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The success of woody plant removal depends on encroachment stage and plant traits

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Woody plants (shrubs and trees) are encroaching across the globe, affecting livestock production and terrestrial ecosystem functioning. Despite the widespread practice, there has been no quantitative global assessment of whether removal of encroaching woody plants will re-instate productive grasslands and open savanna. Here we compiled a global database of 12,198 records from 524 studies on the ecosystem responses of both the encroachment and removal of woody plants, and show that removal fails to reverse encroachment impacts. Removing woody plants only reversed less than half of the reductions in herbaceous structure induced by encroachment, and woody expansion actually enhanced ecosystem functions (+8%). The effectiveness of removal varied with encroachment stage (that is, time since treatment) and the functional traits (for example, deciduousness and resprouting) of the focal woody species, and waned in drier regions. Our results suggest that assessment of woody plant communities before removal is critical to assess the likelihood of successful ecosystem recovery.

Earth's grasslands are shrinking rapidly, yet the area occupied by woodlands continues to expand. The current global extent of woody expansion or encroachment is estimated to exceed 5 million square kilometres[1], equivalent to half of the land mass of Canada. Although most apparent in drylands (arid, semi-arid and dry subhumid biomes), expansion of woody plants is increasingly evident in alpine, boreal, subarctic and arctic tundra environments, with increases in woody plant cover, height and extent[2,3]. The causes of encroachment are varied, ranging from changes in fire regimes, land-use intensification, overgrazing and climate, which result in more variable rainfall and enriched atmospheric carbon dioxide[4–7]. Changes in these drivers can influence the growth of woody plants, potentially initiating a positive feedback loop that promotes further woody expansion[6]. For example, in grasslands, fertile islands formed beneath woody plant patches promote woody plant persistence via resource redistribution[8], and woody expansion in tundra systems can accelerate the thawing of permafrost, releasing more carbon to the atmosphere and leading to higher temperatures that favour woody growth[9]. Woody encroachment is associated with substantial changes in key ecosystem processes and functions, the sign and magnitude of which vary with species and environmental context[10–13]. Encroachment leads to declines in grassland-dependent organisms[14,15] and a loss of important cultural and spiritual services[16], but also enhances shrubland-dependent biota and the sequestration of carbon[8]. Among these changes, dwindling forage production is particularly problematic in drylands[17], which cover approximately 41% of Earth's terrestrial land surface and support 38% of the human population, many of whom rely on forage production to support pastoralist lifestyles[18].

Removal of woody plants has been promoted widely, largely due to the perception that these plants suppress forage production, and the expectation that removal will improve environmental conditions (for example, greater soil stability, carbon storage and hydrological function[12,19,20]). Yet reversing or remediating encroachment effects is extremely challenging, and attempts over the last century have produced highly variable results for a range of different functions[12,21–24]. Despite extensive research on the effectiveness of woody removal[12,20,22,25], there is relatively little clear evidence of the extent to which removal might reverse the impacts of encroachment on multiple functions and ecological processes, and the conditions (that is, removal techniques and ecological contexts) under which this reversibility

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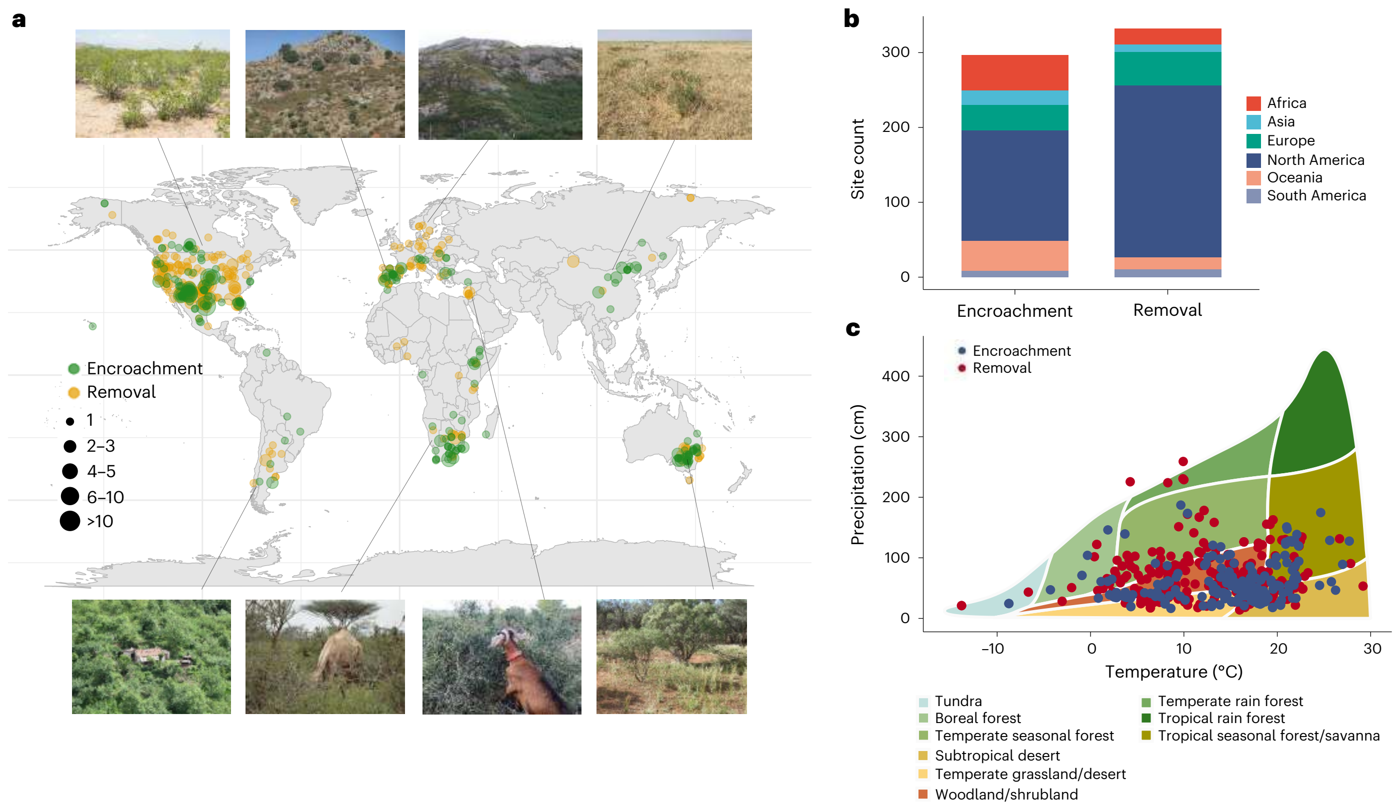

Fig. 1 | Global distribution of woody encroachment and removal sites. **a**, The global distribution of 216 woody encroachment studies and 308 woody removal studies across the globe, with selected photos showing the encroached landscape. **b**, Counts of encroachment and removal studies in each of the six continents. **c**, The location of the sites in relation to the temperature and precipitation envelope.

might be optimized. This information is critical, as organizations and managers seek to promote effective woody management, better allocate restoration funds and make improved predictions of likely outcomes, particularly under different global change scenarios.

Key ecological factors regulating the effectiveness of woody removal are prevailing climatic conditions[12], the traits of the encroached woody species[26] and initial woody cover or density levels[27]. High rainfall seasonality could favour shrubs over herbaceous species[7], which would weaken the effectiveness of reducing woody plant cover. Tall or nitrogen (N)-fixing woody plants can boost the magnitude of ecosystem functions by providing complex habitat for diverse organisms and soil N for supporting plant growth, but such positive effects may diminish when plants attain high densities[28]. Therefore, removing plants with these traits could have detrimental effects on functional processes, particularly when initial woody densities are low[8,29]. Allelopathic species, conversely, negatively affect ecosystem structure by suppressing neighbouring species. Thus, their removal would enhance plant diversity[11,22].

Whether woody removal is beneficial or detrimental is largely unknown because the ecological consequences of encroachment and removal are typically studied in isolation[13,16,20]. Limited evidence suggests that encroachment effects are maximized at intermediate cover levels, for example, 50% cover for carbon sequestration[30]. This suggests that maintaining cover at intermediate levels might optimize ecosystem functioning[29,31], but this is poorly understood. Removal of woody plants in dense stands may be ineffective over long time periods due to positive feedbacks between resource redistribution and woody persistence[21,32]. Despite the extensive literature on encroachment and removal, we still have a poor understanding of the density-dependent effects of woody plant removal, or how this density dependence is regulated by the functional traits of the species removed, the elapsed time since removal or the prevailing environmental conditions. Our limited understanding of these major factors makes it difficult to recommend strategies to effectively return encroached systems to their pre-encroachment state, a major goal of land managers for more than a century[11,12,20].

In this Article, we report the results of a comprehensive global assessment of the association between woody encroachment and woody removal processes, aiming to (1) examine whether removal can reverse the impacts of encroachment; (2) explore how the attributes of encroaching plants (traits and initial cover) affect removal outcomes; and (3) identify the major factors driving the need for, and effectiveness of, removal on different management objectives. To realize these aims, we conducted a global meta-analysis based on 12,198 data records extracted from 524 studies published between 1990 and 2021, distributed globally across all continents except Antarctica, and covering a wide variety of biomes (Fig. 1 and Supplementary Appendix 1). Information on the paired ecological responses to encroachment (encroached or unencroached) and removal (removed or retained) were extracted to compile the database. We used the weighted effect size (log response ratio, LnRR) to compare the effect sizes of paired encroachment and removal studies, and calculated the impact using mixed-effect models. Information on climatic conditions, woody plant traits, encroached woody cover, removal methods and time since removal was obtained to explore the potential regulators of removal effectiveness. We used all the ecological attributes to describe the average ecological response and divided them into three groups: (1) ecosystem structure (those representing plant architecture or spatial distribution of the plant community); (2) ecosystem function (measures depicting ecosystem processes such as production, hydrological processes and nutrient cycling); and (3) ecosystem composition (the variety of species, including species diversity, richness and abundance).

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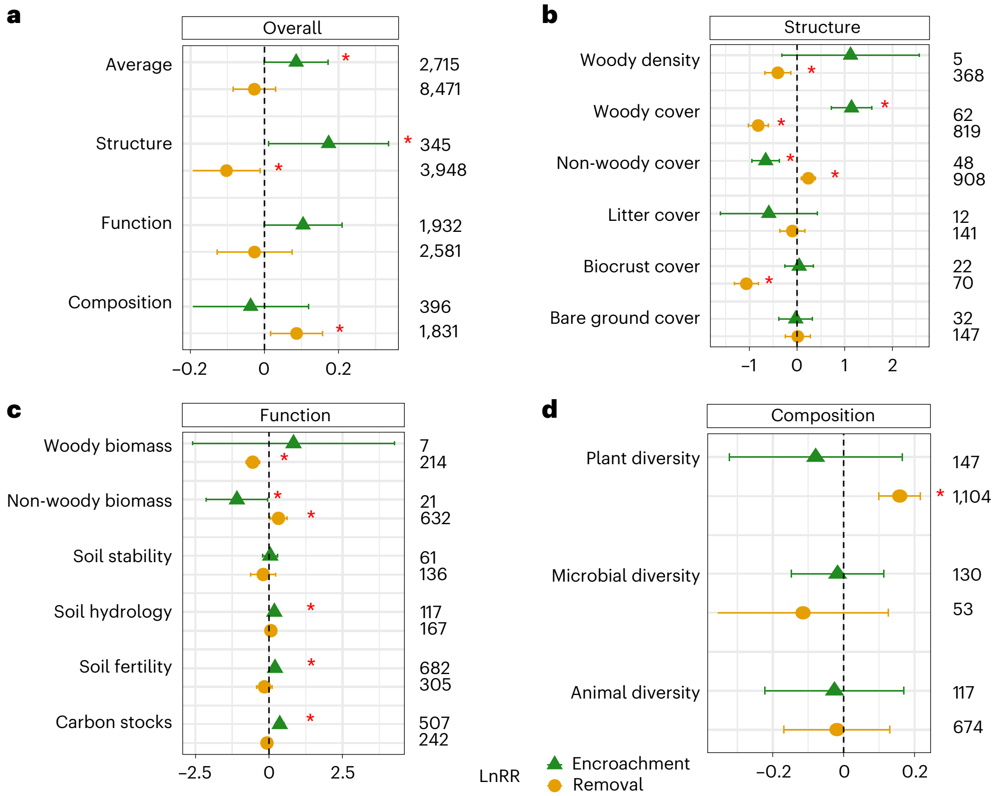

Fig. 2 | Ecosystem response of woody encroachment and removal. a, The response of the overall ecological attributes to woody encroachment and removal. **b**–**d**, The response of attributes within ecosystem structure (**b**), ecosystem function (**c**) and ecosystem composition (**d**). Data are presented as mean ± 95% confidence interval (CI). Numbers on the right of each subplot represent the number of independent observations for each ecological attributes. LnRR = Ln (encroached or unencroached) for woody encroachment database, LnRR = Ln (woody removed or woody retention) for woody removal database. Positive values of LnRR (right side of the zero line) indicate an increase in the value of the response attributes following woody plant encroachment or removal, and negative values of LnRR (left side of zero line) indicate a decline. Red asterisk indicates significant LnRR ($P < 0.05$, t-test on whether LnRR cross zero).

Our results show that removing woody plants only partially reverses the effects of encroachment on ecosystem structure (for example, woody and non-woody cover) and enhances plant composition (for example, plant diversity), but there is no evidence that removal restores ecosystem functions. Attributes of encroaching species such as traits and stage of encroachment are the key factors driving the effectiveness of removal, and their relative importance depends on the removal objective. Moreover, drier and more variable climates dampen the effectiveness of removal. Pre-removal assessment of woody communities is critical to assess the likelihood of successful removal and recovery. Target-orientated management plans are necessary to guide woody removal programmes depending on particular species and environmental conditions, particularly under changing climatic conditions.

Results and discussion

Ecosystem response of encroachment and removal

We first tested whether woody removal could reverse the effects of encroachment, and found that, overall, it reversed only ecosystem structure (Fig. 2a) by reducing woody plants, allowing the recovery of the non-woody component (Fig. 2b). Compared with rapid declines in woody cover immediately following removal, non-woody species showed a smaller response, probably due to a greater access to light, space, and below-ground water and nutrients following relaxation of competitive exclusion[10,33]. Even so, the effect of woody removal was only partial, with a 21% increase in non-woody cover after removal compared with a 48% reduction under encroachment (Fig. 2b). This relatively weak recovery rate was consistent, even when considering different woody genera separately (Fig. 3b), and could be driven by an enhanced growth of previously suppressed exotic species following woody removal[34,35]. It is also potentially due to the fact that encroachment-driven alterations in soils and microclimates, such as reductions in soil infiltration[36], greater soil disturbance[37], changes in microbial composition[38] and elevated soil temperature[39], could have inhibited the ability of non-woody plants to revert to their original state, thereby promoting their re-encroachment (Fig. 4d). Our analyses further revealed that this minor ecosystem recovery, such as ecosystem composition and structure, generally remained consistent, even decades after removal (Fig. 4c). Despite the widespread use of different removal methods and their high cost[17], our results indicate that removal only partially suppresses the effects of encroached woody plants on non-woody components. Non-removal management, either adopting appropriate grazing management that prevents encroachment into current grasslands[40], using prescribed fire[41] or re-instating natural fire regimes, would seem a better long-term strategy.

Contrary to the general notion that encroachment is symptomatic of ecosystem degradation[12,20,42], we found that encroachment actually enhanced the average ecological response by 8%. For example, there was an increase in carbon stocks (+31%), soil fertility (+18%) and soil hydrology (+17%, Fig. 2c) at encroached compared with unencroached sites. This provides evidence of an enhancement of functional processes (for example, carbon sequestration and nutrient cycling) following encroachment rather than the oft-reported declines in function[11]. Compared with grasses, long-lived, taller and wider woody plants have a greater photosynthetic capacity and ability to sequester carbon[43]. Above-ground carbon stocks have been shown to be elevated under encroachment[11,41], with greater nutrient return via litterfall[44]. Moreover, woody plants have a superior ability to scavenge resources[45], are strong facilitators of groundstorey protégé species[46], harbour diverse

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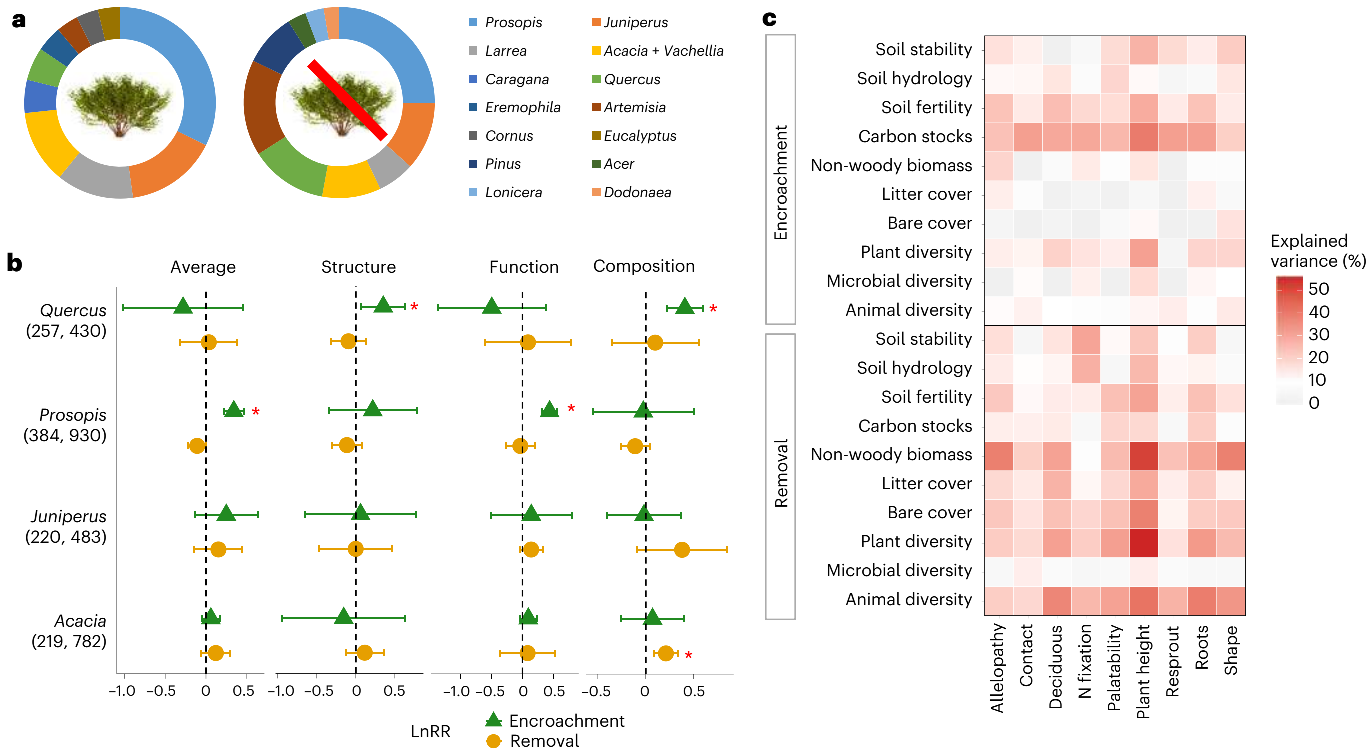

Fig. 3 | Species-specific ecosystem response of woody encroachment and removal. a, The top ten woody genera studied in the woody encroachment and removal literature based on the number of studies. **b**, Ecosystem response (LnRR; mean ± 95% CI) of woody encroachment and woody removal for the averaged ecological response, ecosystem structure, function and composition for the four major woody genera, respectively, with red asterisk indicating significant LnRR ($P < 0.05$, t-test on whether LnRR cross zero), and numbers in brackets indicate the number of independent observations for the average ecosystem response of each genera for woody encroachment and removal, respectively. **c**, The explained variance of plant traits on the ecosystem response to encroachment and removal using random forest analyses (Supplementary Table 7).

microbes and may restrict herbivore access through their dense canopy structure[45,47,48]. Together, these processes reinforce the formation of 'fertile islands' beneath aggregations of woody plants[49], supporting improved levels of soil function and ecosystem multifunctionality[50]. Conversely, the removal of encroaching woody plants had generally neutral effects on ecosystem functions, questioning the general perception that woody removal improves or restores ecosystem functions. The only significant change in ecosystem composition was an increase in plant diversity following removal (Fig. 2d), due to the emergence of diverse plant species associated with waning competition[51].

Drivers of the reversibility of encroachment

To better understand the context dependency of woody encroachment and removal effects, we then used a random forest analysis to explore the relative importance of nine key woody plant traits on encroachment and removal outcomes (Fig. 3c). Such traits are known to regulate woody plant effects on ecological processes[13,14], and our analyses revealed that the same plant traits have contrasting roles in determining the functional consequences of encroachment compared with removal. For example, deciduousness, plant height and root type mainly explained the variance in soil fertility and carbon stocks under encroachment, but accounted primarily for the variance in plant diversity and animal diversity under removal. Encroachment of species with these traits can enhance soil fertility and carbon stocks because taller plants generally have larger canopies with a greater capacity to capture airborne sediment[52]. Similarly, deciduous plants can enhance soil organic matter inputs, and deep and lateral roots enable plants to scavenge resources both vertically and horizontally[53–55]. The removal of species with these traits, however, may not alter these functions because the physical, chemical and microbial signature of woody plant habitat ('fertile islands') persists long after the death of the focal woody plant[56,57]. Removal, however, would be expected to dramatically affect biodiversity, given the immediate loss of physical structure and associated litter, which shades the soil surface and provides habitat for litter-obligate fauna[48,58]. Regardless of the underlying mechanisms, the divergent effects of the same woody functional traits for encroachment and removal processes illustrate that encroachment impacts cannot be used to predict the consequences of woody removal.

The magnitude of woody encroachment would induce a regime shift that affects the likelihood of reversal, but this has often been neglected when assessing the effectiveness of removal[21]. Given their importance, we further explored the influence of woody cover and time since the imposition of treatment using linear and quadratic regression analyses. The effect of removal on functions shifted from neutral to negative as initial woody cover increased, particularly under scenarios where dense stands of encroachment (>50% cover) were removed (Fig. 4a). This led to rapid reductions in carbon stocks (−4% to −40%; removal compared with retention; responses range from the lowest to the highest woody cover) and soil fertility (−15% to −53%), and expansion of bare soil (+37% to +84%) with increasing woody cover (Fig. 4b). Post-removal woody cover significantly increased over time (Fig. 4d), consistent with the general observation of the rapid re-encroachment worldwide due to the fact that many encroached species have the ability to resprout rapidly. This means that any removal is largely ineffective within 5 years (refs. 12,22). For example, most treatment methods such as cutting, burning and browsing only remove the above-ground compartment and fail to kill the plants outright. Thus species with the ability to resprout from epicormic buds can recover, often more vigorously than before treatment, sustaining the woody habitats[16,59,60]. Recovery of the woody community after removal was associated with

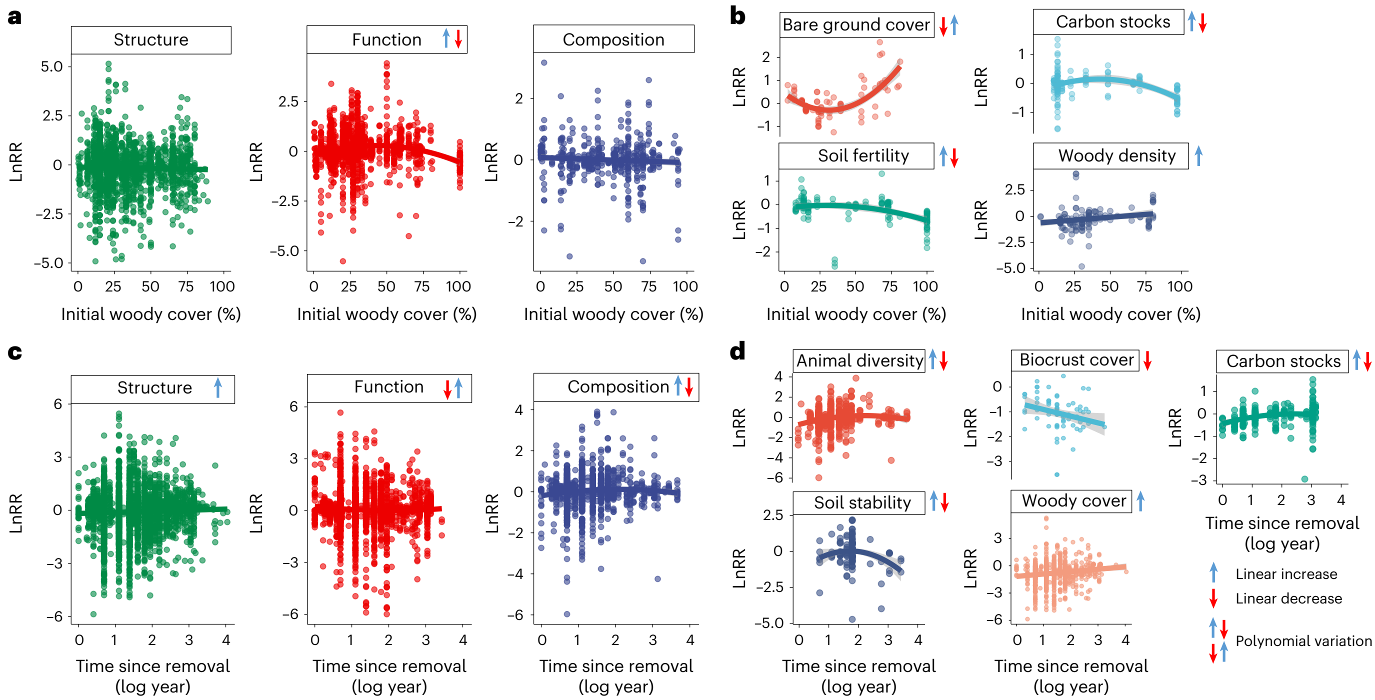

Fig. 4 | Variation in the ecosystem response of woody removal. a,**b**, Variation in the response of ecosystem structure, function and composition (**a**) and ecological attributes (**b**) to woody removal with the increasing initial woody cover (encroachment stage). **c**,**d**, Variation in the response of ecosystem structure, function and composition (**c**) and ecological attributes (**d**) to woody removal with the increasing time since removal (log transformed). Lines are fitted on the basis of linear or polynomial regressions and the shading zone represents the 95% CI. Arrows indicate significant variation trend for linear regression (single arrow) and polynomial regression (double arrows). Negative, neutral and positive LnRR indicate ecological attributes are lower, equal or higher after removal, respectively, compared with encroached scenarios. Only ecological attributes with significant variation ($P < 0.05$) are presented and details of regression model fitting on all attributes are presented in Supplementary Table 10.

changes in animal diversity (−42% to +9%; removal compared with retention; responses range from the nearest to the longest time) and carbon stocks (−36% to +14%) at the expense of biocrust cover (−54% to −80%) and soil stability (−48% to −58%), as time since removal increased (Fig. 4d). Biocrusts, in particular, dominate the inter-spaces and are important drivers of soil stability worldwide[61], but this dominance wanes as woody cover increases[62]. Although overall animal diversity increases as woody plants re-encroach, trade offs among different fauna may still result in encroachment winners and losers[15,63].

Finally, we used structural equation models to explore the relative importance of encroachment attributes and treatment type on three ecosystem responses that dominate the encroachment and removal literature: woody plant cover (the focus of removal studies), non-woody cover (a productivity objective) and animal diversity (a conservation objective; Fig. 5). After accounting for the effects of differences in spatial location and soil texture, we found that woody cover and two woody plant traits (deciduousness and ability to resprout) were the most important determinants of the effectiveness of removal on animal diversity (Fig. 5c). However, treatment type (for example, physical, chemical or multiple removal methods) and time since treatment were the major determinants of the effectiveness of removal on woody and non-woody cover (Fig. 5a,b) (refs. 34,42). The effectiveness of most treatments in suppressing woody cover was short lived, with effectiveness mitigated by prolonged time since removal (Fig. 5b), as most sites (82%) in our study received only a one-off treatment, which is largely ineffective[12]. Our results provide a fresh perspective on the major factors contributing to the success of removal at the global scale: the traits of target species and their initial cover (encroachment attributes), and treatment used (type and time since application). There was also a more limited influence of aridity or rainfall seasonality, with their increases partly suppressing the effectiveness of removal on animal diversity and non-woody cover, suggesting that climate change can weaken future effectiveness of removal.

Conclusions

Our study provides the first global empirical test of the general perception that removal of woody plants can return encroached systems to their pre-encroached state. Removal reinstated less than half of the reductions in non-woody plant cover, and consequently failed to lead to sustained increases in ecosystem services, an implicit goal of most removal programmes. Conversely, woody encroachment enhanced ecological responses by 8% overall, indicating that removing plants to improve ecosystem functions is unrealistic. Rather, the effectiveness of removal was highly contingent upon the stage of encroachment, with the removal outcomes on ecosystem functions shifting from neutral to negative as the cover of encroached woody plant increased. The identity of the focal woody species also regulated the effectiveness of removal on ecological responses via plant traits. Specifically, the ability of the focal woody plants to resprout and whether they were evergreen or deciduous largely determined the post-removal response of non-woody cover (herbs and grasses) and animal diversity. Although woody removal can enhance ecosystem composition, any positive outcomes are likely to wane under drier and more variable climates.

Rather than treating encroachment as a homogeneous process, our results suggest that pre-removal evaluation is essential to assess the likelihood of functional, structural and compositional ecosystem recovery when removing species with different traits and at different densities, particularly as climates change over the next half century. This assessment needs to consider likely production, conservation and socio-political factors, and their trade offs[11]. Further, a greater investment in developing appropriate initial and follow-up treatment

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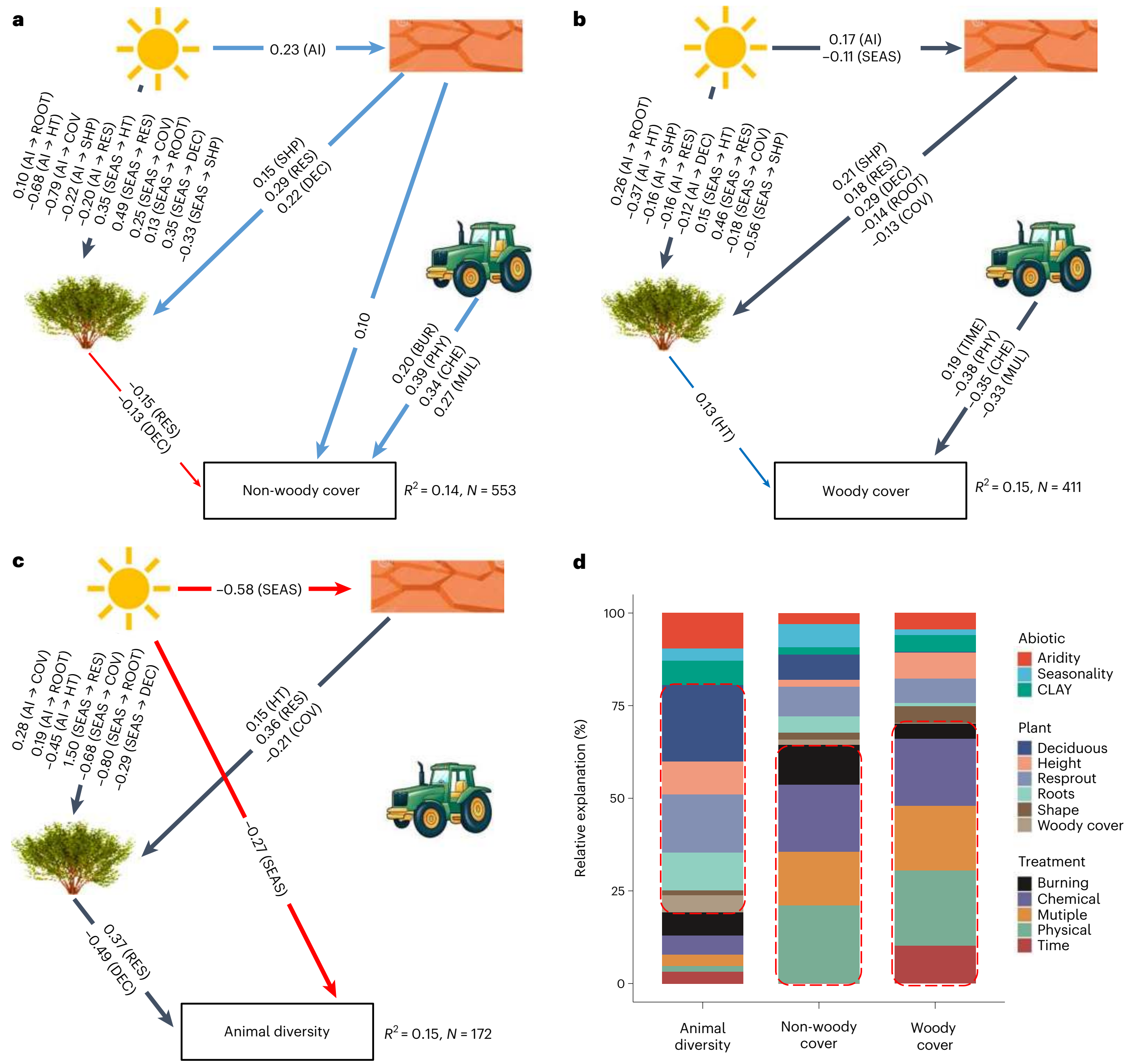

Fig. 5 | Direct and indirect of climate, soil, encroachment attributes and treatment on ecosystem response of removal. **a**–**c**, Structural equation models of the direct and indirect effects of factors (left to right, top to bottom): climate (aridity (AI) and rainfall seasonality (SEAS)), soil clay (CLAY), encroachment attributes (initial woody cover (COV), plant height (HT), root type (ROOT), plant shape (SHP), resprout (RES) and deciduousness (DEC)) and treatment (time since woody removal (TIME), physical removal (PHY), chemical removal (CHE), burning (BUR) and multiple method of removal (MUL)) on the response of non-woody cover (**a**), woody cover (**b**) and animal diversity (**c**) to woody removal after accounting for the effect of spatial location (longitude and latitude), which are not shown in the figure. The detailed model structure is shown in Supplementary Fig. 5 with factors involved directly linked with each other. **d**, Stacked bar plot illustrating the relative explanation of each predictor based on the absolute value of standardized total effects (sum of direct plus indirect effects) derived from each of the structural equation modelling, with dash boxes highlighting the group of drivers accounting for the majority of the explanation. Non-woody cover: model fit: $\chi^2 = 3.92$, degrees of freedom (df) 2, $P = 0.14$, $R^2 = 0.14$, RMSEA 0.04, $N = 553$ and Bollen–Stine 0.10 (2,000 bootstraps). Woody cover: model fit: $\chi^2 = 4.64$, df 2, $P = 0.10$, $R^2 = 0.15$, RMSEA 0.07, $N = 411$ and Bollen–Stine 0.09 (2,000 bootstraps). Animal diversity: model fit: $\chi^2 = 5.6$, df 2, $P = 0.06$, $R^2 = 0.15$, RMSEA 0.10, $N = 172$ and Bollen–Stine 0.02 (2,000 bootstrap).

methods is needed to meet land-holder aspirations regarding improvement in production outcomes. Overall, our study provides a sound basis for more informed sustainable management of encroaching vegetation at the global scale under predicted climate change scenarios, where woody species will unavoidably increase their dominance of dryland plant communities.

Methods

Meta-analysis data building

We used a systematic meta-analytical approach by systematically searching 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[64]. Measures depicting ecosystem processes such as production (for example, biomass), hydrological processes (for example, runoff, infiltration and soil erosion) and nutrient cycling (for example, soil nutrients and plant nutrients) were included as ecosystem functional attributes[11]. Ecosystem compositional attributes comprised variables indicating the variety of species, including species diversity, richness and abundance[65].

For studies on the impact of woody plant encroachment and woody plant removal, we searched multiple databases (Web of Science, Scopus, Proquest Science & Technology and Informit Online/georef); 1950–2021 period) for relevant publications with keywords synonymous with woody encroachment (for example, 'thickening', 'competition' and 'desertification'; see detailed methods in Eldridge et al.[11]) and keywords synonymous with woody plant removal (for example, 'shrub removal' and 'brush management') and terms referring to specific removal treatments (for example 'cut', 'burn', 'fire' and 'herbicide'; see detailed methods in Ding and Eldridge[22]). During screening, we retained only those studies reporting quantitative data on the ecosystem responses that were attributed to woody encroachment or removal only, conducted under natural conditions, with only one dominant encroached or removed woody species, and in plots with and without woody vegetation (that is, encroached and unencroached or removed and retained) located on the same soil type, vegetation community and climatic regions (detailed criteria in Supplementary Appendix 1). On the basis of these criteria, we refined the literature to 216 publications for woody plant encroachment studies and 308 publications for woody plant removal studies (Supplementary Appendix 2).

Data collation and the traits of woody species

For each publication, we recorded the basic geographical information of the study (location, continent and landscape type), land-use history, the identity of the dominant encroached or removed woody species, and the mean, replicates and standard deviation (s.d.) of the ecosystem responses that were assessed on woody plant encroached and not encroached or woody plant removal and retention plots for the encroachment and removal database, respectively. For the woody plant removal database, we also recorded the woody plant encroachment stages (for example, woody plant cover and density) before removal and the time since removal (for example, the number of years after removal). If a study did not report a measure of variance (32% of encroachment data and 3.7% of removal data), we used imputation to calculate missing variances using the relationship between mean and variance, expressed on a log–log scale (Taylor's Law)[66]. Our ability to predict missing variances was high (R^2 = 0.77 for encroachment database; R^2 = 0.81 for removal database). To account for zero values of s.d., we performed a linear regression of $\log_{10}(x) \sim \log_{10}(\text{s.d.})$ and used the regression coefficients to back-calculate s.d. values[66].

Data on temperature and rainfall seasonality were extracted from a global climate database (0′30′ × 0′30′) for the 1970–2000 period from WorldClim Version 2.0 (http://www.worldclim.org/)[67]. Global climatic data were used because not all authors recorded rainfall or temperature. Aridity was identified as 1-precipitation divided by potential evapotranspiration and was derived from the Consortium for Spatial Information for the 1950–2000 period. Soil clay content were obtained from the Harmonized World Soil Database (resolution 1 km) (ref. 68). Data originally published as figures were extracted using Engauge Digitizer V4.1 (http://digitizer.sourceforge.net/). Overall, we compiled two databases: one on woody encroachment (2,912 records; hereafter, encroachment database) and one on woody removal (9,286 records; hereafter, removal database), on a total of 101 ecosystem response variables (Supplementary Table 1).

We compiled data on four structural traits (that is, plant height, root type, plant canopy shape and foliage touching the soil surface) and five functional traits (that is, N fixing, deciduous, allelopathic, palatability and resprouting) for the 213 woody species (including shrubs and trees) that were encroached or removed in the two databases (Supplementary Fig. 3 and Supplementary Table 2) on the basis of online plant traits databases such as BROT[69], PLANTS[70], Woody Plants Database (http://woodyplants.cals.cornell.edu/home) and TRY[71]. Except for the continuous 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 (Supplementary Appendix 3 and Supplementary Table 3).

Effect size and publication bias

We used LnRR 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): $\mathrm{LnRR} = \ln(X_t/X_c)$ (ref. 72) where X_t is the value of the ecological attribute in the woody plant encroachment or removal plot (that is, treatment) and X_c is the value of the ecological attributes in the unencroached or woody plant retention plot (that is, control), respectively. The averaged LnRR was weighted by the sampling error variance, which was calculated according to the formulas presented in Hedges et al.[72] on the basis of standardized deviation following the code used in Mallen-Cooper et al.[73] (https://osf.io/2x53b/). The LnRR was chosen because it is simple to interpret and understand, largely unaffected by non-independent samples and widely used in global meta-analysis[74,75]. 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 ground cover, tree mortality, 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[64]. Publication bias of the two databases was examined using funnel plots, Egger regression and 'trim and fill' approaches[76] for the whole dataset and its subsets for the encroachment and removal database, respectively (Supplementary Appendix 4, Supplementary Fig. 4 and Supplementary Tables 4–6).

Ecosystem impact of woody encroachment and woody removal

Random effect models were used to calculate the estimated mean effect sizes separately for the overall ecosystem response, and ecosystem structure, function and composition, and ecological attributes for the encroachment database and removal database, respectively, after accounting for potential sources of non-independence: (1) data collected from within the same study, (2) residuals of each data record when calculating the variance and the potential bias from sample size and (3) shared controls among observations. To account for shared controls in the encroachment and 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 on the basis of the variance of response attributes and shared control pairs[76] to control for it. Data with extreme variances (>1,000 or <0.0001) were excluded. We adopted an accepted method of pooling ecological attributes into three meaningful groups: ecosystem structure, function and composition (Supplementary Table 1). These provide an overview of how different ecosystem components change after encroachment and removal. This technique has been shown to be appropriate for lumping and combining diverse attributes[64] because the meta-analysis procedure uses LnRR, which brings the different attributes to a common analytical unit. Overall, we ran an intercept-only model (null model) with the LnRR of ecological attributes as the response. The variance matrix calculated above was

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included as the variance to account for the shared control, and the two random factors (that is, a unique ID for each reference and the order of the data within the data file) were included as random effects to account for the non-independence of data collected from same study and residuals of each data within the sample size when estimating mean effect sizes. 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 $P < 0.05$.

Impact of woody species, encroachment stages and time since removal

We selected four major woody genera (*Acacia* or *Vachellia*, *Juniperus*, *Quercus* and *Prosopis* spp.) that account for 44% and 35% of species in the encroachment and removal databases, respectively. We ran separate intercept-only model (null model described above) for each genus, with the LnRR of ecosystem responses (averaged ecological response, ecosystem structure, function and composition) as the response variable to explore the outcomes of woody encroachment and removal across different woody genera. To further explore the relative importance of different plant traits on the woody encroachment and removal processes, we conducted random forest analyses for encroachment and removal, respectively, with the LnRR as response variables and nine plant traits as predictors (Supplementary Table 7).

The impacts of pre-removal woody encroachment stage (that is, initial woody cover) and time since removal on the outcomes of woody removal were explored using regressions. The ecosystem responses tested were (1) ecosystem structure, function and composition, and (2) ecological attributes that are related to structure, function and composition. To ensure the statistical power of the models, response variables that do not have sufficient data (<60 records) were not included. We fitted regressions between the estimated mean effect size (LnRR) of the ecosystem response and the encroachment stages (woody coverage) and time since removal, respectively, to explore how ecosystem response vary as the encroached stages and time since removal changes. For the regression between time since removal (year) and ecosystem response, we log transformed ($\log_e(x+1)$) the time due to the highly left skewed data distribution (52% studies reported short-term effects). According to the distribution of data, we fitted both linear ($y \sim x$) and polynomial ($y \sim \mathrm{poly}(x,2)$) structures for the ecological attributes. Most models (60%) were fitted with a linear structure, and we fitted polynomial models for ecological attributes when the model showed lower Akaike information criterion than the linear structure (Supplementary Tables 8 and 9).

Finally, we used structural equation modelling (SEM)[77] to explore the direct and indirect effects of environmental conditions (aridity, rainfall seasonality and soil clay), treatment (treatment method and time since treatment) and encroachment signature (initial woody cover and traits of woody species) on the effectiveness of woody plant removal after accounting for the effect of spatial locations (latitude and longitude). As the major aims of woody removal are to suppress woody plants, promote non-woody plants (herbaceous, grass and forb) and enhance fauna biodiversity (for conservation or gaming purpose) and they have sufficient records, we selected the impact of removal (LnRR) on woody cover, non-woody cover and animal diversity as the response variables. Aridity, soil texture and time since treatment were continuous variables, whereas treatment was binary and therefore designated as zero or one. Treatment methods used to remove woody plants were either (1) chemical, (2) physical, (3) burning or (4) multiple methods. Other rarely used treatments (for example, grazing or browsing; accounting for 12.7% of the studies) were not explicitly included in our SEM due to their reduced effectiveness in controlling woody plants[51]. We used random forest analyses to select the top five plant traits that had the highest variance explanation (mean plant height, plant shape, roots type, deciduousness and resprout) to include into the SEM. All the variables included in the SEM were not highly collinear on the basis of variance inflation factors test (<3). SEM enabled us to test the hypothesized effects and relationships among the main drivers and ecosystem responses on the basis of an a priori model (Supplementary Fig. 5), allowing us to explore the effect of each driver after accounting for the effects of other attributes included in our model. Models with low χ^2 and root mean error of approximation (RMSEA <0.05), and high goodness-of-fit index and R^2 were selected as the best fit model for our data.

The random effect model and meta-regressions were performed in the 'metafor' package[78], random forest analysis was performed using 'rfPermute' package[79], and all the figures were created using 'ggplot2'[80], 'plotbiome'[81] and 'ggmap'[82] in R version 4.0.3 (ref. 83). SEM analyses were performed using SPSS AMOS 22 (IBM) software.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All the materials, raw data and protocols used in the article are available upon request and without restriction. The meta-analysis database is available in figshare repository (https://doi.org/10.6084/m9.figshare.19915300.v2). Source data are provided with this paper.

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Author contributions

D.E. and J.D. designed the research, collected data and built the databases. J.D. performed the statistical analyses and wrote the first draft. D.E. critically revised the manuscript.

Competing interests

The authors declare no competing interests

Additional information

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Data collection	Data on temperature and rainfall seasonality were extracted from a global climate database (0'30" × 0'30") for the 1970-2000 period from WorldClim Version 2.0 (http://www.worldclim.org/). Aridity was derived from Consortium for Spatial Information (CGIAR-CSI) for the 1950-2000 period. Soil sand content were obtained from the HWSD database (resolution 1km). Data originally published as figures were extracted using Engauge Digitizer V4.1 (http://digitizer.sourceforge.net/). Plant traits of 212 woody species were complied based on online plant traits databases such as BROT, PLANTS, Woody Plants Database (http://woodyplants.cals.cornell.edu/home), TRY database.
Data analysis	The random effect model and meta-regressions was performed in the "metafor" package, all the figures were created using "ggplot2", "plotbiome" and "ggmap" in R version 4.0.379. SEM analyses were performed using SPSS AMOS 22 (IBM, Chicago, IL, USA) software. The code used in the meta-analysis is available at ###

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Study description	In this study, we used a meta-analytical approach by systematically searching the published literature on woody encroachment and woody removal. We totally complied 12,344 records on the ecological impact of woody encroachment and removal (including mean, at least two replicates, standardized deviation) from 520 studies on woody encroachment and removal. We conducted the data analysis following a rigorous procedure on meta-analysis: 1) log response ratio was used to assess the ecological effect of woody encroachment and removal; 2) random-effect model was used to calculate the estimated effect size, with variance matrix included as the variance to account for the shared control, and the two random factors (i.e., a unique ID for each reference, the order of the data within the data file) included as random effects to account for the non-independence of data collected from same study and residuals of each data within the sample size; 3) publication bias of the database was examined using funnel plots, Egger regression and 'trim and fill' approaches; 4) linear and nonlinear regressions were fitted between the estimated mean effect size (LnRR) of the ecosystem response and the encroachment stages (woody coverage) and time since removal, respectively to explore how ecosystem response vary as the encroached stages and time since removal changes; 5) Structural Equation Modelling was used to explore the direct and indirect effects of environmental conditions, treatment, and encroachment signature on the effectiveness of woody plant removal after accounting for the effect of spatial locations.
Research sample	Research sample in this study is 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. 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. Ecosystem compositional attributes comprised variables indicating the variety of species including species diversity, richness and abundance.
Sampling strategy	This study is a meta-analysis in which the dataset was complied based on published studies. We totally complied 12,344 records on the ecological impact of woody encroachment and removal from 520 studies on woody encroachment and removal across all the continents. The ecological attributes involved in the analyses had at least 60 data points. Overall, the sample size is sufficient to support the results performed in the study.
Data collection	For each publication, we recorded the basic geographical information of the study, land use history, the identity of the dominant encroached or removed woody species, and the mean, replicates and standard deviation of the ecosystem responses that were assessed on woody plant encroached (treatment) and not encroached (control) or woody plant removal (treatment) and retention

	(control) plots for the encroachment and removal database, respectively. Data on temperature and rainfall seasonality were extracted from a global climate database (0’30” × 0’30”) for the 1970-2000 period from WorldClim Version 2.0 (http://www.worldclim.org/). Aridity was derived from Consortium for Spatial Information (CGIAR-CSI) for the 1950-2000 period. Soil sand content were obtained from the HWSD database (resolution 1km)68. Data originally published as figures were extracted using Engauge Digitizer V4.1 (http://digitizer.sourceforge.net/). Plant traits of 212 woody species were complied based on online plant traits databases such as BROT69, PLANTS70, Woody Plants Database (http://woodyplants.cals.cornell.edu/home), TRY database.
Timing and spatial scale	Timing: 1950-2021 period, literature searched on 15 September 2021. Spatial scale: Studies were distributed globally across all continents except Antarctica, and covering a wide variety of biomes
Data exclusions	In this meta-analysis, published papers were only included in our database if they met the following a priori criteria: (i) the study was conducted under natural field conditions (greenhouse or growth chamber studies, as well as studies using cultivated plants, were not considered), (ii) the results were quantitative and therefore analysable, and (iii) the variables were collected strictly in plots encroached and without woody vegetation for the woody plant encroachment studies or in plot with woody plant removed and woody plant retained for the woody plant removal studies located in the same geographical area (hereafter encroached and removed plots as treatment, plots without woody plant and woody retained plots as control). This allowed us to be certain that any effects observed at each study could be attributed to the effects of encroachment or removal, and not to variation in climatic or soil type between the treatment and control plots. (iv) studies were included when the impacts resulted only from woody plant encroachment/invasion or woody plant removal rather than the invasion or removal of other plant species. In some studies, many exotic plant species rather than only woody species was invaded in the ecosystem or all the understorey vegetation was removed instead of only removing woody plants, so these studies were excluded; (v) studies were included only if the reported data were representative of whole grassland and encroached plots for encroachment studies and were representative of land that dominated by woody plants and removed plots. Studies that evaluated the effects of woody vegetation or without woody plant on the response variables considered at the microsite level (e.g. comparing the effects of shrub vs. grass canopies on vegetation or soil attributes within the same site) were not considered. For woody plant removal database, studies with shared controls (multiple treatments with one control) were included only if these treatments were conducted in the same geographical area and during the same period. Studies comparing before and after treatment with no specific control treatment were not regarded as paired and were therefore excluded from the database.
Reproducibility	The results of this study can be reproducibility based on the dataset and code that available in Figshare (https://doi.org/10.6084/m9.figshare.19915300.v1) and ###.
Randomization	This study is a meta-analysis and data in this study was allocated into separate ecological attribute group, which do not involve randomization.
Blinding	This study is a meta-analysis which used the data collected from published studies. Therefore blinding is not applicable for this study.

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging