

Shrub encroachment can reverse desertification in semi-arid Mediterranean grasslands

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Abstract

2 The worldwide phenomenon of shrub encroachment in grass-dominated dryland ecosystems
is commonly associated with desertification. Studies of the purported desertification effects
4 associated with shrub encroachment are often restricted to relatively few study areas, and
document a narrow range of possible impacts upon biota and ecosystem processes. We
6 conducted a study in degraded Mediterranean grasslands dominated by *Stipa tenacissima* to
simultaneously evaluate the effects of shrub encroachment on the structure and composition
8 of multiple biotic community components, and on various indicators of ecosystem function.
Shrub encroachment enhanced vascular plant richness, biomass of fungi, actinomycetes and
10 other bacteria, and was linked with greater soil fertility and N mineralization rates. While
shrubs encroachment may be a widespread phenomenon in drylands, an interpretation that this
12 is an expression of desertification is not universal. Our results suggest that shrub
establishment may be an important step in the reversal of desertification processes in the
14 Mediterranean region.

16 **Keywords:** Shrub encroachment, Desertification, Global Change, Mediterranean, semi-arid,
Stipa tenacissima, Plant successional dynamics, Ecosystem functioning

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INTRODUCTION

2 Increases in the density and cover of shrubs in former grasslands, commonly referred as
“shrub encroachment”, have been frequently reported in arid, mesic, alpine and arctic areas
4 worldwide (e.g., van Auken 2000; Parizek *et al.* 2002; Montané *et al.* 2007). This
phenomenon has been extensively studied in dryland ecosystems throughout the world, where
6 the transitions between grasslands and shrublands occurring during the last 150 years have
been dramatic (van Auken 2000). Shrub encroachment is often accompanied by large changes
8 in the spatial pattern of soil resources and vegetation (Schlesinger & Pilmanis 1998), which
have been linked with alterations in the structure and functioning of the ecosystem ultimately
10 leading to its desertification (Schlesinger *et al.* 1990; Archer *et al.* 2001). We define
desertification as land degradation, having socio-economical impacts, in arid, semi-arid and
12 dry sub-humid areas resulting at least partially from anthropogenic activities (Reynolds *et al.*
2007).

14 A variety of triggers, ranging from climate change to grazing to fire suppression, are
implicated in the global shrub encroachment phenomenon (van Auken 2000). In a model
16 based upon the Chihuahuan Desert (North America), it has been proposed that such
disturbances can generate heterogeneity in soil resources, which in turn creates opportunities
18 for shrub colonization (Schlesinger *et al.* 1990). This heterogeneity becomes self-reinforcing
as both abiotic, e.g., sediment transport and moisture availability, and biotic, e.g., root
20 activity, mechanisms result in the translocation of soil resources to the “islands of fertility”
surrounding shrub patches (Schlesinger & Pilmanis 1998). While increased within-site
22 heterogeneity in soil properties and vegetation is a hallmark of shrub encroachment, other
consequences of this phenomenon are more variable. Shrub encroachment can increase runoff
24 and soil erosion (Parizek *et al.* 2002), and reduce soil moisture (Darrouzet-Nardi *et al.* 2006;
but see Schade & Hobbie 2005) and infiltration (Parizek *et al.* 2002). However, there is little

consensus on the consequences of shrub encroachment for nutrient cycling. Some
2 investigations have reported losses of soil carbon and nutrients following shrub encroachment
(Schlesinger *et al.* 1999; Jackson *et al.* 2002), but others have found the opposite (Asner *et al.*
4 2003; Zavaleta & Kettley 2006; Throop & Archer 2008). In addition, the effects of shrub
encroachment on the composition and structure of the biota are complex and depend on which
6 organisms are of concern. While shrub encroachment often diminishes the productivity,
density, cover and recruitment of grasses (Gibbens *et al.* 2005; Zavaleta & Kettley 2006), it
8 also benefits different animals (Whitford 1997; Bestelmeyer 2005). Furthermore, its
consequences for soil organisms like biological soil crusts (BSC) are scarcely understood
10 (Thomas & Dougill 2006).

To account for some of these inconsistencies, Archer *et al.* (2001) proposed a broader
12 model of shrub encroachment, adding some new terminology: i) “xerification” summarizes
the degradation process of the Schlesinger *et al.*’s (1990) model and is the dynamic expected
14 in arid to semi-arid environments, and ii) “thicketization” is a transition from undegraded
grassland or savannah to woodland and occurs in semi-arid to sub-humid areas. Unlike
16 xerification, thickening does not necessarily constitute degradation and can lead to
enhanced provision of some ecosystem services. Nevertheless, the Millennium Ecosystem
18 Assessment Desertification Synthesis, a United Nations-supported document aimed at
informing national and international policies, refers to shrub encroachment as the major
20 ecological expression of desertification in arid and semi-arid rangelands (Millennium
Ecosystem Assessment 2005). Furthermore, and despite that the original Schlesinger *et al.*
22 (1990) model applied to ecosystems at the transition of arid and semi-arid climates, the
message that has propagated and persisted is that in semi-arid rangeland environments, shrub
24 encroachment is a mechanism of desertification (e.g. Archer *et al.* 2001; Peters *et al.* 2006;
Throop & Archer 2008).

Well over half of the studies of shrub encroachment in arid and semi-arid regions have
2 been conducted in the United States, with additional work carried out in Africa, Australia, and
South America (reviewed in van Auken 2000 and Archer *et al.* 2001). Surprisingly, little
4 research has been conducted in the Mediterranean Basin, despite the fact that this region
constitutes a hotspot for biodiversity (Medail & Quezel 1999) and grassland to shrubland
6 transitions are common there (Alados *et al.* 2004). In addition, few investigations have
evaluated the effects of shrub encroachment on both the composition and structure and on the
8 functioning of the ecosystem (Jackson *et al.* 2002; Zavaleta & Kettley 2006), and none has
simultaneously assessed its effects on multiple above- and belowground biotic communities
10 and on ecosystem processes. We studied the effects of the presence of sprouting shrubs in
grasslands dominated by *Stipa tenacissima* L. along a regional climatic gradient. According to
12 Schlesinger *et al.* (1990), we tested the broader hypothesis that shrub encroachment is
consistent with a desertification interpretation in Mediterranean grasslands. Specifically, we
14 evaluated the following predictions: i) vegetation should show a more clumped spatial
organization in plots with shrubs, compared to a more random dispersal of smaller grass
16 patches in plots without shrubs; ii) soil fertility and nutrient cycling should be lower in plant
interspaces due to translocation of resources to shrub canopies, consistent with the
18 development of relatively permanent “islands of fertility” under the later (Schlesinger &
Pilmanis 1998), and iii) shrub encroachment decreases the diversity of vascular plant,
20 biological soil crust, and soil biota communities, and reduces nutrient stocks and cycling and
microbial activity below ground. We also examined whether shrubs could alter the
22 composition of these communities, and whether their effects on ecosystem functioning were
dependent on climatic conditions.

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MATERIALS AND METHODS

2 Study area

We studied 13 experimental sites along a climatic gradient from the center to the south-east of Spain (see Table S1 in Supporting Information). Our sites have annual precipitation and temperature ranging from 265 mm to 497 mm, and from 13°C to 17°C, respectively. Eleven and two sites were located on *Lithic Calciorthid* and *Typic Gypsiorthid* soils, respectively (Soil Survey Staff 1994). Vegetation was in all cases an open grassland dominated by *Stipa*, with total cover values between 31% and 67% (Fig. S1).

It is generally believed that *Stipa* grasslands represent an impoverished, degraded state (i.e. desertified), and that potential vegetation in these grasslands includes more woody vegetation and greater biological productivity (see Appendices S1 and S2 for a discussion). *Stipa* grasslands have been artificially enhanced in Spain over historical times due to shrub removal for fuel, and to the harvesting of *Stipa* fiber (Appendix S1). Nowadays, these grasslands are known or inferred to be undergoing shrub encroachment based upon: i) photographic evidence (in all sites where repeat photography is available, shrub encroachment from 1946 to present is clearly visible and dramatic; Fig. S2); ii) a historical population shift out of rural areas to cities beginning in the 1950s, with a peak in the 1960s, associated with cessation of shrub removal and *Stipa* harvesting (Appendix S1); and iii) widespread reports of shrub encroachment in these and other ecosystems in Spain (Puigdefábregas & Mendizábal 1998; Montané *et al.* 2007; Ramírez & Díaz 2007).

Experimental design

At each site we established two paired 30 m × 30 m plots. One of each pair (S plot) was on land with well-developed adult individuals of sprouting shrubs (26.4% of total perennial cover on average, Table S1). The other (NS plot) was chosen where there were no adult shrubs (0.4% of total perennial cover in average, Table S1); a few of these plots contained

seedlings or saplings of these species. Each pair of S and NS plots were separated by less than
2 1000 m (range 10-1000 m) to ensure that the two plots shared the same climatic conditions.
Each pair also had soils derived from the same parent material, and had very similar slope and
4 aspect values. Thus, all of Jenny's soil forming factors (parent material, climate, topography,
biota, and time; Jenny 1941) were nearly identical among the pairs, except for the
6 presence/absence of shrubs.

Composition and structure of vascular plants and biological soil crusts

8 We assessed the composition and structure of perennial vascular plants using four 30-m long
transects per plot, which were extended parallel to the slope and situated 8 m apart. In each
10 transect we placed 20 consecutive quadrats (1.5 m × 1.5 m size), and the cover of each
perennial species was visually estimated. From these data we calculated indices of the spatial
12 pattern and evenness of perennial plants. Spatial patterns were characterized by the spatial
analysis of distance indices (SADIE, Perry 1998). We used the SADIE index of aggregation
14 (I_a) to summarize such patterns; they were clumped if $I_a > 1$, random if I_a is close to 1, and
regular if $I_a < 1$ (see Appendix S1 for details). Species evenness was calculated as the
16 probability of an interspecific encounter index (PIE, Hurlbert 1971) as detailed in Appendix
S1. We also used the number of perennial species present within each 30 m × 30 m plot as our
18 estimate of species richness.

We recorded the visible components of biological soil crusts (BSC; mosses, lichens
20 and some cyanobacteria), as they strongly contribute to soil stability, hydrology and nutrient
cycling in drylands (Belnap 2006). We randomly placed ten 50 cm × 50 cm quadrats adjacent
22 to the upslope canopy of *Stipa* tussocks and in bare ground interspaces, located at least 50 cm
from the nearest plant. These microsites show sharp differences in the composition and
24 structure of BSC (Maestre *et al.* 2001). Because microsites adjacent to shrubs are typically
covered in leaf litter, BSC were not sampled there. The number of moss and lichen species

was registered in each quadrat. We used these data to evaluate the composition (presence/absence of each species in each quadrat), evenness (PIE), and richness (number of species per plot) of BSC.

Composition and structure of soil microbial communities

We characterized the soil microbial communities by direct extraction and gas-chromatography analysis of ester-linked fatty acids (Schutter & Dick 2000). Analyses were done in three of the five soil samples collected per microsite and plot (see below) as detailed in Appendix S1. Microbial diversity (species richness and PIE) and community structure were evaluated by the relative abundance of fatty acids; these data do not represent diversity at a species-level, but may provide analogous information at a coarse taxonomic resolution. Fatty acids were also grouped by structural classes, including those used as markers of specific microbial groups (fungi, Gram +/- bacteria and actinomycetes, Appendix S1).

Assessment of soil fertility and ecosystem functioning

We obtained data on soil variables related to nutrient cycling, biological productivity, and buildup of nutrient pools (respiration, organic C, total N and P, K, potential N mineralization and pH). Buildup or loss of soil fertility is a “slow variable” proposed as a critical indicator of desertification status (Reynolds *et al.* 2007). We refer to these measures of ecosystem functioning and nutrient pools collectively as “fertility-function”.

We sampled the soil during summer 2006 using a stratified random procedure. In the NS plots, five 50 cm × 50 cm quadrats were randomly placed in the open and tussock microsites. A composite sample consisting of five 145 cm³ soil cores (0–7.5 cm depth) was collected from each quadrat, bulked and homogenized in the field. In the S plots the same scheme was followed, but additional samples were obtained under the canopy of five randomly selected shrubs. In the laboratory, the samples were sieved (2 mm mesh) and separated into two fractions. One fraction was immediately frozen at –80 °C for fatty acid

analyses; the other was air-dried for 1 month for biogeochemical analyses. Soil samples from one of the S plots were accidentally discarded, and could not be analyzed.

Soil respiration was determined by alkali absorption of the CO₂ evolved during an aerobic incubation followed by titration with HCl (Appendix S1). Organic carbon was determined by potassium dichromate oxidation (Appendix S1). Total N and P were obtained on a SKALAR San⁺⁺ Analyzer (Skalar, Breda, The Netherlands) after digestion with sulphuric acid. Potassium was measured with the same analyzer after the soil samples had been shaken with distilled water (1:5 ratio) for 1 hour. Potential N mineralization was estimated as the net increase in NH₄⁺-N and NO₃⁻-N after an anaerobic incubation (Appendix S1). Soil pH was measured with a pH meter, in a 1 : 2.5 mass : volume soil and water suspension.

Statistical analyses

We evaluated the effects of shrubs on the spatial pattern, richness and evenness of perennial vegetation using paired t-tests. The richness and evenness of BSC was analyzed similarly, but by the Wilcoxon sign test because the data were not normally distributed.

The effects of shrubs on the multivariate composition of vascular plants (excluding the sprouting shrubs), BSC and soil microbial communities were evaluated with the semi-parametric PERMANOVA approach (Anderson 2001; see Appendix S1 for details). The model used in the analysis of vascular plants considered site and shrubs (presence/absence) as random factors. That used to analyze BSC and microbial communities (all fatty acids extracted) included site as between-plot random factor, shrubs as a random factor nested within site, and microsite (open/tussock) as a within-plot fixed factor. The same model was used to analyze the richness and evenness of fatty acids, and the relative abundance of particular microbial and BSC groups. To aid our interpretation of the PERMANOVA analyses, we also did a canonical analysis of principal coordinates (CAP, Anderson & Willis

2003). When appropriate, CAP axes were correlated with individual variables included in the ordination by the Spearman correlation coefficients.

To assess the effects of shrub encroachment on plot-scale ecosystem nutrient stocks and cycling, we estimated the value of each soil variable at the scale of each 30 m × 30 m plot using a weighted average of microsite-specific soil measurements, weighted by the cover of the microsites in each plot. Differences between S and NS plots on these estimates were evaluated by paired t-tests. We also calculated the net effect of shrubs in each site with a normalized difference index (see Appendix S1 for details), and related it to the proportion of total perennial cover accounted by sprouting shrubs and to abiotic factors (rainfall, temperature, slope, azimuth, elevation, and geographical co-ordinates) by Spearman correlation analyses. Finally, we evaluated the effects of shrubs at finer spatial scales by analyzing all soil properties measured in the tussock and open microsites with the same PERMANOVA model employed to analyze BSC data.

RESULTS

The spatial clumping of perennial vegetation was virtually identical with ($I_a = 1.43 \pm 0.34$; mean \pm SE) and without ($I_a = 1.42 \pm 0.40$) shrubs ($t_{12} = -0.46$, $P = 0.964$). Our semi-parametric PERMANOVA and canonical (CAP) analyses did not detect a microsite \times shrub interaction in soil fertility-function variables (Fig. 1, $F = 1.25$, $P = 0.15$, Table S2), suggesting that nutrients are not being transported from interspaces to shrub canopies. Rather, our analyses indicated that fertility-function is enhanced in the S plots regardless of the microsite being examined (Fig. 1). The first CAP axis was positively correlated with all soil variables except for total P, and separated the soils from the tussock and open microsites (Fig. 1). The second axis clearly differentiated plots with and without shrubs; soils from the former had greater total soil N, organic C and potential N mineralization. Estimates of total soil N,

organic carbon and potential N mineralization obtained at the plot scale were significantly
2 larger in the S plots (Table 1). The magnitude of the effect of sprouting shrubs on these
variables, as measured with a normalized difference index, was positively related to their
4 relative abundance in the case of organic carbon ($\rho = 0.699$, $P = 0.011$, $n = 12$) and total N (ρ
 $= 0.650$, $P = 0.022$). However, it was not related to the climate or to any other abiotic features
6 of the study sites (Table S3).

The presence of shrubs was found to have several effects upon biotic diversity. More
8 vascular plant species were found in the S (28.92 ± 3.87) than in the NS (20.54 ± 3.10) plots
($t_{12} = -4.36$, $P = 0.001$), albeit the number of BSC species did not differ between them (13.77
10 ± 4.49 against 13.84 ± 4.76 ; $Z = -0.37$, $P = 0.715$). The evenness of vascular plants was also
significantly greater in the S (0.66 ± 0.03) than in the NS (0.46 ± 0.07) plots ($t_{12} = 3.79$, $P =$
12 0.003), but that of BSC was slightly larger in the NS plots (0.89 ± 0.03 compared to $0.87 \pm$
 0.02 ; $Z = -2.28$, $P = 0.023$). The presence of shrubs did not affect the richness and evenness of
14 the microbial community ($F = 0.98$, $P = 0.487$), although significant differences between sites
($F = 3.68$, $P = 0.001$) and microsites ($F = 5.50$, $P = 0.010$) were found (Fig. S3).

16 PERMANOVA analyses conducted for each site revealed that the composition of
vascular plants significantly differed between S and NS plots (Table S4). Corresponding CAP
18 results (Fig. 2A) suggested that this pattern was related with the reduction and increase,
respectively, of the abundances of *Stipa* and *Rosmarinus officinalis* in the S plots (Spearman's
20 ρ with the first CAP axis = 0.932 and -0.564 , respectively, $P < 0.001$ in both cases). The
effects of shrubs on the overall composition of BSC and microbial communities differed
22 between sites and microsites (shrub[site] \times microsite interaction, $P < 0.012$, Table S4). In
most of the sites evaluated, significant effects of shrubs on these biotic communities were
24 evident in at least one of the microsites, but in others these effects were evident in either the
two or none of these microsites (post-hoc results not shown). The first two CAP axes clearly

separated the effects of both microsite and shrubs on the composition of both BSC and microbial communities (Figs. 2B and 2C). The percentages of mosses, gelatinous lichens and cyanobacteria were greater in the S plots, while those of squamulose, fruticose and crustose lichens were lower (Table 2; $P < 0.001$ in all cases, Table S5). The relative abundance of fatty acids representative of fungi, Gram+ and Gram- bacteria and actinomycetes was also greater in the S plots (Table 2; $P < 0.001$ in all cases, Table S5). However, the ratio monounsaturated to saturated fatty acids was decreased by 10 % in these plots (Table 2; $P < 0.001$, Table S5).

DISCUSSION

Evaluating the consequences of shrub encroachment has been a major topic of research in the last two decades. It has been motivated by the extent of the area affected, its relationship to important environmental issues such as desertification (Schlesinger *et al.* 1990) and the global carbon budget (Pacala *et al.* 2001), and its implications for management and policy (Gifford & Howden 2001). Yet, most of the studies carried out on this topic have targeted single components of ecosystems or functions, and have been conducted at one or only a few sites. Our results show important and consistent effects of shrub encroachment on both the composition and structure of multiple biotic communities and the soil fertility and functioning of semi-arid Mediterranean grasslands.

Cascading effects of shrubs on grassland biota

Albeit our design cannot completely exclude potential confounding effects associated to differences in small-scale soil heterogeneity between S and NS plots, which could affect shrub distribution, it controls for all soil forming factors, making the major mechanisms for pre-existing differences between these plots very unlikely. Shrub encroachment increased the diversity and evenness of vascular plants, and promoted important changes in the composition of all biotic communities evaluated. The differences in diversity and composition of the

vascular plant community may be mediated by mechanisms such as direct facilitative
2 interactions, provision by shrubs of perch sites for seed dispersing birds or indirect
interactions involving mycorrhizas or other symbionts. Both shrubs and *Stipa* have been
4 found to facilitate other perennial plants in semi-arid Mediterranean grasslands (Maestre *et al.*
2001; Maestre & Cortina 2005). However, we found that the facilitative effect of shrubs was
6 greater than that of *Stipa* (S.S. and F.T.M., unpublished data). Differences in strategies for
acquiring resources between shrubs and *Stipa* (Puigdefábregas *et al.* 1999), a greater nutrient
8 content under the canopy of shrubs (Fig. S4), and a larger amount of niches in this microsite
(Maestre & Cortina 2005), might explain our results. Furthermore, in Australia shrubs have
10 been described as “water wicks”, and exhibit positive effects on infiltration that may be
enhanced by interactions with BSC (Eldridge & Freudenberger 2005).

12 Perhaps the most intriguing positive impact of shrubs upon other biota and upon
fertility and function of soils occurred in interspaces, a phenomenon which is best explained
14 by biotic mechanisms; leaf and root litter, activity of root symbionts, and altered
microclimate. Although the contrast among plant canopy and interspaces varied among sites,
16 some general responses were observed. Lower monounsaturated: saturated fatty acid ratios
(Table 2), suggest inputs of less easily oxidizable organic C associated with the presence of
18 shrubs (Zelles *et al.* 1995). Such changes can modify the intrinsic rate of nutrient turnover and
the physiological profile of soil communities (Ellis *et al.* 2002). Greater values of fungal fatty
20 acids may suggest a greater development of a hyphal network when shrubs are present.
Finally, compared to *Stipa* tussocks, the greater height of shrubs increase shading, and this
22 may substantially alter soil temperature and subsequently soil moisture. Such microclimatic
changes could impact numerous other organisms, e.g. favoring mosses over some lichens
24 (Bowker *et al.* 2005). The changes observed in this study indicate the existence of a cascading

effect, mediated by sprouting shrubs, affecting different trophic levels and key functional processes depending on them.

Shrub encroachment may advance or reverse perceived desertification

The prevailing model of shrub encroachment-driven desertification of semi-arid rangelands establishes that shrubs increase the spatio-temporal heterogeneity of soil resources (Schlesinger *et al.* 1990). Relatively homogeneous landscapes are replaced by a mosaic of impoverished intercanopy areas and “islands of fertility” under the canopy of shrubs, which accumulate fertility via biotic and abiotic mechanisms (Schlesinger & Pilmanis 1998). This process creates a feedback ultimately leading to the desertification of the ecosystem (Schlesinger *et al.* 1990). This view, developed mostly based upon results obtained in the US portion of the Chihuahuan Desert, and supported by studies from other regions (e.g., Parizek *et al.* 2002), contrasts sharply with our observations. In the grasslands studied, shrubs increased the amounts of organic C and total N, and the potential N mineralization in the soil not only under their canopies (Fig. S4), but also under *Stipa* canopies and in bare ground areas (Fig. 1). In addition, our estimates at the plot scale showed greater values of these soil variables in the S plots, a pattern not apparently driven by either climate or other abiotic features (Table S3). Cascading effects of shrubs upon other biota, and the lack of an obvious abiotic mechanism for such patterns, suggest that these changes may be primarily biotically-mediated. The example described here seems to suggest that a thickening-like dynamic is occurring in Spain, which is resulting in conversion from grassland to woodland, and may potentially lead to even stronger woody plant dominance. However, our system differs from thickening, as described by Archer *et al.* (2001), in that such transition is occurring even in sites with average rainfall values below 300 mm·year⁻¹. It also seems to be driven by the cessation of disturbance, and appears to represent succession away from a state of anthropogenic, ecological and socio-economical impoverishment. Thus we believe this is

more consistent with a reversal of desertification than with a simple fluctuation between two
2 undegraded states, as thickening might imply.

Here we present a model identifying differing scenarios that may arise from shrub
4 invasion into semi-arid grass-dominated ecosystems, and illustrate ways in which shrub
encroachment could lead to either the advancement or the reversal of desertification (Fig. 3A).
6 We hypothesize that the perception of shrub encroachment-linked desertification
advancement or reversal depends upon two key “fulcrum” variables (dark triangles in Fig. 3):
8 traits of the invader shrub compared to the grasses (see also Table S6), and the human use
preference for the landscape, or most highly valued ecosystem services. Coupled natural and
10 human-social drivers are also a major part of recent attempts to synthesize a desertification
paradigm (Reynolds *et al.* 2007). In our conceptual model, effects of shrub encroachment are
12 neutral with regards to desertification, symbolized by lateral arrows. The fulcrum variables
modify the trajectory of these effects toward a dynamic more consistent with reversal
14 (upward, Fig. 3B) or advancement (downward, Fig 3C) of desertification. When a majority of
effects trend upwards or downwards, we suggest that desertification is reversing or advancing,
16 respectively.

The balance of shrub impacts appears to shift from negative to positive as climate
18 becomes wetter (Archer *et al.* 2001, Knapp *et al.* 2008). We propose that an important
mechanism underlying this pattern may be the traits of the woody vegetation that is typical to
20 different climate regimes (Table S6). Traits of the invading shrubs differ between ecosystems,
as do those of the dominant herbaceous species (Figs. 3B and 3C). In general, shrub
22 encroachment literature treats all shrubs as functionally equivalent, but encroaching shrub
properties differ markedly in various ecosystems (Appendix S2). In the Chihuahuan Desert,
24 the invading shrubs tend to be widely-spaced compared to the grasses, invest more in deeper
rooting systems, and have elevated canopies with low basal stem area; on the other hand the

grasses form a relatively homogenous mantle of roots near the soil surface, and have a more
2 continuous basal stem area (Appendix S2). Thus, a fairly continuous horizontal arrangement
of plant biomass is replaced by a punctuated vertical arrangement of plant biomass (Fig. 3C).
4 In direct contrast, the invasion scenario in the *Stipa* grasslands creates a bridging of vertical
plant islands and creates a more horizontal, near-surface zone of plant biomass and organic
6 residues (Fig. 3B). The increase of soil fertility observed far beyond shrub canopies might be
a consequence of architectural and physiological differences between the root systems of
8 *Stipa* and those of sprouting shrubs. While *Stipa* constrains its roots directly under the canopy
(Puigdefábregas *et al.* 1999), sprouting shrubs have sprawling canopies and root systems that
10 can extend horizontally several meters (e.g. *Q. coccifera*, Cañellas & San Miguel 2000).
These shrubs release more of their fixed carbon as root exudates, which are also different
12 from those produced by herbaceous plants (Grayston *et al.* 1996). The wide zone of contact
between the canopy of sprouting shrubs and the soil surface leads to better retention of their
14 own litter, and better interception of mobile resources (Table S6). Increases of root and leaf
litter and root exudates, together with the likely occurrence of hydraulic lift (as found in North
16 American species of *Quercus* and *Juniperus*; Querejeta *et al.* 2007, Leffler *et al.* 2002), might
result in microbial populations sustaining larger metabolic activity and increasing overall
18 nutrient cycling.

In summary, our model suggests that because of combinations of shrub traits relative
20 to those of grasses, and the changes in the spatial pattern of belowground biomass (e.g.
continuous vs. punctuated) promoted when shrubs encroach into grasslands, Mediterranean
22 shrubs enhance retention, aggradation and distribution of mobile resources, whereas those
invading North American grasslands increase ecosystem-level loss of mobile resources. In
24 Australia, the same suite of invading shrubs led to positive impacts upon landscape function
indicators in one herbaceous rangeland ecosystem, and negative impacts in another (Ayers *et*

al. 2001). We suggest that although the shrub traits did not change among the sites, their
2 relative contribution to patch continuity and contact with the surface, compared to that of the
dominant grass species, did change. Undoubtedly, different trait combinations are important
4 in other systems, but we predict that those combinations enhancing the resource sink behavior
of the ecosystem relative to that of the uninvaded grasslands will be more functional.

6 The second component of desertification perception is the relative valuation of various
ecosystem services altered by shrub encroachment. Human society does not value ecosystem
8 function *per se*, rather it values ecosystem goods and services that are required for human
well-being. We do not attempt to illustrate them all here, but shrub encroachment impacts are
10 varied and numerous, and their valuation depends upon the human culture which perceives it.
In the Mediterranean, the primary current use of *Stipa* grasslands is either hunting of small
12 game, which tends to be enhanced by shrub cover (Rueda *et al.* 2008), or livestock
production. The palatability of *Stipa* is similar to that of sprouting shrubs (Ben Salem *et al.*
14 1994), and thus shrub encroachment does not greatly decrease the foraging value of *Stipa*
grasslands. Indeed, compared to the shrubs *Rosmarinus* and *Pistacia lentiscus*, *Stipa* contains
16 less crude protein and digestible organic matter, and was less preferred by both sheep and
camels (Ben Salem *et al.* 1994). In the United States, invasion of palatable livestock forage by
18 shrubs like *Prosopis sp.* is viewed as negative by the current culture because it primarily
values semi-arid regions for pastoralism. However, as evidenced by the widespread use of the
20 *Prosopis* fruit as a food staple by Native American cultures in the distant and recent past
(Harden & Zolfaghari 1988), these valuations are subject to change. *Stipa* itself was also more
22 desirable up until the recent past for its fiber production (Appendix S1). One valuation that is
quite likely to change is that of the role of shrub encroachment as a carbon sink (Archer *et al.*
24 2001). While productivity may decline in some shrub-invasion scenarios and increase in
others, shrub C is likely to be more recalcitrant and could contribute more to long-term C

storage than that of grasses, although this assertion is still a subject of debate and active
2 research (Pacala *et al.* 2001; Asner *et al.* 2003; Knapp *et al.* 2008).

While in many cases the desertification interpretation of shrub encroachment is well-
4 founded, we caution against describing it as such as a universal phenomenon. Our results and
hypothetical model suggest that shrub encroachment could also lead to desertification
6 reversal, or in the case of counterbalancing negative and positive impacts, could have no clear
relationship to desertification. A general model will be attainable when comprehensive studies
8 of encroachment of shrubs with different traits into grasslands of varying cultural value are
conducted in several geographic regions.

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22 cultivated soils. *Plant Soil*, 170, 115-122.

24 **SUPPORTING INFORMATION**

The following Supporting Information is available for this article:

Appendix S1. Detailed materials and methods.

2 **Appendix S2.** Discussion on the importance of the traits of the encroaching woody vegetation relative to those of the grasses as a desertification driver.

4 **Figure S1.** Examples of *Stipa tenacissima* grasslands without and with shrubs.

Figure S2. Photographs of some of the study sites in 1946, 1975 and 2006.

6 **Figure S3.** Richness and evenness of fatty acids measured in plots with and without shrubs.

Figure S4. Values of the surrogates of soil fertility and ecosystem functioning measured in
8 plots with and without shrubs.

Table S1. Main characteristics of the study sites.

10 **Table S2.** Nested PERMANOVA for main treatment effects and interactions on the surrogates of soil fertility and ecosystem functioning measured from the tussock and open
12 microsites across all sites.

Table S3. Correlation matrix between shrub effect size and both the proportion of total cover
14 accounted by sprouting shrubs and the main abiotic features of the study sites.

Table S4. Summary of nested PERMANOVA for main treatment effects and interactions on
16 the composition of vascular plants, biological soil crusts and microbial communities.

Table S5. Summary of nested PERMANOVA for main treatment effects and interactions on
18 the relative abundance of particular biological soil crust and fatty acid groups.

Table S6. Likely effects of plant traits on the functional outcome of shrub encroachment.

20 Additional Supporting Information may be found in the online version of this article.

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Table 1. Effects of shrubs on the surrogates of soil fertility and ecosystem functioning estimated at the scale of 30 m × 30 m plots. Plot-scale estimates were calculated using a weighted average of microsite-specific soil measurements, weighted by the cover of the microsites in each plot. Data represent means ± SE ($n = 12$). Values of P below 0.05 are in bold.

	Plots without shrubs	Plots with shrubs	Paired t-test
Total soil N ($\text{mg}\cdot\text{g}^{-1}$)	1.31 ± 0.11	1.50 ± 0.08	$t_{11} = -2.316, P = \mathbf{0.041}$
Total soil P ($\text{mg}\cdot\text{g}^{-1}$)	0.37 ± 0.03	0.37 ± 0.02	$t_{11} = 0.540, P = 0.600$
Soil K ($\text{mg}\cdot\text{g}^{-1}$)	0.026 ± 0.002	0.030 ± 0.003	$t_{11} = -1.400, P = 0.189$
Soil respiration ($\text{mg C}\cdot\text{CO}_2\cdot\text{g soil}^{-1}\cdot\text{day}^{-1}$)	0.054 ± 0.003	0.059 ± 0.004	$t_{11} = -1.348, P = 0.205$
Soil organic C ($\text{mg}\cdot\text{g}^{-1}$)	29.48 ± 2.11	33.16 ± 1.66	$t_{11} = -2.417, P = \mathbf{0.034}$
Potential N mineralization ($\text{mg N}\cdot\text{kg soil}^{-1}\cdot\text{day}^{-1}$)	0.97 ± 0.21	1.68 ± 0.19	$t_{11} = -3.055, P = \mathbf{0.011}$
Soil pH	7.94 ± 0.08	7.94 ± 0.08	$t_{11} = 0.253, P = 0.805$

Table 2. Effects of shrubs on the frequency and abundance of groups of biological soil crusts (BSC) and fatty acids, respectively, under the canopy of *Stipa tenacissima* (Tussock) and at bare ground areas (Open). Data from all the sites are pooled. Values represent means \pm SE ($n = 130$ and 36 for BSC and fatty acids, respectively). See SI Appendix 1 for the complete list of fatty acids included within each category.

Biological soil crusts (%)	Plots without shrubs		Plots with shrubs	
	Open	Tussock	Open	Tussock
Mosses	19.14 \pm 1.81	36.24 \pm 2.39	21.83 \pm 1.93	38.58 \pm 2.26
Gelatinous lichens	26.81 \pm 2.13	18.21 \pm 1.46	29.80 \pm 2.37	22.69 \pm 1.70
Squamulose lichens	27.04 \pm 1.92	22.31 \pm 1.79	25.90 \pm 2.26	17.45 \pm 1.50
Fruticose lichens	6.73 \pm 1.26	5.64 \pm 1.00	4.03 \pm 1.10	5.39 \pm 1.10
Crustose lichens	9.31 \pm 1.24	8.68 \pm 1.10	7.05 \pm 1.02	7.15 \pm 1.02
Cyanobacteria (<i>Nostoc</i> sp.)	2.51 \pm 0.68	5.09 \pm 0.90	6.77 \pm 1.56	6.43 \pm 1.12
Fatty acids (relative units)				
Monounsaturated: saturated ratio	1.35 \pm 0.05	1.31 \pm 0.05	1.19 \pm 0.04	1.16 \pm 0.04
Polyunsaturated (fungi)	0.208 \pm 0.006	0.209 \pm 0.007	0.228 \pm 0.008	0.206 \pm 0.007
Branched (Gram +)	0.132 \pm 0.004	0.137 \pm 0.007	0.135 \pm 0.004	0.148 \pm 0.007
17:0cy (Gram -)	0.013 \pm 0.001	0.011 \pm 0.001	0.015 \pm 0.001	0.011 \pm 0.001
10Me (Actinomycetes)	0.017 \pm 0.001	0.015 \pm 0.001	0.020 \pm 0.002	0.015 \pm 0.001

Figure captions

Figure 1. Results of the canonical analysis of principal coordinates, showing the effects of shrubs and microsite (Tussock: *Stipa tenacissima* canopies; Open: bare ground areas) on the surrogates of soil fertility and ecosystem functioning measured (soil pH, organic C, total N, total P, K, respiration and potential N mineralization). Significant ($P < 0.05$) Spearman correlations between the original variables and the ordination axes are shown next to them. The data from the different sites were pooled; values represent means \pm SE ($n = 60$).

Figure 2. Results of the canonical analysis of principal coordinates, showing the effects of shrubs on the composition of vascular plants (A), and those of shrubs and microsite (Tussock: *Stipa tenacissima* canopies; Open: bare ground areas) on the composition of biological soil crusts (B) and soil microorganisms (C). Sprouting shrubs were not included in the analysis of vascular plant data. The data from the different sites were pooled; values represent means \pm SE ($n = 1040, 130$ and 36 for A, B and C, respectively).

Figure 3. Shrub encroachment may lead to either advancement or reversal of desertification. Its effects are modulated by two fulcrum variables (plant traits and human values), which may alter the direction of the effects of shrubs, determining impacts upon ecosystem function and utility of the ecosystem for human society (a). Cases where the preponderance of impacts on both function and utility point in an upward direction are consistent with the perception of desertification reversal (b); whereas cases where the point downward are consistent with desertification advancement (c). M = examples pertinent to the Mediterranean, J = examples pertinent to the Chihuahuan Desert. In the Mediterranean example (b), as shrub encroachment progresses (from left to right), the distribution of plant canopy (grasses = black, shrubs = dark

gray) and roots (light gray) takes on a more continuous horizontal orientation, creating a zone of resource accumulation and eliminated resource leaking from interpatch areas. In the Chihuahuan Desert example (c), as shrub encroachment (dark gray) progresses (from left to right) a relatively continuous distribution of plant roots and canopy (light gray) is replaced by a more vertical and punctuated distribution in the fragmentation of resource accumulation zones.

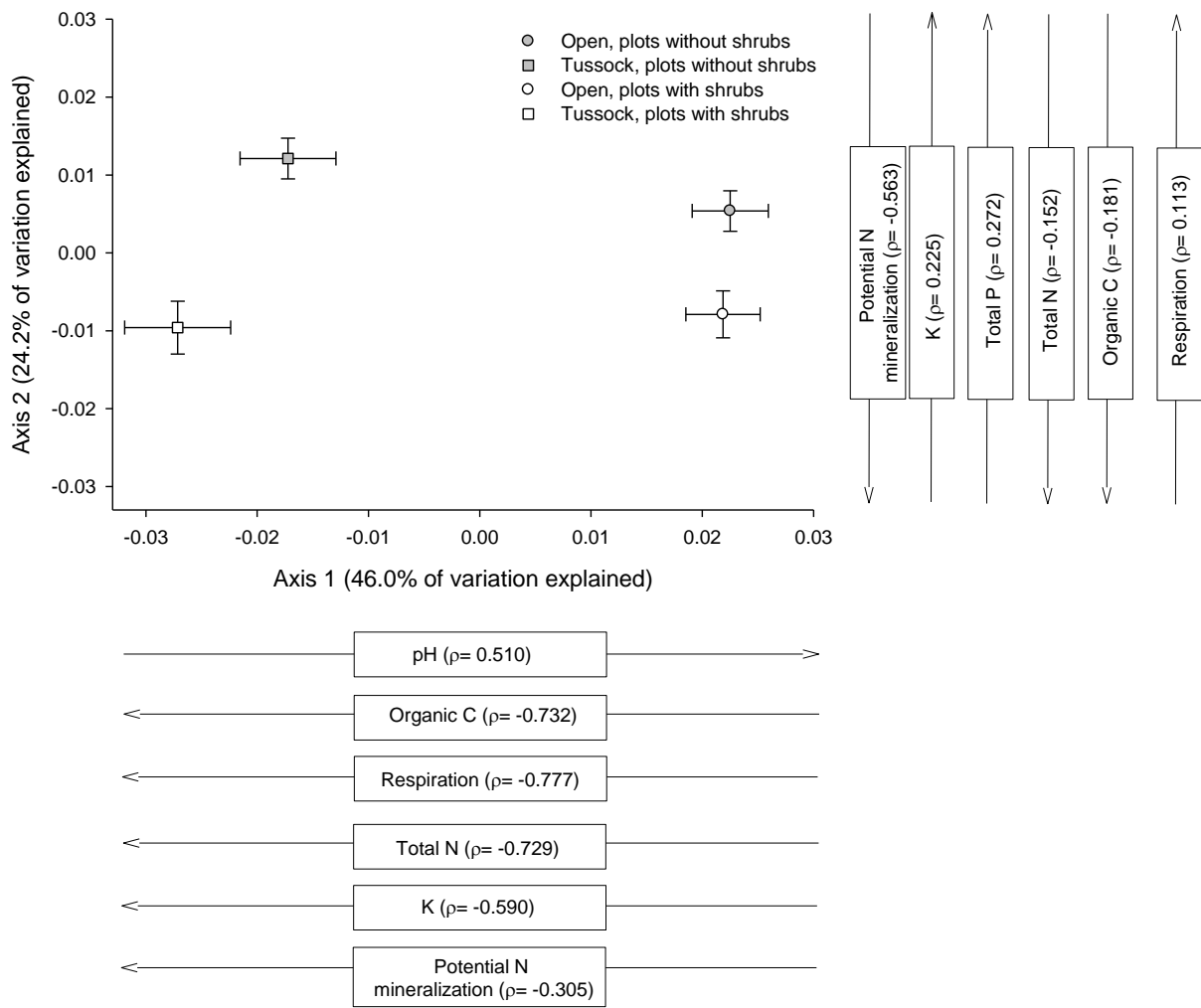


Figure 1

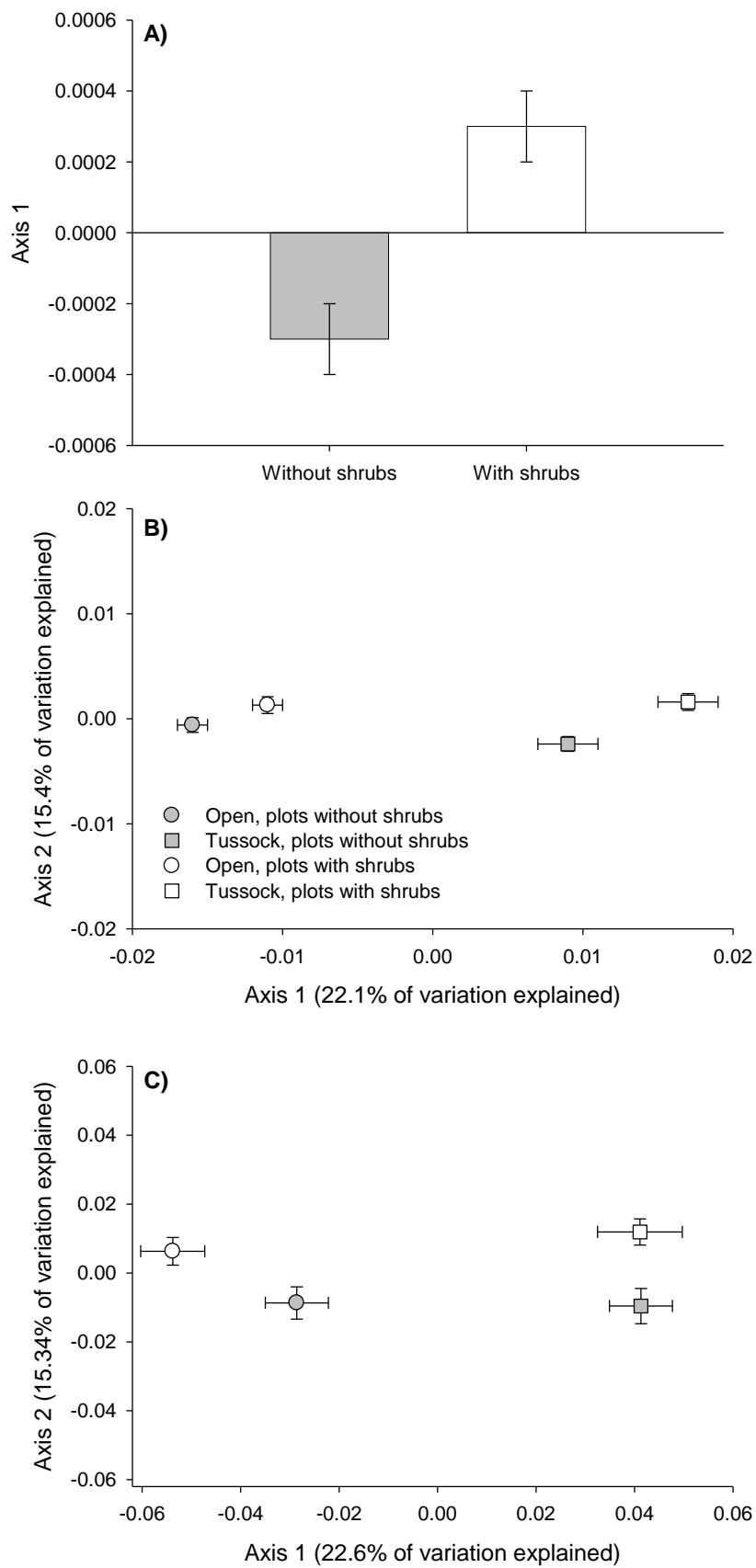


Figure 2

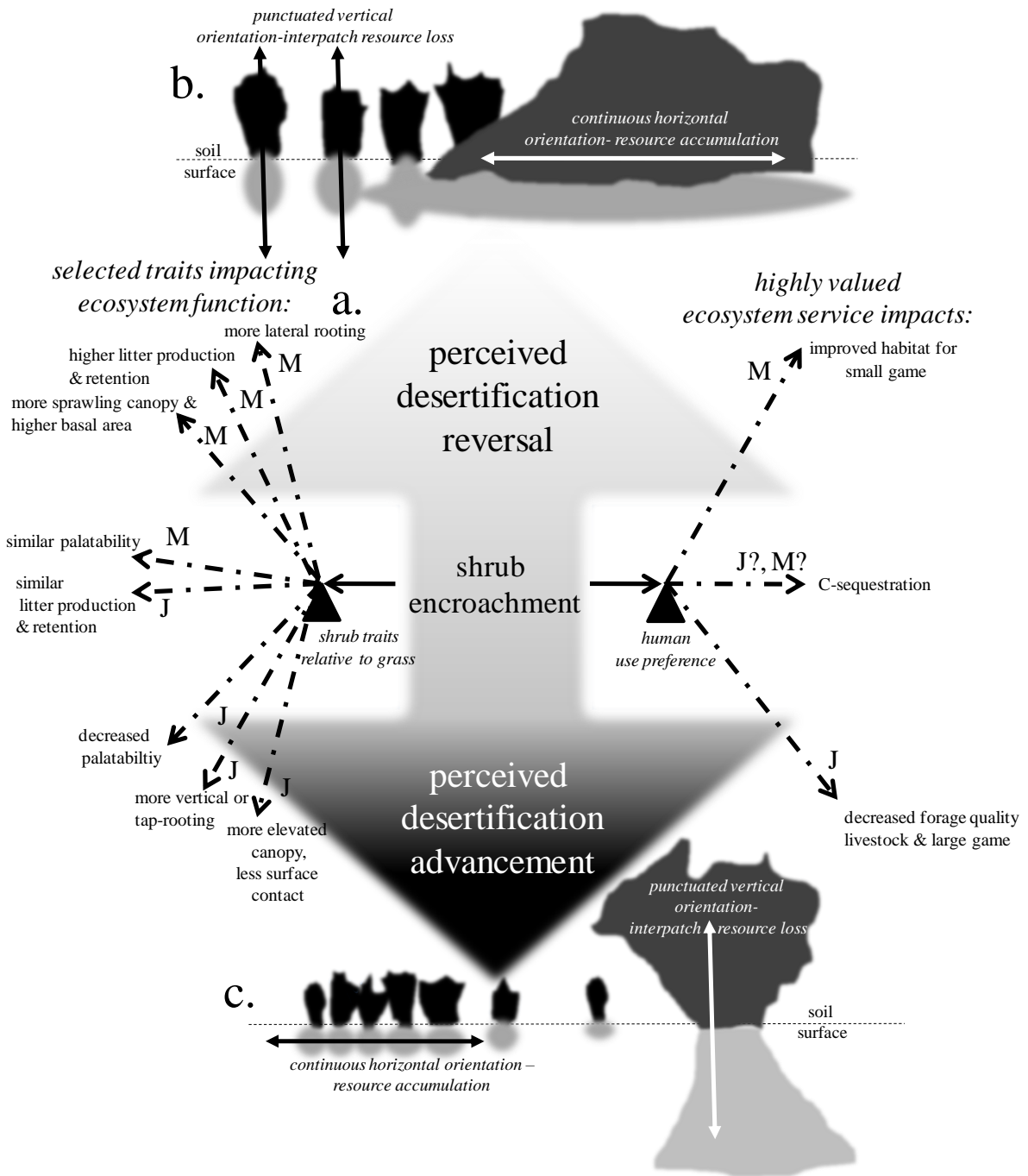


Figure 3