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Contrasting global effects of woody plant removal on ecosystem structure, function and composition

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ABSTRACT

Encroachment of woody plants into savannas and grasslands has increased markedly over the past century due to global changes in climate and intensified land use disturbance (e.g., grazing, fire). Removal of woody plants is mostly used globally to attempt to reinstate open woodlands and grasslands to increase forage plant production for livestock. However, there is still considerable controversy over the effectiveness of different removal programs and a global synthesis of removal impacts on ecosystem processes is still lacking, limiting our ability to provide ecologically-based advice on how best to manage woody encroachment. We used a global meta-analysis to explore the effects of woody plant removal on ecosystems. Analyses of 263 publications revealed that the overall effect of removal varied among different ecosystem response variables, with increases in composition (e.g., grass richness), reductions in structure (e.g., biocrust cover, woody plant cover and density), but no effects on function (e.g., increases in grass biomass, which compensated for reductions in soil roughness and shrub biomass). The outcomes of woody plant removal depended strongly on environmental context and woody plant traits, with removal more effective in mesic areas, but varied depending on both aboveground and belowground traits of the plants (e.g. plant shape, root types). Effectiveness of woody plant removal was relatively short-lived (i.e. within 5 years), but legacy effects on ecosystem function were generally large, negative, and lasted for up to 10 years. Our results highlight the wide disparity in removal outcomes, and reinforce the notion that the impacts of removal are strongly context dependent, vary with treatment methods, and generally ecologically undesirable in the long term. As climate changes, woody plant removal will become less effective due to drier climates and increased woody expansion. Treatment methods should be targeted to specific management goals (e.g., pastoral production or ecosystem conservation), and particular ecosystem outcomes (e.g. ecosystem structure, or function or composition) to improve the efficiency of woody removal in global savannas under the changing climate.

1. Introduction

Savannas occur over extensive areas of the globe and comprise a mixture of trees and grasses occurring in different states and densities (Bond and Midgley, 2012; Stevens et al., 2017). Extensive areas of savanna occur in drylands, which support about a third of the world's human population, many of whose livelihoods are dependent upon pastoralism and therefore grass production (Maestre et al., 2016; Prăvălie, 2016). Encroachment of woody plants into open savannas, woodlands and grasslands (woody thickening, woody encroachment) has increased markedly over the past century and has been attributed to increases in atmospheric CO_2 concentrations, and intensified land use disturbances such as overgrazing and fire (Van Auken, 2000; Eldridge and Soliveres, 2015; Archer et al., 2017; Wilcox et al., 2018). Encroachment shifts the balance from grasses to woody plants, has significant implications for the functioning of savannas and forests, but also presents considerable challenges for land managers.

The effects of woody encroachment on ecosystem properties and processes have been widely reported in the literature (e.g. Eldridge et al., 2013; Archer et al., 2017), but most studies have tended to focus on single locations, with specific woody plant species, and widely different response variables (e.g., plant biomass, soil properties, hydrology). Studies of woody encroachment demonstrate that their ecological effects are highly nuanced; ranging from positive to negative or neutral depending on land use, woody plant type and density, and environmental setting (Eldridge et al., 2011). For example, shrubs at low densities have been shown to have positive effects on understorey herbaceous plants, soils and ecological functions (Eldridge and Soliveres, 2015), but these effects often wane at high densities (Riginos et al., 2009), when sites are overgrazed (Eldridge et al., 2013), or when

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monospecific stands are dominated by shrubs from particular functional groups such as those with specific morphological traits (e.g., resprouters) (Freeman and Jose, 2009).

The prevailing view still remains that dense stands of woody plants are regarded as indicative of degraded, dysfunctional or desertified ecosystems (Schlesinger et al., 1996; Okin et al., 2006), despite the many acknowledged ecosystem benefits that they provide (e.g. Eldridge and Soliveres, 2015). This is primarily because pastoralism, which is still the dominant land use over many of the areas experiencing encroachment, is based heavily on the production of forage (predominantly grass), which is often out competed by woody plants (Scholes and Archer, 1997). Heavily invested, government-sponsored programs to remove woody plants have been implemented widely across global drylands (e.g., Restore New Mexico https://www.blm.gov/press-release/blm-grassland-restoration-treatments-begin-southern-new-mexico) with the objective of reversing the economic loss thought to result from woody encroachment (Hamilton, 2004). Globally, a range of woody plant control methods is used ranging from burning, and browsing by ungulates, to physical removal and the use of herbicides (Archer and Predick, 2014). Despite promoting forage production, removing woody plants also has whole-of-ecosystem effects (Hamilton, 2004) that alter resource aggregation (e.g., the 'fertile island' effect) (Schlesinger et al., 1990), soil function (Chief et al., 2012) and understorey community structure and composition (Bohlman et al., 2016).

Despite the many site-specific or regional studies of woody plant removal on ecosystems (Ansley et al., 2006; Archer et al., 2011; Gillon et al., 1999; Latt et al., 2000; Wu et al., 2016), we still lack a broad understanding of the net effects of their removal on ecosystem processes at a global scale, and to our knowledge, no such global assessment has been attempted, probably because responses vary with environmental context, plant traits and treatment methods (Archer and Predick, 2014; Daryanto et al., 2019). The ecological outcomes of woody plant removal have been shown to vary within similar environment ranges, suggesting the involvement of other site-specific drivers (e.g., removal methods, plant species). Differences in plant functional traits can influence the structural and functional outcomes of woody encroachment *via* plant-plant interactions (e.g., facilitation or competition) (Eldridge et al., 2011), which may be altered once woody plants are removed, thus influencing ecological outcomes. Few studies, however, have compared the ecosystem response of woody plant removal among different woody species, and it remains unclear whether differences in plant traits affect the ecological or management outcomes of different treatment methods. This lack of information hinders our ability to endorse appropriate management guidelines and procedures to meet ecological and management objectives associated with woody plant removal.

The outcomes of woody plant removal are also likely to vary with the time since removal (Archer and Predick, 2014; Daryanto et al., 2019). Reports in the literature suggest a disconnect between effects on woody plants and ecosystem processes. While the effectiveness of different treatments is relatively short-lived, i.e. woody plants recover relatively quickly (< 15 years) after treatment (Eldridge and Soliveres, 2015), any effects on ecological processes are typically prolonged (> 20–40 years) (Archer et al., 2011) and deleterious (e.g., reduced soil function and hydrology) (Chief et al., 2012). With a prolonged time since treatment, ecosystem responses would likely vary due to niche replacement or ecosystem state transitions (Bestelmeyer et al., 2013). However, most studies have tended to focus on short-term effects on the focal plants, so that the legacy effects on ecosystems remain largely elusive. A synthesis of the ecosystem impacts of woody plant removal and how moderating factors such as environment conditions (e.g., soil type, climatic zone), vegetation community type and treatment (e.g., time since removal and removal method) might influence these ecosystem responses is a key knowledge gap. Such a synthesis is timely if we are to be able to strategically tailor removal to specific woody species and/or environmental conditions (Hamilton, 2004; Archer and Predick, 2014).

Here we report on a meta-analytical approach to understand the ecosystem impacts of woody plant removal on three broad ecosystem attributes: structure (the architecture of the system), function (how the system regulates key processes) and composition (the individual components related to species), using 45 individual response variables from 263 studies. The results of our study aim to question the of-reported notion that the removal of woody plants is associated with improved ecosystem functions. Existing studies have only been attempted at regional scales. This study is, to our knowledge, the first global meta-analysis of woody plant removal based on a systematic, meta-analytical approach accounting for the effects of environmental context, treatment methods and target species. In our study we had five predictions. First, we expected that woody plant removal would reduce ecosystem structure and function because woody plants comprise a significant structural element of the plant community (Venter et al., 2018), and the removal of woody plants would lead to reductions in water interception, infiltration and soil stability (Huxman et al., 2005). Further, woody plant removal would increase ecosystem composition by releasing subordinate plants from competitive exclusion, thereby promoting understorey plant richness (Soliveres and Eldridge, 2014). Second, any effects of woody plant removal would likely be greater in more mesic environments with finer-textured soils because such systems are characterized by high productivity and are likely more resilient (Elmqvist et al., 2003). Third, we predicted that the ecosystem response to removal differs between above-ground and below-ground traits of the encroached species because the impact of woody encroachment is species specific (Eldridge et al., 2011). Fourth, the impact of woody removal on ecosystem structure, function and composition would be expected to differ among removal methods due to different effects of disturbance on plants and soils. Finally, any effects of woody removal should decline with time since treatment, consistent with the notion that woody plants recover over time (i.e. resprout or regrow) in the absence of follow-up treatment.

2. Methods

2.1. Database construction

2.1.1. Literature searching and screening

We systematically searched the published literature to identify quantitative studies that reported information on the impact of woody plant removal on ecosystem structure, function and composition. Attributes that represent plant architecture or spatial distribution of the plant community, such as plant cover, density, patch shape and size were included in ecosystem structure attributes (Eldridge et al., 2016). Compositional attributes comprised mainly variables showing the variety of species including species diversity, richness and abundance (Maestre and Cortina, 2004). Attributes of ecosystem function contained measures depicting ecosystem process such as production (e.g., biomass), hydrological processes (e.g., runoff, infiltration, soil erosion) and nutrient cycling, including soil organics (e.g. soil carbon, soil nitrogen, soil phosphorus) and plant nutrients (Eldridge et al., 2011). We searched multiple databases (e.g., Web of Science, Scopus, Proquest Science & Technology, Informit Online, Environment Complete, Biosis and Geobase/georef) in the period of 1900–2017 using the keywords synonymous with woody plant removal and terms referring to specific treatments (see Appendix A for detailed search strings). Our search yielded 3542 publications, which were then screened using the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analysis) procedure (Liberati et al., 2009) (see Fig. A.1 in Appendix A). During screening, we retained those studies that 1) were conducted under natural conditions using field experiments, 2) reported relevant quantitative data, 3) focussed on ecosystem responses to woody plant removal, 4) reported changes restricted to woody plant removal only, 5) compared paired plots with woody plant removal and retention (i.e., treatment and control; see detailed criteria in Appendix A). Based on these criteria, we refined the literatures to 263 publications (see Appendix B). Screening is critical in meta-analyses in order to maintain analytical integrity and to ensure that erroneous conclusions are not reached (Bown and Sutton, 2010).

2.1.2. Data compilation

For each publication, we recorded the basic geographical information of the study (location, continent, landform, landscape type), woody plant removal information (methods, years since treatment), land use history, and follow-up management. In addition, we recorded information on seven morphological traits (e.g., plant height, plant canopy shape, root type, whether allelopathic, capacity to resprout, whether the canopy of the plant touches the soil surface, and the dispersal agent) for the 127 woody species (including shrubs and trees) that were managed or removed in these studies (see Appendix C for woody plant traits list). Data on temperature and rainfall were extracted from global climate database (0′30″ × 0′30″) for the 1970–2000 period from WorldClim Version 1.4. (http://www.worldclim.org/) (Fick and Hijmans, 2017). The Aridity Index (AI = precipitation/potential evapotranspiration) was derived from Consortium for Spatial Information (CGIAR-CSI) for the 1950–2000 period (Zomer et al., 2008) (http://www.cgiar-csi.org/data/global-aridity-and-pet-database) and was used to classify climatic zones (humid $AI \geq 0.65$, dry subhumid $0.5 \leq AI < 0.65$, semi-arid $02 \leq AI < 0.5$, arid $AI < 0.2$). Data on soil physical properties (e.g., soil particle composition, soil carbon, soil texture classification) were obtained from the HWSD database (resolution = 1 km) (http://www.fao.org/soils-portal/soil-survey/soil-maps-and-databases/harmonized-world-soil-database-v12/en/). For each study, we extracted the effects of woody plant removal on measures of ecosystem structure, function and composition on 45 response variables (see Appendix D for the list of response variables). Data originally published as figures were extracted using Engauge Digitizer V 4.1 (http://digitizer.sourceforge.net/). Overall, we compiled a database of 14,110 records of the effects of woody plant removal on 45 ecosystem response variables from 263 studies.

2.2. Statistical analyses

In this study we conducted two analyses. The first examined the direction of ecosystem response to woody plant removal based on a range of ecological attributes, using effect size of response variables from paired woody plant removal and retention sites. The second explored the impact of environmental conditions (e.g., climate zones, soil texture), treatment (treatment method, years since treatment) and woody plant traits (plant height, plant shape, root type, whether allelopathic and capacity to resprout) on the ecosystem response to woody plant removal based on meta-regression models.

2.2.1. Effect size and random effect

To determine the effect of woody plant removal on the measured variables, we calculated the response ratio: $LnRR = \ln(Xt/Xc)$ as the effect size (Hedges et al., 1999) where Xt is the value of the response variable in the woody plant removal plot, and Xc is the value of the response variables in the woody plant intact plot. Positive values of LnRR indicate an increase in the response attributes following woody plant removal and *vice versa*. For ecosystem function, increases in some attributes such as sediment production, runoff and soil nutrient leaching indicate reductions in ecosystem health so that a larger value corresponds to a decline in function. For these variables, therefore, we multiplied the LnRR with -1 to ensure that greater values consistently corresponded to higher function when calculating the overall effect size of ecosystem function. Based on this database, we constructed a dataset of 7055 contrasts of woody plant removal and woody plant retention. We used a random-effects model approach to undertake a multilevel meta-analysis, which would account for the effect of random factors (Nakagawa and Santos, 2012). In the multilevel meta-analytical model, we used study identity (ID) and the order in which data rows were allocated to the datafile as random effects in all models to control for lack of independence from same studies and the potential bias due to the sample size. Furthermore, many studies reported multiple treatments but only a single control. We coded data rows that used the same (shared) control with a unique code and calculated the variance matrix based on the variance of response attributes and shared control pairs (Nakagawa and Santos, 2012) to control for the potential influence of shared controls.

2.2.2. Meta-regression model and publication bias

Meta-analysis models were implemented with LnRR as the response variable, the variance matrix as the within study variance, and an inverse gamma prior for the random effect of reference ID and data order. Using the meta-analysis model, we first ran an intercept-only (null) model i.e., without predictors, to estimate mean effect sizes for the entire dataset (whole ecosystem dataset) and its subsets (structure, function, composition). First, we calculated the overall effect size of the whole dataset on ecosystem responses using a random effect model. Data with extreme variance (> 1000 or < 0.0001) were excluded, and 6206 rows of data were included in the model that calculated the overall effect size. Two subsets of data were extracted in this study. The first was divided into ecosystem structure, function and composition. The second group divided ecosystem structure, function and composition into their constituent ecological attributes (e.g., grass cover, woody plant cover, biocrust cover etc. for ecosystem structure). Analysing the specific attributes can reveal their potential responses and explain differences among the overall response of structure, function and composition to woody plant removal. Considering the statistical power, we mainly analysed attributes with more than 20 observations in the second group. We then used the modified version of I^2, a heterogeneity statistic (ranging from 0 to 1) based on intra-class correlations, to determine the total level of heterogeneity among effect sizes (Nakagawa and Santos, 2012). The substantial heterogeneity ($I^2 = 0.998$) indicated that there are driving factors (predictors or moderators) that could explain the observed variance. We then explored which moderator could explain the observed heterogeneity using a separate meta-regression model each for the ecosystem structure, function and composition datasets. After systematically selecting moderators using pre-assessment and variance inflation factors (VIF) (see Appendix E for VIF results), environment (climatic zone, soil texture), treatment (treatment methods, years after treatment) and woody plant traits (plant height, plant shape, root type, whether allelopathic and capacity to resprout) were incorporated into the model. We then performed separate meta-regression models (with a zero intercept) using each selected categorical moderator as a fixed effect, and the three random effects used above, to compare the estimated effect size for subclasses of each moderator to investigate which moderator would significantly affect the effect size (LnRR) of ecosystem structure, function and composition. The significance of estimated effect size was examined with a t-test, which calculated whether estimated effect sizes differed significantly from zero at $P < 0.05$.

Three approaches (i.e. funnel plot, Egger regression, trim-and-fill) were used to assess publication bias in the whole ecosystem datasets and its subsets (e.g., structure, function and composition) and the results suggested no publication bias in either ecosystem dataset or structure, function and composition dataset (see Appendix F for publication bias examination). Meta-analysis was performed in the ‘metafor’ package (Viechtbauer, 2010) in R 3.4.3 version (R Core Team, 2017). All the figures were created using ‘ggplot2’ and ‘ggmap’ in R version 3.4.3 and Origin software version 9.0 (OriginLab, Northampton, MA).

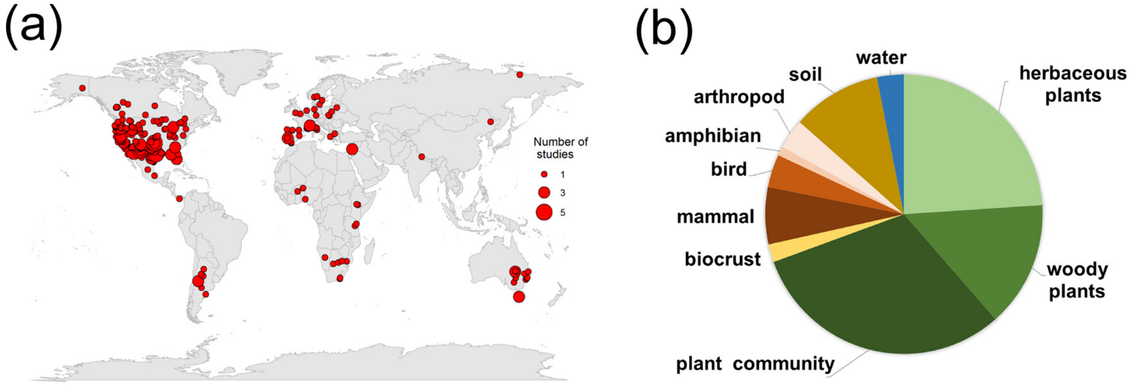

Fig. 1. (a) Global distribution of studies and (b) the relative contribution of different attributes examined.

3. Results

Published studies of woody plant removal were reported across multiple climatic regions worldwide (Fig. 1), but most (57%) were from drylands (n = 151 studies). Most of the 263 studies were conducted in North America (186) and Europe (34), followed by Africa (16) and Australia (12), with studies mainly focused on the response of plants (69%), fauna (15%) and soils (10%) to woody plant removal. Among these studies, woody plants were removed mainly by physical (38%) and chemical (20%) methods, with 70% studies focused on short term (< 5 years) outcomes.

3.1. *Ecosystem effects of woody plant removal*

Woody plant removal resulted in a net increase in composition, reduction in structure, but an equivocal effect on function (Fig. 2). Ecological attributes also exhibited a range of different responses (Fig. 3). For ecosystem structure, woody plant removal resulted in substantial declines in biocrust (66%) and woody plant cover (55%) cover, and woody plant density (43%). Herbaceous plant cover (19%) and density (35%) increased with woody plant removal. Most functional attributes (e.g., soil functions) showed non-significant responses, though soil roughness (47%) and shrub biomass (29%) declined markedly, while grass biomass (30%) and runoff (56%) increased. The positive response of ecosystem composition to woody plant removal resulted mainly from increases in tree (14%) and grass (23%) richness. Woody plant removal had no significant effect on shrub species richness nor animal richness.

3.2. *Ecosystem response mediated by multiple factors*

The response to woody plant removal was more likely to be significant in humid and dry subhumid zones, and the responses were highly variable in arid and semiarid zones (Table 1, see Fig. G.1 in Appendix G). Any effects of soil texture varied with climatic zone. Woody plant removal significantly promoted composition on sandy soils in semi-arid areas, or loamy soils in humid areas, while structure substantially declined on clay soils in dry subhumid areas or on sand soil in humid areas (see Table G.1 in Appendix G).

Ecosystem responses differed with above- and below-ground traits of the woody plant removed (Table 2, see Fig. G.2 in Appendix G). For above-ground traits, removing plants 1–3 m tall increased composition and reduced structure, while removing V-shaped or round-shaped woody plants increased composition and reduced structure, respectively. For below-ground traits, removal of allelopathic woody plants or those with tap roots was more likely to increase composition, while structure declined significantly when resprouting plants or lateral and tap-rooted plants were removed. Ecosystem function only declined when resprouting or weeping plants were removed.

Most of the woody plant removal methods reduced ecosystem structure, with browsing having the greatest reduction on structure, followed by chemical removal and multiple removal (Table 3, see Fig G.3 in Appendix G). Only browsing significantly reduced ecosystem function. Ecosystem composition was promoted when physical or multiple methods (typically physical combined with chemical or burning, which accounted for 57% of studies) were used to remove woody plants. Effects were also related to years since woody plant removal. Effects on ecosystem structure declined marginally, but function declined markedly, with increasing time since treatment (long term; > 10 years). The longevity of different treatment methods also differed (see Table G.2 in Appendix G). Browsing reduced ecosystem structure within 5 years but had a negative effect on function in 5–10 years. Burning and physical removal significantly reduced structure in the short term (< 3 years), but had negative and positive effects,

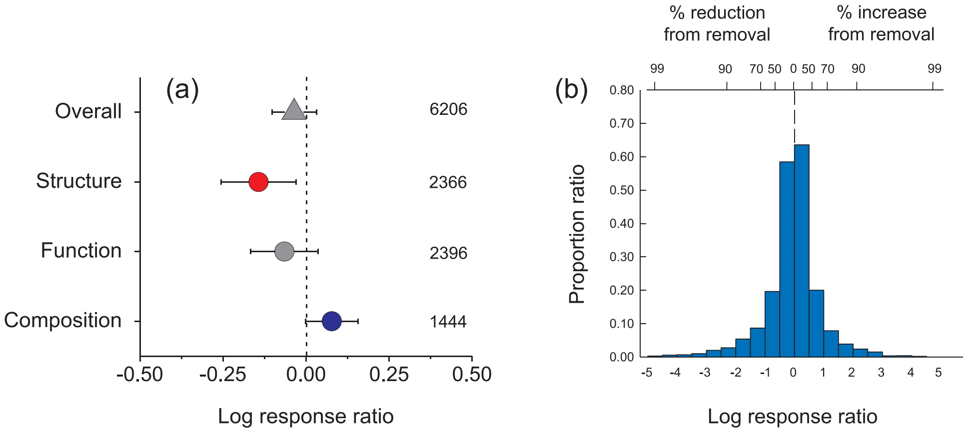

Fig. 2. (a) Overall effect size of ecosystem response and (b) histogram of ecosystem response. Numbers indicate the number of studies. The triangle represents the whole dataset. Significant results are shown in red (negative) and blue (positive), and error bars represent 95% confidence intervals. Sample sizes are indicated. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

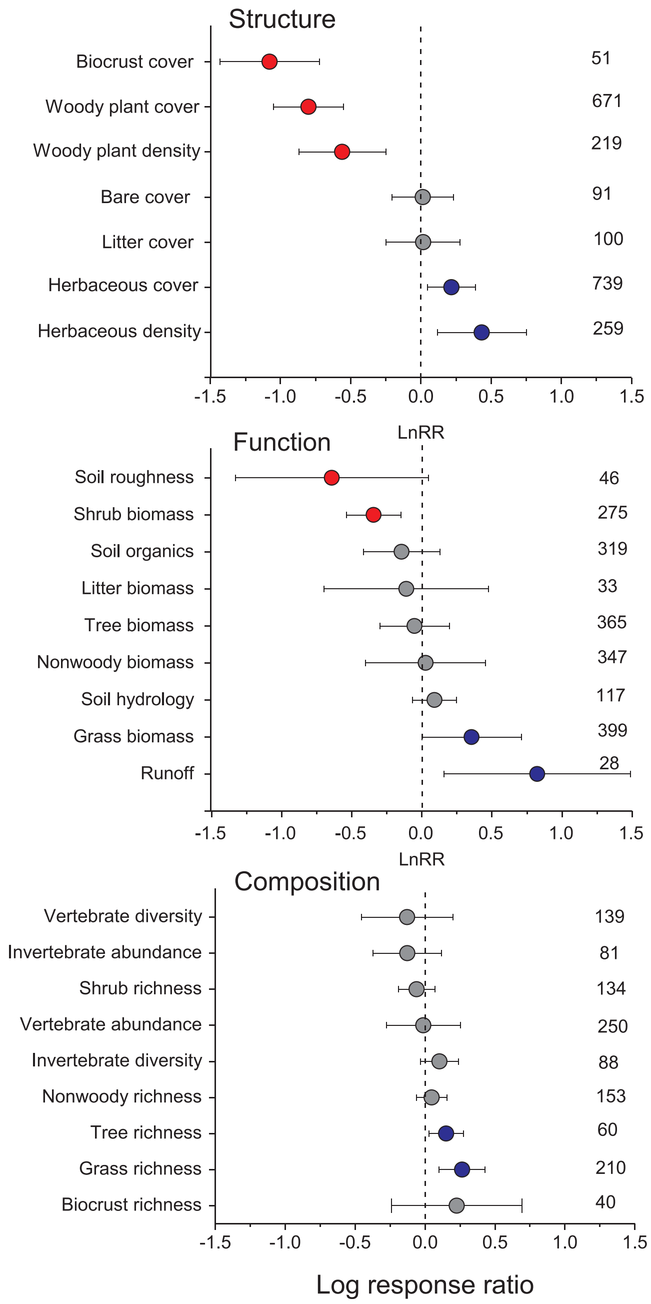

Fig. 3. Response of ecological attributes in ecosystem structure, function and composition. Numbers indicate the number of studies. Significant results are shown in red (negative) and blue (positive), and error bars represent 95% confidence intervals. Sample sizes are indicated. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

respectively, on composition in the long term (> 10 years). Multiple methods (physical, plus chemical or burning) significantly affected structure, function and composition within 5 years, while the significant effect of chemical removal on reducing structure and enhancing composition appeared 5–10 years after treatment (see Table G.2 in Appendix G).

4. Discussion

Considerable controversy and debate surround the issue of woody plants in drylands (Eldridge and Soliveres, 2015), largely because the perspectives on woody plants depend on land use objectives (e.g., conflicts between conservation and production) (Eldridge et al., 2011) and the fact that removal studies have revealed mixed effects due to differences in environmental contexts, treatment types, and reported times since treatment. Using 263 studies from six continents, our analysis revealed five main results. First, the overall effect of removal differed among ecosystem response variables, with increases in composition, reductions in structure, but equivocal effects on function. Second, the ecosystem impact of woody plant removal was more pronounced in mesic areas (e.g., humid, dry subhumid) and did not differ among soil textures. Third, the effects of removal were woody plant species-dependent depending on the above- and below-ground plant attributes, with removal of 1–3 m, allelopathic and V-shaped plants generating similar effects. Fourth, removal methods had different effects on ecosystems, with browsing having the greatest reduction on structure and function, while composition was only promoted by physical and multiple removal. Finally, woody plant removal was generally effective only over short time periods (< 5 years), and had long-term (> 5 years) reductions in ecosystem function and composition especially by browsing and burning removal respectively. Together our results indicate that the effectiveness of woody plant removal is highly context dependent, with generally negative long-term impacts on ecosystem functions (e.g., reduce soil roughness and enhance runoff). Our results provide novel insights into the ecosystem outcomes of woody removal at the global scale. This knowledge is essential to guide successful programs of removal under different environments and treatment scenarios.

4.1. Contrasting ecosystem responses to woody plant removal

The effects of woody plant removal on structure were negative, with cover and density of herbaceous plants increasing in response to reductions in woody cover and density. For example, shrub removal in Argentina resulted in a significant increase in grass cover following dramatic reductions in shrub cover (Blanco et al., 2005). Although woody cover generally exhibited rapid declines, herbaceous structure would be expected to lag behind woody structure in response to relaxation of competitive exclusion, greater access to soil water and nutrients, and reduced levels of shade following woody removal (North et al., 2005). For example, herbaceous cover was found to increase 3 years after physical removal (chaining) in North America (Ansley et al., 2006) or remain unchanged after 4 years in South America (Allegretti et al., 1997) due to the late response to greater light penetration and throughfall precipitation following shrub canopy removal. We also found that woody plant removal resulted in a 66% reduction in biocrust

Table 1
Estimated effect size of ecosystem responses in relation to climate zone and soil texture. Significant ($P < 0.05$) effect sizes shown in bold.

Environment condition	Aridity				Soil texture		
	Arid	Semi-arid	Dry subhumid	Humid	Sand	Loam	Clay
Structure	−0.13	−0.10	**−0.51**	−0.14	−0.30	−0.10	−0.26
Function	−0.10	−0.03	−0.13	−0.07	−0.14	−0.06	0.00
Composition	−0.12	0.00	−0.01	**0.16**	0.10	0.07	0.11

Table 2
Estimated effect size of ecosystem response for aboveground and belowground woody plant traits. Significant ($P < 0.05$) effect sizes shown in bold.

Aboveground	Plant height			Plant shape			
	< 1m	1–3 m	> 3 m	V-shaped	Weeping	Round	Pyramid
Structure	−0.20	**−0.28**	−0.03	**−0.21**	−0.15	**−0.22**	0.03
Function	−0.17	−0.01	−0.07	0.05	**−0.25**	−0.03	−0.10
Composition	0.05	**0.15**	0.04	**0.14**	−0.03	0.06	0.10

Belowground	Allelopathy		Resprout		Roots		
	Yes	No	Yes	No	Lateral	Tap	Lateral & Tap
Structure	**−0.14**	**−0.15**	**−0.17**	−0.09	0.06	−0.11	**−0.21**
Function	−0.03	−0.10	**−0.10**	0.02	−0.14	0.00	−0.11
Composition	**0.12**	0.02	0.05	**0.13**	0.03	**0.12**	0.04

cover. Shrub cover is known to be associated with greater biocrust cover (Soliveres and Eldridge, 2014), so crust reductions likely resulted from direct destruction during the removal treatments such as ploughing (Redmond et al., 2013) or chaining (Ansley et al., 2006) or indirectly, by allowing the ingress of herbivores, which are known to disturb surface crusts (Eldridge et al., 2017; Concostrina-Zubiri et al., 2017). Finally, we found no evidence that woody removal resulted in consistent increases or reductions in the cover of bare soil, as the net effect of shrub removal likely depends on whether removal enhances litter cover and the balance between structural changes in herbaceous and woody plants.

Woody plant removal had an overall equivocal effect on function, with increases in grass biomass balancing out reductions in shrub biomass (Fig. 3). This could be explained by the fact that increases in grass biomass depend heavily on the legacy effects of annual rainfall, historic land use patterns and follow-up treatment effects (Archer and Predick, 2014). Woody plant removal was associated with smoother soil surfaces, which would be expected to enhance runoff by reducing surface storage detention (Helming et al., 1998), thus explaining the increased runoff in our results. The non-significant response of soil hydrology to woody removal is somewhat contrary to the prevailing notion that removal of high water consuming plants would be expected to result in greater infiltration (Eldridge et al., 2015). The most parsimonious explanation is that removal disrupts the hydrological connectivity created by shrub islands (mosaics), leading to greater water loss (Okin et al., 2015; Richardson et al., 1979). Although woody plants are crucial sinks for carbon and nitrogen (de Graaff et al., 2014), we found no evidence of a consistent effect on biotically-derived nutrients after removal. This may relate to the fact that the fertile island effect is known to persist for many years after removal of woody plants (Bechtold and Inouye, 2007).

Woody removal had a net positive effect on ecosystem composition by increasing plant species richness, but we detected no clear effect on faunal richness. Removal could potentially lead to increases in previously suppressed invasive plants, thereby increasing exotic richness. For example, studies in a mixed-conifer forest in Nevada (Bohlman et al., 2016) showed that plant richness was higher on sites where woody plants had been removed, particularly for exotic species that promote ecosystem composition after woody removal. Potential increase in exotic shrub richness might explain why shrub richness was less affected overall after woody plant removal. The lack of a response of vertebrate richness likely reflects idiosyncratic habitat requirements for different faunal functional types. Thus, changes in surface configuration (e.g., litter cover, plant biomass, soil roughness) and landscape connectivity (e.g., patches of woody mosaics) would be expected to have a differential effect on different biota (e.g., variations in different verterbrate assemblages, Fulbright et al., 2013 and mammals, Kutiel et al., 2000) with increase in shrubland obligates at the expense of open-area or grassland taxa such as birds (Coffman et al., 2014) and ants (Radnan and Eldridge, 2018).

4.2. Ecosystem response depends on environmental context and woody traits

Woody plant removal generated pronounced and consistent ecosystem effects (i.e. decline in structure, increase in composition), but only in mesic areas (Table 1), reinforcing the notion that removal is less effective in arid environments due to less reliable rainfall, lower ecosystem resilience and a generally more protracted recovery from disturbance (Maestre et al., 2016). For example, a study in Sierra Nevada (Bohlman et al., 2016) showed that woody removal rapidly reduced woody plant cover (i.e. reduced structure) and promoted understorey richness (i.e. increased composition), whereas a study in the arid Chaco region (Blanco et al., 2005) showed that there was no change in species richness after removing woody plants. The response also depended on soil texture (see Table G.1 in Appendix G), which is a major driver of soil moisture retention (Noy-Meir, 1973) and animal impacts in shrublands (Eldridge and Whitford, 2014).

Ecosystem outcomes were also strongly dependent on the traits of individual woody plant species. Aboveground traits (e.g., height and canopy shape) have been shown to reduce plant α-diversity through competitive effects and over shading (Bohlman et al., 2016), though other work has shown that shrubs can have strong facilitatory effects on herbaceous species (Howard et al., 2012). Plant canopy shape (e.g., pyramidal, V-shaped, round, weeping), affects the ability of understorey plants to access resources (water, light) and has been shown to have a significant impact on the ecosystem structure and function in

Table 3
Estimated effect size of ecosystem response under different treatment method and years since woody plant removal. Multiple is predominantly a combination of physical and chemical removal. Significant ($P < 0.05$) effect sizes shown in bold.

Treatment	Treatment method					Time since treatment (yrs)			
	browsing	burning	chemical	physical	multiple	< 3	3–5	5–10	> 10
Structure	**−0.28**	−0.14	**−0.22**	−0.12	**−0.17**	**−0.18**	**−0.18**	−0.07	−0.16
Function	**−0.17**	−0.07	−0.08	−0.02	−0.08	−0.07	−0.04	0.00	**−0.15**
Composition	0.13	−0.14	0.11	**0.08**	**0.14**	0.07	0.08	0.12	0.09

global shrub encroachment studies (Eldridge et al., 2011). In our study, we found that canopy shape was also an important driver of the outcomes of removal. For example, V-shaped canopies tended to reduce soil moisture availability by intercepting more rainfall, but weeping and round-shaped canopies that reach the ground may provide a safer environment for understorey plants by reducing surface evaporation and reducing water stress (Wang et al., 2013). Woody plants with allelopathic traits have the potential to suppress understorey species *via* belowground soil-mediated effects (Kulmatiski, 2018). Plants might be suppressed from growing beneath tap rooted species by facing fierce water competition at deeper soil depth (Seghieri, 1995), while benefitting from hydraulic lift when growing with tap and lateral rooted woody species (Muñoz et al., 2008). Thus, removal of medium-sized, V-shaped, allelopathic or tap-rooted plants could either weaken resource competition or increase resource availability, thus promoting greater species richness (i.e., increase ecosystem composition).

By contrast, our results show that removing weeping or resprouting species would reduce ecosystem function (e.g., reducing soil infiltration or habitat quality), as resprouting would enable plants to reinforce resource acquisition (e.g. reduce soil moisture, intensify evaporation) after being removed (Freeman and Jose, 2009), and the removal of weeping plants would destroy available sub-canopy habitat. We failed to find, however, any significant functional effect of either different environmental conditions (e.g., aridity, soil texture) proposed by previous studies (Eldridge et al., 2011). This might be because the functional response is highly specific to particular response variables, and woody plant removal likely disrupts critical functional processes when the plant community and associated soil environment are physically disturbed, for example by soil inversion, or chemically contaminated with herbicides, which could contain antimicrobial compounds (Bielińska and Pranagal, 2007).

4.3. *Short-lived gain versus long-term loss*

Our global synthesis showed that, overall, the effectiveness of woody plant removal was relatively short-lived, with either reductions in structure (e.g., reduced woody cover and density) or increases in composition (e.g., increased tree and grass richness) generally diminishing within 5 years of treatment, extending the narrow scope of Archer et al. (2011) to the global scale. For example, a synthesis of woody plant removal from the United States (Archer et al., 2011) showed that the effectiveness of reducing woody cover and increasing herbaceous production (i.e., ecosystem structure) could only be sustained for 5 years before recovering woody species dominated the community, and the increase in herbaceous richness (i.e., increased composition) was marginally 5 years after removal. This short-lived 'ecological fix' indicates the fast regeneration time for woody plants, and the fact that changes in plant composition and resource availability with years since treatment differ markedly among different treatment methods (e.g., regional syntheses from North America [Archer and Predick, 2014] and Australia [Eldridge and Soliveres, 2015]). For example, compared with burning and physical removal, browsing was more effective at short-term reductions ($<$ 5 years) in woody structure (LnRR$=$ -0.44, Table G.2 Appendix G) by removing the actively growing tips and inhibiting woody growth rates, but this effect declines rapidly after 5 years as regenerating species develop strategies to resist further browsing (e.g., spines and secondary metabolites such as terpenes) (Fulbright and Beasom, 1987). By contrast, herbicides had a more prolonged effect of reducing woody cover and increasing species richness (5–10 years), largely by inducing whole-plant mortality and reducing the potential for regeneration (e.g. in North America, Bowes, 1982; Freeman and Jose, 2009). Although multiple methods are generally used as follow-up treatments to prolong the removal of woody plants (Masson et al., 2015), effectiveness lasted no more than 5 years, indicating that a one-off follow-up is insufficient to prevent re-encroachment of treated areas.

Woody plant removal reduced ecosystem function (e.g., reduced hydrological function) for up to 10 years, particularly after browsing or the use of multiple methods (Table 3, Table G.2 in Appendix G). For example, a study in the Chihuahuan Desert (Perkins and McDaniel, 2005) showed that soil infiltration declined 15–18 years after removal. Thus, removal of woody plants could induce long-term legacy effects by altering ecological process that are irreversible in the long run. First, removing woody plants could alter succession process by changing plant composition (e.g. the proportion of C3/C4 species or palatable species), which directly affecting ecosystem productivity and resilience (Van Auken, 2000). Second, woody plant removal could alter hydrological processes by changing soil properties (Redmond et al., 2013), for example, by reducing water-stable aggregation or destroying soil structure due to removal disturbance (e.g. browser trampling) (Perkins and McDaniel, 2005; Daryanto and Eldridge, 2010). Third, removal could alter landscape connectivity by changing the distribution of resource shedding and resource accumulating patches (Schlesinger et al., 1990). For example, Nolte et al. (1994) showed that spatial heterogeneity declined when shrubs were physically removed by root ploughing, resulting in reductions in β-diversity. Ecosystem composition (e.g., plant richness, fauna diversity) can also be negatively affected by burning in the long-term ($>$ 10 years). For example, Killgore et al. (2009) showed that invertebrate and vertebrate diversity (e.g., spider, termite, burrows) declined in burned areas with rapidly regenerated shrubs in an arid area of New Mexico. Fire can promote shrub regeneration by enhancing the dispersal of shrub seeds or reducing reestablishment of herbaceous species, and alter habitat quality by reducing soil organic matter weakening biological activity (Armas-Herrera et al., 2018).

5. Conclusions

Despite the general notion that the removal of woody plants leads to ecosystem 'improvement', our global synthesis showed that removal had both positive and negative ecosystem effects; results that have not previously been reported at such a large scale. Apart from promoting plant diversity, removing woody plants will lead to short-term structural decline by removing midstorey (woody plants) and groundstorey (biocrust) cover, potentially resulting in intensified land degradation, for example, by increasing runoff (Fig. 3). Management goals of reducing woody cover to enhance grass production in the short-term are likely to be eclipsed by longer-term declines in environmental quality (e.g. reductions in ecosystem function and composition). Managers therefore need to be cognizant of the need to balance these short-term productivity benefits with longer-term legacy effects that might result from reduction in function and composition *via* land disturbance. Our global synthesis reinforces the notion that any effects of woody plant removal on ecosystems are highly context dependent. Thus, for example, removal of plants with V-shaped canopies is likely to have a greater impact on composition than removal of those with a weeping shape, possibly due to different effects on hydrological function (Whitford, 2002). Furthermore, our results for specific climatic zones suggest that increases in global dryness predicted by climate change models will further reduce the effectiveness of woody plant removal in savannas worldwide, though drier areas may be less susceptible to encroachment (Sankaran et al., 2005; Scholtz et al., 2018). Managers should consider the most appropriate control methods for specific goals based on the target species in order to manage woodlands and savannas for structural change (browsing/chemical) or plant composition (physical/multiple) under changing climates.

CRediT author statement

Author contributions

Jingyi Ding: Data curation, Formal analysis, Investigation, Writing-original draft. David J. Eldridge: Conceptualization, Funding acquisition, Methodology, Supervision, Resources, Writing-review & editing.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.ppees.2019.125460.

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