Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis

David J. Eldridge[a,*], **Matthew A. Bowker**[b,f], **Fernando T. Maestre**[b], **Erin Roger**[c], **James F. Reynolds**[d], and **Walter G. Whitford**[e]

[a]Department of Environment, Climate Change and Water c/- Evolution and Ecology Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia d.eldridge@unsw.edu.au [b]Área de Biodiversidad y Conservación, Departamento de Biología y Geología, ESCET, Universidad Rey Juan Carlos, 28933 Móstoles, SpainMatthew.Bowker@nau.edu, fernando.maestre@urjc.es [c]Australian Wetlands and Rivers Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia e.roger@unsw.edu.au [d]Nicholas School of the Environment and Earth Sciences and Department of Biology, Duke University, PO Box 90328, Durham, NC 27708, USA. james.f.reynolds@duke.edu [e]USDA-ARS Jornada Experimental Range, PO Box 3003, MSC 3JER, New Mexico State University, Las Cruces, NM 88003, USA. wlawhit@zianet.com

Abstract

Encroachment of woody plants into grasslands has generated considerable interest among ecologists. Syntheses of encroachment effects on ecosystem processes have been limited in extent and confined largely to pastoral land uses or particular geographical regions. We used univariate analyses, meta-analysis and structural equation modeling to test the propositions that 1) shrub encroachment does not necessarily lead to declines in ecosystem functions, and 2) shrub traits influence the functional outcome of encroachment. Analyses of 43 ecosystem attributes from 244 case studies worldwide showed that some attributes consistently increased with encroachment (e.g. soil C, N), and others declined (e.g. grass cover, pH), but most exhibited variable responses. Traits of shrubs were associated with significant, though weak, structural and functional outcomes of encroachment. Our review revealed that encroachment had mixed effects on ecosystem structure and functioning at global scales, and that shrub traits influence the functional outcome of encroachment. Thus, a simple designation of encroachment as a process leading to functionally, structurally or contextually degraded ecosystems is not supported by a critical analysis of existing literature. Our results highlight that the commonly established link between shrub encroachment and degradation is not universal.

Keywords

encroachment; shrubland; ecosystem processes; thickening; shrub; woody; degradation; desertification; invasion

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[*]**Corresponding author**: Department of Environment, Climate Change and Water, c/- Evolution and Ecology Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia. Tel: +61 2 9385 2104 Fax: +61 2 9385 1558. d.eldridge@unsw.edu.au.
[f]Current Address: US Geological Survey, Southwest Biological Science Center, Northern Arizona University, 2255 N. Gemini Drive, Flagstaff, AZ 86001, USA

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INTRODUCTION

The encroachment of woody plants into grasslands, and the conversion of savannas and open woodlands into shrublands, has been a phenomenon widely reported during the past decade (Gibbens at al., 2005; van Auken 2000; Maestre *et al.* 2009; van Auken 2009). Encroachment can be defined as the increase in density, cover and biomass of indigenous woody or shrubby plants (van Auken 2009). The term 'encroachment' is synonymous with other wide-ranging terminologies such as woody thickening (van Auken 2000), regrowth (Eldridge *et al.* 2003), thicketization (Kerley *et al.* 1995, Lechmere-Oertel *et al.* 2005), woody weed invasion (Booth *et al.* 1996, Ayres *et al.* 2001), xerification (Archer *et al.* 2001), shrub invasion (Noble 1997) and bush encroachment (Meik *et al.* 2002).

Encroachment is common over much of the world's arid and semi-arid biomes. In the western United States, for example, dramatic increases in the densities of two shrubs in particular, mesquite (*Prosopis glandulosa*) and creosote bush (*Larrea tridentata*), have largely been responsible for the conversion of extensive areas of former black grama (*Bouteloua* spp.) grasslands into dense shrublands (Buffington & Herbel 1965). This change in vegetation structure has accelerated since the early 1900s (Archer 2010) due to a combination of effects including grazing (see below). Currently in the United States, non-forest lands undergoing shrub encroachment are estimated to cover up to 330 million hectares, mostly in the semi-arid western states (Pacala *et al.* 2001, Knapp *et al.* 2008). In Australia, extensive areas of semi-arid woodland are now occupied by native shrubs at higher densities than thought to exist prior to European settlement (Noble 1997). In southern Africa, 13 million hectares are subject to bush encroachment (Trollope *et al.* 1989), and, along with the loss of savanna systems, are believed to affect more than two billion people worldwide (Adeel 2008). In the Mediterranean Basin, encroachment seems to be associated with the cessation of sheep grazing and activities related to grass fibre cultivation and woody fuel extraction (Maestre *et al.* 2009), and with the natural regeneration of oak woodlands (e.g. Ramírez & Díaz 2008).

Consensus is emerging on the common themes surrounding encroachment (Gardner 1951; Fuhlendorf *et al.* 2008, van Auken 2000). Encroachment appears to result from any of a number of distinct factors or interactions of multiple factors including overgrazing and recovery from anthropogenic disturbance from earlier (traditional) societies (Scholes & Archer 1997, Angassa & Oba 2007, Coetzee *et al.* 2008), increases in CO_2 and N deposition (Archer 2010), reduced fire frequency (Scholes & Archer 1997), long-term climate change (Knapp *et al.* 2008, D'Odrico *et al.* 2010), the presence of exotic plants (Archer 2010), and potentially, predator suppression (Kerley & Whitford 2009). Altered vegetation in long–ungrazed areas suggests, however, that changes in the gaseous composition of the atmosphere are responsible, at least in part, for some of the observed changes in expansion of shrublands. For example, increases in global CO_2 concentrations may have benefited C_3 woody species at the expense of C_4 grasses (Polley *et al.* 1994).

The overgrazing hypothesis is based on the premise that sustained heavy grazing reduces above– and below–ground grass biomass, leading to increased resource availability for the establishment of shrubs, greater shrub recruitment (Coetzee *et al.* 2008) and therefore reduced fire frequency and intensity (Scholes & Archer 1997; Roques *et al.* 2001; Oba *et al.* 2000). Overall, factors that reduce grass biomass or its capacity to exploit surface water and limit recharge will likely enhance woody plant growth (Knoop & Walker 1985) and promote woody recruitment and encroachment (Brown & Archer 1989). Feedback effects modulated by the shrubs themselves can accelerate declines in grass cover, but only under persistent grazing (Roques *et al.* 2001).

Is encroachment synonymous with degradation or desertification?

A substantial body of thought pervading the literature suggests that shrub encroachment is an ecological expression of degradation or desertification (e.g. MEA 2005). Changes in the biotic and abiotic environment, increased soil erosion, reductions in ecosystem functions and long-term, irreversible loss of secondary productivity are typical manifestations of desertification (Whitford 2002). Recent definitions of desertification have been broadened to include the socio-economical impacts of land use, and the roles of financial institutions and governments in its persistence (Reynolds *et al.* 2007).

The desertification paradigm, which emerged out of extensive research in shrub-dominated grasslands in the Chihuahuan Desert of south-western United States ('the Jornada model' *sensu* Schlesinger *et al.* 1990, Peters *et al.* 2006), has a strong emphasis on shrub encroachment. This paradigm arises largely from the fact that shrublands and desertification in the Chihuahuan Desert system are intimately linked. The Jornada model and its various manifestations hold considerable international currency today (e.g. Peters *et al.* 2004; Okin *et al.* 2006, 2009). Indeed, the putative loss of soil function resulting from shrub encroachment is regarded by ecologists worldwide as a precursor to desertification, given the tendency of shrublands to alter the spatial distribution of resources (Schlesinger & Pilmanis 1998), thereby preventing a reversion to grassland (Okin *et al.* 2006, 2009, Archer 2010). The prevailing view among scientists and practitioners is that shrub encroachment and desertification are synonymous (e.g. MEA 2005). However, much of the evidence is drawn from the western United States. We question, therefore, whether encroachment and degradation (or its extreme expression, desertification) are necessarily linked in other arid and semi-arid systems. Overwhelmingly, however, encroachment is a phenomenon typically viewed within the context of pastoral production. Therefore, declines in pastoral productivity, particularly reduced primary and secondary production, are seen as a being directly akin to degradation (desertification). Our understanding of contemporary desertification processes remains synonymous with an increase in woody plants in communities. Shrublands are generally regarded as being of lower pastoral value than grasslands, as they present substantial management challenges to pastoralists and livestock managers, such as increased competition for forage and difficulties associated with mustering livestock. In Australia, the increased density and encroachment of shrubs into arid and semi-arid grasslands, savanna and woodlands have been cited as the most obvious and common forms of desertification (Mabbutt 1978, Ludwig & Tongway 1995). A literature search of published papers using as keywords 'shrubland' and 'desertification' together in the abstract revealed a substantial number (46%) of entries (143 papers) from the Chihuahuan Desert of south-western USA (e.g. Huenneke *et al.* 2002; Jackson *et al.* 2002; Bestelmeyer 2005; Duval & Whitford 2008; Eldridge *et al.* 2009) and South Africa (e.g. Adeel 2008; Sankaran & Anderson 2009). The term 'desertification' has been widely (and loosely) applied and has now been invoked to describe almost any compositional or successional changes in dryland vegetation that are regarded by society in a negative sense, at least in the context of pastoralism. Examples range from Lehman's lovegrass (*Eragrostis lehmanniana*) invasion of *Bouteloua* grasslands in south-western USA (Whitford 1997), cheatgrass (*Bromus tectorum*) invasion of *Artemesia* shrub-steppe in the Great Basin (Roberts 1991) and the encroachment of eastern red cedar (*Juniperus virginiana*) into native grasslands (McKinley *et al.* 2008) and low-elevation sagebrush (*Artemisia tridentata*) steppes (Burkhardt & Tisdale 1976). The overuse of the term 'desertification' has been identified as an issue of concern in the literature (e.g. Drylands Development Paradigm, Stafford Smith & Reynolds 2002).

Functional and structural effects of shrub encroachment

Shrub encroachment is reported to be associated with general reductions in ecosystem functions and processes (van Auken 2000, 2009; Archer 2010). Compared with the original grasslands, the popular view is that shrublands are associated with reduced plant biomass and species richness, and a range of other effects on the vegetation (see below; Zarovalli *et al.* 2007; van Auken 2009). The effects of encroachment on net primary productivity are complex, with reported decreases in ANPP in xeric sites, but dramatic increases at higher precipitation sites (Knapp *et al.* 2008). In other areas, small (~10%) increases in shrub cover can result in marked reductions in pastoral production because of encroachment (Oba *et al.* 2000). The existence of an upper bound on woody cover with increases in mean annual precipitation suggests that shrub encroachment, at least in southern Africa, is limited by the availability of water (Sankaran *et al.* 2005). The obvious extension of this is that global changes in rainfall may be more influential than grazing in driving encroachment (Sankaran & Anderson 2009).

Shifts from grassland to shrubland have been shown to be associated with changes in the spatial distribution of soil resources (Schlesinger *et al.* 1996), altering the patterns of resource flow between shrubs and their interspaces (Li *et al.* 2008) and reinforcing the persistence of shrubs (d'Odorico *et al.* 2007). Wind- and water-transported nutrients, detritus and seeds accumulate under shrub canopies, leading to higher levels of infiltration capacities (Bhark & Small 2003), while the bare interspaces experience higher temperatures and evapotranspiration, retarded organic N incorporation, denitrification, ammonia volatilization, and increased erosion (Schlesinger *et al.* 1990). The combined effect of these processes is a strengthening of the 'fertile island' effect around shrubs, making shrublands extremely resistant to change and enhancing the persistence and development of shrublands at the expense of grasslands (Schlesinger *et al.* 1996, Whitford 2002). Losses of grassland biota with encroachment have been shown to reinforce the shrub-dominant state (Eldridge *et al.* 2009).

Trends in productivity under encroachment are not universally consistent, however. For example, *Juniperus virginiana* encroachment onto lower elevation grasslands and shrublands in the western United States has been shown to increase net ecosystem productivity and alter the quantity and distribution of soil and plant C and N pools (Smith & Johnson 2004; McKinley & Blair 2008). However, conversion of native grasslands to *Juniperus virginiana* forests had relatively minor effects on potential soil N transformations and plant available N, at least half a century after forest establishment (McKinley *et al.* 2008).

Finally, the effects of encroachment on biota are less clearly defined and highly variable. Increases in shrub cover in encroached woodland in eastern Australia have been reported to be associated with increases in some bird species but decreases in others (Ayres *et al.* 2001). Richness of mammalian carnivores, reptiles and tortoises showed no significant trend in relation to increasing shrub cover at sites in the Kalahari (Blaum *et al.* 2007), Arizona (Castellano & Valone 2006) and Texas (Kazmaier *et al.* 2001), respectively. However, Benshahar *et al.* (1992) and Kerley and Whitford (2009) demonstrated increases in ungulates, kangaroo rats and birds respectively with encroachment. Similarly, ant richness has been shown to be variable; sometimes increasing (Bestelmeyer *et al.* 2005; Ayres *et al.* 2001) and sometimes remaining the same (Ayres *et al.* 2001) in response to increasing woody encroachment. In semi-arid *Stipa tenacissima* steppes from the Mediterranean Basin, increases in sprouting shrub cover are associated with higher species richness and diversity of vascular plants, but do not have any effect on the species richness of biological soil crusts and microbial communities (Maestre 2004; Maestre *et al.* 2009).

Towards a global synthesis

The subsequent section indicates that the effects of encroachment on a range of ecosystem functions and products are not universal, with positive effects and negative effects equally probable. This raises an important question about whether degradation (or desertification) is a suitable epithet to attach to shrub encroachment across its entire global range. We believe that it is timely to examine the interconnections between shrub encroachment and degradation, given the results of recent papers suggesting that shrubs do not necessarily lead to negative effects on ecosystem structure and functioning that could be considered consistent with degradation or desertification (e.g. Maestre *et al.* 2009). We define this degradation as reductions in ecosystem structure and/or function, and/or declines in the productive potential of the soil, which reduce its functionality or sustainability (Reynolds *et al.* 2007). We believe that it is timely to examine the interconnections between shrub encroachment and degradation given the results of recent papers suggesting that shrubs do not necessarily lead to negative effects on ecosystem structure and functioning that could be considered consistent with degradation or desertification (e.g. Maestre *et al.* 2009).

Here we advance the proposition that the term 'shrub encroachment' must be decoupled from the concept of degradation, given emerging evidence of the importance of shrubs in ecosystem processes and the fact that existing evaluations are heavily biased towards pastoral production systems. Our first proposition is that shrub encroachment does not necessarily lead to declines in attributes that may be associated with ecosystem structure and functions. Thus far, our examination of the literature strongly suggests that shrubs can increase resource stocks (e.g. below–ground C and N or above–ground NPP) irrespective of any putative changes in landscape heterogeneity (Maestre *et al.* 2009). Thus, we would expect that the effects of shrub encroachment are highly specific to the response variables that one chooses to examine. Increases or declines in particular response variables indicative of ecosystem function would therefore be expected to be equally probable. Second, we advance the notion that the functional traits of individual shrub species influence the functional outcome of shrub encroachment (*sensu* Maestre *et al.* 2009). We test the notion that shrubencroachment is associated consistently with altered ecosystem functions using data drawn from published and unpublished literature using three analyses. The first analysis examines the direction of effect, on a range of biotic and abiotic variables, of a transition from grassland to shrubland. A second analysis employs a meta–analytic approach, using studies with paired grassland (unencroached) and shrubland (encroached) sites, to test the proposition that grasslands undergoing encroachment are more degraded than those that are not. The third analysis links the traits of encroaching shrubs to two metrics derived from functional and structural measures of ecosystem response to encroachment. Finally, we advance a new global conceptual model that considers a range of shrub encroachment outcomes that might result based on community or societal values, shrub traits, and functional and structural components.

METHODS

Scope of the review and database building

We performed a systematic search of the scientific literature to identify quantitative evidence of the impacts of shrub encroachment on ecosystem structure and/or functioning. We searched for relevant studies, using the ISI Web of Knowledge (www.isiwebofknowledge.com) database (1945-2009 period) using the keywords "encroachment", "competition", "shrub", "bush", "thickening", "grassland", "desertification", "arid", "semi-arid", "semiarid", "dryland" and "woody", and searched for published and unpublished material as well as recent reviews (e.g. Hibbard *et al.* 2001; Huxman *et al.* 2005; van Auken 2009). We restricted this review to arid, semi-arid and dry

sub-humid environments ("drylands"; rainfall 850 mm, range: 200-850 mm; median: 400 mm) because land degradation is a key environmental issue in these ecosystems (Reynolds *et al.* 2007), and because the encroachment–degradation (desertification) paradigm was initially developed for the boundary between arid and semi-arid systems around which our dataset is centred (Schlesinger *et al.* 1990). We considered only studies with quantitative data, conducted under natural conditions, in plots with and without woody vegetation (encroached and grassland, respectively) located on the same soil type, vegetation community, and climatic area (see Appendices S1 and S2 in Supporting Information).

Our analyses were based on two separate databases. Database 1 contained information from 273 case studies reported in 144 published articles, book chapters or unpublished reports, on data from grassland and encroached plots. Some papers reported work from extensively studied sites such as the Flint Hills (Kansas, USA), Jornada Experimental Range (New Mexico, USA), and La Copita and Santa Rita Range (Arizona, USA), and therefore individual studies could not be considered independent. Of the 273 studies, 244 were considered spatially independent. Most, but not all, of these data represented encroachment scenarios, except for a few sites from naturally-occurring dense shrubland (e.g. the Succulent Karoo in Southern Africa; see Appendix S1 for additional details on Database 1, and Appendix S2 for the full list of data sources for this database). Database 2 contained information on ten structural (morphological) traits of 76 woody species (shrubs and trees) identified as encroachers in Database 1 (Table S1).

Of the 244 independent plot–level case studies, 111 were from North America (USA, Canada, Mexico), 40 from Africa (Ethiopia, Kenya, Namibia, South Africa, Zimbabwe), 39 from Europe (Spain, Portugal, Greece), 28 from Australia, 19 from Asia (China, Turkey), and 7 from South America (Argentina). Database 1 formed the basis for a quantitative assessment of the effects of encroachment on measures of ecosystem structure and/or functioning. For each study we extracted data on the effects of a change from grassland to encroached (mostly shrubs) vegetation on 43 response variables. Five and 38 variables were structural and functional, respectively (Table 1, see Appendix S3 for a justification of the classification followed). We also recorded the woody species involved in the transition (Table S1) and average annual rainfall. When rainfall data were not presented in the original article, data were obtained by linking site geographical location to the closest measurement on a high resolution $(0'10'' \times 0'10'')$ global climatology dataset interpolated from weather station means of the 1961–1990 period (New *et al.* 2002).

Analytical procedures

Is encroachment consistently associated with increases or decreases in response variables and is any lack of consistency attributable to a dependency on rainfall?—We examined this question using i) a qualitative test of the proportion of increases compared with the proportion of decreases in the 43 response variables across the 244 studies, and, ii) a quantitative and detailed meta-analysis. For each of the case studies evaluated, the effect of encroachment on every variable (Table 1) was recorded as either an increase, decrease or no change. We used a Test of Proportions, reported as a Fisher's Exact Test (Minitab 2007), to test the probability that the proportion of increases differed from the proportion of decreases, where the denominator represents the count of all studies. This test of qualitative data allowed us to examine potential encroachment effects on attributes that had too few (< 10) observations to allow more rigorous meta–analysis.

The following data sets were created: above-ground C and net primary productivity (ANPP), litter cover, bare soil cover, density of perennial plant patches, vascular plant richness, ant richness, vertebrate richness, electrical conductivity, root biomass, exchangeable soil Ca, K,

Mg and Na, total soil C, organic soil C, inorganic soil N, available soil N and total soil N, soil S, potential N mineralization, soil respiration, available soil P, total soil P, soil pH, soil moisture and bulk density (Table 1). If an article reported results from a single site for more than one response variable (e.g. soil C and pH), the results were included in different meta-analyses. Soil data were analysed separately by depth category: 0-15 cm, 15-30 cm and 30-45 cm.

Analyses were restricted to databases with 10 or more case studies coming from three or more sites. To determine the effects of encroachment in the variables measured, we used the response ratio, ln RR = ln(Enc/Grass) in the meta–analyses, where Enc and Grass are the response variable in the plot with and without woody plants, respectively. We tested the normality of lnRR data using Kolmogorov-Smirnov tests. In most of the databases, the ln RR data were not normally distributed. Thus, we used in all cases the Wilcoxon Signed Rank tests to examine whether median response ratios were different from zero. Response variable data were plotted against average annual rainfall to examine any potential moderating effects of rainfall. See Appendix S3 for additional information on the meta-analyses and regression analyses conducted.

Do the traits of encroaching woody plants determine the functional outcome of encroachment?—It is apparent from many studies globally (e.g. Peters *et al.* 2006; Cheng *et al.* 2004; Le Houérou 2001; Ludwig & Tongway 1995) that the degree to which shrub encroachment leads to degradation and desertification can be influenced by the identity of the particular shrub species involved. Indeed, Maestre *et al.* (2009) specifically hypothesized that the effect of woody encroachment on ecosystem function was dependent upon traits of the encroaching shrubs (and trees), relative to those of the perennial grasses that they replace. We tested this hypothesis using both qualitative and quantitative data from Database 2 (Table S1, Appendix S4). Our quantitative data were mean and maximum height of encroaching plants at maturity. Qualitative data on several other traits were obtained, as quantitative data were not universally available. These included: 1) dispersal agent (wind, water, or animal), 2) shape (round, pyramidal, V–shaped, weeping), 3) ground contact (yes, no), 4) deciduousness (evergreen–semi-evergreen, semi–deciduous–deciduous), 5) allelopathic (yes, no), 6) palatable to mammalian herbivores (yes, no), 7) N-fixation ability (yes, no), 8) rooting pattern (tap rooted, laterally rooted, both tap and laterally rooted), 9) associated with banded vegetation patterns (yes, no). We could not find sufficient quantitative data on litter production or quality to include these variables in our analyses.

We constructed a matrix of 43 columns (response variables) by 244 rows (independent studies) and calculated, for each cell, a response ratio statistic (Enc/Grass), which represented a change in ecosystem function (e.g. soil C, N) or structure (e.g. vertebrate richness, ant richness) resulting from encroachment. We then averaged, separately, all response ratio statistics for the 38 functional and five structural variables, to create an additional two columns of data. A logarithmic transformation was applied to each cell in these two columns to create a single ln RR. This allowed us to construct two new synthetic indices; one for ecosystem function (211 values) and the other for community structure (93 values). This process had the effect of reducing all attributes to a common unitless value representing a change in a response variable with encroachment (see Appendix S5). Two outliers, one for each of the structure and function indices, were several standard deviations away from the mean and were omitted from the analyses. Synthetic response variables such as our structural and functional indices have been used extensively in both aquatic (index of biotic integrity, Karr 1991) and terrestrial (terrestrial index of ecological integrity, Andreasen 2001) systems. The approach we used is therefore multi-scale, flexible, measurable and comprehensive, and considers both the functionality of the ecosystem and community structural components of grassland-shrubland states. Using this system one can

integrate over any number of attributes, and the overall effect is largely independent of the conclusions drawn from the individual studies.

We employed Structural Equation Modeling (SEM, Shipley 2000) to examine the relationships among our shrub trait database and the two synthetic functional and structure indices. We constructed separate models for each index; an ecosystem function model, and a community structure model. Both models had the same basic form and had similar assumptions. Bootstrap techniques were used to calculate probability tests for each path in each model using the bias-corrected percentile method. See Appendix S5 for a full description of the SEM analyses conducted.

RESULTS

Encroachment effects on ecosystem structure and functioning

Encroachment was associated with decreases in grass cover and soil pH, and increases in shrub cover, aboveground and total and organic C, total N, exchangeable soil Ca, available soil P and potential soil N mineralisation (Table 1). For the remaining 77% of our response variables (33 out of 43), increases or decreases in response to encroachment were equally probable.

By definition, encroached plots had significantly higher cover of shrubs, but they also supported a lower cover of herbaceous vegetation than grassland plots (Table 2). Encroached plots tended to have higher shrub richness and greater cover of trees ($0.05 < P < 0.08$, Table 2). The response ratio of shrub cover increased with rainfall according to a linear relationship, while that of ant richness, vertebrate richness and vascular plant richness decreased with rainfall (Fig. 1). It must be noted, however, that the relationship between rainfall and ant richness was dependent on a single datum point, and disappeared when it was removed ($R^2 = 0.03$, $P = 0.552$). Shrub encroachment promoted an increase in the richness of these groups at low rainfall levels, an effect that was reduced under high rainfall conditions. The response ratio of bare soil, tree richness and density of plant patches was unrelated to rainfall ($P > 0.10$ in all cases).

For the 0-15 cm soil layer, encroachment increased aboveground C, root biomass, total and organic soil C, total soil N, and soil potential mineralizable N ($P < 0.036$ in all cases, Table 3), but decreased soil pH (Table 3). Encroached plots tended to have more exchangeable Ca (Table 3). The response ratios of litter cover and aboveground C were positively related to rainfall (Fig. 2). Among all the soil variables evaluated at the 0-15 cm depth (Table 3), only soil electrical conductivity and bulk density were related to rainfall (Fig. 2), though for electrical conductivity the curvilinear relationship found was driven strongly by a single datum point. Indeed, when this point was removed, a negative linear relationship between this variable and rainfall was found (y = 3.65 - 0.01x, $R^2 = 0.41$, $P = 0.014$). For the 15-30 cm soil depth, shrub encroachment promoted a significant increase in organic and total soil C and total soil N ($P < 0.001$, Table 3), but had no significant effects on soil pH. No response ratios for the variables evaluated at this depth were related to rainfall ($P > 0.10$ in all cases). At the 30-45 cm depth there were no significant effects on total soil C or N, the only two variables tested ($P > 0.150$; Table 3). Although the response ratio for total soil N did not differ from zero, we found a significant exponential relationship between this variable and rainfall (Fig. 2); shrub encroachment promoted an increase in this variable from low to moderate rainfall levels before reaching a plateau.

Do the traits of encroaching woody plants determine the functional outcome of encroachment?

Our model of community structure variables (richness of vascular plants, birds and ants) was the most successful, explaining 33 % of the variance in the response ratio. The most important variable was a relatively strong negative effect of mean shrub height (Fig. 3). Plant shape, primarily driven by a positive influence of ground contact, also contributed a moderate positive effect, as did allelopathy (Fig. 3).

Our model of ecosystem function variables explained only 14% of the response ratio of compiled ecosystem function measurements. The single greatest contributor was again related to plant height, but in this case was a positive effect of maximum height (Fig. 4). Dispersal method was equally important, and equally driven by positive influences of both water and wind dispersal, indicating that animal dispersal had a negative effect. Allelopathy did have a relatively strong negative effect upon function. N-fixation accounted for a minor positive effect (Fig. 4).

DISCUSSION

The shrub encroachment phenomenon has generated considerable interest over the past two decades. This interest has largely been driven by the global, trans-national nature of encroachment and its putative association with widespread landscape degradation (e.g. desertification in the Chihuahuan Desert; Schlesinger *et al.* 1990), declines in net primary productivity (Huenneke *et al.* 2002), and resulting reductions in pastoral productivity (House *et al.* 2003; Knapp *et al.* 2008). More recently, attention has focused on emerging issues associated with encroachment including global changes in biogeochemical cycles, land surface atmospheric phenomena, CO_2 sequestration (Pacala *et al.* 2001), and emissions of non–methane hydrocarbons (Archer 2010). Although an increasing number of qualitative and semi–quantitative syntheses of shrub encroachment effects on ecosystem processes and properties have been published in recent years (e.g. van Auken 2000, 2009), there has been an apparent emphasis on single ecosystem effects, such as soil C or ANPP, usually at bioregional to continental scales (e.g. western North America; Knapp *et al.* 2008, Archer 2010). Despite some demonstrations of the ubiquity of the shrub encroachment phenomenon in arid and semi-arid areas worldwide (Trollope *et al.* 1989; Noble 1997; Maestre *et al.* 2009; Archer 2010), there have been no attempts, to our knowledge, to formulate a global synthesis of the outcomes of shrub encroachment from utilitarian, ecosystem functional, and community structural perspectives.

Shrub encroachment effects are highly specific to the chosen response variable

Our results indicated a mixture of effects of shrub encroachment on ecosystem structure and functioning, with positive, negative and neutral outcomes of the increase in shrub cover in grasslands. As expected, shrub–dominated sites had consistently lower cover of perennial grasses and greater cover of woody vegetation (shrubs and trees). Somewhat less obvious was that shrub–dominated sites also supported a greater diversity of woody vegetation, rather than being dominated by one or two species. However, this effect may not be attributable to the encroachment phenomenon alone, as the meta–analyses of paired sites with sufficient replication did not reflect any significant change in perennial species richness with changes in shrub cover. Soil fertility was affected by shrub dominance in a variety of ways. Under shrub dominance, soils tended to have 1) lower pH levels, which may be due to leaching of volatile acids from the foliage of some woody plants (Whitford 1992), and which is likely to increase nutrient mobility (Schlesinger & Pilmanis 1998), 2) greater soil C and N pools, and greater potential N mineralisation, and 3) higher levels of exchangeable Ca. Over 77% of our response variables showed no change in response to shrub dominance.

Our meta–analyses of selected response variables largely confirmed the results of our global test of proportions, with no effects of encroachment on the density of persistent plant patches nor richness of vascular plants, and support for the notion of declining soil pH, increased potential N mineralization and soil C and N both at the surface and at depth. This convergence indicates that increases in organic C and N stocks, N mineralization rates, and mobility of some nutrients are associated with shrub encroachment in drylands. This might be due to accumulation of complex organic compounds, which are resistant to decay, in the soil beneath deeply rooted shrubs (Liao *et al.* 2006). Our analyses also indicated that shrub encroachment promoted a non–linear increase in aboveground C, with slight decreases from low to moderate rainfall levels and an important increase from moderate to high rainfall conditions. These results match quite reasonably with the regional studies of ANPP in different biomes of North America by Knapp *et al.* (2008). Jackson *et al.* (2002) found clear relationships between precipitation and SOC and SON pools with increases in woody encroachment. Drier sites in the Chihuahuan desert (< 280 mm rainfall) gained soil C and N with encroachment while more mesic sites (> 850 mm rainfall) lost C and N with encroachment. Our own data, however, are not consistent with observations by Jackson *et al.* (2002). We failed to show that effects of encroachment on soil C pools were rainfall dependent, and at the 30-45 cm depth, shrub encroachment promoted an increase in total soil N from low to moderate rainfall levels, until this effect reached a plateau. This inconsistency may result from the scale of the analysis; while our database synthesized results from 103 sites spanning five continents (Table 2), Jackson *et al.* (2002) focused their analyses on the United States and were not restricted to drylands (e.g., included sites with more than 1000 mm of rainfall). Thus, the patterns noted by these authors may pertain primarily to the United States rather than to drylands globally.

Overall, variable responses to either shrub dominance or shrub encroachment illustrate the fact that the collective outcome of encroachment depends on the particular variables that one chooses to examine. Studies that examine, for example, C and N stocks and cycling, are more likely to conclude that there are positive effects of shrub encroachment, whereas those that examine, for example, micronutrient content, are likely to conclude that encroachment effects are mostly neutral. Following from this, we argue further that the ecosystem effects of shrub encroachment will be highly context dependent and vary according to one's interests and background, and our notion of degradation. It is important to note, however, that positive and neutral effects of shrub encroachment are much more abundant than negative effects among the different response variables evaluated.

Plant functional traits influence the functional outcome of shrub encroachment

Using the shrub dominance database, we tested the hypothesis that the outcome of shrub encroachment is partially due to a set of key traits of potential encroachers (Maestre *et al.* 2009). This test is indirect, because a few cases within the database were not instances of direct encroachment. Rather, we conducted the best test that we could do using the data available in the literature. It reflects therefore the traits that tend to determine whether a dominant shrub increases or decreases surrogates of ecosystem function or structure. By extension, we would expect these same traits to be important in encroachment scenarios.

Our trait variables were moderately successful in explaining the indices of community structure and ecosystem function, but overall, they had only low predictive power (R^2 values ranging between 0.12 and 0.33). Interestingly, the effects of traits upon function and structure were generally asynchronous. Except for plant height and to a lesser extent allelopathy, a different set of traits promoted functional changes in soils than the set of traits that altered community structure. The shrub trait that had consistently highest path coefficient for both function and structure was plant height. While its effect on the structural index was negative, it had a positive effect on the functional index (Fig. 3). Taller, generally

larger, shrubs would have wider canopies with more leaf biomass, increasing the extent to which they entrain sediments (Okin *et al.* 2006). Larger shrubs would also be more effective nutrient pumps, with greater deposition of root exudates within the rhizosphere. They would also provide more shade, reducing the photo-oxidation of surface organic matter. The combination of a greater litter mass and increased resource capture would be likely to promote higher levels of microbial decomposition, leading to enhanced C and N pools (McClaran *et al.*, 2008; Throop & Archer 2008). Larger shrubs would be expected to support higher levels of biological activity (and hence be associated with a strongly positive structural score) as they provide more habitat (canopy area) and therefore greater resources (e.g. seed, fruit, sap, flowers, leaf–borne invertebrates) for birds and mammals. It is somewhat counterintuitive, therefore, that we found the opposite to be the case in our SEM analyses. The most parsimonious explanation is that the canopies of shrubs and trees have complex community level effects on the rest of the plant community and its component organisms (Schenk & Mahall 2002), which may be either positive or negative. Shading may promote facilitation in drylands due to its effects in reducing evapotranspiration and improving soil moisture (Maestre *et al.* 2003). Increases in plant height and size may also promote a higher diversity of understorey plants because of the "perch effect" (Pausas *et al.* 2006) and the increase in habitat heterogeneity under shrub/tree canopies (Maestre & Cortina 2005). On the other hand, rainfall interception by shrub/tree canopies may reduce available soil moisture in areas where rain falls mostly as small events, a response that may increase competitive effects under these canopies (Bellot *et al.* 2004).

Allelopathy had similar effects to those of shrub height, with positive and negative effects on the structural and functional indices, respectively (Figs. 3 & 4). Initially, this seems difficult to reconcile, although there is a prominent example in the literature. In the Chihuahuan Desert, the encroacher creosote bush (*Larrea tridentata*) tends to have deep tap roots (Gibbens & Lenz 2001) and reduces the continuity of plant cover by competitive or allelopathic mechanisms (Mahall & Callaway 1992). This would likely mitigate against the accumulation of organic matter, nutrients and microbial biomass beneath their canopies by suppressing the growth of forbs and grasses, which have lower C:N ratios and therefore decompose more readily than woody material (Throop & Archer 2008). Our diversity index comprised a mixture of plant and animal richness data, including vertebrates and invertebrates. Indeed, Báez and Collins (2008) demonstrate that *Larrea* encroachment reduced plant diversity, but the same response is not necessarily found when analyzing animal diversity. Bestelmeyer and Wiens (2001) found relatively high ant diversity, and Whitford (1997) found comparable or slightly higher diversity of birds and mammals in *Larrea*-encroached ecosystems. In a grassland, the addition of *Larrea* could enhance the diversity of some shrub-obligate animals such as desert woodrats (*Neotoma lepida*; Meyer & Karasov 1989) and some invertebrates (creosote bush grasshopper, *Bootettix argentatus*, Otte & Joern 1976). Perhaps because shrub encroachment induces heterogeneity of resources at a coarser spatial scale (Schlesinger *et al.* 1990), the same reason it is proposed to result in degradation in some habitats, it also increases niche space, which could enhance animal diversity. An allelopathic plant might be expected, therefore, to be especially effective at generating coarse-scale heterogeneity.

Other trait effects were fairly intuitive, such as positive effects of N-fixation upon soil function. Plant canopy shape was also influential for structure, with the strongest positive influence being a shape that contacts the surface. This suggests a mechanism consistent with the deposition of both wind- and water-eroded material, possibly via increases in surface threshold wind velocities (Whitford 2002; Okin *et al.* 2006).

Finally, we observed a substantial positive effect of dispersal mechanism on function, which was driven equally and positively by both wind and water dispersal modes. Positive effects

of wind and water dispersal indicate a suppressive effect of animal dispersal on function. We find this difficult to interpret, but perhaps it relates to the fact that few of the woody plants included in the analyzed databases were animal-dispersed. On one hand, sole reliance on animals for dispersal may make it difficult for shrubs to increase their abundance rapidly and thus exert large functional changes. On the other hand this may be a sampling bias reflecting the properties of the species studied in the papers that happened to report useful data for our analysis rather than encroachers in general. Whether encroacher species truly do tend to be wind or water dispersed is unknown, and ought to be investigated further.

Overall, our trait variables had low predictive power (<33% of variance explained). We emphasize, however, that our dataset is based on multiple approaches, plant communities and methodologies and is therefore inherently noisy. The large majority of our input data were qualitative, as we were unable to obtain quantitative data on traits such as litter production rates, nutrient content, and decomposition rates. Consequently, we used surrogates of tissue nutrients such as the binary variable "deciduousness." Despite these problems, we were still able to detect significant effects of shrub traits on two components of possible encroachment outcomes, and this certainly argues that this question should be pursued further when quantitative trait data, and a larger encroachment-focused database, become available. Such a global analysis will therefore not be without its problems. Given this, we believe that low values of our coefficients of determination are not unreasonable and should be considered a conservative estimate of the true variance explained by shrub traits.

Synthesizing the outcomes of shrub encroachment: linking land use, shrub traits and abiotic gradients

Several attributes of shrubs could be important in relation to the functional outcome of encroachment. For example, plant height and shape indicate the potential for encroaching plants to alter microclimate, and capture mobile resources such as airborne sediments, and therefore their potential to create fertile islands around their stems (Garner & Steinberger 1989). Plant shape and height may determine animal use and habitat, and therefore deposits of exogenous resources such as urine, faeces and carcasses. Root morphology, N fixation, deciduousness and allelopathic effects influence the heterogeneity of plant roots, hydraulic lift, litter stock and C: N ratios and therefore soil nutrient pools, decomposition rates, retention and interception of mobile resources and overall soil fertility (see Maestre *et al.* 2009).

To synthesize these observations, we argue the need for a broader conception of shrub encroachment outcomes and degradation. We can envision the interplay of the various factors that determine the outcome of shrub encroachment using a flowchart (Fig. 5). The flowchart considers various shrub encroachment outcomes that might result from several scenarios. An encroachment outcome has at least three conceptually unique components: 1) a utilitarian (societal values *sensu* Gliken & Fairbrother 2000) component, 2) a functional component and 3) a structural or community diversity component. Each component may experience ecosystem degradation (negative effect) or ecosystem enhancement (positive effect) due to shrub encroachment. Neutral effects are also likely, but are omitted for simplicity. The overall outcome of encroachment is predicted therefore to be a combination of various groupings of the three different types of ecosystem enhancement or degradation. The utilitarian (societal) component of the encroachment outcome is highly dependent on the intended use to which the land is to be put ('human use preference' in Figure 5). The functional and structural components are partly determined by trait assemblages of encroaching shrubs and partly by abiotic contingencies such as aridity. Our SEM analyses demonstrated that various assemblages of shrub traits can have different outcomes. For example, encroaching species that tend to be taller, are dispersed by wind or water, or fix N

tend to be associated with higher functional scores. Conversely, encroaching allelopathic species tend to be associated with low functional scores. The effects of a given assembly of traits may or may not have similar effects on structure. Figure 5 depicts these concept using four idealized types of trait assemblages: those that enhance both function and structure, those that degrade both structure and function, those that enhance function and degrade structure, and those that degrade function and enhance structure. The functional component may be further contingent upon abiotic gradients such as aridity (driven by average annual rainfall), which we have shown has a large effect on above-ground C, likely due to the effects of moisture availability on variables related to C cycling and hence plant growth.

The interplay of the different components (utilitarian/functional/structural) in determining the overall encroachment outcome is best understood in an example. Eight different encroachment outcomes might be expected to result from the single human use preference, pastoralism, depicted in Figure 5. Because of a preference for grasses (e.g. Heady & Child 1999), shrub encroachment is likely to result in a degradation of utilitarian value with respect to sheep and cattle grazing, but a positive effect on utilitarian value for goat grazing, given the predilection of goats for woody browse (Heady & Child 1999). Various possible trait assemblages of the encroaching shrub produce four different responses in terms of functional and structural encroachment outcomes for both sheep/cattle grazing, and goat grazing. Thus, for a single preferred human use, pastoralism, there are a total of eight different encroachment outcomes ranging from purely positive to purely negative, and containing multiple mixed responses. If, on the other hand, the preferred human use is C-sequestration, then climatic gradients come into play and dictate the utilitarian component of the encroachment outcome because of its control on aboveground C production.

CONCLUDING REMARKS

In this work, we advance the first global synthesis of the outcomes of shrub encroachment in drylands based upon observed responses reported in the literature and land use objectives. Our work demonstrates that a single interpretation of shrub encroachment as a form of degradation is not possible, and that many outcomes ranging from desertification to ecosystem enhancement may occur. The interpretation of shrub encroachment depends strongly on the measured responses. Several measures of ecosystem function seem likely to improve under shrub encroachment, including soil C and N, whereas others decline. Some of these responses are also contingent upon aridity; in general, ecosystems closer to the more arid end of the gradient have a greater likelihood of experiencing increasing ecosystem degradation. Further, our work shows that not all encroaching woody species are equivalent. Traits of various woody plants known to encroach into herbaceous communities can influence the overall impact on ecosystem function in soils and especially in community structural attributes such as biodiversity. The literature on the negative effects of shrub encroachment has been strongly influenced by the prevalence of a single land use; pastoralism involving grass-feeding livestock. We consider that if coupled human and natural systems are considered, there are multiple components of the encroachment outcome; utilitarian, functional and structural. If a broader conception of degradation is applied to shrub encroachment, which encompasses all of these components, it is easy to see that a variety of positive, negative, and neutral effects are plausible. Such a broader conception must be taken into account when designing conservation and management plans for drylands, which has often been guided by the notion that shrub encroachment is a form of degradation/desertification, and when further exploring the particular mechanisms underlying the ecological consequences of shrub encroachment.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

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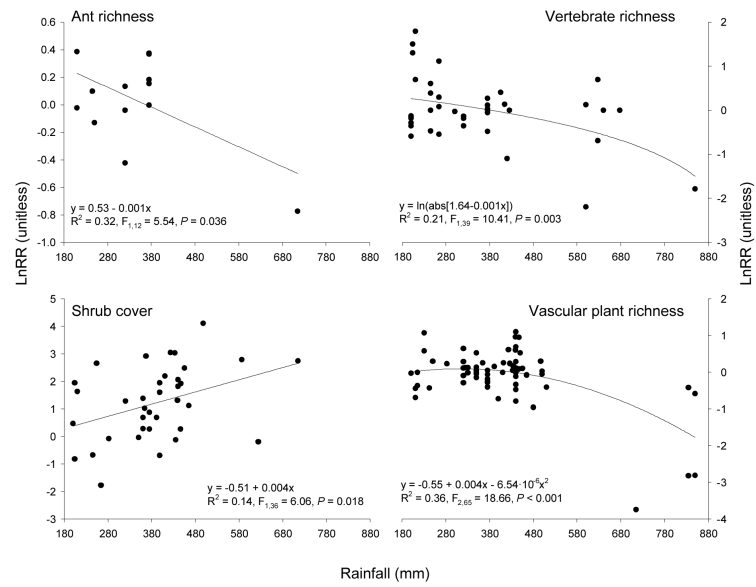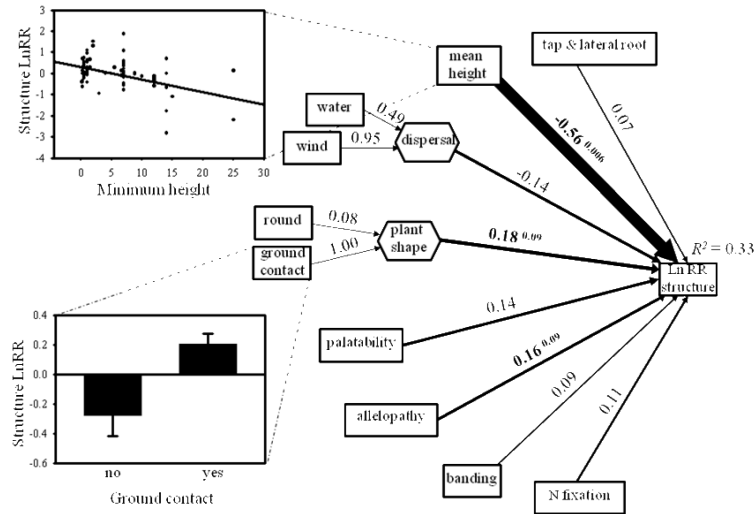
Figure 1.
Regressions of rainfall with the response ratio (lnRR) of shrub cover, ant richness, vertebrate richness and vascular plant richness. Details of the models fitted are given within each panel.
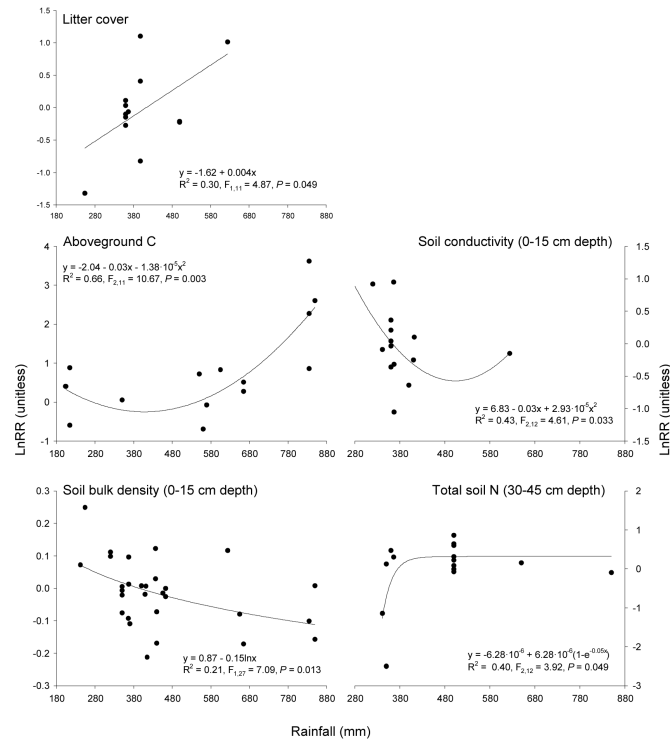
Figure 2.
Regressions of rainfall with the response ratio (lnRR) of litter cover, aboveground carbon, soil bulk density (0-15 cm depth), soil conductivity (0-15 cm depth) and total soil nitrogen (N, 30-45 cm depth). Details of the models fitted are given within each panel.

Figure 3.
Final structural equation models depicting effects of plant traits upon the surrogate of ecosystem structure (Ln RR statistic). Boxes indicate measured variables entered in the model. Hexagons indicate composite variables used either to model multi-level categorical predictors, or to pool effects of a group of otherwise conceptually related predictors. Arrows represent "paths", i.e. hypothesized effects that one variable has on another. Numbers adjacent to paths are path coefficients, and are an effect size statistic directly analogous to regression weights. When $P < 0.10$, the associated bootstrap probability value is presented in superscript. In the case of paths leading from predictors to the response variable, the path widths are scaled proportionally to the path coefficient. Paths leading into composites are "loadings"; multiplying them by a path coefficient leaving a composite yields the effects of individual indicators on the response variable. Although not shown to simplify graphs, all predictors are freely allowed to covary.

Figure 4.
Final structural equation models depicting effects of plant traits upon the surrogates of ecosystem function (Ln RR function). The remainder of the legend is as in Fig. 3.

Figure 5.

Potential outcomes of shrub encroachment in former grasslands in relation to three factors: 1) human use preference, 2) the trait assemblage of encroaching shrubs, and 3) abiotic contingencies (e.g., average annual rainfall). These outcomes are separated according to the utilitarian (U; e.g. grazing, recreation), ecosystem functional (F; e.g., soil physio-chemical variables related to nutrient cycling and C storage), and community structural (S; e.g. cover, biodiversity and spatial pattern) perspectives. Four possible trait assemblages (identified by the SEM analyses) can conceivably result in: 1) enhancement of both functional and structural components, 2) reduction of both components, 3) enhancement of one component and reduction of the other, in addition to various combinations that are neutral for either soil function or community structure. The function component may be further contingent upon abiotic gradients such as aridity due to the apparent effects of moisture availability on variables related to C cycling. Thus, for a single preferred human use such as biodiversity conservation there are a four different encroachment outcomes ranging from purely positive for utility (+), function (+) and structure (+) to purely negative for all three, as well as multiple mixed responses. In the case of the human use preference recreation, the encroachment outcome in terms of utility will be mixed (m) depending on whether the preferences of recreationalists align with environments that are shrub-encroached or shrub-free.

Table 1

Summary of trends for the 43 variables in response to a change from grassland to shrubland; na = not analyzable; [a] data from Australia and Spain only.

Response variable	Type	Number of cases				*P*-value	Trend
		Increasing	Declining	Unchanged	Total		
Grass cover	Functional	5	37	11	53	<0.001	Decrease
Soil pH	Functional	0	7	51	58	0.013	Decrease
Shrub cover	Functional	22	2	14	38	<0.001	Increase
Total soil C	Functional	33	6	20	59	<0.001	Increase
Total soil N	Functional	57	18	26	101	<0.001	Increase
Above-ground C	Functional	10	2	2	14	0.006	Increase
Soil organic C	Functional	24	10	33	67	0.009	Increase
Exchangeable soil Ca	Functional	11	3	11	25	0.025	Increase
Available soil P	Functional	11	3	12	26	0.027	Increase
Potential soil N mineralization	Functional	10	3	13	26	0.052	Increase
Root biomass	Functional	12	5	7	24	0.069	no change
Shrub richness	Structural	4	0	10	14	0.100	no change
Total soil P	Functional	10	4	15	29	0.123	no change
Tree cover	Functional	5	1	5	11	0.149	no change
Above-ground N	Functional	4	0	2	6	0.150	no change
Soil moisture	Functional	8	3	16	27	0.175	no change
Vertebrate richness	Structural	12	6	23	41	0.184	no change
Exchangeable soil K	Functional	9	4	25	38	0.220	no change
Vascular plant richness	Structural	21	25	22	68	0.235	no change
Exchangeable soil Mg	Functional	6	2	13	21	0.238	no change
Plant inter-patch distance	Functional	10	5	16	31	0.240	no change
Electrical conductivity	Functional	8	4	7	19	0.295	no change
Cryptogam cover	Functional	4	1	5	10	0.300	no change
Soil bulk density	Functional	3	7	38	48	0.317	no change
Inorganic soil N	Functional	5	2	2	9	0.335	no change
Density of perennial plant patches	Functional	5	8	18	31	0.490	no change
Soil stability index [a]	Functional	6	4	22	32	0.730	no change
Soil respiration	Functional	8	10	9	27	0.773	no change
Above-ground net primary productivity	Functional	19	20	9	48	1	no change
Available soil N	Functional	3	4	4	11	1	no change
Bare soil cover	Functional	6	5	17	28	1	no change
Cation exchange capacity	Functional	0	0	6	6	1	no change
Decomposition	Functional	0	1	0	1	1	no change
Exchangeable soil Na	Functional	3	3	4	10	1	no change
Ant richness	Structural	2	1	11	14	1	no change
Litter cover	Functional	2	2	9	13	1	no change
Microbial biomass	Functional	0	1	0	1	1	no change

Response variable	Type	Number of cases				P-value	Trend
		Increasing	Declining	Unchanged	Total		
Plant tissue N	Functional	2	0	0	2	1	no change
Soil erosion	Functional	2	2	1	5	1	no change
Soil infiltration index [a]	Functional	1	2	27	30	1	no change
Soil nutrient index [a]	Functional	2	2	26	30	1	no change
Total soil S	Functional	3	2	9	14	1	no change
Tree richness	Structural	0	0	9	9	1	no change

Table 2

Summary of the meta-analyses conducted with structural attributes and ground cover components. Median response ratios are reported in all cases. Statistical results indicate results from Wilcoxon Signed Rank tests (Z). The null hypotheses of these tests are that median values do not differ from 0. P values below 0.05 are in bold. n = number of study cases included in the analysis, S = number of studies included in the analyses.

Response variable	Response ratio	n	S	Z	P
Bare soil cover	0.037	28	9	0.3	0.785
Shrub cover	1.206	38	19	−3.9	**<0.001**
Grass cover	−0.491	53	29	4.4	**<0.001**
Tree cover	0.591	11	5	−1.9	0.062
Vascular plant richness	−0.004	68	28	0.4	0.721
Shrub richness	0.693	14	8	−1.8	0.074
Density of plant patches	−0.119	31	5	1.4	0.150
Ant richness	0.116	14	5	−0.5	0.594
Vertebrate richness	0	41	22	0.2	0.826

Table 3

Summary of the meta-analyses conducted with functional variables. C = carbon, N = nitrogen, P = phosphorus, ANPP = aboveground net primary productivity, EC = electrical conductivity, PMN = potentially mineralisable soil nitrogen. The remainder of the legend is as in Table 2. 0-15, 15-30 and 30-45 indicate the three soil depths (in cm) evaluated.

Response variable	Response ratio	n	S	Z	P
Aboveground C	0.615	14	14	−2.1	**0.035**
ANPP	−0.223	48	35	1.5	0.124
Litter cover	−0.101	13	7	0.6	0.552
Root biomass (0-15)	0.651	17	13	−2.2	**0.028**
Total soil C (0-15)	0.224	51	32	−3.1	**0.002**
Organic soil C (0-15)	0.126	52	28	−2.3	**0.020**
Total soil N (0-15)	0.176	73	43	−3.8	<**0.001**
Available soil N (0-15)	0.028	10	7	0.2	0.878
PMN (0-15)	0.322	23	14	−2.2	**0.031**
Total soil P (0-15)	0.007	23	8	−1.3	0.191
Available soil P (0-15)	0.186	20	15	−0.4	0.654
Soil respiration (0-15)	0.042	21	13	0.1	0.903
Soil moisture (0-15)	0.015	18	17	−0.5	0.586
Soil pH (0-15)	−0.008	44	25	2.3	**0.020**
Soil calcium (0-15)	0.189	19	14	−1.8	0.070
Soil potassium (0-15)	−0.009	30	12	−0.5	0.644
Soil magnesium (0-15)	0.048	17	10	−0.8	0.446
Soil EC (0-15)	−0.036	15	8	0.7	0.496
Soil bulk density (0-15)	−0.007	29	22	0.7	0.456
Soil sulphur (0-15)	0.013	10	5	0.2	0.878
Total soil C (15-30)	0.276	13	9	−2.2	**0.028**
Organic soil C (15-30)	0.151	32	17	−3.2	<**0.001**
Total soil N (15-30)	0.174	32	17	−4.3	<**0.001**
Soil pH (15-30)	−0.017	14	13	1.4	0.158
Soil bulk density (15-30)	−0.040	10	11	1.6	0.114
Total soil C (30-45)	0.060	11	7	−1.2	0.248
Soil N (30-45)	0.154	15	9	−1.1	0.281

Table 4

Path coefficients and *P*-values for the shrub traits used in the exploratory SEM process using the structural, functional and combined index scores.

Attribute	Structural score (R^2=0.33)		Functional score (R^2=0.14)		Combined score (R^2=0.12)	
	Estimate	**P - value**	**Estimate**	**P - value**	**Estimate**	**P - value**
N–fixation	0.11	0.38	**0.17**	**0.03**	**0.25**	**0.003**
Palatability	0.14	0.35			0.17	0.21
Banding	0.09	0.41	−0.04	0.61	0.11	0.20
Dispersal mechanism	−0.14	0.25	**0.38**	**0.002**	**0.27**	**0.03**
Allelopathy	**0.16**	**0.09**	**− 0.37**	**<0.001**	−0.03	0.75
Plant shape	0.18	0.09	0.16	0.47	**− 0.30**	**0.03**
Deciduousness			0.02	0.92	**− 0.09**	**0.08**
Plant height	**− 0.56**	**0.006**	**0.39**	**<0.001**	**− 0.31**	**0.02**
Rooting^2	0.07	0.83	−0.04	0.85	−0.09	0.80