New Phytologist

Research

Remove or retain: ecosystem effects of woody encroachment and removal are linked to plant structural and functional traits

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Received: *11 August 2020*
Accepted: *23 October 2020*

New Phytologist (2020)
doi: 10.1111/nph.17045

Key words: brush management, global synthesis, meta-analysis, multifunctionality, plant traits, thickening.

Summary

- The impacts of woody encroachment and removal on ecosystems are highly variable and are thought to be related to the traits of the individual woody species. Decisions on whether to remove or to retain woody plants are hampered by a lack of empirical evidence of the relationship between woody traits and the ecosystem consequences of their removal or retention.
- We used a global meta-analysis of 149 ecosystem attributes from 172 woody species to evaluate the relative effects of woody plant traits and abiotic environmental variables on the ecosystem consequences of woody encroachment and removal.
- The ecosystem consequences were closely related to woody plant traits. For example, encroachment of plants characterized by high structural traits (e.g. tall, mixed tap and fibrous roots) reduced ecosystem composition, while removal of plants characterized by high functional traits (e.g. nitrogen fixing, deciduous) reduced ecosystem function. Structural and functional traits of woody plants mainly regulated soil stability during woody encroachment and herbaceous cover after woody removal. Conversely, environmental conditions mainly affected herbaceous cover under encroachment and soil stability under removal scenarios.
- We demonstrate that the ecosystem consequences of encroachment and removal are closely linked to the structural and functional traits of the target woody species. Furthermore, biotic (woody plant traits) and abiotic (climate, soils) factors have different impacts on regulating trade-offs between ecosystem responses under these two management scenarios. Our study provides empirical support for management decisions on whether to retain or remove different woody taxa under various environments across the globe.

Introduction

Woody encroachment is a global issue characterized by an increase in the cover and/or density of woody plants, generally at the expense of the herbaceous or grassy understorey (Van Auken, 2000; Maestre *et al.*, 2009; Archer & Predick, 2014; Eldridge & Soliveres, 2015). The causes of woody encroachment are varied and complex, and relate to legacy effects of overgrazing, lack of competition from herbaceous vegetation, the absence of fire, and increases in atmospheric CO_2 concentrations, all of which confer a competitive advantage on woody plants over herbaceous vegetation, especially under the ongoing changing climate (Bond & Midgley, 2000; Eldridge *et al.*, 2013; Ward *et al.*, 2014; Scholtz *et al.*, 2018). Encroachment is a critical issue for global food security because more than half a billion people depend on livestock grazing for food (e.g. milk, meat, fuel), shelter and financial security, and therefore to sustain their livelihoods (Campos *et al.*, 2018). Encroachment, therefore, has the potential to threaten the social and ecological viability of pastoral enterprises, presenting substantial challenges for global ecosystem sustainability and human well-being.

Encroachment is considered to be a form of land degradation due to its generally negative effects on pastoral production (Scholes, 2009). Consequently, considerable resources have been invested in woody plant removal using physical, chemical and biological methods (Archer & Predick, 2014). Notwithstanding the putative negative effects of encroachment, woody plants have been shown to support a wide range of ecosystem goods, services and functions (e.g. Bestelmeyer, 2005; Maestre *et al.*, 2009; Archer *et al.*, 2011; Eldridge *et al.*, 2011; Eldridge & Soliveres, 2015). For example, woody plants provide habitats, facilitate understorey protégé plants, and increase soil carbon and nitrogen, and many of these functions are known to increase with the intensity of encroachment (Eldridge & Soliveres, 2015). The outcomes of removal, however, are typically mixed and generally short-lived, and do not always create the desired effects (Ding & Eldridge, 2019). In addition, the responses are dependent upon the traits of the target woody species (Ding *et al.*, 2020). Knowledge of the ecosystem impacts of different woody species and their traits is essential to guide decisions about whether removal or retention will have the desired effects.

Two contrasting scenarios are associated with the global issue of encroachment: one in which plants are increasing in density and cover (encroachment), and an opposing scenario in which plants are being removed (removal). The tendency of particular woody species to encroach, or to respond to removal, is thought to be related to their structural and functional traits (Eldridge *et al.*, 2011; Ding *et al.*, 2020), which would be expected to affect ecosystem structure and function, and therefore influence the consequences of these two scenarios. For example, encroachment of *Acacia* spp. might be expected to improve soil function in xeric environments because acacias produce nitrogen (Barnet & Catt, 1991; Mureva *et al.*, 2018). Similarly, encroachment of deep and fibrous-rooted plants would likely lead to increased hydrological function and greater soil stability due to a greater abundance of root-created macropores and associated microarthropods (Reubens *et al.*, 2007; Eldridge *et al.*, 2015). Consequently, removal of woody plants with deep and fibrous roots, or those that fix nitrogen, would be expected to reduce ecosystem functions associated with nitrogen production and ecosystem stability. Larger, denser shrubs whose foliage reaches the soil surface might be expected to provide better habitat for woodland- and shrubland-dependent birds, invertebrates and mammals, be more effective traps for aeolian-deposited material, and accumulate more resources beneath their canopies (Ravi *et al.*, 2011; D'Odorico *et al.*, 2012). Thus, removing woody plants with these traits would be expected to lead to declines in vegetation cover (ecosystem structure) and habitat for biota.

Despite the likely effects of woody plant traits on ecosystem structure and function, these relationships have yet to be tested empirically, across both encroachment and removal scenarios. Our study aims to test this using global data on the effects of encroachment (Eldridge *et al.*, 2011) and removal (Ding *et al.*, 2020) on multiple ecosystem response attributes. Our study is novel because it links different woody species with their ecosystem impacts using plant structural and functional traits that are widely applicable across global woody taxa. Further, our study explores potential relationships between woody encroachment and woody removal, improving our understanding of how management decisions to remove or retain woody plants might affect ecosystem processes.

Here we conducted a global meta-analysis using data from 433 studies covering 149 ecosystem responses and 172 woody species across the globe to evaluate the impact of woody plant traits on ecosystem responses, and whether biotic (woody plant traits) or abiotic (climate, soils) drivers control the consequences of woody encroachment and removal. This study is, to the best of our knowledge, the first study linking the traits of woody plants to the ecosystem consequences of both encroachment and removal processes based on a systematic, meta-analytical approach. In this study we had three hypotheses. First, we hypothesised that encroachment of woody plants with high values of structural and functional traits that confer a superior ability to maintain habitat quality (e.g. tall stem, pyramid-shaped canopy, foliage touching the soil surface; De Soyza *et al.*, 1997; Okin *et al.*, 2006), support nutrient cycling (e.g. deciduous, mixture of tap and fibrous roots; Attiwill & Adams, 1993; Van Breemen, 1995), facilitate ground-storey species (e.g. nitrogen (N)-fixing, nonallelopathic; Gómez-Aparicio & Canham, 2008; McKinley & Blair, 2008) and increase resilience against disturbance (e.g. resprouting, unpalatable; Heisler *et al.*, 2004; Eldridge *et al.*, 2016) would optimize ecosystem multifunctionality (the overall ecosystem response, *sensu* Manning *et al.*, 2018; Fig. 1a, Pathway E). Conversely, removal of plants with these traits would lead to reductions in the overall ecosystem responses (Fig. 1a, Pathway R). To explore the relationships among woody traits and ecosystem structure and function, we further examined how four structural traits (i.e. height, root type, plant canopy shape, foliage touching the soil surface) and five functional traits (i.e. N-fixing, deciduousness, allelopathy, palatability, resprouting) of our target woody plants would influence overall empirical measures of ecosystem structure, function and composition (Eldridge *et al.*, 2011; Ding *et al.*, 2020). Specifically, we hypothesised that woody plants with high values of structural traits (e.g. tall stem, mixed tap and fibrous roots, pyramid-shaped canopy, foliage touching the ground surface) would have a greater effect (i.e. greater increase or reduction) on ecosystem structure (Fig. 1b,c), while those with high values of functional traits (e.g. N-fixing, deciduous, nonallelopathic, unpalatable, resprouting) would have a greater effect on ecosystem function (Fig. 1d,e) under both encroachment and removal scenarios. Third, we aimed to identify the main drivers of the consequences of woody encroachment and removal. We predicted that the ecosystem response under encroachment would be driven primarily by a mixture of structural and functional traits of the encroaching woody plants, which affect a range of ecological processes such as infiltration (root types) and nutrition cycling (N-fixation, deciduous; Supporting Information Fig. S1a), whereas the ecosystem response to removal would be driven by abiotic factors (e.g. aridity, rainfall seasonality, soil texture) that regulate ecosystem productivity and stability in the absence of woody plants (Fig. S1b).

Materials and Methods

Meta-analysis data building

We used a systematic meta-analytical approach (Nakagawa & Santos, 2012) to evaluate the impact of woody plant traits on the ecological consequences of woody plant encroachment and woody plant removal. We systematically searched the published literature to identify quantitative studies that reported information on the impact of woody plant encroachment and woody plant removal on ecosystem structure, function and composition. Ecosystem structural attributes included those representing plant architecture or spatial distribution of the plant community, such as plant cover, density, patch shape and size (Eldridge *et al.*, 2016). Measures depicting ecosystem processes such as production (e.g. biomass), hydrological processes (e.g. runoff, infiltration, soil erosion) and nutrient cycling (e.g. soil nutrients, plant nutrients) were included as ecosystem functional attributes (Eldridge *et al.*, 2011). Ecosystem compositional attributes comprised variables indicating the variety of species, including species diversity, richness and abundance (Maestre & Cortina, 2004).

For studies on woody plant encroachment, we searched the ISI Web of Knowledge (http://apps.webofknowledge.com/) database

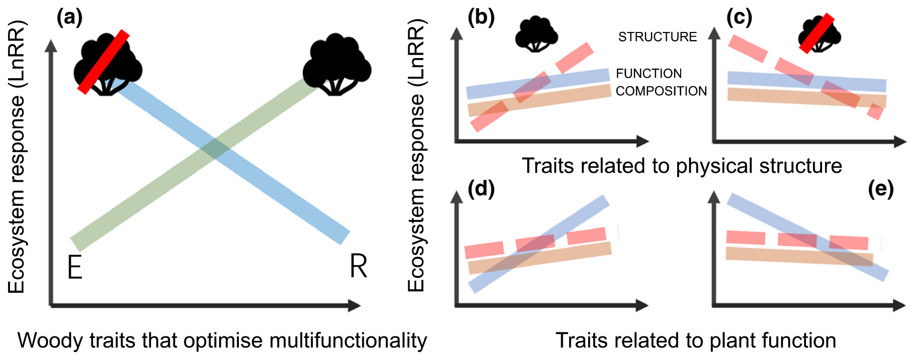

Fig. 1 Predicted relationships (a) between woody traits that optimize ecosystem multifunctionality and the ecosystem response, based on results from global meta-analyses of effects due to woody encroachment or removal. Ecosystem response is measured as the log response ratio (LnRR) of a range of ecological attributes for either encroachment (pathway 'E' in (a); encroached cf. unencroached sites), or woody plant removal (pathway 'R' in (a); woody plants present cf. removed). Plants that optimize multifunctionality are characterized by being taller, unpalatable, N-fixing, deciduous, pyramid-shaped, nonallelopathic resprouters whose foliage reaches the soil surface, and which have both tap and fibrous roots. (b–e) Predicted responses (LnRR) of ecosystem structure, function and composition to changes in either structural (plant height, plant canopy shape, ground contact, root type) or functional (deciduousness, palatability, N-fixation, allelopathy, resprouting ability) traits under encroachment (b, d) and woody plant removal (c, e) scenarios.

(1945–2015 period) for relevant publications with keywords synonymous with woody encroachment (e.g. 'thickening', 'competition', 'desertification'; see detailed methods in Eldridge *et al.*, 2011). For studies on woody plant removal, we searched multiple databases (Web of Science, Scopus, Proquest Science & Technology, Informit Online/georef; 1950–2017 period) using keywords synonymous with woody plant removal (e.g. 'shrub removal', 'brush management') and terms referring to specific treatments (e.g. 'cut', 'burn', 'fire', 'herbicide'; see detailed methods in Ding & Eldridge, 2019). During screening, we retained only those studies reporting quantitative data, conducted under natural conditions, with only one dominant encroached or removed woody species, in plots with and without woody vegetation (i.e. encroached/unencroached, removed/retained) located on the same soil type, vegetation community, and climatic regions (detailed criteria in Notes S1). Based on these criteria, we refined the literature to 175 publications for woody plant encroachment studies and 258 publications for woody plant removal studies (Notes S2).

Data collation and multifunctional traits of woody species

For each publication, we recorded the basic geographical information of the study (location, continent, landscape type), land use history, the identity of the dominant encroached or removed woody species, and the mean and standard deviation of the ecosystem responses that were assessed on woody plant encroached and not encroached plots or woody plant removal and retention plots for the encroachment and removal databases, respectively. Data on temperature and rainfall seasonality were extracted from global climate database ($0'30'' \times 0'30''$ resolution) for the 1970–2000 period from WorldClim v.1.4 (http://www.worldclim.org/) (Fick & Hijmans, 2017). Global climatic data were used because not all authors recorded rainfall or temperature. Aridity was calculated as 1 − (precipitation/potential evapotranspiration) and was derived from the Consortium for Spatial Information (CGIAR-CSI) for the 1950–2000 period (Zomer *et al.*, 2008) (https://cgiarcsi.community/2019/01/24/global-aridity-index-and-potential-evapotranspiration-climate-database-v2/). Soil sand content data 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/). Data originally published as figures were extracted using Engauge Digitizer v.4.1 (http://markummitchell.github.io/engauge-digitizer/). Overall, we compiled two databases: one on woody encroachment (1828 records; hereafter encroachment database) and one on woody removal (6965 records, hereafter removal database), on a total of 149 ecosystem response variables (Table S1).

We compiled data on four structural traits (height, root type, plant canopy shape, foliage touching the soil surface) and five functional traits (N-fixing, deciduousness, allelopathy, palatability, resprouting) for the 172 woody species (including shrubs and trees) that were encroached or removed in the two databases (see Table S2) 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/). Plant height is related to the ability of a species to accumulate resources, with generally taller plants having larger canopies and a greater ability to entrain sediments (Okin *et al.*, 2006) or provide habitat or refugia for biota. Except for the continuous trait plant height, we ranked the eight categorical traits numerically such that a larger number equated with greater function in terms of its own growth or for facilitating surrounding conditions. These traits are as follows: plant canopy shape – ranked according to a greater ability to obtain resources (water and light) for the understorey, with greater resource accumulation under v-shaped plants but greater rainfall accumulation under pyramid-shaped (inverted v-shaped) plants (v-shaped = 1, weeping/round = 2, pyramid = 3; De Soyza *et al.*, 1997); foliage reaching the soil surface – high values were ranked according to the ability to protect habitat for understorey species (no = 1, yes = 2; Okin *et al.*, 2006; Wang *et al.*, 2013); deciduousness –

higher values relate to the ability of species to benefit their growth conditions, such as greater litter inputs to the soil nutrient pool (evergreen = 1, deciduous = 2; Van Breemen, 1995); allelopathy – lower values for species that exclude or compete with protégé species (allelopathic = 1, no-allelopathy = 2; Gómez-Aparicio & Canham, 2008); nitrogen fixation – higher value for N-fixing plants (non-N fixing = 1, N-fixing = 2; McKinley & Blair, 2008); root type – higher values relate to potentially greater nutrient cycling and water infiltration (tap roots = 1, fibrous roots = 2, tap and fibrous roots = 3; Attiwill & Adams, 1993); resprouting – a higher value was associated with resprouting species being able to sustain woody plant habitat (nonresprouting = 1, resprouting = 2; Heisler *et al.*, 2004); palatability – higher values for woody species that maintain their structure (palatable = 1, unpalatable = 2; Eldridge *et al.*, 2016).

Based on the numeric values of the nine woody plant traits, we standardized the value of each trait across the 172 woody species (*z*-score transformation) to make them comparable. The average of the standardized values of all nine traits was used as our measure of multifunctional traits of each woody species, with higher values indicating greater ecosystem multifunctionality (overall ecosystem response) supported by woody plants. Using the same procedure, we then calculated separate values for structural traits, using the four structural traits (height, root type, plant canopy shape, whether foliage reaches the soil surface) and functional traits, the five functional traits (N fixation, deciduousness, allelopathy, palatability, resprouting), with higher values indicating more structurally or functionally complex woody plants (see the conceptual diagram of woody trait values in Fig. S2).

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 encroachment or removal on the overall ecosystem response, and for separate responses (ecosystem structure, function, and composition): $\mathrm{LnRR} = \log_e(X_t/X_c)$ (Hedges *et al.*, 1999) where X_t is the value of the ecological attribute in the woody plant encroachment or removal plot (i.e. treatment), and X_c is the value of the ecological attributes in the woody unencroached or woody plant retention plot (i.e. control), respectively. Positive values of LnRR indicate an increase in the response attributes following woody plant encroachment or removal, and vice versa. For ecosystem structure and function, increases in some attributes such as bare soil cover, sediment production, runoff and soil nutrient leaching indicate reductions in ecosystem quality so that a larger value corresponds to a decline in structure or function. For these variables, their LnRR values were 'coined' (multiplied by -1) to ensure that greater values corresponded to higher structure or function when calculating the overall effect size of ecosystem structure and ecosystem function (Eldridge *et al.*, 2016).

Random effects models were used to calculate the estimated mean effect sizes separately for the overall ecosystem response, and ecosystem structure, function and composition for each woody species in the encroachment database and removal database, respectively after accounting for the effects of random factors (i.e. data from different reference sources, different sample size) within the database. Data with extreme variances (> 1000) were excluded. We used the variance of LnRR as the variance in the random effect model for the woody plant encroachment database. To account for shared controls in the removal database, for example, where a study 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 & Santos, 2012) to control for it. We ran an intercept-only model (null model) with the LnRR of ecological response variables as the response. Within-study variance was included as the variance (i.e. the variance for the encroachment database or the variance matrix for the removal database), and the two random factors listed above were included as random effects to estimate mean effect sizes. We ran the null model for the overall ecosystem response, and ecosystem structure, function, and composition for each woody species in the encroachment and removal databases, respectively. The significance of the estimated effect size was examined with a *t*-test to determine whether the estimated effect size differed significantly from zero at $P < 0.05$. We then fitted linear regressions between the estimated mean effect size (LnRR) for the ecosystem response (overall ecosystem response, and ecosystem structure, function and composition) and the values of woody traits that optimize multifunctionality (multifunctional traits), related to physical plant structure (structural traits) and plant function (functional traits), respectively, to examine the relationship between ecosystem responses and woody plant traits.

Publication bias of the two databases was examined using funnel plots, Egger regression and 'trim and fill' approaches (Nakagawa & Santos, 2012) for the whole dataset and its subsets for the encroachment and removal databases respectively (see Methods S1; Fig. S3; Table S3–S5). The meta-analysis was performed in the METAFOR package (Viechtbauer, 2010), all the figures were created using GGPLOT2 (Wickham, 2016) and GGMAP (Kahle & Wickham, 2013) in R v.3.4.3 (R Core Team, 2018).

Structural equation modelling

We used structural equation modelling (SEM; Grace, 2006) to explore the direct and indirect effects of environmental conditions (aridity, rainfall seasonality and soil sand content) and the traits (structural, functional) of encroached or removed woody plants on the log response ratio for two attributes: herbaceous cover and soil stability. These were selected because they represent the major types of ecosystem structure (forage cover) or function (stability) that are of most concern to managers when they decide to remove or retain woody vegetation (Archer & Predick, 2014; Eldridge & Soliveres, 2015). Structural equation modelling enabled us to test the hypothesized effects and relationships among the main drivers and ecosystem responses based on an *a priori* model (see Fig. S1), allowing us to explore the effect of each driver after accounting for the effects of other attributes included in our model. Our *a priori* model predicted that aridity and rainfall seasonality would affect soil sand content, and have direct effects on herbaceous cover and soil stability, as well as indirect effects (mediated by the traits of encroached or removed plants), because they directly regulate ecosystem productivity, soil stability and woody plant growth (Delgado-Baquerizo *et al.*, 2013). Models with low χ^2 and root mean square error of approximation (RMSEA < 0.05), and high goodness of fit index (GFI) and R^2 were selected as the best fit models for our data. Analyses were performed using Amos 22 (IBM, Chicago, IL, USA) software.

Results

Studies of woody encroachment and removal were concentrated in five geographical nodes: Europe, North America, southern Africa, and to a lesser extent, Australia and China (Fig. S4). Based on their trait signatures, the distribution of woody plants was strongly geographically explicit. Plants in North America and Europe had high structural trait values (e.g. tall stem, pyramid-shaped canopy, mixed tap and fibrous roots, foliage touching the ground surface) but low values of functional traits (e.g. non-N fixing, allelopathic, palatable, nonresprouting, evergreen). Conversely, woody plants encroaching or being removed from southern Africa and Australia had mainly low structural, but high functional, trait values. The few woody plants recorded from Asia had a mixture of low and high values of structural and functional traits.

We found partial support for our first hypothesis of an association between multifunctional traits of woody plants and the overall ecosystem response. Under encroachment scenarios, there was no relationship between multifunctional traits and the overall ecosystem response. By contrast, removal of woody plants with increasing multifunctional trait values was associated with significant declines in the overall ecosystem responses (Fig. 2; Tables S6, S7). The impact of woody structural and functional traits on ecosystem responses differed between encroachment and removal scenarios, partly supporting our second hypothesis. For example, encroachment of woody plants with increasing values of structural traits resulted in strong declines in ecosystem composition but not ecosystem structure (Fig. 3a; Table S6). However, consistent with our expectation, we found that ecosystem function declined when woody plants with greater values of functional traits were removed (Fig. 3d; Table S7).

Our final hypothesis, that woody plant traits are important drivers of encroachment effects, but not removal effects, was partially upheld (Figs 4, S5). For example, the structural traits of woody plants were important drivers of soil stability, but not herbaceous cover, under encroachment. Under removal scenarios, however, increases in aridity had the greatest positive effect on soil stability, but for herbaceous cover, there were only weak negative effects of woody plant structural and functional traits.

Discussion

Our study provides clear evidence that the ecosystem consequences of either removing or retaining woody plants are closely associated with different structural and functional traits of the target woody plants across the globe. For example, encroachment

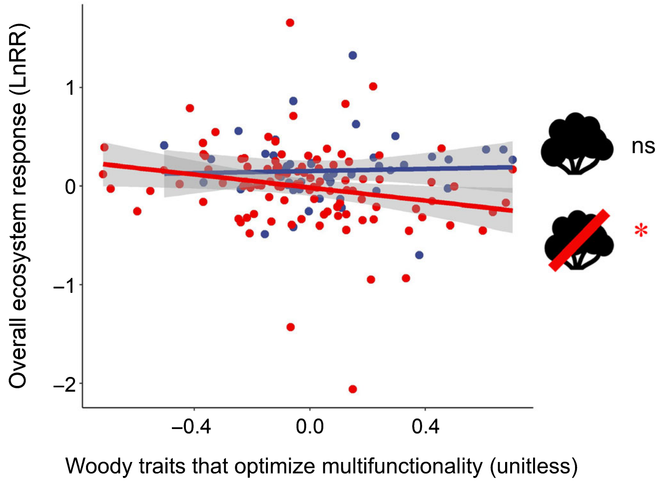

Fig. 2 Variation in overall ecosystem response (LnRR) with the multifunctional traits of woody plants under woody encroachment and woody removal scenarios. Solid lines were fitted with linear regressions. The asterisk indicates a significant ($P < 0.05$) linear relationship and 'ns' indicates an insignificant linear relationship between LnRR and multifunctional traits of woody plants that are removed. The grey shaded zone is the 95% confidence interval.

of woody plants with greater values of structural traits reduced ecosystem composition, and removing woody plants with greater values of functional traits reduced ecosystem function. Furthermore, we demonstrate that the impacts of woody plant traits on ecosystem consequences differed with different management scenarios (encroachment or removal). Contrary to the general notion, our results indicate that woody encroachment does not necessarily reduce herbaceous production, with environmental conditions (rainfall seasonality, soil texture) controlling herbaceous performance under both encroachment and removal scenarios. However, the traits of woody plants only had negative legacy effects on herbaceous cover after having been removed. Similarly, woody plants with greater values of structural traits were associated with more stable soils under encroachment, and the impact of woody removal on soil stability depended more on environmental setting (aridity, soil texture) than plant trait signature. Overall, our study indicates that biotic (plant traits) and abiotic (climate, soils) factors play different roles in regulating trade-offs between ecosystem responses under the two management scenarios. This has important implications for woody plant management because decisions about whether to retain or remove different woody taxa will vary under various environments across the world.

Ecosystem response is related to woody plant traits

The ecosystem impacts of either retaining or removing woody plants are associated with a range of different structural and functional woody traits. For example, we found that removal of woody plants that optimize multifunctionality was associated with significant reductions in the overall ecosystem responses. Woody plants characterized by high values of multifunctional traits (e.g. tall stem, foliage touching ground, N-fixing, non-

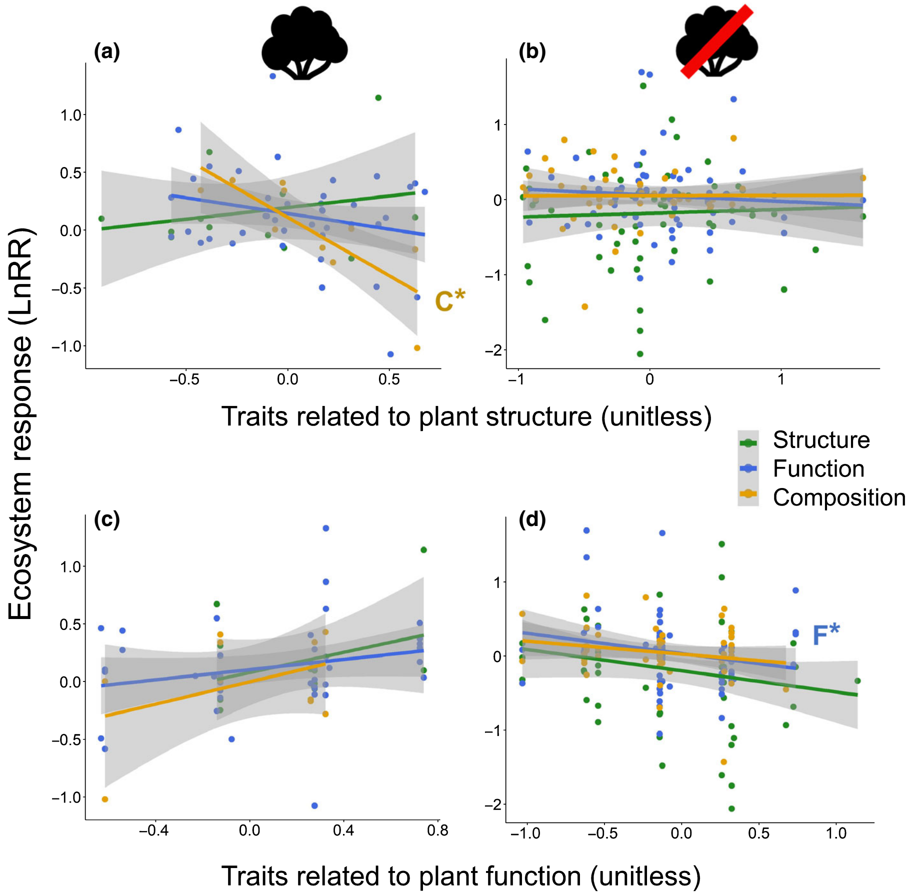

Fig. 3 Variation in ecosystem response (LnRR) of ecosystem structure (S), ecosystem function (F) and ecosystem composition (C) with the structural traits and functional traits of woody plants under (a, c) woody encroachment and (b, d) woody removal scenarios. Solid lines were fitted with linear regressions. The asterisks indicate significant ($P < 0.05$) linear relationships between LnRR and woody plant structural or functional traits. The grey shaded zone is the 95% confidence interval.

allelopathic) are more likely to benefit ecological processes such as facilitating protégé species, enhancing nutrient cycling, and providing diverse habitats (De Soyza *et al.*, 1997; Ward *et al.*, 2018). Thus, their removal leads to reductions in the overall ecosystem responses, reinforcing the view that the consequences of removal depend upon the targeted woody species (Ding *et al.*, 2020). When we examined the relationship among woody traits and our three measures of ecosystem performance (structure, function, composition), we found that removing woody plants with traits that optimized functions such as N fixation, unpalatability or non-allelopathy, strongly reduced ecosystem function but had no effects on ecosystem structure or ecosystem composition. Removal of N-fixing woody plants is known to reduce soil nitrogen concentrations (John *et al.*, 2012) and may have feedback effects on soil phosphorus (P) cycling, given the strong links between extracellular phosphatase enzymes that require N investment (Vitousek, 2004), coupling P availability to biological processes (Olander & Vitousek, 2000). Similarly, the removal of unpalatable plants such as *Larrea tridentata* (Elakovich & Stevens, 1985) or shrubs with high concentrations of secondary compounds such as *Quercus ilex* (Rogosic *et al.*, 2006) could expose highly palatable protégé species to herbivory through the relaxation of associational resistance (Smit *et al.*, 2005; Ida *et al.*, 2018). Conversely, there were no strong impacts of woody plant traits on the ecosystem consequences of encroachment, but a negative effect of structural traits on ecosystem composition and a mixture of nonsignificant effects on ecosystem structure and function were observed. Woody plants with higher values of structural traits (e.g. tall stem, mixed tap and fibrous roots, foliage touching ground) are characterized by a greater ability to scavenge resources (Ward *et al.*, 2018), potentially competitively excluding other species. The mixed effects on ecosystem structure and function might be explained by the highly nuanced impact of encroachment reported globally (Eldridge *et al.*, 2011), with the ecological effects of woody plants also depending on climatic conditions, disturbance regimes (grazing; Eldridge *et al.*, 2013) and encroachment stages (Eldridge & Soliveres, 2015).

Drivers of forage production and ecosystem stability differ with management scenario

Pastoral land management is geared towards maximizing pastoral productivity, and therefore livestock production, while maintaining a stable ecosystem (Blake *et al.*, 2018; Campos *et al.*, 2018).

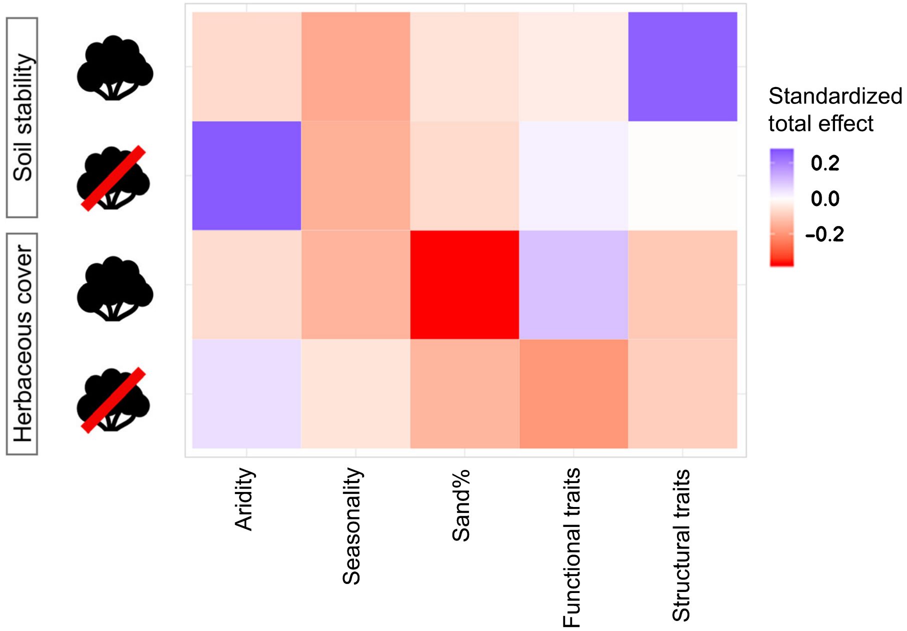

Fig. 4 Standardized total effects (sum of positive and negative effects; derived from the structural equation modelling in Supporting Information Fig. S5) of aridity, seasonality of rainfall, sand% (soil sand content), and woody plant functional and structural traits on two ecosystem response measures, soil stability and herbaceous cover, under encroachment and removal scenarios.

Our results indicate strong trade-offs among a range of specific ecosystem responses under woody retention and removal scenarios. The retention of woody plants had positive effects on stability but mixed, and therefore nonsignificant, effects on pastoral production (e.g. herbaceous cover) due to the wide-ranging differences in shrub effects on understorey protégé species. Conversely, under woody removal, traits were important only for herbaceous cover but not for soil stability, which was regulated by changes in environmental variables (soil sand, rainfall seasonality).

In agri-pastoral systems, the generally accepted paradigm is that woody encroachment reduces pastoral productivity through competitive exclusion (Scholes & Archer, 1997; Oba *et al.*, 2000). Woody plants are removed, therefore, in the hope that this will result in increased pastoral production for livestock (Archer *et al.*, 2011), though the results are generally short lived (Archer *et al.*, 2011; Eldridge & Soliveres, 2015; Ding & Eldridge, 2019). However, using global data on woody removal and retention scenarios, our structural equation modelling showed that the extent to which encroachment reduces herbaceous cover depends on environmental conditions, with highly seasonal rainfall and sandy soils suppressing herbaceous cover due to highly variable rainfall and low soil water retention (Noy-Meir, 1973). Conversely, woody plants only affected herbaceous performance under removal, with herbaceous cover negatively associated with removal of woody plants with high values of functional, and to a lesser extent, structural traits. Protégé species can benefit from their association with structurally (e.g. tall stem, developed roots) or functionally (e.g. N fixing, unpalatable) complex woody plants through greater moisture and nutrient availability, and less disturbance under woody species (e.g. ameliorated microclimates, fertile patches; Yoder & Nowak, 1999; D'Odorico *et al.*, 2010) or the ability of woody species to extract water from the subsoil (hydraulic lift, Caldwell *et al.*, 1998). These facilitatory effects could potentially outweigh any competitive effects of woody plants on herbaceous species in water-limited environments. Thus, removing structurally or functionally complex woody plants would lead to forage reductions (Dohn *et al.*, 2013). Additionally, the effects of woody plant removal on the herbaceous understorey will likely also depend on a number of factors including post-removal herbivory, climatic conditions, the density and proximity of nearby woody patches, and the presence of a viable seed bank, to name a few (Archer *et al.*, 2011; Ding *et al.*, 2020). These factors vary markedly across different regions and different shrub types. Consequently, the overall effects of woody removal on pastoral production are likely to be strongly nuanced, consistent with the results of our study.

Consistent with prediction, woody traits mainly affected soil stability under retention, but not under removal scenarios. This suggests that pyramid-shaped tall plants with mixed tap and fibrous roots, and with foliage reaching the ground play an important role in soil stabilization compared with the bare interspaces, by reducing disturbance, binding soil particles and acting as resource traps (D'Odorico *et al.*, 2010, 2012). Under removal, stability was most strongly associated with environmental variables, strengthening with increased aridity and lower sand content. The positive links between aridity and stability are well-founded in drylands where soil surfaces are often dominated by biocrusts, surface aggregations of biological organisms such as lichens, bryophytes, bacteria and fungi, and the uppermost layers of the surface soils (Ferrenberg *et al.*, 2017). These nonvascular communities enhance surface stability and resilience (Eldridge & Greene, 1994) and have been shown to have their greatest development in more arid environments (Rodriguez-Caballero *et al.*, 2018; Ding & Eldridge, 2020). Arid areas might also be expected to support lower levels of vertebrate grazing, lower population densities and reduced levels of human exploitation (Martínez-Valderrama *et al.*, 2020) and, consequently, would be expected to have greater ecosystem stability. Conversely, we show that sites dominated by sandy soils had lower levels of stability, consistent with observations of greater erosion in areas dominated by sandy soils, such as coppice dune systems in New Mexico (Ravi *et al.*, 2011).

Concluding remarks

Our global synthesis reveals that the consequences of woody retention or removal on ecosystem responses vary with woody plant traits. For example, compositional effects will be reduced when plants with high values of structural traits encroach, but not necessarily when they are removed. Similarly, functional processes will decline when plants with high values of functional traits are removed, but the opposite does not necessarily ensue when they increase under encroachment. Furthermore, our studies identify the trade-offs between forage production and ecosystem stability, with the relative effects of woody traits and environmental conditions varying with encroachment or removal scenarios. Thus, management decisions on whether to retain or remove woody plants will depend on whether the end game is to increase diversity, for example, under a conservation management setting where small stature plant species are favoured (e.g. *Euphorbia barnardii*, Knowles & Witkowski, 2000). Similarly, the management objective might be to enhance biodiversity (e.g. to benefit shrub-dependent birds or mammals; Coffman *et al.*, 2014) or to enhance ecosystem function (e.g. maximising pastoral productivity and available biomass for livestock grazing). With these objectives, managers might wish to retain woody plants with high values of functional traits (Scholes, 2009). All of these decisions on woody plant management will depend on trade-offs between various land use competitors (Eldridge *et al.*, 2011; Archer & Predick, 2014), but the effectiveness of both retention and removal will depend on the specific traits characteristic of the particular woody species, and the environments in which management is implemented.

Acknowledgements

We thank Shinichi Nakagawa and Max Mallen-Cooper for assistance with the meta-analysis. This study was supported by Holsworth Wildlife Research Endowment & The Ecological Society of Australia and a PhD scholarship from China Scholarship Council (no. 201706040073).

Author contributions

DJE and JD designed the research, collected data, and built the databases. JD performed the statistical analyses. DJE wrote the first draft and JD critically revised the manuscript.

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Data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 *A priori* model structure.

Fig. S2 Woody trait conceptual diagram.

Fig. S3 Funnel plots.

Fig. S4 Global distribution of structural and functional trait values.

Fig. S5 Structural equation models for herbaceous cover and soil stability.

Methods S1 Publication bias examination.

Notes S1 Detailed background information on the procedure for selecting relevant studies.

Notes S2 List of literature used to compile the woody plant encroachment and woody plant removal databases.

Table S1 List of 149 response variables on ecosystem structure, function and composition.

Table S2 The database of nine attributes of the 172 woody species.

Table S3 Test for funnel plot asymmetry.

Table S4 Egger regression results.

Table S5 Trim and fill results.

Table S6 Summary of linear model results for woody encroachment.

Table S7 Summary of linear model results for woody removal.

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