Extreme climatic events change the dynamics and invasibility of semi-arid annual plant communities

Abstract

Milagros A. Jiménez,^{1,2,3*} Fabian M. Jaksic,¹ Juan J. Armesto,^{1,2,4} Aurora Gaxiola,^{1,2,4} Peter L. Meserve,⁵ Douglas A. Kelt⁶ and Julio R. Gutiérrez^{2,7} Extreme climatic events represent disturbances that change the availability of resources. We studied their effects on annual plant assemblages in a semi-arid ecosystem in north-central Chile. We analysed 130 years of precipitation data using generalised extreme-value distribution to determine extreme events, and multivariate techniques to analyse 20 years of plant cover data of 34 native and 11 exotic species. Extreme drought resets the dynamics of the system and renders it susceptible to invasion. On the other hand, by favouring native annuals, moderately wet events change species composition and allow the community to be resilient to extreme drought. The probability of extreme drought has doubled over the last 50 years. Therefore, investigations on the interaction of climate change and biological invasions are relevant to determine the potential for future effects on the dynamics of semi-arid annual plant communities.

Keywords

Disturbance, drought, El Niño Southern Oscillation, exotic, long-term studies, native, precipitation.

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INTRODUCTION

Natural ecosystems are being altered in numerous ways by global change processes (Vitousek *et al.* 1997; Smith *et al.* 2009). Changes in land use, atmospheric CO₂ concentration, nitrogen deposition, climate change and biotic exchange have been identified as the major drivers of global change (Sala *et al.* 2000). The relevance of extreme climatic events (ECEs) for biodiversity has not been fully explored presumably because data for unusual or ECEs generally are rare, whereas average environmental values are more often available in existing databases (Jentsch *et al.* 2007). However, understanding the effects of abrupt climate change and shifts in disturbance regimes is critical in light of increased probability of exceeding transitional thresholds between alternative stable states in ecosystems (Scheffer *et al.* 2009).

An ECE is an episode or occasion in which a statistically rare or unusual climatic period alters ecosystem structure and/or function well outside the bounds of what is considered typical or normal variability (Smith 2011a). Because these events are historically unprecedented (in duration and intensity) or extremely rare, most species from these ecosystems are unlikely to have evolved adaptive responses to them (Holt 2008). Thus, changes in the frequency and/or intensity of ECEs may have profound consequences for natural ecosystems (Easterling *et al.* 2000). Such alterations may be driven by changes in species abundances, loss of key species, and/or invasion by new species with different functional traits. Likely outcomes of ECEs include periods of prolonged recovery, significant hysteresis and/or persistent state changes (Smith 2011a).

Extreme drought and temperature variables have often been correlated with shifts in species composition, diversity, and functional attributes in natural ecosystems as divergent as temperate grasslands and moist evergreen tropical forests. For instance, two drought events (in 1995 and 2003) affected the community composition of temperate grassland in Wytham (UK), but vegetation recovered completely 1 to 3 years after each drought event (Grime et al. 2008). In contrast, persistent extreme drought caused high plant mortality that reset plant community dynamics and induced 9 years of oscillations in a North American grassland community (Haddad et al. 2002). Major shifts in the boundary between pine forest and juniper woodland in the 1950s were associated with extreme drought in northern New Mexico that remain today (Allen & Breshears 1998). In temperate meadows from the southern Alps, an extreme drought caused changes in species composition that persisted 12 years later (Stampfli & Zeiter 2004). Recently, stochasticity of succession (as measured by the synchrony in the development of species composition of twin plots) was strongly altered by the extreme warm, dry summer of 2003 and diverged since then (Kreyling et al. 2011). Thus, the prevalence of these impacts is highly variable in different ecosystems (Parmesan et al. 2000; Smith 2011b).

In part, differences among studies may be caused by speciesand/or system-specific attributes; thus, we need to understand effects of ECEs in multiple ecosystems (Smith 2011a). For instance, one general prediction is that intensification of extreme rainfall regimes will reduce the frequency (and duration) of stressful periods for plants and soil processes in xeric ecosystems, whereas mesic sites may be

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subject to more frequent and longer periods of soil and plant water stress (Knapp et al. 2008). Extreme wet precipitation events greatly modify the structure and composition of arid and semi-arid ecosystems (Gutiérrez & Meserve 2003; Holmgren et al. 2006 and references therein; Miriti et al. 2007; Thibault & Brown 2008; Previtali et al. 2010). In arid and semi-arid regions of South America, strong rain pulses trigger biotic processes such as massive seed germination (Vidiella et al. 1999), plant growth (Gutiérrez et al. 2010), rodent outbreaks (Lima et al. 1999; Previtali et al. 2009) and vertebrate predator responses (Jaksic 2001; Stenseth et al. 2002; Holmgren et al. 2006). The biota of such ecosystems is adapted to low water availability, and consequently extreme droughts have seldom been considered as drivers of community change. However, at a similar community in the Colorado Desert, massive die-offs of most of the common perennial species have been attributed to severe droughts (Miriti et al. 2007).

Extreme droughts may have also strong implications for community composition, as they can alter the competitive balance between species and susceptibility to invasions (invasibility) (Kreyling et al. 2008; Mills et al. 2009). Under the 'fluctuating resources model' (Davis et al. 2000) a community becomes more susceptible to invasion when resources are released by the death of resident plants and/or when they increase faster than they can be sequestered (Davis et al. 2000). According to this model, if individuals are killed by disturbance, more resources may be available and/or a greater number of sites would be open for colonisation, presumably increasing the invasibility of the community (Davis et al. 2000; Clark & Johnston 2011). Few studies have considered the potential facilitative effect of extreme droughts by enhancing invasibility in semi-arid environments; further, many have either confounded drought effects with other explicit sources of variation, or lacked temporal continuity and/or spatial resolution in their design (Stampfli & Zeiter 2004).

The extent to which community changes are coupled with disturbances such as extreme droughts is not well-known. Key issues are identifying what comprises 'extreme' climate conditions, and clearly attributing ecological responses to the period of climate extremity (Smith 2011a). In addition, our understanding of modifications in the water balance of ecosystems and the resilience of communities in response to ECEs remains incomplete and requires more insight from long-term studies. We hypothesise that ECEs will change the composition of the annual herb community and will provide windows of opportunity for invasion by exotic annual plants. The semi-arid zone of north-central Chile is an excellent natural laboratory to test this hypothesis because a longterm ecological investigation has been in progress here since 1989. Rainfall dramatically affects the dynamics of annual plants in this region; cover of annual plants ranged from 0% during La Niña years to 80-86% during El Niño Southern Oscillation (ENSO) rainy years (Gutiérrez et al. 2010). Small mammal and vertebrate predator densities and biomass increase 2-3 orders of magnitude during ENSO years (Jaksic et al. 1997; Gutiérrez et al. 2004, 2010). We apply extreme-value distribution to determine the magnitude of extreme precipitation events and how their frequency and probability of occurrence has changed in the last 50 years. We then report how extreme rainfall events have changed the dynamics and invasibility of the annual plant community, by causing shifts in abundance and composition of native vs. exotic species and providing a window of opportunity for the spread and dominance of exotic plant species.

METHODS

Study site

Our study area is in Bosque Fray Jorge National Park (FJ henceforth), located in north-central Chile (71°40′W, 30°38′°S, c. 80°m elevation). The climate is semi-arid Mediterranean with 90% of the 131 mm of mean annual precipitation falling between May and September. Mean monthly temperatures range from 24 °C (January) to 4 °C (July) (Gutiérrez *et al.* 2004).

Our study area is characterised by a thorn-scrub shrubland, composed mainly of perennial shrubs (e.g. *Porlieria chilensis, Proustia cuneifolia* and *Adesmia bedwellii*) and an assemblage of ephemeral plants (geophytes and annuals) during the winter–spring growing season (Gutiérrez *et al.* 2004). A long-term study site was established here in 1989 and the associated experimental design has been maintained for more than 20 years, making this the longest such study in temperate South America (Gutiérrez *et al.* 2010).

The ENSO phenomenon has a direct influence on the biota of FJ (Gutiérrez & Meserve 2003; Previtali *et al.* 2009). During the study span (1989–2007), our site experienced five El Niño/high rainfall events (1991–1992, 1997, and 2000–2002, 2004 and 2006), with two to three times normal rainfall (Gutiérrez *et al.* 2010). Additionally, there were two La Niña events, one lower than normal (1995) and one particularly strong (1998), with the lowest annual rainfall (11 mm) in over two decades (Gutiérrez *et al.* 2010). Consequently, this site offers a unique opportunity to assess the effects of ECEs on the dynamics of semi-arid ecosystems.

Data collection

Since 1989, we have measured ephemeral plant cover during the peak of the growing season each year (September or October), using the point-intercept method on 10 random 1.5-m long segments subdivided into 30 points (5-cm intervals) along four 75-m permanent transects in 75×75 m plots. In this study, we used data only from four control plots within a larger experimental manipulation; these had low (1-m high) fencing with 2.5-cm mesh, buried c. 40 cm. Openings (5 cm diameter) in the fencing provided access to all rodent species (Gutiérrez et al. 1993, 2010). The total number of points per plot was 1200 and we utilised a total of 72 samples (4 plots \times 18 years). The cover of each annual species was estimated as the proportion of points in which they were recorded. We used these data to analyse changes in species composition. Total herbaceous cover ranged from 10.8 to 114.4%. We used cover data of 45 annual herb species (33 native and 11 exotic) from each of the four plots. We excluded species that were present in < 5% of all the plots from all years (< 3/72 samples) for species composition analysis. We excluded data from 1998 as the annual herbaceous cover that year was 0% but included all species for analysing changes in species richness.

Data analysis

Unusual or extreme events can be determined by assessing extraordinary deviations from the median of probability distributions (Jentsch *et al.* 2007). The amount of rainfall representing a statistically extreme precipitation event was determined by analysing precipitation data since 1867 for La Serena, a city located *c.* 100 km to the north of our site. The correlation coefficient between precipitation data from the last 20 years in our study site and the precipitation in La Serena for this period was 0.91. We were interested in determining a minimum extreme value of precipitation, which represented an extreme drought. To examine how extreme precipitation events have changed in La Serena, we calculated the 5th and 95th percentiles of precipitation bounded by 0 mm, with a 30-year window by using extreme-value distribution (Katz *et al.* 2005). We also used these data to determine how the probability of an extreme minimum precipitation event (5th percentile determined by extreme-value distribution) had changed during this period. We calculated the cumulative distribution function that corresponded to this value with a moving-average analysis and a 30-year window, using a generalised extreme-value distribution (Katz *et al.* 2005).

Community responses to environmental perturbations are often expressed as changes in species composition and abundance, and these multispecies responses can be quantified using multivariate techniques (McCune *et al.* 2002). We relativised data by largest values in columns (species) to use analytical tools based on distance measures (McCune *et al.* 2002). To visualise the multivariate patterns, we performed non-metric multidimensional scaling (NMDS) on Bray– Curtis distances among the four plots for 18 years. We determined whether community composition of the ordination obtained by NMDS was significantly correlated with environmental variables such as rainfall and occurrence of extreme drought. We included the occurrence of drought as a factor (years grouped in 'before 1998' and 'after 1998' levels). The significance of this correlation was assessed by using 10 000 permutations of environmental variables.

To determine whether there were significant temporal changes in species composition assemblages between consecutive years, we conducted a PERMANOVA (Anderson 2001) with 10 000 permutations using each plot as an experimental unit for each year (excluding 1998). The resulting temporal analysis of similarity allowed us to characterise the extent of resilience in our plant community (Kreyling *et al.* 2011). We used Bray–Curtis distance between 1989 and all other years as a baseline to determine whether there was any resilient behaviour in changes in similarity between consecutive years.

Once we identified the consecutive years that were significantly or marginally different with the PERMANOVA test, we performed an Indicator Species Analysis (ISA) to determine which, if any, plant species were most strongly associated with changes in composition. ISA compares a priori groups, and in our analyses, these comprised the matrices of abundance for species recorded in the period before vs. after the year in which PERMANOVA detected significant changes in species composition. To explore resilience in the community, we performed ISA in years before or after the year of change. ISA involves the calculation of a test statistic, the indicator value (IVij), that is simply the product of the abundance and frequency of each species in a given group (Dufrêne & Legendre 1997; Bakker 2008). Species are generally considered to be strong indicators of a certain group if their IVij is higher than 25 (Dufrêne & Legendre 1997). To determine the probability of obtaining an IVij equal to or greater than the calculated value in a given group, we performed a bootstrap with 9,999 permutations. We conducted ISA separately for each of the four plots and then we combined the results from the plots using metaanalytical techniques described by Bakker (2008).

Finally, we calculated the mean annual total cover and mean species richness of native and exotic annual plants to explore whether there have been temporal changes in these variables, associated with extreme rainfall events. For all analyses we used CRAN software R (R Development Core Team 2011), with the packages lmom (functions 'samlmu', 'pelgev', 'quagev' and 'gevfit'), vegan (functions 'vegdist', 'metaMDS', 'envfit' and 'adonis') and, for ISA, we executed in R the script developed by Bakker (2008).

RESULTS

Assessment of extreme drought

The 5th percentile of the extreme-value distribution was $15.125 \text{ mm year}^{-1}$. Only 6 of 130 years in our dataset had < 15 mm and the 95% percentile was 269.045 mm year⁻¹. Therefore, we considered years with < 15 mm and > 270 mm of rain to be rare for this ecosystem, and to represent a statistically extreme and infrequent climatic event for the study site (Fig. 1a). Over the last 130 years the 5th percentile (using a 30-year window) has oscillated between 5.83 and 33.83 mm. In contrast, the value of the 95th percentile ranged from 183.5 to 397.42 mm. The maximum precipitation (again a 30-year window) has declined notably since 1919, reflecting a decline in the variability of high rainfall events during this period. On the other hand, 30-year mean minimum precipitation has remained relatively constant, with a slight decrease in the last 50 years, indicating that the variability of extreme droughts has increased slightly during this period (Fig. 1b).

Five of 6 years of extreme low precipitation have occurred since 1960 (Fig. 1a). The probability of extreme drought conditions (< 15 mm rainfall) increased from 1900, reaching a peak of 0.07 in 1920. From 1930 to 1960, it decreased to 0.008, and then increased again to 0.14 (Fig. 1c). Therefore, during the last 50 years, the probability of an extreme drought has increased an order of magnitude compared with that of 1900, and was double as that of the previous dry period in 1920–1935.

Plant assemblage changes and invasibility

Most of the variation in our NMDS was explained by the first axis NMDS1 which is significantly correlated with the precipitation vector $(r^2 = 0.30; P = 0.0001, Fig. 2a-d)$. Extreme drought as a factor explained significant but small proportions of compositional change between years ($r^2 = 0.14$; P = 0.0001), mostly aligned along NMDS2 (Fig. 2a-d). All points corresponding to years of high precipitation before 1998 are located close to the extreme of the precipitation vector (1991, 1992 and 1997) in all plots and some of the points corresponding to years of very high precipitation after 1998 (except 2006) are not near the extreme of the precipitation vector (Fig. 2a,c). In contrast, years with low precipitation before 1998 are located in the opposite direction of the precipitation vector. Most of the points corresponding to years after 1998 are located in the negative region along NMDS2 axis, except for 2006 whose points are again in the positive region of the NMDS2, near the centroid of the level 'before' of drought factor.

Exotic species (except *Linaria texana* and *Oenothera rosea*) are separated from most native species along the NMDS2 axis and are more closely associated with species composition after 1998 and near the centroid of the level after of disturbance (Fig. 3). The native species *Cuscuta micrantha*, *Chaetanthera linnearis*, *Pasithea coerulea* and *Bromus berterianus* and the exotic species *Malva parviflora*, *Erodium moschatum* and *Urtica urens* were positively correlated with precipitation, because they are near the extreme of the precipitation vector. Further, the native species *Stachys grandidentata*, *Bowlesia incana*, *Schizanthus*



Figure 1 Analysis of extreme drought events in the climatic data from La Serena, Chile. (a) Accumulated annual precipitation since 1867. Lower dashed line represents 15 mm annual precipitation, determined to be the minimum extreme of precipitation, whereas upper dashed line represents 272 mm annual precipitation, the maximum extreme for our study site. Circles indicate years when annual precipitation was lower than 15 mm and ticks in upper x-axis indicate El Niño rainy events. (b) Variability of annual precipitation in La Serena calculated with a moving-average analysis with a 30-year window. Continuous line represents moving median (50th percentile), and dashed lines represent the 95th and 5th percentiles of extreme-value distribution. (c) Changes in the probability of occurrence of years with an annual rainfall of < 15 mm in La Serena, Chile, during the last 130 years, calculated with a moving-average analysis and a 30-year window.

litoralis, Moscharia pinnatifida, Parietaria debilis, Olsynium junceum and Alstroemeria magenta and exotic species Galium aparine and Erodium malacoides are positively correlated to precipitation but not located in the extreme of the precipitation vector. Thus these species are affected by moderately high precipitation events (Fig. 3). In contrast, the native species *Apium laciniatum*, *Valeriana bridgesii* and *Rhodophiala phycelloides* were negatively correlated with the precipitation vector and mainly occur in years of low precipitation.

Species composition changed significantly between 1990 and 1991 (PERMANOVA, pseudo- $F_{1,6} = 5.23$; P = 0.029), between 1997 and 1999 (pseudo- $F_{1, 6} = 2.26$; P = 0.028) and between 2006 and 2007 (pseudo- $F_{1, 6} = 2.01$; P = 0.028). Additionally, three other pairwise comparisons tended towards strong differences in composition: 1989 vs. 1990 (pseudo- $F_{1, 6} = 2.14$; P = 0.057), 1992 vs. 1993 (pseudo- $F_{1, 6} = 2.22$; P = 0.086) and 2005 vs. 2006 (pseudo- $F_{1, 6} = 1.55$; P = 0.084) (Fig. 4a). Most of the years where changes in community composition were detected were characterised by the occurrence of El Niño/high rain events or La Niña strong events. There were no significant changes from 1996 vs. 1997, despite the latter was a strong El Niño year (Fig. 4a). There were not similar patterns in composition changes between consecutive years and between each year vs. 1989, so there is no resilient behaviour in the dynamics of composition change in our ecosystem (Fig. 4a)

Only native species were indicators of change from 1989 to 1991 (Table 1) and most of them were correlated with years of high precipitation and located near the centroid of the 'before drought' level (Fig. 3). From 1992 to 1997, there were no significant changes, although we documented strong trends towards differences in species composition; these were associated with the exotic Urtica urens in 1993 and in 1996. Three exotic species are indicators of the significant change from 1997 to 1999, spanning 1998, an extreme La Niña year: M. parviflora, Schismus arabicus and Erodium cicutarium. The first was correlated with very high precipitation and the latter two were located near the centroid of the 'after drought level' (Fig. 3). From 2005 until 2007, there are no species identified as significant indicators of change, and marginally significant indicator species were almost all native annuals, the only exception was the exotic Erodium malacoides (Table 1). Native annuals that have been indicators of change consistently in the same years as exotic annuals were B. berterianus, which is affected by very high precipitation, and Lastarriaea chilensis.

Cover of native annuals varied from 0 to 114.4% and was clearly affected by water availability (Fig. 4b). In contrast, cover of exotic annual plants was low (0–18.4%) and stable during 1989–1998. There were small increments in exotic plant cover during all El Niño / rainy years, when the availability of water was higher. Since 1998, however, cover of exotics increased an order of magnitude, irrespective of rainfall but since 2005 cover of exotics has gradually declined (Fig. 4b). Cover of 12 of 15 exotic species in this ecosystem increased from 1999 to 2007.

Native species richness varied from 0 to 20 species year⁻¹. However, if we exclude 1998, native richness increased by 5–10 species typically during rainy years. Exotic species richness varied from 1 to 4 from 1989 to 1997, and was either 4 or 5 from 1999 until 2004 (Fig. 4c). Parallel to changes in exotic species cover, exotic richness decreased after 2004 (Fig. 4c). In general, analyses reported here are consistent in indicating that since 2005 this community has been returning to pre-drought (e.g. pre-1998) conditions.

DISCUSSION

We document an extreme drought event in north-central Chile (in 1998) and demonstrate that this event constituted a major disturbance to annual plant communities, promoting changes in species composition



Figure 2 Non-metric multidimensional scaling analysis of temporal changes in species composition at Fray Jorge, Chile. (a) Community composition of each year is represented with numbers (1989–1997, 1–9, respectively; 1999–2007, 10–18, respectively), (a–d) represent four different plots. Vector represents correlation between annual precipitation in FJ and community composition; 'd-before' and 'd-after' labels represent centroids of years before and after drought. 1998, a year of extreme drought, was excluded from the analysis. (Final stress = 14.37, rmse = 0.002, max resid = 0.007, stress-based $R^2 = 0.98$, fit-based $R^2 = 0.90$.)

and facilitating invasion by exotic species. Nevertheless, our data also indicate that this plant community is resilient and that it appears to be returning to its previous state.

Annual rainfall < 15 mm represents an extreme drought for our study system, and the frequency and probability of occurrence of such an event has increased since 1960. In contrast, annual rainfall > 272 mm represents an extreme wet period. At our study site, variability in high rainfall events has decreased whereas variability in drought conditions has increased slightly; in combination, these patterns reflect greater probability and frequency of drought conditions over the past 50 years. However, we have observed that the variability of extreme wet events has been steady during the last decade (Fig. 1) and we have reported an increase in the frequency of high rainfall events in 2000–2009 compared with 1990–1999 (Previtali *et al.* 2009). This is consistent with predictions of global climate change at mid-latitudes of increasing frequency and intensity of droughts and extreme wet events (Easterling *et al.* 2000; Breshears *et al.* 2005).

Our results are consistent with extreme drought precipitating major ecological change in this ecosystem. Germination of ephemeral plants in this region (Vidiella & Armesto 1989) is triggered by 10–15 mm of precipitation year⁻¹ (consistent with our definition of extreme drought); years with lower precipitation elicit no evident plant growth. Consequently, the occurrence of an event of 15 mm of annual precipitation is both statistically and biologically extreme for our study system.

In contrast to the drought, two extreme wet precipitation events (1997, 2002) did not generate compositional changes in our system. However, two high rainfall events (1991, 2006) did, although in both cases it was native annual species rather than exotics that were indicators of change. Therefore, native annuals would respond to high rainfall events that are part of the regular variability of precipitation in this ecosystem. The latest high rainfall period in our ecosystem (2006) evidently provided an opportunity for native annual species to recover and for the system to return to pre-drought conditions after 8 years. The ecological response to extreme drought that we document is similar to that reported from a North American grassland community (Haddad et al. 2002) both in time of recovery and also in impact (reset of community dynamics); however, extreme drought appears to have promoted invasibility in our ecosystem, whereas it did not do so in the North American grassland. Our semi-arid plant community appears to be more resilient than an experimental grassland community in



Figure 3 Correlation of annual plant species cover with the NMDS1 and NMDS2 Axes. Position of species codes represents the correlation of species cover with the axes. Exotic species have grey labels whereas native species have black labels. Species codes are given in Appendix 1.

Germany, which is predicted to continue diverging from its original state (Kreyling *et al.* 2011), if the frequency of extreme drought in our study site is the same as that of the last 50 years, this ecosystem may experience a new event of this magnitude in the near future. Such an event might preclude this system from fully recovering from the 1998 drought, and could shift this system to an alternative stable state (Scheffer *et al.* 2009). If climate change alters the frequency of drought in this region, the extent to which this system will be able to return to original floristic conditions (e.g. its resilience) is likely to be a function of the duration of interdrought intervals.

Because mesic ecosystems are predicted to be more strongly impacted by extreme droughts than xeric ecosystems (Knapp *et al.* 2008), direct comparisons with semi-arid annual plant communities should be interpreted conservatively. On the other hand, if drought conditions have this level of influence on arid-adapted floras such as that in northern Chile, and if drought conditions are likely to be more frequent in the future, then this study may suggest greater resilience to climate change in xeric systems compared with more mesic systems.

However, not only exotic species increased in abundance or cover under drought conditions; some native annual weeds that are affected by very high precipitation such as *B. berterianus* responded similarly. Under such conditions, when the entire assemblage of annual plants is exposed to identical changes in ecological processes, some plants will be better able to capitalise on the increased availability of resources, and these will have the opportunity to increase their cover, regardless of their status as natives or exotics.

In other semi-arid deserts, temporal heterogeneity in water availability and differences in germination strategies and requirements allow the coexistence of annual plants through the 'storage effect'. This is a general mechanism of species coexistence based on differences in life-history traits (Warner & Chesson 1985; Adondakis & Venable 2004; Chesson *et al.* 2004; Facelli *et al.* 2005). In our study, exotics did not exclude native plant species, or vice versa. Furthermore, the species that account for most of the dissimilarity in the pre-1998 assemblage were native annuals, whose germination thresholds



Figure 4 Temporal trends in variables describing community dynamics in Fray Jorge, Chile: (a) Bray–Curtis distance between consecutive years and between each year vs. 1989; *, statistically significant distance between consecutive years; +, marginally significant distance between years; black bars in the upper x-axis represent El Niño rainy years whereas white bars represent La Niña dry years. (b) Total annual species cover and (c) species richness.

are higher than 20 mm. In contrast, the exotic annual species that accounted for most of the dissimilarity and had significant indicator values following the drought event have lower seed germination thresholds (Vidiella & Armesto 1989). Additionally, these native species have different bet-hedging strategies than exotics, which may allow them to maintain greater long-term fitness and contribute to community resiliency (M. Jiménez, C. Gonzalez-Browne, F. Jaksic, J. Armesto, A. Gaxiola, P. Meserve, D. Kelt & J. Gutiérrez, unpublished data). This lack of competitive exclusion through different germination requirements and different bet-hedging strategies may explain coexistence and invasibility in our system through a form of the 'storage effect' (Chesson et al. 2004; Melbourne et al. 2007; Davis 2009). Further research should explore potential differences in germination strategies and requirements, and other life history traits of native and exotic species in local plant assemblages to determine the invasibility of semi-arid communities.

 Table 1 Indicator Species Analysis (ISA) of annual plants from FJ in consecutive years with significant differences in species composition

Species	Origin	Group	IV	P-value
1989 vs. 1990				
Alstroemeria diluta	Ν	В	73.2	0.084
Pectocarya dimorpha	Ν	В	90.7	0.091
Eryngium coquimbanun	Ν	В	86.0	0.097
Menonvillea litoralis	Ν	А	32.4	0.068
1990 vs. 1991				
Alstroemeria diluta	Ν	В	50.9	0.064
Moscharia pinnatifida	Ν	А	92.4	0.029
Camissonia dentata	Ν	А	82.1	0.060
Bromus berterianus	Ν	А	79.7	0.068
Oxalis micrantha	Ν	А	82.3	0.087
Lastarriaea chilensis	Ν	А	71.9	0.091
1992 vs. 1993				
Cryptantha glomerata	Ν	В	40.8	0.162
Alstroemeria diluta	Ν	В	38.8	0.165
Plantago hispidula	N	В	59.7	0.171
Bromus berterianus	Ν	А	72.2	0.036
Urtica urens	E	А	32.1	0.044
1995 vs. 1996	_		0	
Cistanthe sp	N	В	31.7	0.051
Ervnoium coquimbanun	N	B	52.0	0.053
Urtica urons	F	A	31.5	0.033
Bromus hortorianus	N	A	76.8	0.011
Schismus arabicus	E	A	70.8	0.013
Listoch amic on	N	Δ	18.5	0.013
1996 vs. 1997	18	Λ	40.3	0.007
Leucocoryne purpurea	Ν	В	58.1	0.048
Eryngium coquimbanun	Ν	В	50.3	0.058
Urtica urens	E	А	35.6	0.003
Bromus berterianus	Ν	А	79.4	0.005
Schismus arabicus	E	А	74.7	0.012
Hypochaeris sp.	Ν	А	55.2	0.027
Malva parviflora	Е	А	50.0	0.030
Lastarriaea chilensis	Ν	А	54.3	0.080
1997 vs. 1999				
Leucocoryne purpurea	Ν	В	64.1	0.019
Eryngium coquimbanun	Ν	В	51.9	0.045
Plantago hispidula	Ν	В	65.7	0.062
Olsynium junceum	Ν	В	49.0	0.070
Schismus arabicus	Е	А	81.9	0.003
Hypochaeris sp.	Ν	А	63.2	0.009
Bromus berterianus	Ν	А	75.7	0.010
Malva parviflora	Е	А	55.6	0.014
Lastarriaea chilensis	Ν	А	55.6	0.073
Erodium cicutarium	Е	А	50.9	0.076
1999 vs. 2000				
Olsvnium junceum	Ν	В	56.5	0.028
Leucocorvne burburea	Ν	В	61.7	0.028
Plantaoo histidula	N	В	65.4	0.071
Viola tusilla	N	B	55.8	0.073
Frongium coquimbanun	N	B	45.3	0.092
Schismus arabicus	E	A	84 7	0.002
Bromus herterianus	N	A	73.9	0.002
Intica urons	F	A	30.1	0.012
Hypochaeric sp	N	A	61.2	0.014
I astarriaga chiloweie	1N N	A	60.6	0.010
Enodium cicutania	TN E	A	50.7	0.043
Malua bamillan	F	Δ	20.7	0.070
iviaiva parvijiora Erodiana cicat-nium	E	Λ Δ	32.3 26.0	0.009
2000 m 2001	Ľ	11	20.0	0.093
2000 vs. 2001	N	D	66.0	0.015
Leuwovyne purpurea	LN NT	D D	00.2	0.015
riantago inspidula	IN N	D	08.0	0.056
Oisynium junceum	IN	В	50.6	0.060

Table I (Continued)	Table	1	(Continued)
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Species	Origin	Group	IV	P-value
Viola pusilla	Ν	В	56.0	0.080
Schismus arabicus	Е	А	78.1	0.011
Lastarriaea chilensis	Ν	А	64.8	0.029
Bromus berterianus	Ν	А	65.2	0.045
Urtica urens	Е	А	25.7	0.050
Hypochaeris sp.	Ν	А	54.3	0.052
Koeleria phleoides	Е	А	35.7	0.084
Erodium cicutarium	Е	А	50.0	0.086
2005 vs. 2006				
Viola pusilla	Ν	В	69.5	0.131
Camissonia dentata	Ν	В	54.7	0.295
Adesmia tenella	Ν	В	59.5	0.298
Valeriana bridgesii	Ν	А	32.8	0.164
Bowlesia tropaeliflora	Ν	А	25.5	0.226
Rhodophiala phycelloides	Ν	А	60.4	0.234
2006 vs. 2007				
Moscharia pinnatifida	Ν	В	90.4	0.141
Adesmia tenella	Ν	В	86.0	0.160
Oxalis micrantha	Ν	В	86.8	0.178
Alstroemeria magenta	Ν	А	30.0	0.057
Erodium malacoides	Е	А	50.0	0.058
Cistanthe sp	Ν	А	25.0	0.060

ISA was performed separately in each of the four plots to account for spatial variation, and results were combined with meta-analytical techniques, to calculate the values provided here. Origin of plant species: Native (N), Exotic (E). Group: Before (B) of After (A) change detected; IV: Indicator Value, *P*-value: probability values, calculated by permuting the data 9999 times. Species are ordered by lower *P*-values inside each group. Bold numbers indicate *P*-values lower than 0.05. Years when changes in composition were detected by PERMANOVA, are highlighted in bold characters.

The 'fluctuating resources model' posits that the invasibility of a community may be promoted either by increasing the gross supply of a limiting resource or by changing the uptake of this resource (Davis et al. 2000). Previous investigations in semi-arid ecosystems have reported that invasibility is often promoted by increasing the main limiting resource (water) rather than by decreasing this (e.g. drought; Cleland et al. 2004; Kreyling et al. 2008). In our study site, gross water supply is associated with very high rainfall/El Niño events. However, the occurrence of these wet events did not lead to an increase in the cover of exotic annuals prior to 1998. Consequently, we suggest that it may be more plausible that invasibility at our site was facilitated by a change in the rate of uptake of a limiting resource. This change may be influenced by mortality of seeds resulting from the 1998 drought as a disturbance, and by a conservative bet-hedging strategy of native species (M. Jiménez, C. Gonzalez-Browne, F. Jaksic, J. Armesto, A. Gaxiola, P. Meserve, D. Kelt & J. Gutiérrez, unpublished data).

In the face of global change, however, the frequency and probability of such events may be increasing. In addition, because of their effects on the physiology, ecology and evolution of the organisms that live in semi-arid ecosystems, we contend that extreme droughts deserve more attention from researchers studying arid and semi-arid ecosystems as well as more mesic environments. To our knowledge, this is the first long-term study to document that extreme drought enhances the susceptibility of a semi-arid community to invasion by otherwise uncommon exotic annuals, and that high but not extreme wet events may provide the opportunity for community recovery. Further longterm research is needed to document rare climatic extremes and to understand the factors governing the resilience of biodiversity to these extreme events.

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AUTHOR CONTRIBUTIONS

M.A.J. performed the data analyses. P.L.M., J.R.G. and D.A.K. developed and installed the experimental design at the research site and collected the data. M.A.J. wrote the first draft of the manuscript, and all authors contributed substantially to revisions. We declare that we do not have conflict of interests.

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