



Co-occurring grazing and climate stressors have different effects on the total seed bank when compared to the persistent seed bank

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Keywords

Altitudinal gradient; Dry scrub; Ecuador; Environmental filter; Environmental stress; Grazing; Herbivory; Seed bank; Semi-arid system; Similarity indices; Tropical ecosystem

Nomenclature

Jørgensen & León-yáñez (1999)

Abbreviations

RDI_{rTP} = relative dominance index for the total and persistent seed banks in terms of richness; RDI_{aTP} = relative dominance index for the total and persistent seed banks in terms of abundance; RDI_{rAB} = relative dominance index for above-ground and below-ground components in terms of richness

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Introduction

The transition from seed to plant is a key process determining community structure and dynamics (Eriksson & Ehrlén

Abstract

Questions: (1) Does climate amelioration in semi-arid ecosystems increase seed bank richness and seed density in both total and persistent seed banks? (2) Does herbivory modulate climate effects on soil seed banks? (3) Is this effect mediated by changes in the above-ground vegetation? (4) To what extent do environmental conditions affect similarity between the total and persistent seed banks, and between above-ground (vegetation) vs below-ground (seed bank) community compartments?

Location: Ecuadorian Dry Mountain Scrub Ecosystem.

Methods: Our study was conducted along a climatic gradient (altitude) under two different management conditions: undisturbed and grazed. The effect of grazing, altitude and their interaction on seed abundance and richness of the total and persistent soil seed banks were evaluated with non-linear mixed models.

Results: Altitude, grazing and their interaction exerted a significant effect on richness and abundance of the total seed bank, but not on the persistent seed bank. At highly stressful climate conditions, differences in species richness between the total and persistent seed banks were small or absent, while at milder environmental conditions the total seed bank showed greater seed species richness and abundance than the persistent one. However, under grazing conditions, species richness in both seed banks was rather similar along the climatic gradient. Relationships in terms of species richness between above-ground vs below-ground compartments, shifted from being dominated by the above-ground component at low altitudes (more stress) to being dominated by the seed bank component at higher elevations (milder conditions). In grazed locations, vegetation and seed bank showed similar species richness throughout the altitudinal gradient.

Conclusions: This study demonstrates that not only climate acted as a key environmental filter on soil seed bank properties, but also that grazing greatly modulated the primary effect of climate. Nevertheless, the effect of climate and grazing was restricted to the total seed bank (the fertility compartment) and no effect was observed in the persistent seed bank (longevity compartment). In this tropical dry scrub, richness and abundance of seeds increased upwards along the altitudinal gradient, most likely because at higher altitudes environmental conditions improve and become more benign for plant development.

1992). As a consequence, knowledge of seed bank function and the interaction with standing vegetation has become a priority for plant ecologists (Chambers & MacMahon 1994). This seems especially critical in stressful habitats

such as drylands, where soil seed banks are important ecosystem components (Busso & Bonvissuto 2009) that allow species persistence during unfavourable periods (Kinloch & Friedel 2005) and promote community stability by reducing the impact due to environmental stochasticity (Fenner 1995).

In stressful ecosystems, a two-phase vegetation structure prevails, with patches interspersed among bare ground areas. Several studies have found a profound effect of plant patches and their dynamics on seed bank properties. For instance, seed bank density and richness are much higher inside patches than in bare areas (Pugnaire & Lázaro 2000; Caballero et al. 2008a; Busso & Bonvissuto 2009). This spatial structure is related to higher seed production within patches (seed source effect) and to the capacity of patches to trap seeds from surrounding areas (trapping effect) (Flores & Jurado 2003; Bullock 2004). As a consequence, plant patches prevent seed losses from superficial run-off and act as seed sources during secondary dispersal. Further investigation on how this 'patch effect' on seed bank properties varies with the presence and intensity of some stressors has become a key research topic. For instance, several studies have highlighted the important influence of climate on the relationship between the seed bank and above-ground vegetation patches (Hopfensperger 2007; Chaideftou et al. 2008), and even relationships between the total and persistent seed banks along environmental gradients (e.g. Milton 1939; Thompson 1978; Hopfensperger 2007). Other studies have shown the profound effect of grazing intensity on soil seed bank composition and structure (Cavieres & Arroyo 2001; Funes et al. 2003; Miller & Cummins 2003; Ma et al. 2010a). However, the mechanisms that modulate the 'patch effect' along stress gradients when several stressors such as harsh climatic conditions and herbivory co-occur remain unknown.

Studies on the effect of climatic stress on seed bank properties have shown contrasting results; some studies reporting a decrease of richness and density with stress (Ortega et al. 1997; Cummins & Miller 2002) and others finding positive trends between stressful conditions and seed bank richness and density (Funes et al. 2003). Although some mechanisms have been proposed to explain these apparently contradictory results, they still remain inconclusive. Some authors have suggested that the higher seed densities found at more stressful locations are the consequence of increased seed longevity at low soil water conditions (Cavieres & Arroyo 2001; Turner et al. 2006), related to the decrease in seed viability found in wet and mild conditions (Walck et al. 2011) due to fungal pathogens (Wagner & Mitschunas 2008; Walck et al. 2011). These mechanisms of seed persistence in the soil will be called the 'seed longevity hypothesis'. However, in

benign sites, the better performance of plants usually promotes seed production (Miller & Cummins 2003; Ma et al. 2010a,b) and, consequently, it may lead to higher seed species richness and densities at milder conditions, this will be referred to as 'seed productivity hypothesis'. We suggest that both hypotheses contribute to seed bank properties and that the differences found among several studies are simply a confounded interpretation related to the different weight given in each study to the persistent (seed longevity component) and to the total (fertility component) seed bank compartments. Thus, it is crucial to understand how the balance between the two soil seed bank compartments shifts along environmental gradients. How each seed bank compartment varies along environmental gradients can be tested along an altitudinal gradient, since altitude is a good surrogate of climatic gradients because most climate variables vary in a predictable way (Körner 2003).

Evidence of grazing impact on size, richness and composition of seed banks is also contradictory (Kinloch & Friedel 2005). Some studies have suggested positive responses of seed abundance to grazing (Navie et al. 1996), while others have found neutral effects (Meissner & Facelli 1999; Kinucan & Smeins 2008) or even negative response with increasing grazing pressure (Bertiller 1996). These apparently contradictory effects of grazing rely on the different response of above-ground vegetation to grazing pressure (Pazos et al. 2007; Kinucan & Smeins 2008; Kassahun et al. 2009), i.e. grazing usually affects more intensively the perennial component of the community (Bestelmeyer et al. 2003), improving the conditions for annual species development (Navie et al. 1996), which may increase the importance of annual species in the seed bank.

On the other hand, it is also well known that stressful ecosystems tend to maintain high similarity between above- and below-ground species composition (Thompson & Grime 1979; Henderson et al. 1988; Hopfensperger 2007). The unpredictable environment in drylands favours species that build persistent seed banks and this may lead to high similarity between seed bank and above-ground vegetation (Henderson et al. 1988). In this study, we wish to improve our understanding on the effect of plant patch on soil seed bank properties and, more specifically, how these seed reservoirs (seed bank patches) are affected by the main biotic (i.e. herbivory) and abiotic (i.e. climate) filters and how they interact with the standing vegetation.

With this in mind, we conducted a field survey in the Ecuadorian Dry Mountain Scrub Ecosystem. This ecosystem is especially suitable because the community is dominated by a unique nurse/engineer plant along a very long altitudinal gradient, having locations subject to different grazing pressures. In this dry ecosystem, the relationship between environmental stress and altitude is opposite to that in other latitudes: climate at low elevations is more

stressful, with low water availability and high temperatures, while climate becomes milder towards higher altitudes with an increase in precipitation and a decrease in maximum temperatures. Our working hypotheses are based on the following points: (1) climate amelioration with altitude may increase seed bank density and richness by means of improvement to above-ground vegetation performance and fruit production; (2) climate effect on seed bank properties will most likely be modulated by herbivory; (3) we expect that both stressors will affect the total and persistent seed banks, specifically we expect that under highly stressful conditions differences between the two seed banks will be small or absent, while when environmental conditions become milder, then differences would increase; and (4) we expect that under high climatic stress the difference in richness between above-ground (vegetation) and below-ground (seed bank) components would be smaller than under milder conditions, and that these differences would be also modulated by grazing.

Methods

Study site

The fieldwork was undertaken in the Ecuadorian Dry Mountain Scrub Ecosystem, a scrubby variant of Tumbesian dry forests that occur from north Peru to south Ecuador in some inter-Andine valleys along a 1000-m altitudinal gradient (Harling 1979; Espinosa et al. 2011). Mean annual temperature is 27.5 °C (Catamayo airport; 1500 m a.s.l.), the average maximum temperature is 30.8 °C (in October) and the minimum average temperature is 17.9 °C (in June). Average precipitation and evapotranspiration are 383 mm·yr⁻¹ and 1112 mm·yr⁻¹, respectively (Richter & Moreira-Muñoz 2005). From May to December rainfall does not compensate for the local evapotranspiration, which causes an intense water deficit. Mean annual precipitation decreases and mean temperature increases towards lower elevations, probably due to the rain shadow effect induced by the high mountains around the Catamayo valley. Thus, stressful conditions decline towards high altitudes, where environmental conditions became milder and a steady transition occurs from dry scrub vegetation to cloudy montane forests. The geological substrate is conformed of Paleozoic metamorphic rocks intermingled with volcanic and sedimentary rocks from the Cretaceous and Tertiary periods, which create basic (pH 7.6), nutrient-rich, sandy to stony soils.

Vegetation forms conspicuous perennial patches interspersed in bare soil areas dominated by annual plants in the rainy season. *Croton wagnerii* (Müll) Arg. (*Euphorbiaceae*) is the dominant patch-forming scrub plant. *C. wagnerii* is an evergreen shrub up to 2-m high with autochorous or myrmecochorous seed dispersal

(Jara-Guerrero et al. 2011). Other rare xerophytic and spiny species conform the vegetation patches together with *Croton* plants, such as some cacti-like plants of the genera *Euphorbia* and some trees up to 7-m high such as *Acacia macracantha* Humb. & Bonpl. ex Willd. (*Fabaceae*) and *Bursera graveolens* (Kunth) Triana & Planch (*Burseraceae*) (Sierra 1999; Fig. 1).

Experimental design

We selected two locations 20-km apart from each other in the valley of Catamayo (Loja-Ecuador): Chinchas with altitude from 1490 to 2090 m, and Alamala ranging from 1530 to 1950 m. They constitute an ideal natural system model to test our hypotheses because they share the same climate, slope, orientation, altitude range, substrate and similar vegetation type, differing only in their livestock density. Chinchas has high livestock densities ranging from 1 to 3 head·ha⁻¹ whereas Alamala remains almost undisturbed. Cattle grazing occurs during the rainy season at the phenological optimum of the vegetation. At each location, we established four sites distributed along the altitudinal gradient (Chinchas: 2070, 1950, 1620 and 1480 m a.s.l.; Alamala: 1900, 1670, 1600 and 1530 m a.s.l.). Within each site, two 30 m × 30 m plots were located <100 m apart and with an altitudinal difference ranging from 10 to 55 m a.s.l. (i.e. 16 plots, eight per location). Climate conditions were more stressful at the lower edge of the gradient with less precipitation and higher temperatures. At the upper edge, the dry scrub community is sharply transformed into a relatively moist forest (Richter & Moreira-Muñoz 2005).

Soil seed bank sampling

We randomly selected nine *Croton* individuals per plot. The seed bank of each *Croton* patch was sampled in the upper, middle and bottom sides and the three samples (10 × 10 × 3 cm) were merged to conform our sampling unit. The upper 3 cm of soil were sampled since they accumulate most of the germinable seed bank in arid environments (Caballero et al. 2008a). Soil seed bank was sampled in June 2010 (persistent seed bank) following seedling emergence and before seeds had been shed; the same patches were re-sampled in February 2011 after seeds had been dispersed and prior to seedling emergence (total seed bank). Note that this seed bank type has usually received the name 'transient' seed bank in the literature, but be aware that the soil samples collected in February contain every seed in the soil, not only the transient but also persistent seeds.

A total of 288 samples were collected, sifted and placed in 12 × 12 cm plastic cells in a greenhouse at 25 °C; samples were irrigated every 2 d. Pots contained sterile

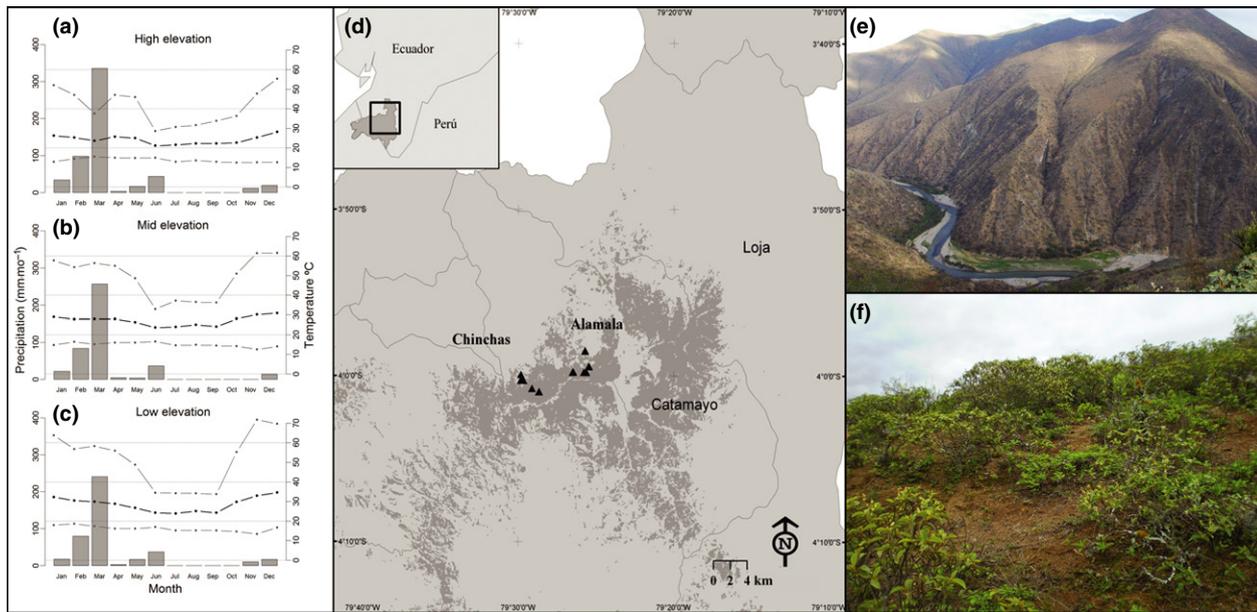


Fig. 1. Monthly precipitation (grey bars), maximum, mean and minimum temperatures at high (a: 2000 m), mid (b: 1700 m) and low (c: 1400 m) elevations of the study site. (d) The dry mountain scrub ecosystem is represented in dark grey and the eight experimental sites are represented with black triangles. Half of the plots were located in Alamala ($4^{\circ}16.37'S$, $79^{\circ}29'51.07''W$) and the other half in Chinchas ($3^{\circ}59'51.07''S$, $79^{\circ}26'30.93''W$) the coordinates correspond to the centre of each location. (e) a view of the steep slopes of Alamala and Chinchas study sites, (f) *Croton wagneri* plants, note the patch–open area structure, typical of these dry scrub ecosystems.

substrate of pumice stone to maintain humidity of soil samples and a mesh to prevent the contact of soil with the pumice stone. Control trays with sterile soil were randomly located in order to control for local incoming seed. Monitoring was conducted for 4 mo, until almost no new seedlings emerged; emerged seedlings were identified and removed, species that could not be identified were transplanted until identification was possible (ter Heerdt et al. 1996). All emerging plants were considered.

Vegetation sampling

Vegetation was sampled at three different spatial scales: (1) The plot scale (30 m × 30 m): our 16 plots were monitored; vegetation richness of each plot was estimated by means of four 30-m long transects, parallel to the slope and 8-m apart in which we placed 20 contiguous 1.5 m × 1.5 m quadrats. We recorded the presence and abundance of every perennial plant species in each quadrat and weighted averaged species abundance at the plot level; (2) The patch scale: in each plot, presence and abundance of every perennial species in each selected *Croton* patch was recorded, together with the maximum patch length and width; and (3) The neighborhood scale: distance between each target patch and the five nearest

patches was measured and species occurrences inside neighbouring patches were also recorded; average distance to neighbouring patches for each selected individual was calculated.

Biotic indices

We calculated three biotic indices based on the relative interaction index (RII) normally used to measure biotic interactions (Armas et al. 2004). In order to estimate changes in the relative dominance of species richness between the persistent and total seed banks (June and February, respectively) we built the following relative dominance index (RDI_{rTP}):

$$RDI_{rTP} = \frac{TSB - PSB}{TSB + PSB}$$

where, TSB stands for species richness of the total seed bank, and PSB for species richness of the persistent seed bank. Similarly, another RDI was built to evaluate changes in the relative importance in seed abundance also between the total and persistent seed banks (RDI_{aTP}). Finally, we also built another RDI in order to evaluate shifts in the relative importance of below-ground (i.e. soil seed bank) vs

above-ground (i.e. standing vegetation) species richness at patch scale (RDI_{rAB}):

$$RDI_{rAB} = \frac{SB - AGV}{SB + AGV}$$

where, SB is the accumulated seed richness of perennial species found in both the total and persistent seed banks, and AGV is the above-ground perennial vegetation species richness. In this case, we focused only on the perennial component since most annuals are ephemerals and very difficult to survey.

These indices range from -1 to 1 . For the RDI_{rTP} and RDI_{aTP} indices these values represent dominance of the persistent (-1) and of the total ($+1$) seed banks. For the RDI_{rAB} these values represent species richness dominance in the standing vegetation (-1) and in the seed bank ($+1$).

Data analyses

Nonlinear mixed models were used to model our two different types of data due to their versatility for dealing with any form of data: (1) abundance and richness of both total and persistent seed banks; and (2) relative dominance indices (RDI). We used altitude, grazing and their interaction as predictors. We also included the average distance to the five neighbouring patches, the patch area, and the perennial species richness at plot, neighbour and patch scales. All these predictors were considered fixed factors. Plot was included as a random factor in order to account for spatial autocorrelation and other potential biases due to some unobserved trends related to our field experimental design (Warren 2010). The convenience of including the quadratic term of altitude and their interaction to account for non-monotonic responses along the gradient was also considered. We built models with these quadratic terms, and by using an AIC criterion the convenience of including these terms was evaluated. In the RDI_{rAB} index, we did not include the fixed factors related to the above-ground vegetation.

Since our variables were asymptotically bounded between a minimum and a maximum observed value, we fitted models based on two-parameter logistic functions (i.e. $= \frac{e^{a+bx}}{1+e^{a+bx}}$), expanded and translated to fit the responses between the corresponding bounding limits (Legendre & Legendre 1998). This approach releases the analysis from the need to transform the data in order to fit any of the probability distributions usually assumed by GLMs (O'Hara & Kotze 2010; Warton & Hui 2011). We performed the usual model diagnostics and when apparent violations were found, we refitted the SE of the coefficients by adjusting the estimated variance-covariance matrix by means of sandwich estimators (White 1996).

Statistical analyses were performed with the packages stats, nlme (Pinheiro & Bates 2000) and nls (Bates & Chambers 1992) in the R environment (R Foundation for Statistical Computing, Vienna, AT).

Results

In this study, 2842 seedlings of 15 species emerged from the total seed bank and 1286 seedlings of 16 species from the persistent seed bank. Overall, we detected 22 species (21 species mentioned in Appendix S1 and one taxon that could not be identified to species). Ten of these species (three perennials and seven annuals) appeared in both seed banks, six species (five perennials and one annual) were only present in the total seed bank and six species (all of them perennials) only occurred in the persistent seed bank. Average species richness per soil sample was very similar in total (2.9 ± 0.11 species) and persistent (2.8 ± 0.15 species) seed banks, ranging from zero to seven and eight species, respectively. Seed density was lower in the persistent seed bank (mean: 297.7 ± 27.2 seeds·m⁻²; range: 0–2066.6 seeds·m⁻²) than in the total seed bank (mean: 658 ± 59.1 seeds·m⁻²; range: 0–4666 seeds·m⁻²).

Altitude, grazing and their interaction exerted a significant effect on seed richness and seed abundance of the total seed bank; however, no significant effect was observed on the persistent seed bank (Table 1). Richness and abundance of the total seed bank increased upwards

Table 1. Coefficients of fitted models for the total and persistent seed bank richness and abundance. Altitude²: the quadratic term of altitude. Altitude:Grazing: interaction between altitude and grazing. Rich_{patch}: plant richness in the target patch. Rich_{neighbor}: plant richness in the five nearest neighbour patches. Rich_{plot}: plant richness in the plot. Area_{patch}: patch area. AverD: average distance between the target patch and the five nearest patches. The significance is shown as *** $P < 0.01$, ** $P < 0.05$. n.i.: variables not included in the model (see Methods).

Predictors	Total seed bank		Persistent seed bank	
	Richness	Abundance	Richness	Abundance
Intercept	37.81**	-11.6	-3.9**	-3.4
Altitude	-0.05***	0.005***	0.001	-0.00003
Altitude ²	0.00001***	n.i	n.i	n.i
Grazing	-32.24**	10.3***	2.5	0.6
Altitude: Grazing	0.04**	-0.005***	-0.001	-0.00001
Altitude ² : Grazing	-0.00001**	n.i	n.i	n.i
Rich _{patch}	0.05	0.14**	0.09	0.4***
Rich _{neighbor}	-0.09	-0.004	0.01	0.06
Rich _{plot}	0.01	0.022	0.05	0.05
Area _{patch}	-0.03	-0.08	-0.05	-0.24***
AverD	0.06	0.28***	0.03	0.37***

along the altitudinal gradient, however both parameters remained rather constant under grazing conditions all along the altitudinal gradient towards milder environmental conditions (Fig. 2). Most species abundances increased towards the milder higher altitudes in ungrazed locations (Appendix S1). Moreover, many seed species only occurred at the highest altitudes of ungrazed areas (i.e. *Llagunoa nitida*, *Tragus berterianus*, *Opuntia cylindrica*, etc.). Otherwise, under grazing conditions, most species seemed to be favoured by grazing at least in terms of seed abundance in the soil seed bank (i.e. *Acacia macrantha*, *Poa* sp., *Sida acuta*, *Gaya calytrata*, *Urochloa fasciculata*, etc.), while a few species seem to have been removed by grazing, e.g. *Opuntia cylindrica* and *Llagunoa nitida*. Thus, an important shift in species composition between grazed and ungrazed locations, as well as along the altitudinal gradient, was observed.

Above-ground plant richness measured at patch scale significantly increased seed abundance, both in the total and persistent seed banks; however, no other above-ground plant richness predictor measured at different spatial scales affected seed bank characteristics (Table 1). Patch size showed a negative effect on seed abundance of the persistent seed bank. In addition, the longer the distance to neighbouring patches the greater the seed abundance in the target *Croton* individual.

There was a significant interaction between altitude and grazing for the relative contribution in species richness (RDI_{rTP}) and seed abundance (RDI_{aTP}) of the total vs the persistent seed banks (Table 2, Fig. 3). At low altitudes (high stressful climate conditions) differences in species richness between the total and persistent seed banks were small or absent, while at higher altitudes (milder environmental conditions) the total seed bank showed increased

seed species richness and abundance than the persistent one. However, under grazing conditions, species richness in both seed banks was rather similar throughout the climate gradient. In terms of seed abundance, the dominance of the total seed bank increased upwards along with altitude in ungrazed conditions; the opposite occurred under grazing conditions and the RDI_{aTP} index decreased towards higher altitudes until seed abundance was nearly the same in both seed banks.

Table 2. Coefficients of fitted models for relative dominance indices. RDI_{rTP} : relative dominance index between total and persistent seed banks in terms of richness; RDI_{aTP} : relative dominance index between total and persistent seed banks in terms of abundance; RDI_{rAB} : relative dominance index between above-ground (vegetation) and below-ground (accumulated seed bank) in terms of richness. Altitude²: the quadratic term of altitude. Altitude:Grazing: interaction between altitude and grazing. Rich_{patch}: perennial plant richness in the target patch. Rich_{neighbor}: perennial plant richness in the five nearest neighbour patches. Rich_{plot}: plant richness in the plot. Area_{patch}: area of the target patch. AverD: average distance between the target patch and the five nearest patches. The significance is shown as *** $P < 0.01$; ** $P < 0.05$; n.i.: predictors not included in the model (see Methods).

Predictors	RDI_{rTP}	RDI_{aTP}	RDI_{rAB}
Intercept	32.35	-5.53**	-4.73***
Altitude	-0.04	0.003***	0.002**
Altitude ²	0.00001	n.i.	n.i.
Grazing	-59.5**	8.07***	4.94**
Altitude:Grazing	0.07***	-0.004***	-0.003**
Altitude ² :Grazing	-0.00002***	n.i.	n.i.
Rich _{patch}	0.06	0.08	n.i.
Rich _{neighbor}	-0.05	0.09	n.i.
Rich _{plot}	-0.004	-0.01	n.i.
Area _{patch}	-0.06	-0.04	-0.06
AverD	0.03	0.04	0.13

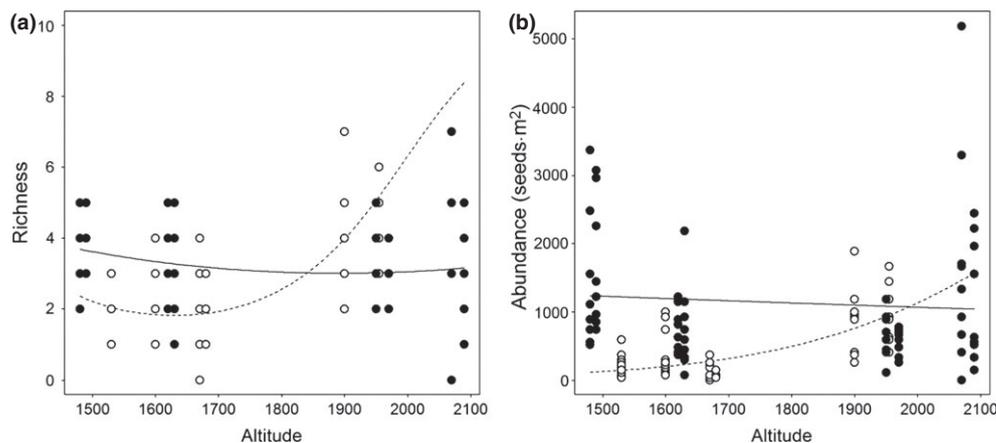


Fig. 2. Shifts in the total seed bank species richness (a) and seed abundance (b) with altitude under two grazing conditions. Patches are represented with circles; black circles represent the grazed patches and white circles the undisturbed ones. Fitted models are shown for each location, solid line for the grazed location and dotted line for the undisturbed one.

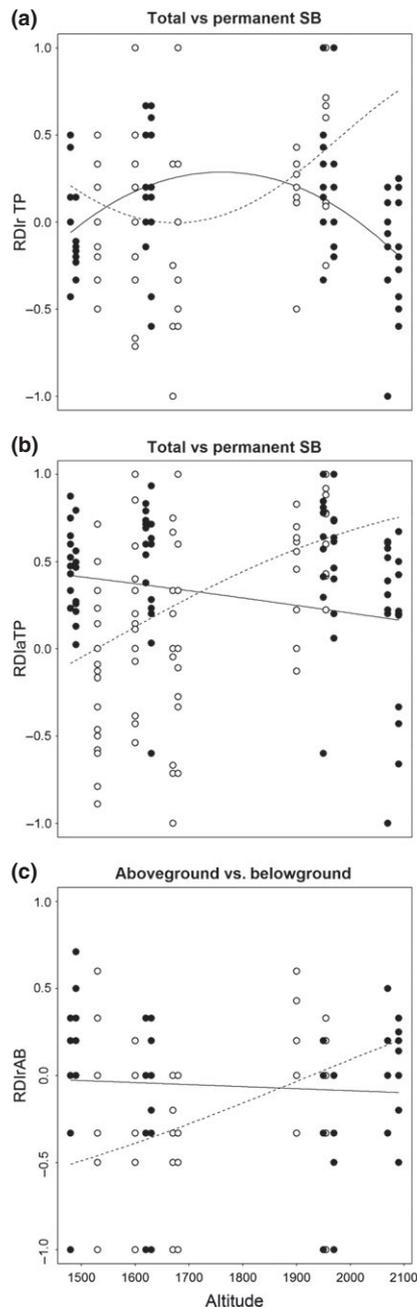


Fig. 3. Shifts in the relative dominance indices (RDI) with altitude and under two different grazing regimes. RDI_{rTP} : relative dominance index between total and persistent seed banks in terms of richness; RDI_{aTP} : relative dominance index between total and persistent seed banks in terms of abundance; RDI_{rAB} : relative dominance index between above-ground (vegetation) and below-ground (accumulated seed bank) in terms of richness. Positive values indicate dominance of the total seed bank over the persistent one (a and b) or dominance of the below-ground component over the above-ground component (c) (see Methods for more details). Patches are represented with circles; black circles represent the grazed patches and white circles the undisturbed ones. Fitted models are shown for each location, solid line for the grazed location and dotted line for the undisturbed one.

At low altitudes (dry conditions), perennial species richness was higher in above-ground (vegetation) than below-ground (accumulated seed bank), and this relationship shifted towards being dominated by the below-ground compartment at higher altitudes (Table 2: see RDI_{rAB} in Fig. 3). However, this relationship was not observed in the grazed locations, where above-ground and below-ground species richness were rather similar throughout the altitudinal gradient.

Discussion

As expected, our study demonstrates that climate, indirectly estimated by altitude, acted as a key environmental filter for the development of the soil seed bank and that, concurrently, grazing modulated the effect of this primary climate filter on soil seed bank properties. In our tropical dry scrub system, we observed a marked increase in seed species richness and abundance in the total seed bank towards higher altitudes, most likely related to amelioration of environmental conditions, from water shortage at the lowest edge to milder conditions at the upper limit (Richter & Moreira-Muñoz 2005). Under milder conditions the number of species able to survive and reproduce, as well as seed production of each species were probably larger. This improvement of above-ground vegetation richness and productivity would eventually be translated to soil seed bank properties, such as richness and abundance. Other studies carried out in very stressful habitats, such as alpine mountains and arctic ecosystems, reported a decrease in seed bank richness and abundance with altitude (Funes et al. 2003; Ma et al. 2010b); however, these ecosystems, unlike our tropical mountain dry ecosystem, are characterized by increasing climatic stress with altitude that greatly constrain seed production (Thompson 1985).

Nevertheless, the above-mentioned trend was completely out-weighted by grazing. We detected a decisive effect of grazing modulating the climate trend. More specifically, grazing led to an increase in most species seed abundances, probably because grazing produced more available open space as a consequence of a higher eating pressure on *Croton* patches, thus creating larger open areas among patches. This also implied a homogenizing effect of grazing on the total seed bank in terms of seed abundance throughout the altitudinal gradient, most probably due to cattle wandering up and down this gradient, which might have favoured propagule dispersal from species-rich zones to species-poor ones. Eventually, grazing reduced total seed bank richness at high elevations and promoted species richness at low altitudes. Specifically, shrubs or trees such as *Caesalpinia glabrata*, *C. spinosa* and *Lycianthes lycioides* only appeared at low elevations in the grazed locations, while other trees or shrubs, e.g. *Acacia macrantha*, increased

their presence in the seed bank towards higher elevations (see Appendix S1). Overall, species of the *Poaceae* family increased towards high altitudes under grazing conditions. Although we did not evaluate the mechanisms underlying this pattern, we suggest that larger biomass productivity of the more mesic high altitudes may induce cattle to spend more time grazing, and thus it may greatly affect the presence of species intolerant to grazing (see Ortega et al. 1997), while at lower altitudes plant species sheltered below shrubs may be able to avoid grazing and reproduce in order to refill the soil seed bank.

Nevertheless, although altitude increased richness and abundance in the total seed bank within a patch, we did not detect any effect of altitude on the persistent seed bank. Since the persistent seed bank is mainly composed of long-lasting seeds, processes that alter longevity of seeds may have had a large impact on composition and structure of the persistent seed bank. The expected positive effect of altitude on this compartment might have been overridden due to a decrease in seed longevity in the more benign environmental conditions (Cavieres & Arroyo 2001), as increasing soil moisture enhances fungal infection and predation of seeds (Funes et al. 2003).

The average distance to neighbouring patches had an unexpected positive effect on the abundance of both seed banks, i.e. the larger the distance to neighbouring patches the larger the seed abundance in the target patch. This could be due to secondary seed dispersal, via anemochory, as well as due to run-off events on the soil surface that may have swept away superficial seeds, these being the more isolated shrubs that collected more seeds. Patch size negatively affected seed abundance in the persistent but not in the total seed bank. This decline could be explained due to two non-exclusive mechanisms related to higher soil moisture beneath plant patches: on the one hand, soil moisture may have favoured fungal infection and the corresponding loss of viability; on the other hand, it may have promoted seed germination of the superficial seed bank, and thus fewer seeds would enter the persistent seed bank, causing seed bank depletion.

Changes in co-occurrence of both biotic and abiotic stressors seem to induce shifts in the balance in terms of dominance of the species richness between the total and the persistent seed banks. Under ungrazed conditions, the total seed bank became dominant both in richness and abundance at high altitudes (less stress), whereas under the more stressful conditions of lowland areas the total and the persistent seed banks showed similar seed abundance and number of species. The development of the persistent and total seed banks is largely influenced by seed production of the above-ground vegetation and seed longevity in the soil (Cavieres & Arroyo 2001; Ma et al. 2010a,b). Thus, the rainy climate of high altitudes may have induced seed

production (i.e. fertility component) (Ortega et al. 1997) together with a decrease in seed longevity (Cavieres & Arroyo 2001), and consequently, it may have increased the importance of the total seed bank. On the other hand, stressful climatic conditions may have limited the production of seed, but simultaneously, these dry conditions may have enhanced seed longevity, causing the persistent and the total seed banks to be very similar in richness (Ortega et al. 1997).

Balance between the dominance of above-ground and below-ground community compartments in terms of richness varied greatly along altitude and under different grazing conditions. In contrast to expectations, under the more stressful climate conditions of lowland locations, above-ground vegetation dominated in terms of species richness, at least in ungrazed conditions. Facilitation mechanisms may be acting on the above-ground plant community under stressful conditions, and thus positive interactions may have promoted plant species richness in this community compartment (Bertness & Callaway 1994). Nevertheless, in line with our hypothesis, grazing leveled off above-ground and below-ground species richness, which suggests that under high stress conditions the seed bank and the extant vegetation are closely related and that both compartments respond in a similar way. Our results support the 'spiral dynamics model' proposed in Caballero et al. (2008b) for semi-arid gypsum environments. Current theory suggests that the close relationship between above-ground and below-ground components will be maintained over time, and that small changes in one component will lead to dynamic shifts in the system over time.

In conclusion, our results show that although climate is the primary factor determining soil seed bank properties, its effect was profoundly modulated by grazing, as suggested by the existence of an important interaction between the two stressors. Not only seed abundance and richness but also the relative dominance of total and persistent seed banks were affected by both environmental stressors. Our results support that both the 'seed productivity hypothesis' and the 'seed longevity hypothesis' contributed to conform the soil seed bank, and even more we suggest that shifts in seed bank properties were mainly related to local conditions. Specifically, the seed productivity hypothesis may explain the dominance of the total seed bank at high altitudes, due to the improvement in plant performance under benign climatic conditions and the corresponding increase in seed input into the seed bank; at the same time, the seed longevity hypothesis may be responsible for the dominance in the persistent seed bank detected under the high stress conditions of the lowlands, where the total and persistent seed bank abundances converge to similar species number. Changes in these

patterns produced by grazing were probably linked to changes in the above-ground vegetation.

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Appendix S1. Mean seed densities per m² (3-cm deep) at each location in grazed vs undisturbed sites and at each of the four altitudes. Standard errors are indicated. GF, Growth form; LC, Life cycle; T, Tree; Sh, Shrub; Su, Succulent; F, Forb; G, Grass; P, Perennial; A, Annual.