Seed bank of desert annual plants along an aridity gradient in the southern Atacama coastal desert

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Keywords
Chile; Coastal desert; Ephemeral plants; Soil seed bank; Species co-existence

Nomenclature
Marticorena et al. (2001); Squeo et al. (2008)

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Abstract
Questions: What is the species composition and density of the seed bank in one of the most arid deserts of the world: the Atacama Desert? Do composition and density vary along the aridity gradient? Are they affected by the sampling season and soil nutrient content?

Location: Southern Atacama coastal desert, Chile.

Methods: Seed bank composition and density were estimated via direct counting of seeds extracted from soil samples collected in eight localities separated by 0.5°, between 26–30° S along the study geographic gradient. This sampling protocol was conducted at three different seasons: after seed set and before and after germination in the rainy season. We also estimated soil nutrient content and obtained local climatic data from the WorldClim database to perform an ordination of seed banks along the aridity gradient.

Results: The entire seed bank was composed of 89 species (38 endemic), including 51 annuals (20 endemic). Annuals represented 82.4% of all seeds counted. Exotic plants were represented by 11 species, including nine annuals, with higher seed densities towards the more mesic localities. Aridity was by far the main factor driving seed bank composition and seed density along the study gradient. Seed banks were similar among seasons across all localities. Soil nutrient content played an important, but secondary, role in species-specific relationships. In comparison to other ecosystems, the seed bank densities found in this study correspond to the lowest figures reported to date.

Conclusions: This study represents the first report on seed banks via direct counting for the southern part of the Atacama coastal desert. The level of aridity mainly determines annual plant communities in this desert, including exotic species. Their responses to the aridity level and soil nutrient content are species-specific, which allows for species co-existence under extreme abiotic conditions.

Introduction
In arid and semi-arid environments scarce precipitation exerts strong control on the composition of biotic communities, species life histories and their physiological traits (Noy-Meir 1973; Chesson et al. 2004). Rainfall is also highly variable within and between years, occurring in infrequent and discrete events with a large stochastic component and a pulse-driven nature (Noy-Meir 1973). Among desert biota, desert plants have two main strategies to cope with these conditions: drought tolerance, shown by most perennial species (e.g. succulents, shrubs); or drought evasion, characteristic of ephemeral plant species (Whitford 2002). By producing seeds (e.g. annuals) or perennial vegetative structures (e.g. geophytes), ephemeral species are able to remain dormant in the soil for several years until appropriate conditions for their development occur (Vidiella 1992; Ward 2009). In some deserts, such as the coastal southern Atacama Desert, annual species are an important component of the plant community biodiversity (Armesto et al. 1993), enduring successive years with limited or absent rainfall, as their seeds can remain dormant in the soil for several years. Seed banks result from a lack of germination that buffers against reproductive failure of cohorts of germinated seeds not surviving long enough to produce new seeds, and
Seed banks constitute the stored seeds buried in the soil for variable time periods (Thompson & Grime 1979). They are crucial to maintain the presence of annual species populations and communities (Pake & Venable 1996) and their genetic diversity (Honnay et al. 2008). Furthermore, seed banks are the basis of a diverse trophic chain (Inouye 1991; Gutiérrez 2001) and mediate the outcome of interactions among consumers (Veech 2000). Seeds enter the seed bank via seed rain or through physical- and animal-mediated dispersion (Louda 1989), and leave it via germination, secondary dispersal, seed predation, seed decay and parasite attack (Fenner 1985; Traba et al. 2006). Nutrient content, through its effects on plant productivity, also determines seed production and, in turn, seed banks (Nelson & Chew 1977; Gutiérrez & Whitford 1987; Davis et al. 2000). Seed banks act as the ‘memory’ of ecosystems, contributing to habitat re-colonization (King 2007), habitat restoration (Holmes 2002) and can be of major importance to cope with environmental changes produced by climate change (Ooi et al. 2009). However, they are also exposed to invasion processes with exotic plants; even when exotics are eradicated from above-ground vegetation, their seeds may remain in the seed bank (Vilá & Gimeno 2007).

Hence, seed banks have ecological and applied importance, and their study warrants deep insight into ecosystem functioning and prediction under different scenarios of environmental change.

Seed banks are highly variable in time and space (Reichman 1984; Gutiérrez et al. 2000; Gutiérrez & Meserve 2003; Facelli et al. 2005); however, the influence of large environmental gradients on seed banks has been less investigated, particularly in desert regions. Only three studies on seed banks of the Atacama coastal desert are available to date. In Bosque Fray Jorge National Park (31° S), at the southern tip of the Atacama Desert, Gutiérrez & Meserve (2003) found that seed abundance in the seed bank increased five- to ten-fold after the wet 1991–1992 El Niño–Southern Oscillation (ENSO) event, while Gutiérrez et al. (2000) reported that in Aucó, south of Fray Jorge (31.5° S), seed abundance increased three- to five-fold after the 1997–1998 ENSO event. Both reports correspond to single and geographically close field sites on the southern and less arid end of the Atacama Desert. Vidiella (1992) instead performed germination assays with soils collected from an aridity gradient encompassing a larger geographic area in the Atacama coastal desert (26–30° S), but this study presents an incomplete estimate of the seed bank since it was based on the germinable fraction. The need for a better understanding of seed bank composition and dynamics is of particular importance in the arid region of north Chile, since many local communities persist because productivity of the annual vegetation is the main source of forage for their livestock (Gutiérrez 2008).

The main objectives of this study were to determine the seed bank composition, seed density and their drivers in eight sites located along a latitudinal rainfall gradient in the southern Atacama coastal desert. We specifically aimed to answer the following questions: (1) what is the seed bank composition and density in the Atacama coastal desert; (2) do seed banks differ along the aridity gradient; (3) do they vary with sampling season; and (4) are they driven by soil nutrient content? We hypothesize that differences in species richness, composition and seed density of seed banks should occur along the north–south aridity gradient. Seed banks in the less arid (southern) end of the gradient should be more diverse and have more seeds because of higher resource availability for plant growth and reproduction. We also expected seasonal variation in the seed bank to be higher at the less arid end of the gradient since plant development and germination will be favoured by the higher amount of rainfall. Finally, we expected soil nutrient content to play a minor role in seed bank dynamics due to the overriding influence of rainfall scarcity in arid zones (Noy-Meir 1973).

**Methods**

**Study site**

The southern part of the Atacama Desert is located between 26–31° S. This desert is an arid environment with a Mediterranean climate characterized by a dry period (7–10 mo) and a single rainy season during the winter (di Castri & Hajek 1976). Between 80% and 90% of the annual rainfall occurs between Jun and Aug (Juliá et al. 2008). The north–south aridity gradient corresponds to a latitudinal gradient, where mean annual rainfall increases from 23 mm at the northern tip to 131 mm at the southern tip (Vidiella 1992; Table 1). The inter-annual rainfall variability is high, decreasing in a north–south direction (Díez et al. 1994; Vidiella 1992; Table 1). Aridity, as calculated with the De Martonne index (De Martonne 1926), also decreases in a north–south direction. Due to the lack of meteorological data for most of the localities within the study gradient, De Martonne indices were calculated with data retrieved from the WorldClim database (Hijmans et al. 2005). This area experiences drought for 2–5 yr (Vidiella 1992), followed by a noticeable increase in plant cover after winter rain events of at least 15 mm (Vidiella & Armesto 1989). Even though rainfall is scarce, this desert...
has permanently high humidity, which increases in the winter months and is evident as frequent cloud cover and high relative humidity (di Castri & Hajek 1976). In 2009, when this study was conducted, weather stations at Coquimbo (30° S) and Romeral (29°45’ S) reported a dry year, with 56.9 and 47.9 mm rainfall, respectively (data available at http://www.ceazamet.cl), figures that are below the average values for these stations (Coquimbo 2006–2009 average: 60.4 mm, Romeral 2006–2009 average: 52.9 mm). The previous year, 2008, was a wet year, with Coquimbo and Romeral receiving 103.3 and 85.6 mm rainfall, respectively. There are no available weather stations in the northernmost locations.

In this geographically large aridity gradient we selected eight coastal localities (Fig. 1), all of them within 1 km of the coastline, and all in flat marine terraces with gentle slopes, sand-clayish soils, derived from fossil dunes, with high drainage, deposited over a layer of calcium carbonate rock. These localities from north to south are: Rodillo (26°40’ S), Cisne (27°15’ S), Pajonales (27°45’ S), Carrizal

<table>
<thead>
<tr>
<th>Locality</th>
<th>Latitude</th>
<th>De Martonne AI</th>
<th>Closest localities with weather data (Almeyda 1950)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rodillo</td>
<td>26°40’</td>
<td>0.1259</td>
<td>Chaharal 26°21’ 23 87 18</td>
</tr>
<tr>
<td>Cisne</td>
<td>27°15’</td>
<td>0.1250</td>
<td>Caldera 27°03’ 24 94 58</td>
</tr>
<tr>
<td>Pajonales</td>
<td>27°45’</td>
<td>0.1168</td>
<td>Copiapó 27°21’ 25 94 74</td>
</tr>
<tr>
<td>Carrizal</td>
<td>28°00’</td>
<td>0.1299</td>
<td>–</td>
</tr>
<tr>
<td>Bronces</td>
<td>28°30’</td>
<td>0.1643</td>
<td>Vallenar 28°35’ 55 73 26</td>
</tr>
<tr>
<td>Choros</td>
<td>29°15’</td>
<td>0.2482</td>
<td>–</td>
</tr>
<tr>
<td>Romeral</td>
<td>29°45’</td>
<td>0.3175</td>
<td>La Serena 29°54’ 124 65 140</td>
</tr>
<tr>
<td>Lagunillas</td>
<td>30°6’</td>
<td>0.3643</td>
<td>Lagunillas 30°6’ 131 51 23</td>
</tr>
</tbody>
</table>

Fig. 1. Location of the study localities in the aridity gradient in the southern Atacama coastal desert.
(28°S), Bronces (28°30’S), Choros (29°15’), Romeral (29°45’ S) and Lagunillas (30°6’ S). All localities experience moderate levels of grazing during wet years; however, the southernmost localities that have more mesic conditions experience grazing more frequently. Within each locality we installed four randomly selected 50 × 20 m plots, separated by at least 200 m from each other. Plant communities in all localities are composed of shrubs, geophytes, perennial and annual herbs. Plant cover, particularly of annuals, increases towards the southern part of the gradient, as does exotic species density and richness (Armesto et al. 1993).

Sampling and determination of seed banks

A total of 20 soil samples per plot were randomly collected in three sampling seasons: Dec 2008, to collect seed banks after seed set and dispersal at the end of the growing season; Apr 2009, to collect the remnant seed bank after germination (Gutiérrez & Meserve 2003). We used a corer of 3-cm diameter and 5-cm depth (35.4 cm³) because previous sampling demonstrated that <10% of the seeds within the seed bank are located below 4-cm depth (Gutiérrez & Meserve 2003). Moreover, Vidiella & Armesto (1989) showed that in Lagunillas the highest proportion of viable seeds was located within the first 3–5 cm of soil. Seed determination was conducted at the Universidad de La Serena, following the protocol detailed in Gutiérrez & Meserve (2003). Seeds were initially separated from soil particles using sieving meshes (mesh size 0.50–3.35 mm), and the smallest seeds were extracted by flotation. Extracted seeds via flotation were dried, identified to species level and directly counted using a reference scope (Nikon SMZ-10), by comparison with a reference seeds database (Leps & Smilauer 2003). Seeds of annual species amounted to 82.4% of the seed bank, ranging from 52.1% at Pajonales to 96.8% at INIA at La Platina-Santiago following the guidelines compiled in Sadzawka et al. (2006).

Data analysis

To compare total and annual species richness and seed density among localities and seasons we performed a repeated measures ANOVA (rmANOVA), with season as the within subject factor, using the software STATISTICA (v 7; Statsoft, Tulsa, OK, US). Tukey post-hoc comparisons were performed to determine differences at P < 0.05. We tested the influence of environmental variables on seed bank composition among localities and seasons using canonical correspondence analysis (CCA) in CANOCO (ter Braak & Smilauer 2003). The CCA included only 26 annual species, those that had a density > 100 seed m⁻² in at least one of the sampled localities. We included soil N, P and K content and mean annual rainfall as environmental variables, while season was included as a dummy variable (Leps & Smilauer 2003). Rainfall data were obtained from the WorldClim database (Hijmans et al. 2005) due to the lack of meteorological data for most of the localities under study. De Martonne aridity indices, calculated based on WorldClim data (Hijmans et al. 2005), were not included in this analysis because they were highly correlated with rainfall data readily available from the WorldClim database (r = 0.9988, r² = 0.9972, P < 0.0001). The influence of environmental variables on species responses and sample vectors provided by the CCA was further visualized with an ordination diagram displaying the vectors. Vector position indicates the relative influence and direction of such environmental variables on species responses (Leps & Smilauer 2003). Finally, we used a generalized additive model to fit the number of species across samples to the variation contained within the first two canonical axes of the CCA ordination (Leps & Smilauer 2003).

Results

Seed bank composition

Overall, a total of 89 plant species were found in the seed bank (Appendix S1), 51 (57.3%) annual herbs, 17 (19.1%) shrubs, 15 (16.9%) perennial herbs, two (2.2%) parasitic plants and four (4.5%) geophytes. In addition, 38 (42.7%) of them were endemic to Chile, with 20 annual endemics (39.2% of all annuals), nine shrubs (52.9% of all shrubs), two geophytes (50% of the geophytes) and seven perennial herbs (46.7% of all perennial herbs). We found 11 (12.4%) exotic species: nine annuals (17.6% of all annuals), one perennial herb (6.7% of the perennial herbs) and one shrub (5.9% of all shrubs).

Seeds of annual species amounted to 82.4% of the seed bank, ranging from 52.1% at Pajonales to 96.8% at...
Romeral. The most abundant native annuals were Cistanthe coquimbensis and Eryngium coquimbamum, while the most abundant exotic annuals were Erodium cicutarium and Erodium moschatum (Table 2). Seeds of shrubs were the second most abundant in all localities, with the exception of Pajonales and Choros, where they were replaced by perennial herbs (Table 2).

Seed bank density

The total number of species and of annual species in the seed bank was significantly different among localities (F7,24 = 27.94, F7,24 = 33.14; respectively, P < 0.0001), but did not show seasonal differences (F2,48 = 0.087; P = 0.91; F2,48 = 0.48; P = 0.62, respectively). The localities with the highest number of total and of annual species were Choros and Romeral, while Rodillo had the lowest numbers (Fig. 2a). Significant differences in total seed density (i.e. all life forms included) and annual seed density were found among localities (F7,24 = 15.18; F7,24 = 14.69, respectively, P < 0.0001), but there were no differences among seasons (F2,48 = 0.82, F2,48 = 0.68; P = 0.44, P = 0.51, respectively). Romeral had the highest total and annual seed densities, while the Pajonales seed bank had the lowest values (Fig. 2b). Romeral had the highest seed density and species richness of exotic annuals, with Erodium spp. accounting for much (ca. 12%) of the total seed density (Table 2).

Relationship with environmental variables

The first four axis of the CCA retained ca. 50% of the total variance and ca. 100% of the species–environment variance relationship. All environmental variables were significant within the canonical model, but only the continuous variables (i.e. mean annual rainfall, N, P, K) showed high correlations with canonical axes (Table 3). The main environmental variable determining the composition of seed banks was mean rainfall, as it presented the highest correlation with the first axis of the CCA (Table 3). Along this axis, there were three distinct groups of seed banks (Appendix S2): (1) the northernmost arid localities, Rodillo, Cisne and Pajonales; (2) the intermediate localities within the aridity gradient, Carrizal, Bronces and Choros; and (3) the southernmost rainier localities, Romeral and Lagunillas. The second CCA axis was related to soil nutrient concentration (i.e. K and N; Table 3) and, together with the first axis, discriminated the study localities even further, especially the Romeral–Lagunillas group that presented contrasting nutrient concentrations (Table 4). Northern localities of Rodillo, Cisne, Pajonales and Carrizal were distributed along a gradient of K concentration. Romeral was clearly different from the other localities with the highest soil N and K concentrations (Table 4), coupled with the presence in its seed bank of the three exotic annuals included in the ordination analysis: Erodium spp., Galium aparine and Scirpus mariqueter. The southernmost locality, Lagunillas, was also separated from the other localities by the presence of native species such as Adesmia tenella, Plantago hispida and Cistanthe sp. The increase in species richness was first related to the increase in mean annual rainfall, and second to an increase in soil nutrient content, especially K and N (Appendix S2). Seasonal variation explained a small proportion of variance within the CCA model and poor correlations with canonical axes (Table 3).

Discussion

This study represents the first report on seed bank composition and density along the southern Atacama coastal desert. It was based on direct tallying of seeds including both transient and persistent seed banks (Thompson & Grime 1979). Overall, aridity exerted strong control on seed banks, with southern less arid localities having significantly higher species richness and seed density than northernmost localities. Seeds of annual plants represented 82.4% of all seeds extracted, which is higher than previously reported in the literature for deserts in general (ca. 60%), but in accordance with several studies showing that annual plants are the most abundant life form in desert seed banks (e.g. Gutiérrez & Meserve 2003; Stenberg et al. 2003; Cano-Salgado et al. 2012). We also showed that ca. 50% of all species found were annuals, which supports previous reports on plant species richness from the Atacama Desert (Armesto et al. 1993; Gutiérrez 2008), which determined that annual plants are the life form with the highest species richness. Notwithstanding this large proportion of annual plants, we did not find any seasonal differences in species richness and density of the seed bank at any locality of the gradient, similar to Gutiérrez & Meserve (2003) during a 6-yr study at Bosque Fray Jorge National Park (30° S). In our study, the absence of a seasonal effect could be caused by the low germination during the growing season of 2009 (D.A. Sotomayor, unpubl. data) because of the paucity of rainfall events that year (ca. 50 mm total annual rainfall). The lack of significant germination after a single growing season and the large proportion of annual plants highlight the ecological importance of seed banks for this desert. Further studies on the longevity of seeds in the soil are thus needed to better understand the temporal dynamics of the seed banks in the Atacama coastal desert.

The seed densities reported here for the drier localities (Rodillo, Pajonales, Carrizal and Bronces) are among the lowest reported for deserts to date (Fig. 3). This is probably
Table 2. Seed mass and density (±1 SE) of the ten most abundant species within the seed banks of the study localities in the southern Atacama coastal desert. All ten species are annuals.

<table>
<thead>
<tr>
<th>Species</th>
<th>Density (seed·m⁻²)</th>
<th>Weight (mg)</th>
<th>ROD</th>
<th>CIS</th>
<th>PAJ</th>
<th>CAR</th>
<th>BRO</th>
<th>CHO</th>
<th>ROM</th>
<th>LAG</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Bromus berterianus</strong></td>
<td>2.13 (0.28)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>109.3 (16.1)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>958.8 (134.9)</td>
<td>0.0 (0.0)</td>
<td></td>
</tr>
<tr>
<td><strong>Cistanthe coquimbensis</strong></td>
<td>0.23 (0.01)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>526.4 (142.7)</td>
<td>3972.7 (211.6)</td>
<td>1022.3 (166.4)</td>
<td>0.0 (0.0)</td>
<td></td>
</tr>
<tr>
<td><strong>Cistanthe longiscapa</strong></td>
<td>0.07 (0.00)</td>
<td>7.1 (7.1)</td>
<td>360.7 (96.0)</td>
<td>310.2 (52.1)</td>
<td>334.9 (43.3)</td>
<td>1149.2 (106.7)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td></td>
</tr>
<tr>
<td><strong>Crassula closiana</strong></td>
<td>15.3 (8.9)</td>
<td>16.5 (10.8)</td>
<td>3.5 (3.5)</td>
<td>3.5 (2.5)</td>
<td>5.9 (3.2)</td>
<td>4.7 (3.6)</td>
<td>850.7 (104.5)</td>
<td>5.9 (3.7)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Erodium spp.</strong>*</td>
<td>3.30 (0.19)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>1.2 (1.2)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>1247.9 (125.2)</td>
<td>0.0 (0.0)</td>
<td></td>
</tr>
<tr>
<td><strong>Eryngium coquimbanum</strong></td>
<td>0.15 (0.01)</td>
<td>0.0 (0.0)</td>
<td>2.4 (1.6)</td>
<td>0.0 (0.0)</td>
<td>4.7 (4.7)</td>
<td>4.7 (3.2)</td>
<td>3872.8 (750.5)</td>
<td>477.1 (74.4)</td>
<td>0.0 (0.0)</td>
<td></td>
</tr>
<tr>
<td><strong>Helieum urmenatae</strong></td>
<td>0.10 (0.01)</td>
<td>3.5 (2.5)</td>
<td>22.3 (9.3)</td>
<td>55.2 (15.3)</td>
<td>532.3 (267.6)</td>
<td>298.5 (154.6)</td>
<td>278.5 (133.2)</td>
<td>349.0 (76.1)</td>
<td>2.4 (1.6)</td>
<td></td>
</tr>
<tr>
<td><strong>Oenothera coquimbensis</strong></td>
<td>0.10 (0.01)</td>
<td>1.2 (1.2)</td>
<td>1196.2 (358.9)</td>
<td>8.2 (5.9)</td>
<td>142.2 (58.0)</td>
<td>0.0 (0.0)</td>
<td>1.2 (1.2)</td>
<td>1.2 (1.2)</td>
<td>0.0 (0.0)</td>
<td></td>
</tr>
<tr>
<td><strong>Plantago hispifula</strong></td>
<td>2.17 (0.08)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>7.1 (7.1)</td>
<td>15.3 (9.4)</td>
<td>99.9 (81.1)</td>
<td>2.4 (1.6)</td>
<td>780.2 (217.8)</td>
<td></td>
</tr>
<tr>
<td><strong>Quichamalium chiliense</strong></td>
<td>0.20 (0.02)</td>
<td>867.2 (165.0)</td>
<td>824.9 (132.3)</td>
<td>7.1 (3.7)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.0)</td>
<td></td>
</tr>
</tbody>
</table>

*Total annuals: 1155.0 (163.2) 2936.3 (444.4) 849.5 (39.1) 1364.2 (284.5) 1947.0 (169.5) 5521.3 (614.9) 10516.3 (445.2) 2250.1 (315.3)*

*Total shrubs: 447.7 (51.0) 304.3 (73.8) 152.8 (30.9) 508.8 (105.6) 200.9 (20.5) 329.0 (37.6) 84.6 (29.8) 980.0 (241.5)*

*Total geophytes: 0.0 (0.0) 0.0 (0.0) 0.0 (0.0) 34.1 (17.4) 0.0 (0.0) 16.5 (6.2) 12.9 (6.4) 0.0 (0.0)*

*Total parasites: 0.0 (0.0) 7.1 (4.8) 17.6 (8.2) 34.1 (18.2) 18.8 (7.2) 7.1 (2.7) 8.2 (2.7) 2.4 (1.6)*

*Total perennials: 14.1 (6.9) 232.7 (40.9) 412.4 (63.5) 255.0 (34.7) 1387.1 (46.7) 628.6 (67.4) 42.3 (8.3) 670.9 (158.1)*

*Undetermined: 204.5 (52.4) 77.6 (25.7) 250.9 (80.7) 264.8 (44.7) 124.6 (20.6) 179.8 (31.5) 193.9 (11.4) 59.9 (23.5)*

*TOTAL: 1821.3 (133.3) 357.9 (526.5) 1632.1 (76.4) 2422.9 (321.2) 2429.9 (173.7) 6682.2 (591.3) 10858.2 (444.3) 3963.3 (459.7)*

*Denotes exotic species.
due to the fact that the studied area is one of the most arid environments in the world. In contrast, seed density of annuals at Romeral, one of the mildest environments in our gradient, was relatively high (>10,000 seed m\(^{-2}\)) compared to previous reports from South American deserts in non-ENSO years (e.g. Ohga 1992; Gutiérrez & Meserve 2003). This could be related to the higher grazing disturbance and higher resource availability at Romeral compared to the other localities in our gradient that also favoured the presence of exotic annual species (Davis et al. 2000). In general, our results showed that the size of seed banks of the southern part of the Atacama coastal desert are within the range reported for other arid environments worldwide, although they belong to the most arid region, and lower figures available in the literature. These figures are also of major importance for the management and conservation of natural resources, and showcase the importance of conservation in this desert, in particular given the high proportion of endemism and the current threats to biodiversity in the Atacama Desert.

Fig. 2. Seed banks along an aridity gradient in the southern Atacama coastal desert. (a) Total (black bars) and annual (white bars) species richness (± 1 SE). (b) Total seed density and annual species seed density (± 1 SE). Different letters indicate significant differences among localities (Tukey test, \(P < 0.05\)).
In terms of seed bank composition, we found a higher proportion of exotics towards the southern more mesic part of the gradient, with Romeral having the highest exotic species richness, as well as the largest exotic species seed density. The higher proportion of exotics towards the southern part of the gradient supports the findings of

Table 3. Results of CCA performed on the seed banks present along the southern Atacama coastal desert. Significant values are in bold.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Lambda A</th>
<th>P-value</th>
<th>F</th>
<th>Correlations</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Axis 1</td>
<td>Axis 2</td>
</tr>
<tr>
<td>Rainfall (PREC)</td>
<td>0.65</td>
<td>0.001</td>
<td>27.04</td>
<td>-0.9720</td>
</tr>
<tr>
<td>Phosphorus (P)</td>
<td>0.35</td>
<td>0.001</td>
<td>17.00</td>
<td>-0.0534</td>
</tr>
<tr>
<td>Potassium (K)</td>
<td>0.29</td>
<td>0.001</td>
<td>16.48</td>
<td>-0.2933</td>
</tr>
<tr>
<td>Nitrogen (N)</td>
<td>0.14</td>
<td>0.001</td>
<td>8.79</td>
<td>-0.6401</td>
</tr>
<tr>
<td>Season 2 (STA2)</td>
<td>0.01</td>
<td>0.001</td>
<td>0.55</td>
<td>0.0014</td>
</tr>
<tr>
<td>Season 1 (STA1)</td>
<td>0.01</td>
<td>0.001</td>
<td>0.41</td>
<td>0.0145</td>
</tr>
<tr>
<td>Season 3 (STA3)</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>-0.0160</td>
</tr>
</tbody>
</table>

Table 4. Mean values of soil nutrient and chemical characteristics (± 1 SE) at the study localities in the southern Atacama coastal desert.

<table>
<thead>
<tr>
<th>Locality</th>
<th>pH</th>
<th>Organic matter (%)</th>
<th>Electrical conductivity (mmho-cm⁻¹)</th>
<th>N (ppm)</th>
<th>P (ppm)</th>
<th>K (ppm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rodillo</td>
<td>8.9 (0.1)</td>
<td>0.2 (0.0)</td>
<td>6.7 (1.8)</td>
<td>1.3 (0.3)</td>
<td>9.3 (1.0)</td>
<td>70.3 (8.2)</td>
</tr>
<tr>
<td>Cisne</td>
<td>9 (0.1)</td>
<td>0.2 (0.0)</td>
<td>6.3 (0.9)</td>
<td>1.3 (0.3)</td>
<td>6 (0.7)</td>
<td>163.3 (27.4)</td>
</tr>
<tr>
<td>Pajonales</td>
<td>8.2 (0.2)</td>
<td>0.5 (0.0)</td>
<td>5.2 (0.3)</td>
<td>1.3 (0.3)</td>
<td>8.8 (0.9)</td>
<td>230 (7.9)</td>
</tr>
<tr>
<td>Carrizal</td>
<td>9.4 (0.1)</td>
<td>0.5 (0.1)</td>
<td>6.7 (1.6)</td>
<td>1.3 (0.3)</td>
<td>13 (4.1)</td>
<td>261.5 (7.0)</td>
</tr>
<tr>
<td>Bronces</td>
<td>9.7 (0.1)</td>
<td>0.5 (0.1)</td>
<td>11.1 (1.0)</td>
<td>1.3 (0.3)</td>
<td>34.3 (7.6)</td>
<td>76.8 (4.3)</td>
</tr>
<tr>
<td>Choros</td>
<td>9.2 (0.1)</td>
<td>0.4 (0.1)</td>
<td>7.3 (1.6)</td>
<td>2.5 (1.5)</td>
<td>26.8 (3.5)</td>
<td>95 (11.3)</td>
</tr>
<tr>
<td>Romeral</td>
<td>7 (0.1)</td>
<td>1.3 (0.1)</td>
<td>1.5 (0.2)</td>
<td>6 (0.0)</td>
<td>10 (0.4)</td>
<td>293 (15.7)</td>
</tr>
<tr>
<td>Lagunillas</td>
<td>8.3 (0.1)</td>
<td>0.5 (0.1)</td>
<td>1.9 (0.2)</td>
<td>1.3 (0.3)</td>
<td>10.3 (1.7)</td>
<td>61.8 (7.8)</td>
</tr>
</tbody>
</table>

Fig. 3. Seed bank abundance based on direct counting of seeds for different deserts in the world in relation to their average annual rainfall. Empty circles correspond to values from this study; filled circles are values from: Abella et al. (2013) (2; Mojave Desert, US), Guo et al. (1999) (3; Great Basin, Mojave Desert, Sonoran Desert and Chihuahuan Desert, US), Gutiérrez & Meserve (2003) (4; north-central desert, Chile), Gutiérrez et al. (2000) (5; north-central desert, Chile), López (2003) (6; Prepuna Desert, Bolivia), Marone & Horno (1997) (7; Monte Desert, Argentina), Nelson & Chew (1977) (8; Sonoran Desert, US), Ohga (1992) (9; coastal desert, Peru), and Pake & Venable (1996) (10; Sonoran Desert, US).

\[ y = 47.89x + 3084.10 \]
\[ r^2 = 0.2782, P = 0.0019 \]
Vidiella (1992), Armesto et al. (1993) and Gutiérrez (2008). This pattern might be explained by both the higher water availability that allows exotics to renew their presence with a higher frequency in the seed bank, and the larger impacts of human activities. Patterns of this type have been found elsewhere for above-ground vegetation and are related to invasibility due to higher amount of available resources and scale-dependent processes (Tilman 1997; Davis et al. 2000; Kreuling et al. 2008). Increased native species richness may counter the establishment of invasive exotics, but this might depend on whether vacant niches, not occupied by native species, are available for colonization by new and exotic species (Tilman 1997). Furthermore, aridity reduces the susceptibility to invasion while large rainfall events increases it (Kreuling et al. 2008). It can be argued that at Romeral there were vacant niches that have been filled by exotic species, whereas towards the northern part of the gradient, aridity acted as a limiting factor for the establishment of exotics despite the fact that vacant niches might be available. Scarce rainfall may therefore protect arid environments from substantial invasion by limiting the establishment of exotic species.

We hypothesized that the composition, diversity and seed density of seed banks in the southern Atacama coastal desert would vary along the aridity gradient in the studied area. Our results showed that rainfall was the dominant factor controlling biota, seed banks in particular, as has been postulated by several authors (e.g. Noy-Meir 1973; Chesson et al. 2004; Ward 2009). Indeed, in our study the diversity and abundance of species in the seed bank decreased towards the north, where rainfall is more limiting and unpredictable. However, this trend might be species-specific since seed banks of *Quinchamalium chilense* were particularly large at Rodillo and Cisne, the driest northernmost localities. These species-specific effects might not only be governed by large physical gradients (e.g. rainfall, soil nutrients), but might also be associated with biotic interactions, such as the host–parasite relations of the parasitic *Q. chilense*. Conversely, this trend might be related to specific climatic conditions, such as large rainfall ENSO-related events that replenished their seed banks in the past (Holmgren et al. 2001; Squeo et al. 2006).

Rainfall was highly correlated with the first axis of our multivariate analysis, while the second axis can be attributed to soil nutrient content, mainly K and N. The relative importance of soil nutrients has been described by Gutiérrez & Whitford (1987) and Gutiérrez (1992). They reported N as the second most important factor for plant development after water in arid environments. In our study, the range of soil N content values along the gradient was small in comparison to the range of K content values, which suggests that under N limiting conditions, K might assume a dominant role in the density and composition of the seed bank when water availability is less limiting. Moreover, the relatively large seed bank at Choros (even larger than the southernmost Lagunillas) was probably due to combined effects of larger rainfall and higher P and K content. Certainly, different species displayed different relationships with their environment, which may promote species co-existence through spatial niche partitioning (Chesson 2000; Chesson et al. 2004). The storage effect theory proposes that co-existence in highly variable environmental conditions, such as those occurring in deserts, would be possible when species have differences in germination and resource consumption rates and a buffered population growth evidenced in seed banks (Chesson et al. 2004), both encountered in this study. Further testing of this theory warrants an improved understanding of the mechanisms that maintain biodiversity in this desert and in extreme conditions in general.

In conclusion, the results of this study highlight the importance of water scarcity for plant community development, but also provide insights into the mechanisms governing species co-existence in this desert. Future studies should focus on testing more specifically for species co-existence mechanisms and also on designing experiments to test the potential effects of global warming on the composition and abundance of plants of the Atacama Desert. Conservation initiatives should address the importance of soils to preserve biological diversity and provide a deeper understanding on how aridity limits the presence of exotic plants.

**Acknowledgements**

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**References**


**Supporting Information**

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

**Appendix S1.** Seed density (±1 SE) of all the species found within the seed banks of the studied localities in the southern Atacama coastal desert.

**Appendix S2.** Multivariate analysis of seed banks along an aridity gradient in the southern Atacama coastal desert.