Multiple trade-offs regulate the effects of woody plant removal on biodiversity and ecosystem functions in global rangelands

Running title: Trade-offs under woody plant removal

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ABSTRACT

Woody plant encroachment is a major land management issue. Woody removal often aims to restore the original grassy ecosystem, but few studies have assessed the role of woody removal on ecosystem functions and biodiversity at global scales. We collected data from 140 global studies and evaluated how different woody plant removal methods affected biodiversity (plant and animal diversity) and ecosystem functions (plant production, hydrological function, soil carbon) across global rangelands. Our results indicate that the impact of removal is strongly context dependent, varying with the specific response variable, removal method, and traits of the target species. Over all treatments, woody plant removal increased grass biomass and total groundstorey diversity. Physical and chemical removal methods increased grass biomass and total groundstorey biomass (i.e., non-woody plants, including grass biomass), but burning reduced animal diversity. The impact of different treatment methods declined with time since removal, particularly for total groundstorey biomass. Removing pyramid-shaped woody plants increased total groundstorey biomass and hydrological function but reduced total groundstorey diversity. Environmental context (e.g., aridity and soil texture) indirectly controlled the effect of removal on biomass and biodiversity by influencing plant traits such as plant shape, allelopathic or roots types. Our study demonstrates that a one-size-fits-all approach to woody plant removal is not appropriate, and that consideration of woody plant identity, removal method, and environmental context is critical for optimizing removal outcomes. Applying this knowledge is fundamental for maintaining diverse and functional rangeland ecosystems as we move towards a drier and more variable climate.

Keywords: encroachment, thickening, shrub removal, removal method, woody plant traits, rangeland management, meta-analysis, global synthesis

1. INTRODUCTION

Rangelands cover about half of Earth's land surface and account for about a third of the terrestrial net primary productivity (Hassan, Scholes, & Ash, 2005). Moreover, they support much of the world's livestock production and are critical for human well-being and global ecosystem sustainability, particularly in developing countries (Steinfeld et al., 2006). Climate change and land degradation threaten the social and ecological viability of rangeland pastoral enterprises and thus present substantial challenges for rangeland managers. Over the past few decades, land use (e.g., overgrazing, tree clearing) and climate change (e.g., increasing atmospheric carbon dioxide), combined with biophysical feedbacks across episodic climate cycles and altered fire regimes (Maestre et al., 2016), have resulted in a proliferation of woody plants, particularly shrubs, across the world's rangelands (Archer & Predick, 2014). This phenomenon, known variously as woody encroachment or thickening, is characterized by pronounced, rapid increases in the cover and density of woody plants at the expense of herbaceous species, particularly grasses (Eldridge et al., 2011). Despite the extensive literature reporting positive effects of woody plants on soil fertility and on understorey vegetation globally (Eldridge, Soliveres, Bowker, & Val, 2013; Soliveres et al., 2014; Ward et al., 2018), encroachment is commonly believed to have negative impacts on biodiversity and ecosystem functions and is often associated with ecosystem degradation (Eldridge et al., 2011; Schlesinger et al., 1990). Consequently, the removal of woody plants has been promoted as a method to restore grassland function across global rangelands (Archer & Predick, 2014).

Recent studies, however, have questioned the efficacy of woody removal to promote ecosystem biodiversity and function (Archer et al., 2010; Archer & Predick, 2014; Soliveres & Eldridge, 2015). For example, Eldridge, et al. (2011) showed that the effects of woody plant encroachment on ecosystem functioning ranged from positive to negative, depending on land use objectives (e.g., conservation *cf.* grazing). In addition, the impacts of shrub removal have been found to vary within similar environmental conditions (Archer & Predick, 2014), suggesting the involvement of other site-specific drivers (e.g., plant species, removal methods). For example, a meta-analysis of

North American data showed that the largest response in herbaceous biomass to woody removal occurred within a specific range of environmental conditions (300-700 mm rainfall range; Archer & Predick, 2014). Other studies suggest that removal is predicted to be less effective and recovery from disturbance more protracted in arid environments due to lower ecosystem resilience (Maestre et al. 2016), and that under similar climates, the effect of woody removal on groundstorey biomass is greatest on finer textured soils (Hughes et al., 2006). Although previous studies have advanced our understanding of woody removal effects on ecosystem functioning, a global synthesis of its effects on biodiversity and ecosystem function is still lacking (but see Archer et al., 2011 for a regional synthesis). This hampers our ability to optimize the outcomes of woody plant removal in rangelands.

Herein, we posit that the effectiveness of woody removal for regulating ecosystem functions and biodiversity is context dependent (e.g., shrub type and removal method) and varies across contrasting ecological settings. For example, the traits of woody plant are important proxies of the extent to which they regulate the responses of biodiversity and functions to woody plant removal globally (Eldridge et al., 2011). The balance of plant-plant interactions (i.e. facilitation and competition) depends on woody functional attributes such as allelopathy, nitrogen fixation and ability to resprout (Callaway & Walker, 1997), and therefore, the removal of shrubs with different functional traits might differentially affect the outcomes of woody plant removal in rangelands. Faunal diversity is also affected by particular traits associated with woody encroachment, with different plant architecture leading to a range of diverse habitats. For example, plant height and shape directly affect habitat features, the capacity for rainfall interception, radiation, shelter and food provision, and advantage taxa that are woody habitat specialists at the expense of open habitat species (Eldridge & Soliveres, 2015; Lloyd & Vetter, 2019). Thus, the effects of woody removal on biodiversity and ecosystem function might be a direct consequence of specific plant traits. Another ecological cost of woody encroachment is the change in hydrological function with reductions in interspace infiltration, accelerated groundwater recharge and transpiration losses (Huxman et al., 2005). Such effects also differ with different root systems and canopy size, with large and deep-rooted species having a strong capacity to access groundwater, scavenge resources from the interspaces, and intensify evaporation (Schlesinger et al., 1990). The impact of woody plants on erosion control and soil fertility has also been shown to vary with plant traits, with soil function peaking at intermediate levels of woody plant cover (Soliveres et al., 2014). Carbon sequestration, a function known to be enhanced by woody encroachment (Archer et al., 2010), also depends on the water use efficiency (Huxman et al., 2005) and growth form (e.g., leaf area and deciduousness; Knapp et al., 2008) of woody species. Despite the potential importance of plant functional traits, studies that have comprehensively evaluated how differences in woody plant traits regulate the effects of removal on biodiversity and ecosystem function are sorely lacking.

In addition, we further propose that removal method is a major regulator of the responses of biodiversity and function to woody plant removal. Woody management often involves physical removal, herbicide, fire, browsing by herbivores, or various combinations of these (Archer et al., 2011). Although physical removal is costly and labour intensive, it is still widely used in the USA, Africa and Australia to increase plant production for livestock. To date, however, there has been little or no critical assessment of the effectiveness of different treatment methods, the longevity of possible effects, and any co-benefits that might arise for biodiversity conservation and ecosystem functions following removal, apart from a regional assessment from North America (Archer et al., 2011). Moreover, the impacts of woody removal on biodiversity and ecosystem functions such as hydrological function, soil carbon and plant production, are likely to be mediated by differences in climate, treatment type, identity (traits) of the encroaching species, and the current land use (Archer & Predick, 2014). Synthesizing the net impacts and interactions of different drivers on woody plant removal would advance our understanding of the effects of removal and help us to optimize the ecosystem outcomes under changing climates.

Here we report on a study where we collected data from 140 studies from rangelands worldwide to synthesise the impacts of woody plant removal on biodiversity (groundstorey plant and animal diversity) and ecosystem functions (plant production, hydrological function and soil carbon sequestration). We used a combination of meta-analyses and structural equation modelling to address three key predictions. First, we examined whether the effects of woody plant removal on biodiversity and ecosystem functions vary with the response variables. For example, plant production (grass biomass or total groundstorey biomass) and total groundstorey diversity would be expected to increase following woody removal due to competitive release, while the impacts on animal diversity, hydrological function and soil carbon would more likely be varied because effects depend on soil properties and removal methods, which vary in their level of disturbance. Second, we expected that removal methods and functional plant traits would be significant factors regulating the response of biodiversity and functions to woody plant removal because these directly determine the magnitude of disturbance and species interactions. Third, environmental context would indirectly determine (e.g., by influencing plant traits), to a large extent, the response of biodiversity and ecosystem function to removal, as environmental factors regulate ecosystem productivity and resilience. For example, we might expect woody plant removal to increase ecosystem responses in more mesic areas, or on finer soils, as such ecosystems support higher productivity species that indirectly contribute to high ecosystem resilience following disturbance.

2. MATERIALS AND METHODS

2.1 Meta-analysis data building

We used a systematic meta-analysis approach (Nakagawa & Santos, 2012) to evaluate the general impact of woody plant removal on the rangeland function and biodiversity and explore the factors driving the variations. Meta-analyses are used widely in ecology to synthesise evidence from a large number of studies, to test hypotheses, and to evaluate ecological outcomes at global scales (Gurevitch, Koricheva, Nakagawa, & Stewart, 2018). We compiled a comprehensive database of ecosystem responses to woody plant removal from published global literature. First, we searched multiple databases (e.g., Web of Science, Scopus, Proquest Science & Technology, Informit Online, Environment Complete, Biosis and Geobase/Georef) for any online study published between 1900 and 2017, reporting an ecosystem impact of woody plant removal using search terms related to woody plant removal and treatment type (see detailed search string in Fig. S1.1 in

Appendix S1). We then screened studies on the ecosystem impacts of woody plant removal using the PRISMA procedure (Liberati et al., 2009), ensuring that all studies: 1) were conducted under natural conditions using field experiments, 2) reported relevant quantitative data, variance and number of observations, 3) focused on ecosystem responses to woody plant removal, 4) specified the removal method, 5) reported changes related to woody plant removal, and 6) compared plots where woody plants had been removed and retained (i.e., treatment and control; see Appendix S1 for detailed criteria). This yielded 263 publications. We then focused on six ecosystem responses that are valued by land managers, pastoral producers or conservation managers, and for which we had sufficient data to perform analyses. We used plant biomass as our measure of plant (forage) production with (1) grass biomass (i.e. annual or perennial grass) and (2) total groundstorey production (non-woody plant biomass, including grass, forb and herb). Total groundstorey diversity (3) (i.e. non-woody plant diversity, including grass, graminoid, forb and herb) and (4) animal diversity were used to represent the diversity of rangeland flora and fauna. Finally, (5) hydrological function (i.e. evaporation, soil infiltration, runoff, water recharge) and (6) soil carbon represents the capacity of the soil to conduct water and sequester carbon in the soil (i.e., labile carbon, organic carbon, total carbon content). Based on these criteria, 140 publications met our criteria for inclusion in the analyses, and 29 response variables were included under the six ecosystem responses (see Fig. 1 for the global distribution of studies; A list of the data source is found in Appendix S2; Table S3.1 in Appendix S3 for response variables).

2.2 Data collation

From each publication we extracted the following information: geographical location, woody plant removal treatment (i.e., physical, chemical, burning, multiple), years since treatment, sample size, and the mean and standard deviation of the ecosystem responses that were assessed on woody plant removal and retention plots. Numeric values were extracted from figures using the software Engauge Digitizer V 4.1 (http://digitizer.sourceforge.net/). We also recorded the identity of the removed woody plant species in each study and compiled data on 10 plant traits for each of these 64 species. These traits described plant function and allowed us to explore their effects on the outcome of woody plant removal. Plant traits included three continuous measures of maximum, minimum and mean plant height; two categorical measures of plant shape (v-shaped, round, weeping and pyramid) and root type (tap root, lateral root, both tap and lateral roots), and five binary measures of whether the species is allelopathic, fixes nitrogen, has the ability to resprout after disturbance, has foliage that reaches the ground surface, and whether it is deciduous or evergreen (Table S4.2, Appendix S4) based on online plant traits databases such as BROT (Tavşanoğlu & Pausas, 2018), PLANTS (USDA 2019), Woody Plants Database (http://woodyplants.cals.cornell.edu/home), TRY (Kattge et al., 2011), and Wikispecies (https://species.wikimedia.org/wiki/). Environmental conditions (i.e. Aridity Index and soil texture) for each study location were extracted from global databases. The Aridity Index (AI = precipitation/potential evapotranspiration) was derived from the Consortium for Spatial Information (CGIAR-CSI) for the 1950-2000 period (Zomer, Trabucco, Bossio, & Verchot, 2008) (http://www.cgiar-csi.org/data/global-aridity-and-pet-database) and soil clay content were obtained from the HWSD database (resolution 1km) (http://www.fao.org/soils-portal/soil-survey/soil-maps-and-databases/harmonized-world-soil-database-v12/en/). In this study, we defined aridity as 1 minus Aridity Index so that increases in aridity corresponded to greater dryness. The validation of soil texture derived from HWSD dataset is shown in Appendix S5.

2.3 Effect size and estimate mean effect sizes

We used a log response ratio of the effect size to determine the relative effect of woody plant removal on selected ecological attributes for the six ecosystem responses: LnRR= $\ln(X_t/X_c)$ (Hedges, Gurevitch, & Curtis, 1999) where X_t is the value of the ecological attribute in the woody plant removal plot (i.e. treatment), and X_c is the value of the ecological attributes in the woody plant retention plot (i.e. control). Positive values of this ratio indicate an increase in the value of the ecological attributes after woody plant removal and *vice versa*. We constructed a dataset of 1774 contrasts of woody plant removal and woody plant retention based on the data from 140 studies (Table S3.1). For hydrological function, increases in the values of most ecological attributes indicate a positive effect on hydrological function, but for others (e.g., runoff), increases indicate a reduction in hydrological function. The LnRR for the latter case were therefore 'coined', i.e. multiplied by -1, so that increasing LnRR scores indicated an increase in hydrological function (Eldridge, Poore, Ruiz-Colmenero, Letnic, & Soliveres, 2016).

We used a random effects model to calculate the estimated mean effect sizes for the six ecosystem responses after accounting for the effects of random factors within the database. In the random effects model, we used random factors and a variance matrix to control for three potential sources of non-independence. First, we included reference identification (ID) to account for non-independence among observations from a single study. Second, we included a unique data record ID corresponding to data order to account for non-independence among the residuals of each data record and the potential bias from sample size. Third, to account for the lack of independence in studies with multiple treatments but a single control, we coded observations that used the same (shared) control with a unique code and calculated a variance matrix based on the variance of response attributes and shared control pairs (Nakagawa & Santos, 2012). For the meta-analysis model, we ran an intercept-only model (null model) with the LnRR of each ecological attribute as the response, the variance matrix as the within-study variance, and an inverse gamma prior for the random effect of reference ID and data order to estimate mean effect sizes for these six ecosystem responses. Data with extreme variances (>1000 or <0.0001) were excluded, resulting in 1482 rows of data used to calculate the overall effect size in Fig. 2. The significance of the estimated effect size was examined with a *t*-test on whether estimated effect size differed significantly from zero at $P < 0.05$. Publication bias was examined using funnel plots (see Fig. S6.2 in Appendix S6), Egger regression and 'trim and fill' approaches (Nakagawa & Santos, 2012) for the whole dataset (see Appendix S6). The meta-analysis was performed in the 'metafor' package (Viechtbauer, 2010) in R 3.4.1 version (R Core Team, 2018).

2.4 Structural equation modelling

We used Structural Equation Modelling (SEM; Grace, 2006) to explore the direct and indirect effects of environmental conditions (aridity and soil texture), treatment patterns (treatment method and time since treatment) and traits of removed woody plants on each of the six ecosystem responses to woody plant removal. Aridity, soil texture, and time since treatment were continuous variables whereas treatment was binary and therefore designated as zero or one. Categorical plant traits (Fig. S7.3 in Appendix S7) were converted to numerical values (Table S7.4 in Appendix S7). To avoid collinearity among the 10 plant traits (Appendix S4), we systematically selected moderators using variance inflation factors (VIF; see Tables S8.5 to S8.8 in Appendix S8) which result in six traits (mean plant height, plant shape, roots type, the ability to resprout after disturbance, allelopathy, nitrogen fixation) included into the SEM. Structural equation modelling allowed us to test the hypothesized effects and relationships among the main drivers and six ecosystem responses based on an *a priori* model (see Fig. S9.4 in Appendix S9). Our *a priori* model predicted that environmental conditions (i.e. aridity and soil texture) would have direct effects on the six ecosystem responses, as well as indirect effects, mediated by the traits of the removed woody plants. The different woody plant removal treatments were fixed according to the particular studies, as selection of removal method depends on many variables such as environment conditions, cost and availability of techniques, feasibility of removing encroached species, and the preference of managers, to name a few. Therefore, we only explored the direct effects of treatments on ecosystem responses in this meta-analysis due to the lack of sufficient data on the factors that determine the selection of different treatments. We used soil clay content as our measures of soil texture. The traits of removed plants comprised the six woody plant traits described above. Plant height and allelopathy was excluded in the soil carbon SEM due to their high correlation with nitrogen fixation ($r = 0.94$) and plant shape ($r = 1.00$) respectively, resulting in an overfitted model (path coefficient >1). Treatment methods used to remove woody plants were either 1) chemical, 2) physical, 3) burning or 4) multiple methods. Other rarely used treatments (e.g., grazing, browsing) were not explicitly included in our SEM. We also included a component that represented time since treatment (Time). We used the effect size (LnRR) of each value of the relevant ecosystem responses as the response variable in each model. Thus, the model evaluated the direct effects of time since treatment, treatment method and plant traits, and the direct and indirect effects of aridity and soil clay on the outcome of woody plant removal compared to woody plant retention.

Overall goodness-of-fit probability tests were performed to determine the absolute fit of the best models, using the χ^2 statistic. The goodness of fit test estimates the likelihood of the observed data given an *a priori* model structure. Thus, high probability values indicate that these models have highly plausible causal structures underlying the observed correlation. Models with low χ^2 and Root Mean Error of Approximation (RMSEA < 0.05) and high Goodness of Fit Index (GFI) and R^2 were selected as the best fit model for our data. Standardized direct, indirect effects and variance explained by each factor for the six SEM models were shown in Table S10.9 in Appendix S10. We also calculated the standardized total effects of each explanatory variables to show the total effect of each variables. Analyses were performed using AMOS 22 (IBM, Chicago, IL, USA) software.

3. RESULTS

3.1 Ecosystem response to woody plant removal

The responses of biodiversity and functions to woody plant removal were varied, resulting in groups of winners and losers. For example, woody plant removal resulted in a 30% increase in the response of grass biomass, but no significant difference in the response of total groundstorey biomass (Fig. 2). Removing woody plants, overall, increased the response of total groundstorey diversity (11%) but had no net effect on the response of animal diversity. The response of soil carbon and hydrological function to woody plant removal was negative, but highly variable and insignificant overall (Fig. 2).

3.2 Drivers of ecosystem responses to woody plant removal

Our SEMs provide further evidence that the effects of woody removal on biodiversity and functions are context-dependent and varied across plant traits and removal methods. For example, we found that removing nitrogen fixing or resprouting plants reduced biomass or hydrological function (Table 1). Moreover, we found some trade-offs in the effects of woody removal on biodiversity and ecosystem functions. For example, the removal of pyramid-shaped plants tended to be associated with greater total groundstorey biomass and hydrological function (Figs. 3c, 5a) but reductions in total groundstorey diversity (Fig. 4a). Removal of resprouting or non-allelopathic plants consistently reduced biomass (i.e. grass biomass or total groundstorey biomass; Figs. 3a, 3c) but has contrast effect on total groundstorey diversity (Fig. 4a). Similarly, removing tall plants or those with deep and lateral roots reduced animal diversity, and removing non-allelopathic plants reduced hydrological function (Fig. 4c, Fig. 5a). In contrast, soil carbon was unaffected by any plant traits (Fig. 5c).

Removal method was another crucial factor regulating ecosystem responses, with burning and physical removal being the most influential (Table 1). For example, in the SEMs, the response of grass and total groundstorey biomass to woody removal was strongly affected by removal method, with physical or chemical removal methods significantly increasing the biomass response (STE = 0.15 to 0.31, Figs. 3b, 3d). Burning reduced animal diversity (Fig. 4c), whereas no removal method significantly affected total groundstorey diversity, hydrological function or soil carbon. Time since woody removal has a significant, but small effect on total groundstorey biomass (Fig. 3c).

We also found that environmental factors were important regulators of the responses of biodiversity and functions to woody removal. Increases in aridity resulted in positive biomass responses but reduced the soil carbon response (Table 1). In addition, from our SEMs, we found that aridity directly increased grass and total groundstorey biomass and hydrological function, with the greatest increases occurring in drier areas (Figs. 3a, 3c, 5a). We also detected some weak, indirect mixed effects of aridity and soil clay on several ecosystem responses. Increasing aridity reduced the response of grass and total groundstorey biomass to woody plant removal by intensifying the negative effects of removing non-allelopathic woody plants (Figs. 3a, 3c). Similarly, increasing soil clay content enhanced the suppressive effect of pyramid shaped plants, or tall plants, on groundstorey and animal diversity (Figs. 4a, 4c). Increasing aridity reduced hydrological function by either suppressing the positive effect of removing pyramid-shaped plants or enhancing the negative effect of removing non-allelopathic plants (Fig. 5a).

4. DISCUSSION

4.1 Impacts of woody removal depend on the functions assessed

We showed that, on average, woody removal increased grass biomass and total groundstorey diversity, but its effects on total groundstorey biomass, animal diversity, hydrological function and soil carbon were mixed, and largely insignificant overall. Woody plants are known to compete strongly with groundstorey plants, including grasses, by either altering environmental conditions (e.g., shading and rainfall interception) or by intensifying belowground resource competition (e.g., exploiting water and nutrients; Scholes & Archer, 1997). Consequently, removing woody plants can release understorey plants from competitive exclusion (Abule, Smit, & Snyman, 2005), promoting fast growing grass species (Reich, 2014), and increasing the diversity and cover of groundstorey plants. Compared with grass biomass, the response of total groundstorey biomass was highly variable, potentially due to complex interactions (e.g., competition or facilitation) among woody and non-woody species (Ludwig, Dawson, Prins, Berendse, & De Kroon, 2004). For example, deeply-rooted species compete with woody plants for water, while shallow-rooted species are often facilitated by woody plants through hydraulic lift (Caldwell, Dawson, & Richards, 1998). Thus, the removal of woody plants can alter species interactions to favour competitive species at the expense of facilitated species, with no overall net effect.

Woody removal, overall, had no significant effect on animal diversity with reductions only in amphibian abundance, while arthropod, bird and mammal abundance and diversity displayed mixed responses (Fig. 2, Table S3.1 in Appendix S3). The overall insignificant response may reflect the changing balance between grassy open and woody habitats. Removing woody plants may favour grassland specialist birds or rodents (Coffman, Bestelmeyer, Kelly, Wright, &

Schooley, 2014; Kutiel, Peled, & Geffen, 2000) at the expense of woody-obligate taxa such as reptiles (Jones, Fox, Leslie Jr, Engle, & Lochmiller, 2000; Germano & Hungerford, 1981), resulting in no overall significant difference (Fig. 2, Table S3.1 in Appendix S3). In addition, time lags in the response of different faunal groups to habitat change may explain the insignificant effects. For examples, a study in North America showed that bird community richness did not differ between the control 3 years after burning due to rapid succession in the groundstorey vegetation, which compensated for changes in the woody community (Newman, Potts, Tingley, Vaughn, & Stephens, 2018). Similar results were also found in long-term (10-30 year) studies of mammals such deer (Ruthven III, Hellgren, & Beasom, 1994) and rats (Fulbright, Alejandro Lozano-Cavazos, Ruthven III, & Lite, 2013), which were unaffected by root-plowing due to the rapid reestablishment of the vegetation community. Furthermore, increases in grassland species may accompany declines in woody dependent species, resulting in no net change in total animal diversity (Archer & Predick, 2014). An insignificant effect on fauna may also result from non-linear responses of grass obligate fauna to changes in woody cover (McCleery et al., 2018; Macchi et al., 2019).

We also failed to detect any signal of hydrological recovery or soil carbon reduction following woody plant removal, consistent with previous studies (Acharya, Kharel, Zou, Wilcox, & Halihan, 2018; Huxman et al., 2005). Rather, the response was highly variable, reinforcing our view that woody removal produces context-dependent results. Hydrological effects of woody removal are likely depended on spatial scale and plant traits. At the plant scale, infiltration beneath woody plants is greater than in the interspaces due to root- and invertebrate-derived macropores (Eldridge, Wang, & Ruiz-Colmenero, 2015). Thus, different roots distributions could produce varied effects on infiltration. At landscape scales, dense woody encroachment could reduce hydrological function by altering the downward flux of water and therefore recharge rates (Acharya et al., 2018), or reduce surface and subsurface flows (Qiao, Zou, Stebler, & Will, 2017). Although we found no evidence for a direct effect of woody plants on soil carbon, our STEs suggest a general depression, particularly for burning (Fig. 5d). Moreover, studies conducted over a longer time periods since treatment, or at different levels of encroachment, may have revealed different responses. Less than 10% of our data represented studies conducted over decadal time scales, making it difficult to capture changes in ecosystem states and transitions that occurs over large temporal scales. Soil carbon, for example, takes many centuries to recover after grassland restoration (Rosenzweig, Carson, Baer, & Blair, 2016) and can take decades to detect significant carbon loss by frequent burning (Pellegrini et al., 2018).

4.2 Ecosystem responses to plant removal are driven by removal method

Removal can promote grass and total groundstorey biomass when physical (e.g., cutting, chopping, root ploughing) or chemical (e.g., herbicide) methods are used. Physical and chemical methods are effective for reducing woody plants as they often induce whole plant mortality (e.g., herbicide, chaining, root-ploughing), inhibiting regrowth (Bates, 2005; Hodgkinson & Harrington, 1985; Wiedemann & Cross, 2001). Despite this, increases in total groundstorey biomass are relatively transient, as responses decline with time since treatment (Fig. 3c). In contrast, burning significantly reduced animal diversity effects (Fig. 4c). This result seems inconsistent with the general view that burning is often used to increase biodiversity through its effect on heterogeneity (Parr & Andersen, 2006), thereby generating a greater range of faunal resources (e.g., Smith, 2000). However, the effect of burning as a restoration technique is highly taxon dependent (Pastro, Dickman, & Letnic, 2011), and burning has been shown to indirectly reduce the some faunal groups by reducing coarse woody debris, which is important habitat for invertebrates, small mammals and amphibians (Bunnell, 1995; Smith, 2000; Kwok & Eldridge, 2016). For example, an Australian study showed that bird richness declined after burning, but vertebrates were less affected (Lindenmayer, Wood, MacGregor, Hobbs, & Catford, 2017). Other studies range from rapid recovery of bird richness within 3 years (Newman et al., 2018) to no effect 7 years after burning (Long, Jensen, & Matlack, 2014), indicating lag response in fauna groups. Responses to burning may also be related to pre-treatment encroachment levels. For example, shrub removal by fire is more effective in low density stands that support greater fuel loads (Hodgkinson & Harrington, 1985).

4.3 *Response of biodiversity and functions to woody removal vary with trait and environment*

Our study provides further evidence, from a global synthesis, that the ecosystem outcomes of removing woody plants are species-specific, varying with the traits of the focal species and consistent with findings in the literature (Bestelmeyer et al., 2013; Eldridge et al., 2011). Woody plant height and shape mainly affected the ecosystem response by altering plant-plant interactions. Removal of tall woody plants reduced animal diversity (Fig. 4c). Large-sized plants can provide more food resources and refugia for small mammals and invertebrates (Derraik, Closs, Dickinson, Barratt, & Sirvid, 2002), so their removal likely reduces habitat quality. Unlike tall woody plants, removing pyramid-shaped plants had contrasting effects on groundstorey biomass and diversity. We found that pyramid-shaped plants with wider canopies, which can intercept more rainfall and moderate fluctuations in temperature and evaporation, can support a more diverse understorey species compared with those with narrow canopies (De Soyza, Franco, Virginia, Reynolds, & Whitford, 1996; Gómez-Aparicio, Gómez, Zamora, & Boettinger, 2005) and such facilitate effect would be weaken once these woody plants were removed (Fig. 4a). By contrast, the weak positive effect of removing pyramid plants on total groundstorey biomass (Fig. 4c) indicated the fact that removing facilitate species lead to a homogenous landscape dominated by the highly productive weedy plants with study found that forb dominant (73% cover) the landscape after 2 years of shrub removal in a encroached mesic grassland (Lett & Knapp, 2005).

Root type and allelopathic features also exert considerable effects on the outcomes of woody removal. Plants with deep and lateral roots are effective ionic pumps, extracting nutrients from lower in the profile (Attiwill & Adams, 1993) and advantaging understorey plants *via* hydraulic lift (Scott, Cable & Hultine, 2008). Removing species with deep and lateral roots would therefore disadvantage ground dwelling fauna such as invertebrates and amphibians that rely on dense understorey cover (Smith, 2000; Kwok & Eldridge, 2016). Non-allelopathic plants such as *Larrea divaricata* and *Prosopis glandulosa* have been shown to advantage understorey species by increasing soil nutrients (Schade & Hobbie, 2005; Zhou, Boutton, & Wu, 2018) and increasing plant biomass, but these effects waned following woody removal. The ability to resprout after disturbance is important for retaining woody habitat (Clarke, Lawes, & Midgley, 2010) but is also a crucial factor inhibiting the success of woody removal as it stimulates post-removal resource competition. Studies have shown that the effects of woody removal on increased herbaceous production vanished with the reestablishment of woody plants (Archer & Predick, 2014), consistent with our findings that the removal of resprouting species reduces grass biomass and groundstorey diversity.

Contrary to expectations, aridity and soil clay had only weak overall effects on the response of different functions, with most effects mediated by plant traits. Aridity directly affected the response to removal, with our data suggesting that removal from drier locations promotes plant biomass and recovery of hydrological function (Figs. 3a, 3c, 5a). Consistent with a regional synthesis (Archer et al., 2011), our results suggest that there are few effects in mesic areas, potentially because highly productive mesic systems can buffer reductions in woody cover, unlike arid and semi-arid systems. In addition, woody removal could potentially increase the capacity of invasive plants to flourish in mesic areas where resources are less limiting (Muvengwi, Mbiba, Jimu, Mureva, & Dodzo, 2018). Aridity and soil clay were more likely to affect the ecosystem response indirectly by regulating the occurrence of woody plant species of different traits. For example, aridity and soil clay content reduced the response of animal diversity to woody plant removal by increasing the occurrence of tall plants or those with deep and lateral roots (e.g., *Artemisia tridentata*, *Prosopis glandulosa*) in drier and finer soils, thus increasing the risk of losing species that facilitate protégé species and soil conditions (Attiwill & Adams, 1993; Scott et al., 2008) after woody removal (Figs. 4c, 4d).

Finally, our global synthesis highlighted some major gaps in the current literature, and therefore a number of limitations of our study. First, although the meta-analysis covered studies across different spatial and temporal scales, most (72%) reported short-term (< 5 years) effects and were limited to small spatial scales. Second, many studies failed to report important moderators such as initial level of encroachment, level of grazing and potential interactions with different treatments. This lack of explanatory data makes it more difficult to arrive at a truly global consensus given the wide range of histories, environments and approaches used to study woody removal. Finally, we pooled much of our data across different taxa and environment conditions into general ecosystem responses, partly to overcome this lack of data. Our study therefore is limited to an assessment of those factors (climate, soils, treatment patterns, encroached species) that are widely reported in the literature and should be interpreted as general findings on broad ecosystem responses that may differ from results reported in specific taxa/environment.

5. CONCLUSIONS

Our work provides compelling evidence that the impacts of woody plant removal on biodiversity and ecosystem function are strongly context dependent, varying across species with contrasting functional traits, environmental conditions and removal method, with no single condition can optimizing all ecosystem responses. Despite the limitations of the current literature, our meta-analysis provided a robust assessment of the impact of woody removal on rangeland ecosystems, and the effects of these factors on removal outcomes. Although regular removal and follow-up treatments with multiple techniques are likely to sustain the short-term effect of woody removal, the negative effect of removal treatment on animal diversity found in our study suggests that widespread and indiscriminate removal of woody plants may not be the best strategy for sustainable long-term rangeland management practices, particularly under drier, hotter climates that are predicted for Earth’s rangelands (Huang, Yu, Guan, Wang, & Guo, 2016).

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Table 1. Pearson's *r* correlations among the six ecosystem responses and the attributes used in the structural equation models. Only significant ($P < 0.05$) relationships are shown.

Attribute	Grass biomass	Total groundstorey biomass	Total groundstorey diversity	Animal diversity	Hydrological function	Soil carbon
Aridity	0.15	0.13	-	-	-	-0.24
Soil clay	-	-	-	-	-	0.21
Plant height	-	-	0.16	-0.18	-	0.22
Plant shape	-	-	-	-	-	-0.25
Nitrogen fixation	-0.09	-0.07	-	-	-	-
Allelopathy	-	-0.07	-	-	-	-0.25
Resprouting	-0.21	-0.17	0.27	-	-0.15	-
Root type	0.15	0.07	0.19	-	-	-
Physical	0.11	0.12	-	-	0.22	-
Chemical	0.18	-	-	-	-	-
Burning	-0.21	-0.12	-	-0.33	-	-
Multiple	-	-	0.17	-	-0.47	-0.21
Time since treatment	-	-	-	-	-0.23	-

Figure captions

Figure 1. Global distribution of 140 woody removal studies with different removal treatments

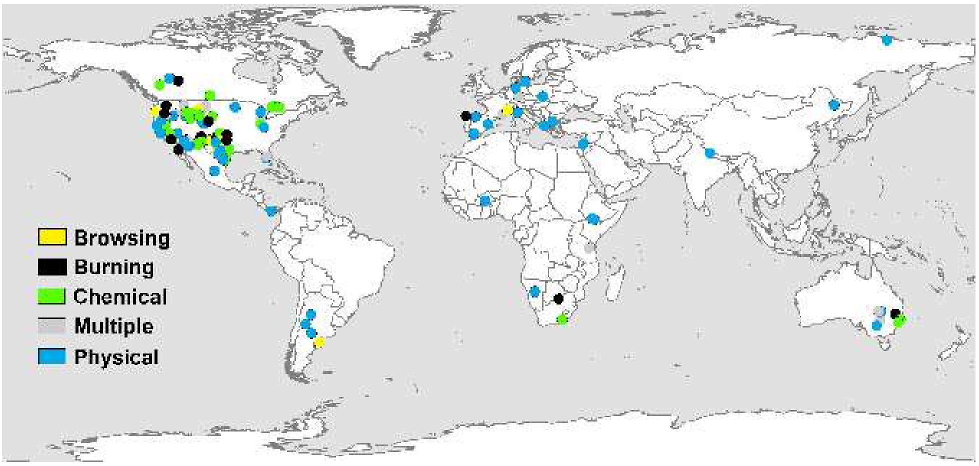
Figure 2. Mean (± 95% CI) log response ratio for the six ecosystem responses. Numbers indicate the number of observations. Blue circles represent response attribute significant increase ($P < 0.05$), grey circles represent non-significant response ($P > 0.05$).

Figure 3. Structural equation models of the direct and indirect effects of Aridity, Soil clay, Traits of the removed woody plants, Treatment, and Time since woody plant removal on the response of (a) grass biomass and (c) total groundstorey biomass to woody plant removal. Histograms illustrate the standardised total effects (STE: sum of direct plus indirect effects) derived from the structural equation modelling for (b) grass biomass and (d) total groundstorey biomass. 'Traits of removed plants' are represented by six plant traits (HT, mean plant height; SH, plant shape; RT, roots type; RE, the ability to resprout after disturbance; AL, allelopathy; NF, nitrogen fixation), 'Treatment', the method used to remove woody plants, comprises physical (PHY), chemical (CHE), burning (BUR) and multiple (MLT) methods. Time is years since woody plant removal. Standardized path coefficients, adjacent to the arrows, are analogous to partial correlation coefficients, and indicative of the effect size of the relationship. Pathway arrows are negative (red), positive (blue), mixed negative and positive (black), or non-significant (grey). Model fit: Grass biomass: $\chi^2 = 1.60$, df = 1, $P = 0.21$, GFI = 1, R^2=0.14, RMSEA = 0.03, Bollen-Stine = 0.08 (2000 bootstrap). Total groundstorey biomass: $\chi^2 = 1.14$, df = 2, $P = 0.57$, GFI = 1, R^2=0.11, RMSEA = 0, Bollen-Stine = 0.47 (2000 bootstrap).

Figure 4. Structural equation models of the direct and indirect effects of Aridity, Soil clay, Traits of the removed plants, Treatment, and Time since woody plant removal on the response of (a) total groundstorey diversity and (c) animal diversity to woody plant removal. Histograms illustrate the standardised total effects (STE: sum of direct plus indirect effects) derived from the structural

equation modelling for (b) total groundstorey diversity (d) animal diversity. Colours, symbols and abbreviations are same as Figure 3. Model fit: Total groundstorey diversity: $\chi^2 = 4.55$, df = 6, $P = 0.60$, GFI = 1, $R^2=0.28$, RMSEA = 0, Bollen-Stine = 0.19 (2000 bootstrap). Animal diversity: $\chi^2 = 3.17$, df = 3, $P = 0.37$, GFI = 1, $R^2=0.22$, RMSEA = 0.02, Bollen-Stine = 0.21 (2000 bootstraps).

Figure 5. Structural equation models of the direct and indirect effects of Aridity, Soil clay, Traits of the removed plants, Treatment, and Time since woody plant removal on the response of (a) hydrological function and (c) soil carbon to woody plant removal. Histograms illustrate the standardised total effects (STE: sum of direct plus indirect effects) derived from the structural equation modelling for (b) hydrological function (d) soil carbon. Colours, symbols and abbreviations are same as Figure 3. Mean plant height (HT) and allelopathy (AL) were not included into the model of soil carbon. Model fit: hydrological function: $\chi^2 = 0.63$, df = 1, $P = 0.43$, GFI = 1, $R^2=0.29$, RMSEA = 0, Bollen-Stine = 0.41 (2000 bootstrap). Soil carbon: Model fit: $\chi^2 = 1.55$, df = 1, $P = 0.21$, GFI = 1, $R^2=0.18$, RMSEA = 0.07, Bollen-Stine = 0.11 (2000 bootstraps).



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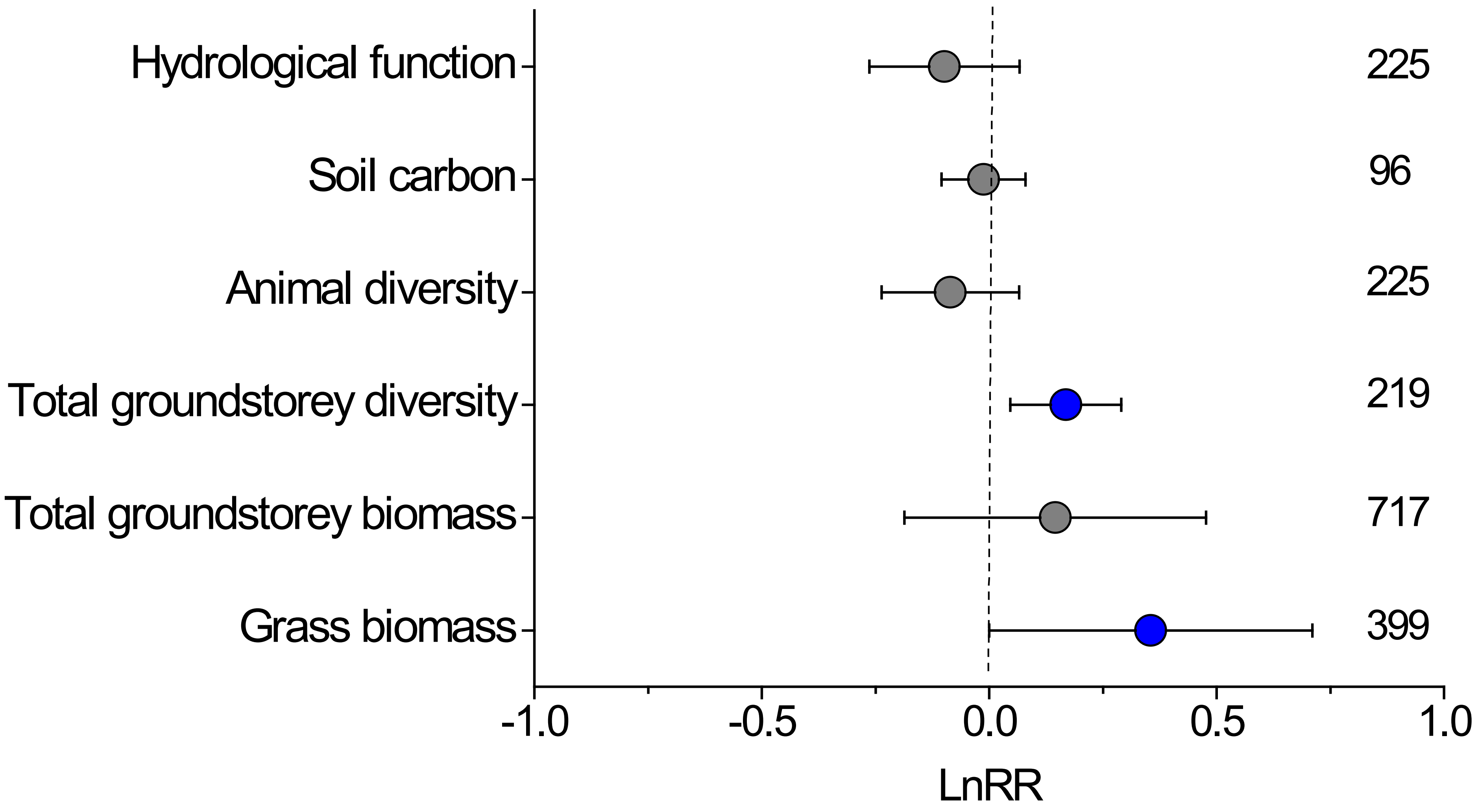
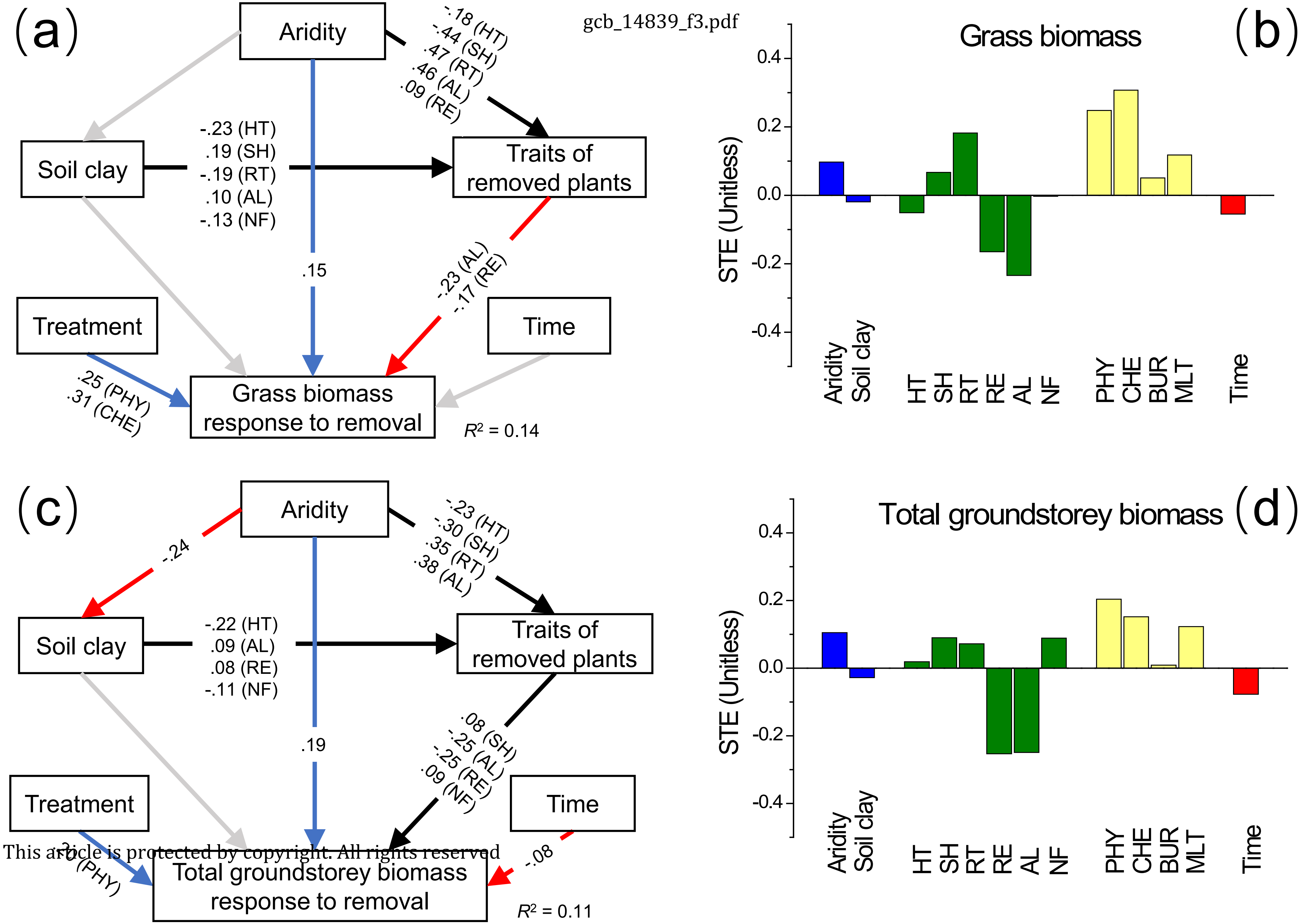
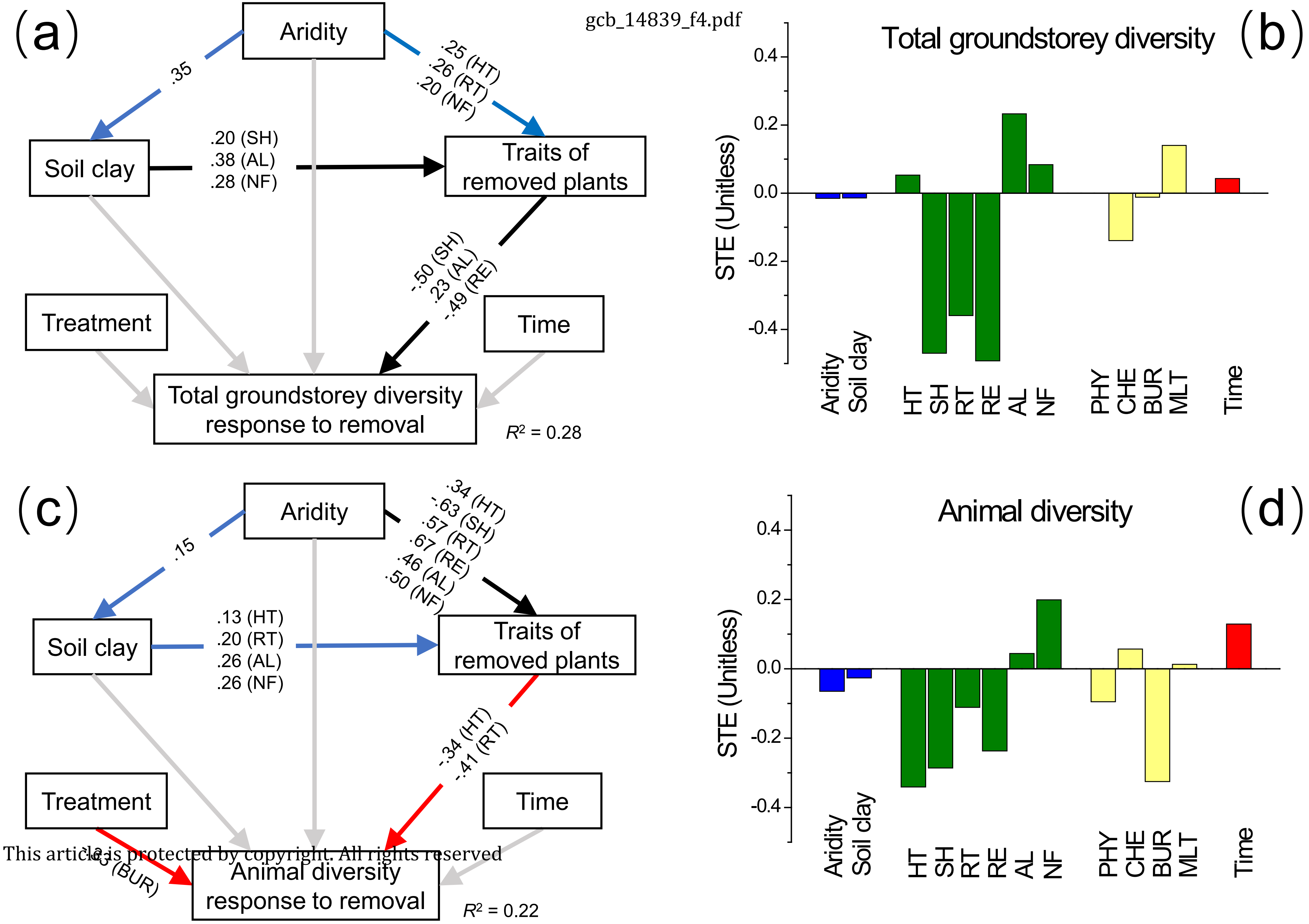
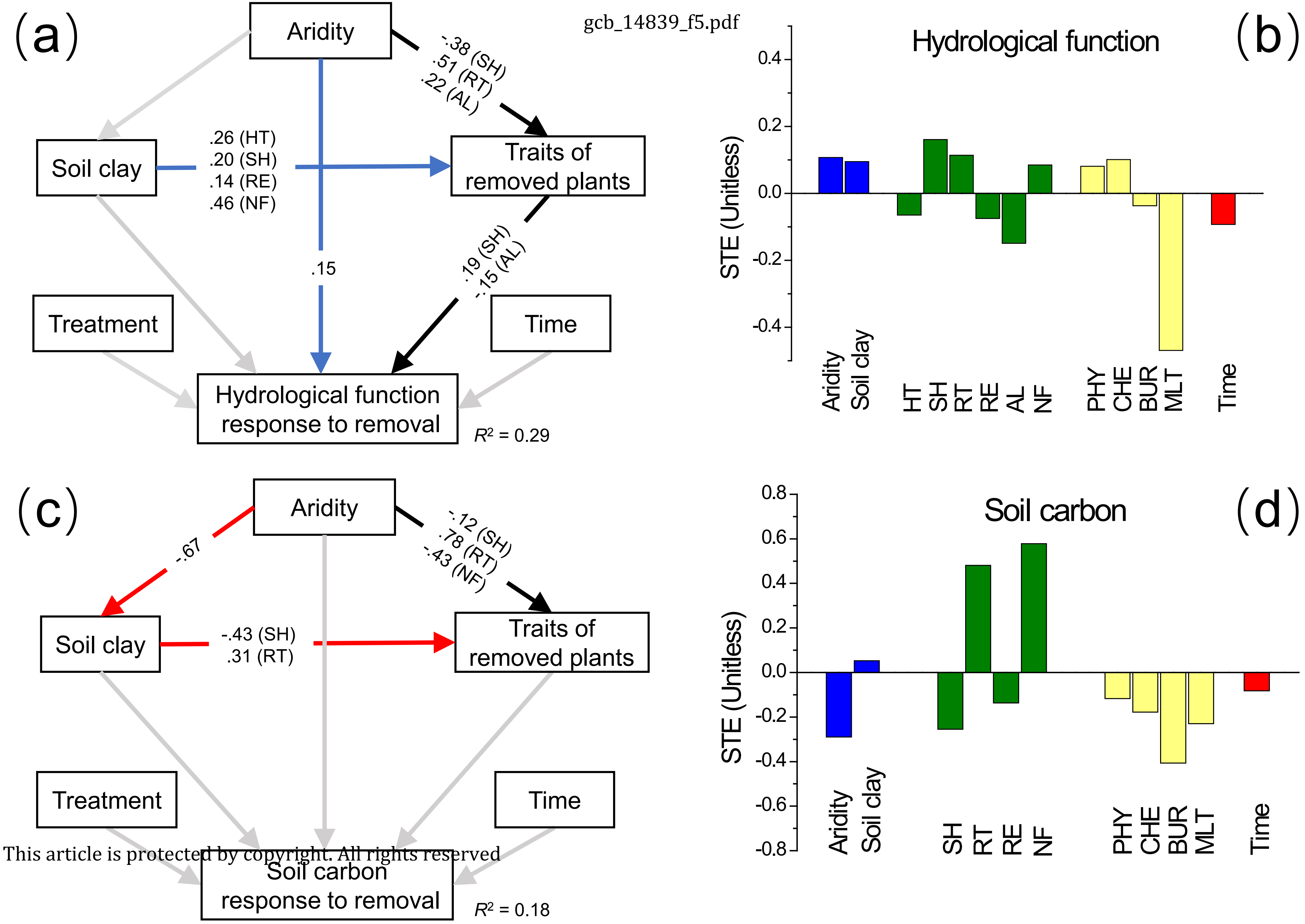

Hydrological function
Soil carbon
Animal diversity
Total groundstorey diversity
Total groundstorey biomass
Grass biomass
225
96
225
219
717
399
-1.0
-0.5
0.0
0.5
1.0
LnRR


(a)
Aridity
-.18 (HT)
-.44 (SH)
.47 (RT)
.46 (AL)
.09 (RE)
Soil clay
-.23 (HT)
.19 (SH)
-.19 (RT)
.10 (AL)
-.13 (NF)
Traits of removed plants
.15
-.23 (AL)
-.17 (RE)
Treatment
Time
.25 (PHY)
.31 (CHE)
Grass biomass response to removal
R^2 = 0.14
(b)
Grass biomass
STE (Unitless)
0.4
0.2
0.0
-0.2
-0.4
Aridity
Soil clay
HT
SH
RT
RE
AL
NF
PHY
CHE
BUR
MLT
Time
(c)
Aridity
-.24
-.23 (HT)
-.30 (SH)
.35 (RT)
.38 (AL)
Soil clay
-.22 (HT)
.09 (AL)
.08 (RE)
-.11 (NF)
Traits of removed plants
.19
.08 (SH)
-.25 (AL)
-.25 (RE)
.09 (NF)
Treatment
Time
.20 (PHY)
-.08
Total groundstorey biomass response to removal
R^2 = 0.11
(d)
Total groundstorey biomass
STE (Unitless)
0.4
0.2
0.0
-0.2
-0.4
Aridity
Soil clay
HT
SH
RT
RE
AL
NF
PHY
CHE
BUR
MLT
Time


(a)
Aridity
.35
.25 (HT)
.26 (RT)
.20 (NF)
Soil clay
.20 (SH)
.38 (AL)
.28 (NF)
Traits of removed plants
-.50 (SH)
.23 (AL)
-.49 (RE)
Treatment
Time
Total groundstorey diversity response to removal
R^2 = 0.28
(b)
Total groundstorey diversity
STE (Unitless)
0.4
0.2
0.0
-0.2
-0.4
Aridity
Soil clay
HT
SH
RT
RE
AL
NF
PHY
CHE
BUR
MLT
Time
(c)
Aridity
.15
.34 (HT)
-.63 (SH)
.57 (RT)
.67 (RE)
.46 (AL)
.50 (NF)
Soil clay
.13 (HT)
.20 (RT)
.26 (AL)
.26 (NF)
Traits of removed plants
-.34 (HT)
-.41 (RT)
Treatment
Time
-.13 (BUR)
Animal diversity response to removal
R^2 = 0.22
(d)
Animal diversity
STE (Unitless)
0.4
0.2
0.0
-0.2
-0.4
Aridity
Soil clay
HT
SH
RT
RE
AL
NF
PHY
CHE
BUR
MLT
Time


(a)
Aridity
-.38 (SH)
.51 (RT)
.22 (AL)
Soil clay
.26 (HT)
.20 (SH)
.14 (RE)
.46 (NF)
Traits of removed plants
.15
.19 (SH)
-.15 (AL)
Treatment
Time
Hydrological function response to removal
R^2 = 0.29
(b)
Hydrological function
STE (Unitless)
0.4
0.2
0.0
-0.2
-0.4
Aridity
Soil clay
HT
SH
RT
RE
AL
NF
PHY
CHE
BUR
MLT
Time
(c)
Aridity
-.67
-.12 (SH)
.78 (RT)
-.43 (NF)
Soil clay
-.43 (SH)
.31 (RT)
Traits of removed plants
Treatment
Time
Soil carbon response to removal
R^2 = 0.18
(d)
Soil carbon
STE (Unitless)
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
Aridity
Soil clay
SH
RT
RE
NF
PHY
CHE
BUR
MLT
Time