013b)
6	(-) High stocking rate increases soil compaction and bulk density (Pulido *et al.*, 2016), therefore reduces infiltration and macroporosity (Castellano & Valone, 2007; du Toit *et al.*, 2009), as well as nutrients and stability indices (Eldridge *et al.*, 2013).
7	(+) Healthy soils with higher plant, litter and crust cover will increase organic inputs into soil, that support diverse microbial community and enrich the soil nutrient pool will promote overall ecosystem functions.

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Table 2. Mean, standard deviation, minimum and maximum values of relevant attributes and response variables used in the structural equation models. [#] woody (shrub + tree) cover can exceed 100% where shrubs occur beneath trees. Aridity = 1 – FAO Aridity Index

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| Attribute	Mean	SD	Min	Max
Aridity	0.36	0.08	0.19	0.63
Soil health index (%)	44.1	8.3	17.4	80.2
Grazing intensity				
Livestock tracks area (cm^2 100 m^{-1})	122.7	319.0	0.0	3060.0
Mass of cattle dung (kg ha^{-1})	142.0	481.1	0.0	4539.5
Mass of sheep/goat dung (kg ha^{-1})	12.1	40.2	0.0	302.7
Mass of kangaroo dung (kg ha^{-1})	52.8	41.6	0.5	270.2
Mass of rabbit dung (kg ha^{-1})	12.2	29.1	0.0	232.8
Plants				
Woody cover (%)	41.9	22.6	4.0	116.0[#]
Plant biomass (t ha^{-1})	1.14	0.63	0.19	3.16
Soil enzymes				
β-glucosidase (nmol g^{-1} soil^{-1} h^{-1})	74.0	34.9	9.7	192.8
cellobiosidase (nmol g^{-1} soil^{-1} h^{-1})	63.4	32.7	8.8	176.3
N-acetyl-β-glucosaminidase (nmol g^{-1} soil^{-1} h^{-1})	66.6	33.3	8.9	179.8
phosphatase (nmol g^{-1} soil^{-1} h^{-1})	112.9	44.5	26.3	248.8
Soil chemistry				
Labile carbon (mg kg^{-1})	436.2	105.7	221.0	658.7
NH$_4$ (mg L^{-1})	1.74	1.09	0.51	7.09
NO$_3$ (mg L^{-1})	0.95	1.46	0.05	9.59
Colwell P (mg kg^{-1} soil)	14.37	8.47	4.55	55.20
Total C (%)	2.08	0.73	0.79	4.54
Total N (%)	0.15	0.04	0.08	0.30

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Table 3. Mean cover (%) of plant taxa occurring at sites with a high intensity of rabbit

grazing (dung > 100 kg ha^{-1})

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| Species	Group	Origin	Life cycle	Response to grazing	Cover (%)
Echium plantagineum L.	Forb	Exotic	Annual	Increase	16.7
Stipa scabra Lindl.	Grass	Native	Biennial	Benign	13.9
Hordeum leporinum Link	Grass	Exotic	Annual	Increase	12.4
Arctotheca calendula Levyns	Forb	Exotic	Annual	Increase	9.9
Vulpia spp.	Grass	Exotic	Annual	Increase	4.8
Erodium crinitum Carolin	Forb	Native	Annual	Increase	4.8
Sisymbrium irio L.	Forb	Exotic	Annual	Increase	4.0
Trifolium arvense L.	Forb	Exotic	Annual	Increase	4.0

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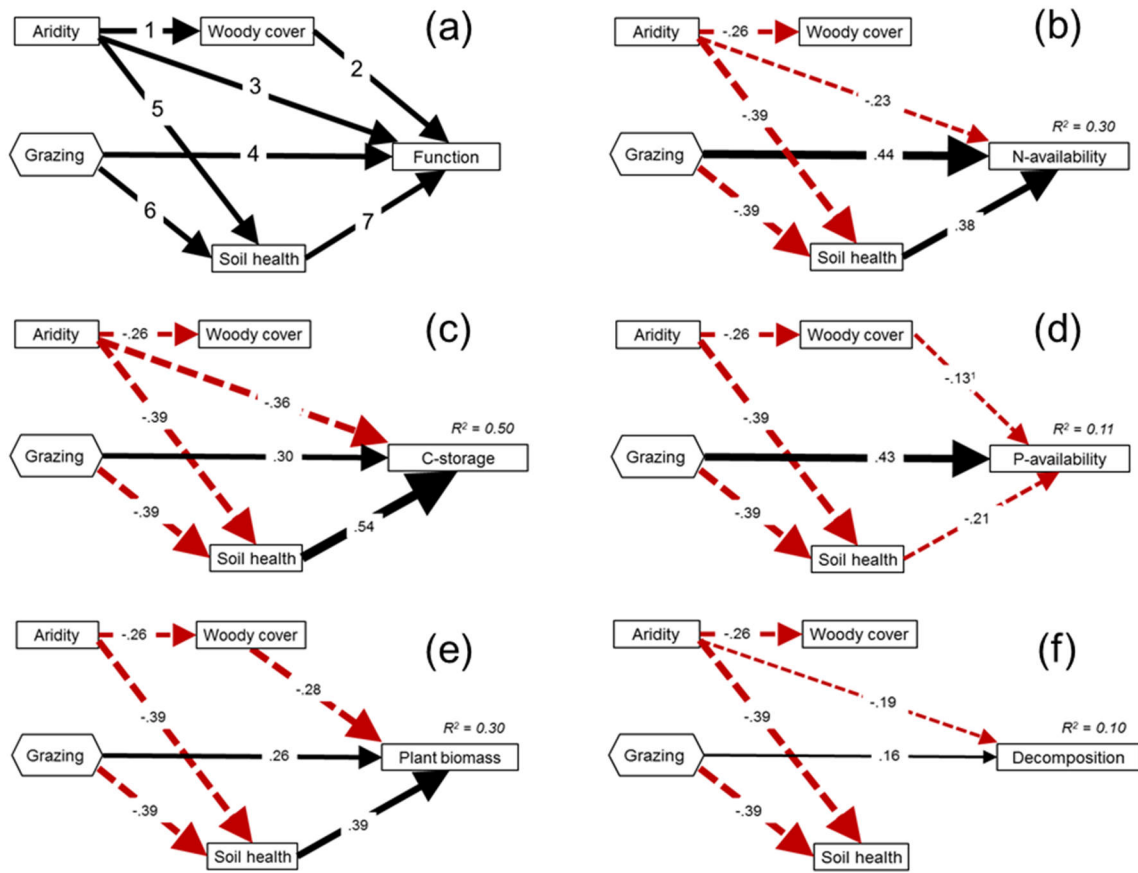
Figure 1. Structural equation models for (a) the *a priori* model and (b)–(f) five ecosystem services. Grazing is a composite variable comprising recent grazing by all herbivores, and historic grazing by livestock. Standardized path coefficients, embedded within the arrows, are analogous to partial correlation coefficients, and indicate 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 is shown in each figure. Only significant pathways are shown in the models. Model fit: $\chi^2 = 8.48$, df = 9, $P = 0.49$. [1] $P = 0.09$, [2] $P = 0.10$.
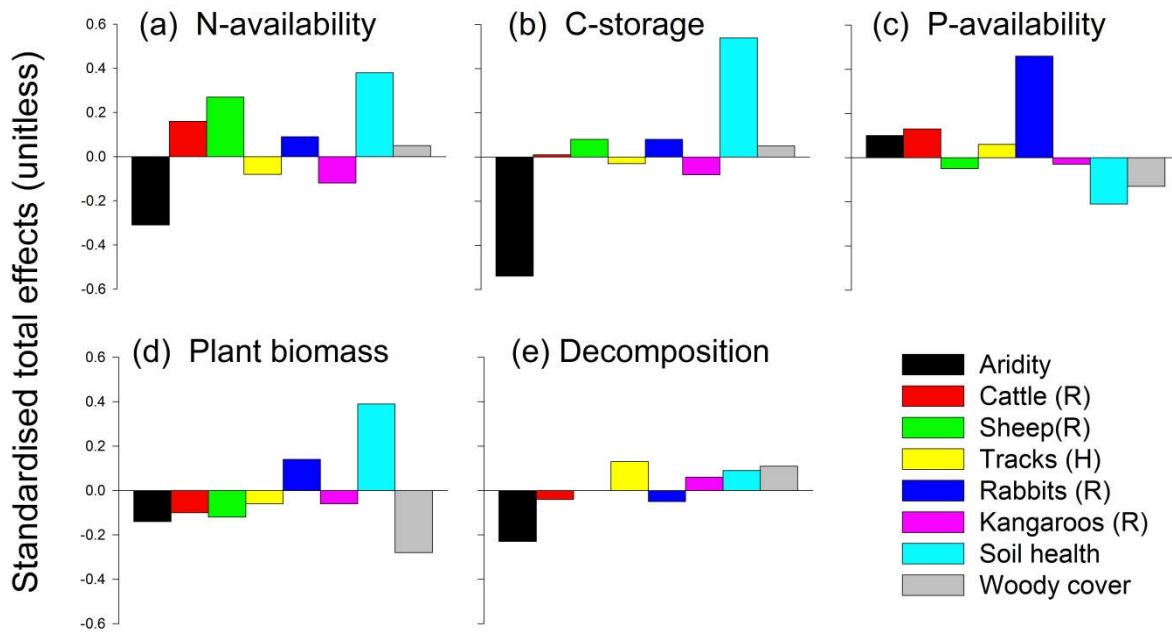
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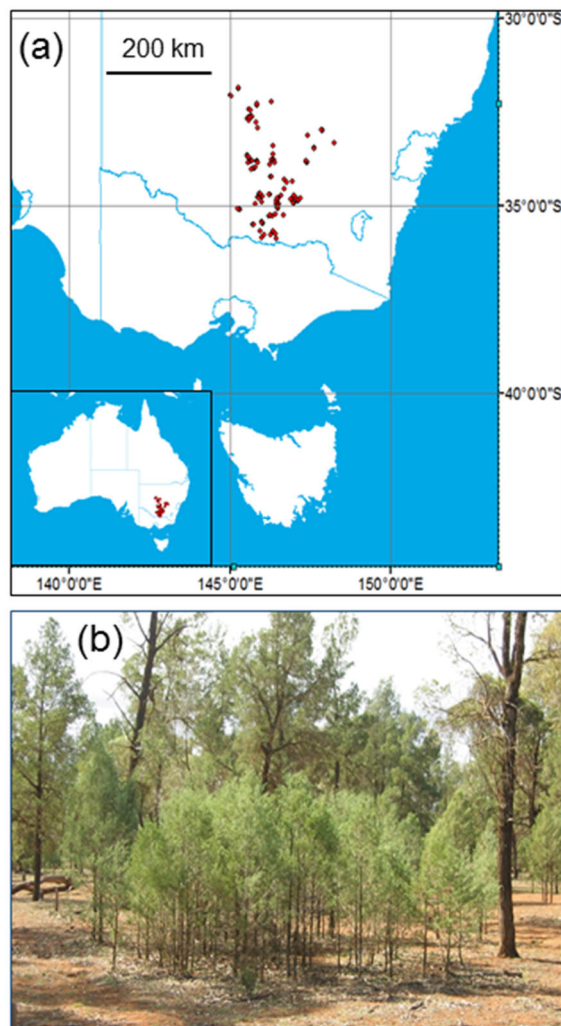
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818 Figure 2. (a) Location of the 151 sites in eastern Australia and (b) a view of a typical *Callitris*
819 *glaucophylla* woodland showing mature trees (background) and young saplings (foreground).

822   Figure 3. Standardised Total Effects (STE) of aridity, the five measures of grazing, soil health

823   and woody cover on the five ecosystem services indices. The STE is the sum of direct and

824   indirect effects on a particular response variable. R = recent grazing, represented by Cattle,

825   Sheep, Kangaroos and Rabbits. H = historic grazing, represented by Tracks.

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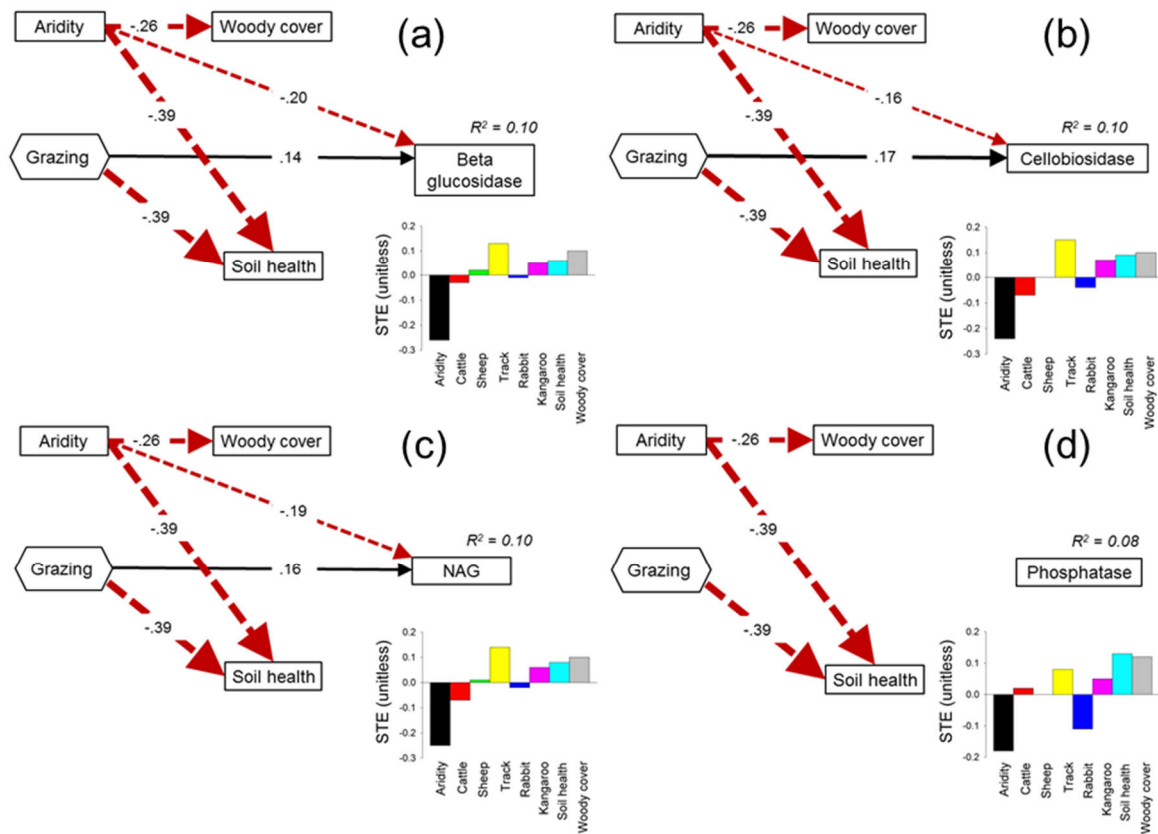
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829   Figure 4. Structural equation model for extracellular enzyme activities: a) β-glucosidase, b)

830   cellobiosidase, c) NAG (N-acetyl-β-glucosaminidase), and d) phosphatase including the

831   standardised total effects of aridity, measures of grazing, soil health and woody cover.