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RESEARCH ARTICLE

Loss of native herbivores triggers diversity decline of ephemeral plant communities

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Abstract

Aim: Evaluate the temporal changes in species diversity, composition, and structure of ephemeral plant communities and the seed bank in response to long-term herbivore exclusion over 11 years in plots with and without herbivores.

Location: North-central Chile.

Methods: We obtained information on ephemeral vegetation cover in August and September using the intercept point method and recorded seed abundance in April. The Bosque Fray Jorge National Park Long-Term Socio-Ecological Research (LTSER) provided these records covering 11 years (2009–2019). From the original experiment of 20 plots, we used eight plots divided into two treatments: four plots allowed free access to all herbivores (with herbivores), while the other four plots excluded herbivores (without herbivores).

Results: We found that Hill–Shannon diversity increased in plant communities with herbivores and a temporal increase in the cover of the dominant species, *Plantago hispidula*, under herbivore exclusion. In wet years, species richness and temporal turnover of plant communities increased independently of treatment. Although seed abundance differed among treatments and years, population structure remained constant over time and among treatments, suggesting that the seed bank acts as a buffer against shocks that modify plant community dynamics. Structural equation modeling revealed that precipitation, via its positive effects on *Plantago hispidula*, increases native plant richness to a greater extent than herbivores. However, in the absence of herbivores, precipitation directly affects native species richness. Moreover, we found that precipitation also influences the native species richness of the seed bank, both directly and indirectly, although its impacts exhibit a time lag.

Conclusions: Our study demonstrates that the temporal dynamics of ephemeral plant communities and seed banks in semi-arid ecosystems are strongly coupled to climate variability, highlighting the vulnerability of these communities to biodiversity loss and climate change.

KEYWORDS
dominance, herbivores, long-term experiments, plant diversity, *Plantago hispidula*, seed bank, small mammals, temporal turnover

1 | INTRODUCTION

Species loss is a consequence of global change, leading to changes in community structure and abundance that can profoundly affect ecosystem functioning (Cardinale et al., 2002; Hooper et al., 2012). The loss of an entire group of species, that is, a guild, that perform similar functions in an ecosystem, such as herbivores, could impact ecosystem functioning to a greater extent than the loss of individual species because of functional redundancy (Bardgett & Wardle, 2003; Wardle et al., 2004; Hooper et al., 2012; Pardo et al., 2015). Regulation of plant communities by herbivores can occur through various mechanisms—decreased survival, biomass, abundance, and reproduction, increased plant diversity due to consumption of dominant and common species, and reduced competitive exclusion—which can result in the persistence of rare species and increased species turnover (Grime, 1998; Maron & Gardner, 2000; Larios et al., 2017; Jia et al., 2018; Mortensen et al., 2018). As plant communities also are regulated by competition (Chesson, 2000; Tilman, 2004; Ploughe et al., 2020) as well as abiotic conditions such as precipitation and temperature (Anderson et al., 2007; Maestre et al., 2012), the relative importance of herbivores in mediating plant community dynamics is uncertain (Anderson et al., 2007; Hillebrand et al., 2007; Young et al., 2013).

The impacts of large herbivores on the richness and diversity of plant communities are due mainly to soil trampling and direct consumption of plants (Bakker et al., 2004; Hester et al., 2006). In contrast, small herbivores can be more selective, consuming only palatable species, and have a smaller range of displacement, which results in a greater impact on the local vegetation and disturbing the system by building burrows or digging for bulbs (Forbes et al., 2019). Most studies on the effects of vertebrate herbivores on plant communities have been conducted in seminatural ecosystems such as grasslands (Olff & Ritchie, 1998; Bakker & Olff, 2003; Bakker et al., 2004; Seabloom et al., 2015; Gao & Carmel, 2020). The use of herbivore exclusions to study plant communities is essential for accurately estimating the actual effect of herbivory, as they eliminate variation caused by random events, such as environmental factors. However, fewer studies have utilized the long-term exclusion of native herbivores in natural areas. Long-term monitoring is necessary to fully comprehend the role of herbivory in natural ecosystems (Jia et al., 2018).

Whereas we know that herbivores regulate the structure and composition of plant communities (Allen et al., 2021; Orr et al., 2022), it is difficult to predict the community response of exotic species in the absence of herbivores (Allen et al., 2021). The enemy release hypothesis (Keane & Crawley, 2002) postulates that the consumption of more palatable or abundant native species may give way to the establishment of exotic species that may become abundant rapidly. On the other hand, the biotic resistance hypothesis (Levine et al., 2004) suggests that exotic species may be more palatable to herbivores, thus limiting the distribution of these species. Additionally, indirect interactions may play a key role in herbivore response and on the balance between exotics and natives (Vavra et al., 2007). Previous research has demonstrated that exotic plants are more tolerant than native species to herbivore impacts on soil, which gives them an advantage over native species (Funk, 2008, 2013).

In arid and semi-arid ecosystems, a significant percentage of total plant biomass consists of ephemeral vegetation, covering bare soil, thereby reducing evapotranspiration and run-off of rainfall. Ephemeral plants, which include herbaceous annuals and herbaceous perennial geophytes, have a life cycle linked to the rainy season, leading to a strong coupling between precipitation and productivity (Ogle & Reynolds, 2004; Miranda et al., 2009). Similarly, plant community dynamics are intimately linked with variation in climatic conditions. For example, high intra-annual climatic variability promotes the coexistence of species with different survival strategies, that is, bet-hedging; this strategy refers to an individual forgoing opportunities for immediate reproductive gain in the hopes of greater reproductive success over the long term (Cohen, 1968; Gremer & Venable, 2014). A classic example of bet-hedging is the delay of germination in desert annuals; this mechanism is critical in communities with extreme environmental conditions, such that in years of low precipitation, a significant percentage of seeds do not germinate and remain stored in the soil until years with favorable conditions permit germination (Ooi, 2012). Bet-hedging varies among species and may be a common strategy in water-limited ecosystems, where precipitation fluctuates markedly, within and between years (Clauss & Venable, 2000). Yet, this adaptive mechanism is not the only one that may affect the soil seed bank (Ooi, 2012); granivory may decrease soil seed bank density and diversity (Chang et al., 2001; Sternberg et al., 2003). The relative importance of the effects of abiotic (precipitation) and biotic (herbivory) influences on ephemeral plant communities—and especially on their seed banks—in water-limited ecosystems is uncertain.

The diversity of plant communities can be modified depending on the selectivity of herbivores (Bakker et al., 2004; Jia et al., 2018). For instance, the direct consumption of highly palatable plants can result in temporary periods of increased dominance by one or a few species (so-called "dominance pulses"; Hillebrand et al., 2008). Prolonged dominance pulses have the potential to result in losses of subordinate species (Wilsey & Polley, 2004; Mortensen et al., 2018), which can persist for multiple years, depending on colonization rates (Cadotte et al., 2006) and the sequence and timing of species joining communities (referred to as "priority effects"; Chase, 2003;

Fukami, 2015). These processes can be further influenced by abiotic factors, such as precipitation and nutrient availability, particularly in arid ecosystems (Wainwright et al., 2012; Gao & Carmel, 2020).

In this study, we address the following questions: (1) how do herbivores influence patterns of interannual variation in native and exotic species and their seed banks; (2) are the temporal dynamics of ephemeral plant communities and seed banks de-coupled, as predicted by bet-hedging; and (3) how does the abundance of herbivores influence the impacts of dominant species on plant and seed bank diversity of native and exotic species? To address these questions, we established a long-term experimental exclusion of herbivores in a semi-arid ecosystem to evaluate both the direct and indirect effects of small mammalian herbivores and climate on the temporal dynamics of ephemeral plant communities and the soil seed bank. We examine temporal changes in complementary measures of ephemeral plant diversity and the soil seed bank over 11 years in response to the long-term exclusion of herbivores.

2 | MATERIALS AND METHODS

2.1 | Study site

We performed this study in Quebrada de Las Vacas, located in the Bosque Fray Jorge National Park, Chile (Figure 1a). The climate at the study site is semi-arid mediterranean with cold, wet winters and hot, dry summers (Di Castri & Hajek, 1976; Luebert & Pliscoff, 2006; Meserve et al., 2020). The mean maximum temperature in the warmest month (January) is 24°C, while the mean minimum temperature in the coldest month (July) is 4°C (CEAZAMET, 2019). Precipitation is concentrated in the austral winter months (May–September), distributed in pulses of 2–60 mm (CEAZAMET, 2019). Mean annual precipitation (1991–2021) is 125 mm/year; El Niño–Southern Oscillation (ENSO) events amplify interannual precipitation variation, resulting in either extremely wet or dry years (red line in Figure 1b). In the present study, we used data from 11 years (2009–2019), during which three years are considered wet (2011, 2015, and 2017) and three years can be considered very dry (2012, 2014, and 2019) (Figure 1d).

The herbivore assemblage at Fray Jorge comprises two invasive lagomorphs and several species of native rodents. European hares (*Lepus europaeus*) and European rabbits (*Oryctolagus cuniculus*) reached Fray Jorge in 2000–2002 (D. A. Kelt, pers. obs.) and have since become established. Common rodents (all native) include the diurnal herbivorous degu (*Octodon degus*) and two nocturnal/crepuscular species, the omnivorous olive grass mouse (*Abrothrix olivacea*) and the herbivorous Darwin's pericote (*Phyllotis darwini*). Additionally, the herbivorous and generally nocturnal Bennett's chinchilla rat (*Abrocoma bennettii*) and the moon-toothed degu (*Octodon lunatus*) occur in lesser numbers, and the herbivorous fossorial cururo (*Spalacopus cyanus*) occurs sporadically throughout the park. Finally, the omnivorous/insectivorous long-haired grass mouse (*Abrothrix longipilis*) and the granivorous long-tailed pygmy rice rat (*Oligoryzomys longicaudatus*) occur episodically in our study sites, usually during rainy periods.

The experimental design consists of 20 plots pf 75 × 75 m (0.56 ha) separated by a minimum distance of 50 m (for additional detail, see Gutiérrez et al., 2010; Kelt et al., 2013; Meserve et al., 2016). We use data from two treatments: control (hereafter: with herbivores) and exclusion (hereafter: without herbivores). Plots with herbivores are encircled with low fencing equipped with large holes to allow full access by all species (e.g., herbivores, predators, and others) (Figure 1c). In contrast, plots without herbivores have taller fences (1.5 m high and buried 0.5 m deep to hinder burrowing) constructed with a wire mesh with small openings and whose upper part has metal flashing that prevents the entry of rodents that can climb the mesh fencing (Figure 1d).

2.2 | Ephemeral plant community sampling

The flora of Bosque Fray Jorge National Park is diverse and includes 65 ephemeral plant species to date (Appendix S1). The cover of ephemeral plant species (native and exotic) in the experimental plots was recorded monthly using the point intercept method (Ellenberg & Mueller-Dombois, 1974). All plots were assessed along four 50-m transects; 10 sections (length 1.5 m) of each transect were randomly selected for vegetative measurement using a point frame with 30 sampling pins at 5-cm intervals. The species and the number of individuals that occur at each point were recorded at each sampling point. The total number of points per plot was 1200 (30 samples on 10 segments on each of four transects). Vegetation cover per species was then estimated as the proportion of points where each species was recorded. In subsequent analyses, we use data from the months with the highest plant coverage (August and September), when plant diversity typically is greatest (Gutiérrez et al., 1997, 2010; Fernández-Murillo, 2016), as our focus is on interannual dynamics.

2.3 | Soil seed bank

In April of each year, prior to the germination, soil samples (3 cm diameter × 5 cm depth, hence 35.34 cm^3 vol) were collected at five random points within each plot and taken to the laboratory where samples were sieved manually, and seeds counted by hand. The smallest seeds (<0.5 mm) were extracted by flotation (in water) and were identified with a microscope (Gutiérrez & Meserve, 2003). Sixty percent of the species recorded in the plant community were represented in the seed bank, of which we identified 30% to genus and 70% to species.

2.4 | Statistical analyses

For all analyses, we use the average of August and September for each plot and each year. For all plots, we calculated temporal

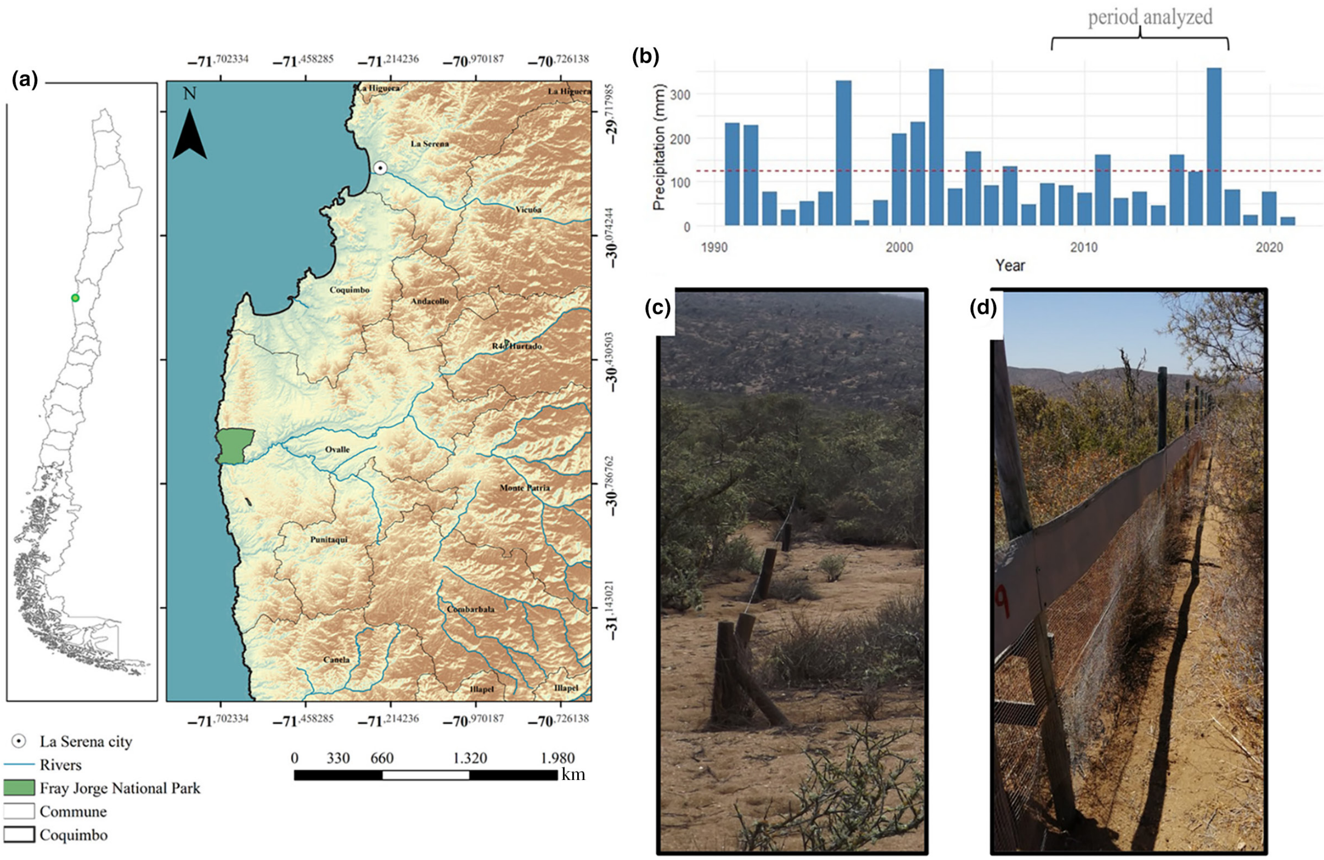

FIGURE 1 Overview of the experimental design and study site. (a) The study site is in Bosque Fray Jorge National Park in north-central Chile. This study examines the joint effects of climate and herbivores, whose abundance was manipulated experimentally. The climate is characterized by high interannual variation in precipitation (b). Mean annual precipitation is 125 mm/year (red line). The study period covers 2009–2019, of which three were rainy years (2011, 2015, and 2017). The two experimental treatments, with small mammal herbivores (c) and without small mammal herbivores (d), were established in 1989 and are part of Fray Jorge Long-Term Socio-Ecological Research (LTSER).

diversity indices with the *codyn* package (Hallett et al., 2016) in R v. 4.1.0 (R Core Team, 2020), focusing on species turnover, which is a measure that allows us to quantify the rate of change in species composition from year to year. Species diversity of plant communities and the seed bank for each plot in each year were quantified using Hill numbers (^qD) with the *hillR* package (Chao et al., 2014; Li, 2018). Hill numbers, or order diversity (e.g., $q=0$ or 1), reflect the sensitivity of the index to relative species abundances. We used two values of q: $q=0$, which is species richness and gives equal weight to all species, and $q=1$, equivalent to Shannon's diversity index, which gives more weight to more abundant species. We converted all diversity orders to the effective number of species to facilitate interpretation (Jost, 2006). For plants, we report patterns of species richness (q_0) and Hill–Shannon diversity (q_1; Roswell et al., 2021) for all species as well as for native and exotic species separately. We analyzed responses of species richness, Hill–Shannon diversity, and turnover to the experimental treatment and year with generalized additive mixed models (GAMMs), treating treatment as a fixed factor and plot as a random factor. We assesed temporal autocorrelation including a temporal correlation structure in the fitted models. We fitted these models using the R package *gamm4* (Wood et al., 2017). Results were plotted using the *ggplot2*package in R (Wickham, 2016).

We analyzed temporal changes in species rank abundances for each treatment for ephemeral plant communities and the seed bank. First, the three most abundant species were classified as dominant species (Appendix S2). The three dominant species in our study were *Plantago hispidula*, *Bromus berteroanus*, and *Oxalis micrantha*. Temporal changes in the abundance rank of a species can be visualized using "rank clock plots" (per Collins et al., 2008), where sequential radii represent years, and the location on each radius corresponds to abundance rank. If a species retains the same rank order in each year of analysis, it would be presented as a perfect circle; deviations from this reflect temporal changes in rank abundance. We calculated two sets of rank clocks, one for plant cover and the other for seed abundance, for both experimental treatments for each year of the study period. We analyzed the abundance of the three dominant species and the native/exotic groups with an additive mixed model with treatment variable as a fixed effect (with and without herbivores) and plot as a random factor, also considering temporal correlation.

We examined how the abundance of herbivores influences the impacts of dominant species on ephemeral plant and seed bank diversity of native and exotic species over time and between experimental treatments, using piecewise structural equation modeling with the *piecewiseSEM*R package, using linear mixed models (LMM) including the plot as a random effect and temporal autocorrelation (Lefcheck, 2016). We formulated a hypothetical causal model based on ecological theory and our knowledge of the study ecosystem. Our hypothetical model evaluates (1) the indirect effects of herbivory and precipitation on the species diversity of native and exotic ephemeral species via the abundance of *Plantago hispidula* and (2) the direct effects of herbivory on plant species, as well as its indirect effects on seed species richness (of the following year) via the abundance of *Plantago hispidula* (Appendix S3). Our models incorporated the plot as a random factor and accounted for temporal autocorrelation by including a temporal correlation structure in the fitted models. We used four parameters to evaluate model fit: AIC, χ^2 value (with $p>0.05$), Fisher's C value (with $p>0.05$), and the adjusted marginal and conditional R^2. To improve the fit, we included paths with lower probabilities than the recommended $p<0.05$ in directed separation tests, as long as the Fisher's and χ^2 test probability for model fit remained significant ($p>0.05$). We fitted separate models for each treatment. To meet assumptions of normality, we applied a log-10 transformation. Additionally, we included the annual abundance of the dominant herbivore, *O. degus*, in both models to account for their presence, albeit minimal (less than 200 individuals per year), in the herbivore exclusion plots. For detailed information on rodent captures, refer to Meserve et al. (2016). We fitted SEMs using the "psem" function of *piecewiseSEM*package in R (Lefcheck, 2016). We provide the script of the final SEMs in the Data Availability Statement section. Data manipulation, visualization, and analysis were performed using R v. 4.1.0 (R Core Team, 2020).

3 | RESULTS

3.1 | Temporal change in the ephemeral plant community

We observed no significant difference in ephemeral plant species richness (q_0) across treatments (Figure 2a), and this held for analyses solely on native species as well (Figure 2c). In contrast, exotic ephemerals demonstrated a non-significant trend, with plant species richness being slightly greater in the presence of herbivores (Figure 3e). Furthermore, species richness varied significantly over the years (Figure 2a). Approximately 20% more species were recorded in years with higher precipitation (2011, 2015, and 2017) than in dry years (2014 and 2019; Figure 2). We observed 41 ephemeral plant species in the herbivore treatment, including ten exotic species (*Erodium malacoides*, *Erodium cicutarium*, *Linaria texana*, *Urtica urens*, *Galium aparine*, *Schismus arabicus*, *Vulpia bromoides*, *Microseris pygmaea*, *Pectocarya linearis*, and *Rotraria cristata*). In contrast, we observed 31 species in the treatment without herbivores, seven of which were exotic (*Erodium malacoides*, *Erodium cicutarium*, *Schismus arabicus*, *Linaria texana*, *Microseris pygmaea*, *Galium aparine*, and *Rostraria cristata*). Hill–Shannon diversity (i.e., diversity order 1) for the ephemeral plant community was also significantly higher in the presence than in the absence of herbivores (Figure 2b). Similar patterns were observed for the Hill–Shannon diversity of native species but not exotic species, exhibiting minimal differences across treatments (Figure 2d,f respectively). The Hill–Shannon diversity of both, the entire community and its constituent groups (native and exotic species), exhibited significant intra-annual variation, regardless of the treatment. These findings align with the observed patterns in species richness.

In the seed bank, we observed an apparent shift between treatments, with higher species richness in the presence of herbivores. Additionally, seed species richness varied markedly over time, with 2016, 2017, and 2018 exhibiting the highest levels of species richness (Figure 3a). Similar patterns were observed for native species (Figure 3c; p Treat = 0.01 and Year = 6.65 e^{-06}). However, we found a different pattern for the seed bank of exotic species, whose species richness did not change significantly between treatments or years (Figure 3e; p Treat = 0.07; Year = 0.72) Seed Hill–Shannon diversity showed no significant differences between treatments, but differed significantly between years, with 2017 being the year with the highest diversity (Figure 3b). Differences in Hill–Shannon diversity between years were also observed for native and exotic taxa (Figure 3d,e).

Total plant turnover showed significant differences between years ($p=0.006$) but not between treatments ($p=0.07$). Furthermore, there were no observed differences in turnover between the native and exotic plant species (Appendices S4 and S5). In terms of turnover of the soil seed bank, no consistent directional changes were observed over time. Similarly, there were no significant turnover differences between treatments for native or exotic species (Appendices S4 and S5).

3.2 | Changes in ephemeral plant cover and seed abundance

The total cover of ephemeral plants differed significantly between years but not between treatments, and similar patterns were found for native and exotic plant species. Yet, the cover of native plants was higher without herbivory, in contrast to exotic plants (Table 1; Figure 3). In addition, the years with the highest vegetation cover were 2010, 2011, and 2013, with an average of 53.9%, while the year with the lowest cover was 2019, with a cover of 1.38%.

Ephemeral plant communities without herbivores were dominated by *Plantago hispidula*, *Zephyranthes physeloides*, and *Bromus berteroanus*, while communities with herbivores were dominated by *Plantago hispidula*, *Oxalis micrantha*, and *Bromus berteroanus* (Appendix S2). Ephemeral plant communities without herbivores exhibited a higher plant cover of *Plantago hispidula* and almost no plant cover of exotic plant species compared to communities with herbivores (Figure 4a, Table 1). The structure of communities without herbivores was more consistent between years than that

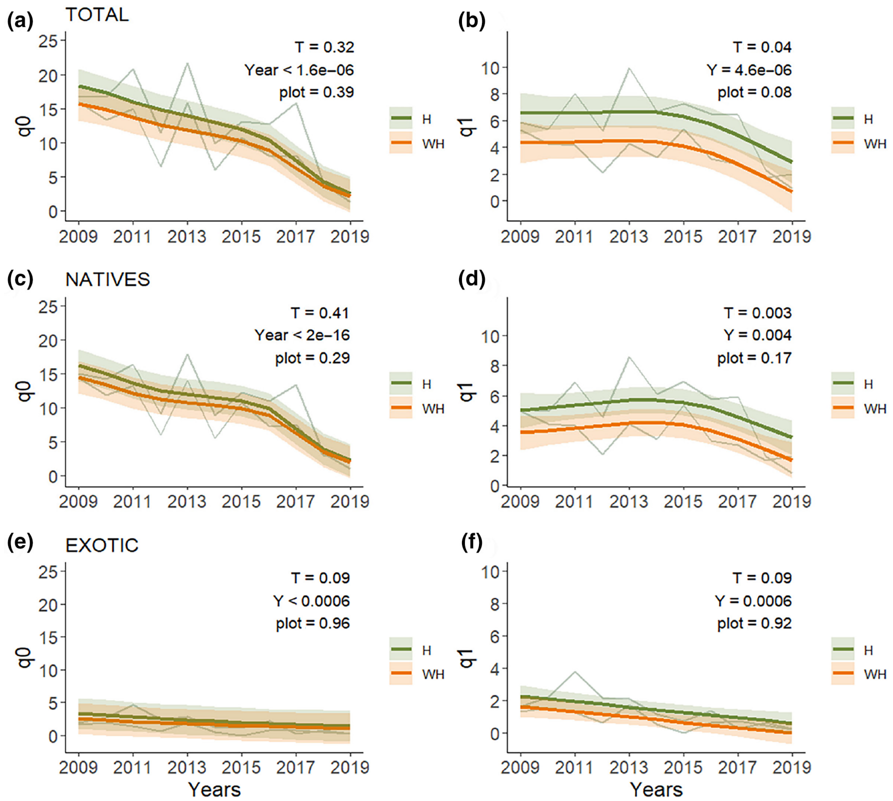

FIGURE 2 Temporal variation of ephemeral plant species diversity in a semi-arid ecosystem in central Chile, where herbivores are experimentally excluded; the treatment without herbivores is represented by WH and with herbivores by H. The diversity of ephemeral plant species was quantified using Hill numbers; q_0 represents the effective number of species, which indicates species richness, and q_1 represents the Hill-Shannon diversity. (a, c, e) Total, native, and exotic richness (q_0) of the ephemeral plant community, respectively. (b, d, f) Total, native, and exotic Hill–Shannon diversity of the ephemeral plant community, respectively. Each figure shows *p*-values for the generalized additive mixed model (GAMM), year (*Y*), treatment (*T*), and random factor (plot). The gray lines show the mean plot per treatment, the colored lines show the smoothed mean of the GAMM model for each treatment, and the shaded area shows the variance.

of communities with herbivores, with 2010 and 2015 being the only years with a higher cover of native species and a lower cover of *Plantago hispidula* than other years. The structure of communities with herbivores was dominated by *Plantago hispidula*, and native plant species generally had a lower plant cover, except in 2012 when the native species *Bromus berteroanus* had an unusually high plant cover (Figure 4a). The composition of the ephemeral plant communities indicates that in both treatments, the number of species decreased in recent years, and we recorded no new species from those in the first year. However, the number of shared species in the communities without herbivores is greater than those with herbivores, although the latter had a higher plant species richness (Figure 4b).

In the seed bank, total abundance varied significantly among treatments and years (Table 1). The years with the highest seed abundance were 2016 and 2018 (200 seeds/cm^3), and 2015 was the year with the lowest seed abundance (20 seeds/cm^3). Communities with herbivores, on average, had higher seed abundance (110 ± 11; mean ± SE) than those without herbivores (60 ± 8; mean ± SE) (Table 1). The seed bank was dominated by *Oxalis micrantha*, *Bromus berteroanus*, and *Apium* in plant communities without herbivores. In contrast, the seed bank in plant communities with herbivores was dominated by *Oxalis micrantha*, *Plantago hispidula*, and *Bromus berteroanus* (Appendix S2).

For seeds of native and exotic species, we observed significant statistical differences between years and some between treatments (Table 1). Specifically, whereas the abundance of *Oxalis micrantha* decreased in the absence of herbivores, we found that *Plantago hispidula* exhibited considerably lower abundance in plant communities with herbivores (Figure 4a). Conversely, both *B. berteroanus*, native species, and exotic species showed no significant differences between treatments.

Community structure did not significantly differ between treatments. Across all years, native plant species remained dominant, followed by *O. micrantha* (Figure 4a). The composition of the seed bank was different from that of ephemeral plants; although the number of species in the seed bank decreased in the last year for both treatments, the number of shared species was lower in the treatment without herbivores (Figure 4c). Moreover, the number of species recorded only in the first year of monitoring was higher in communities without herbivores than in those with herbivores (Figure 4c).

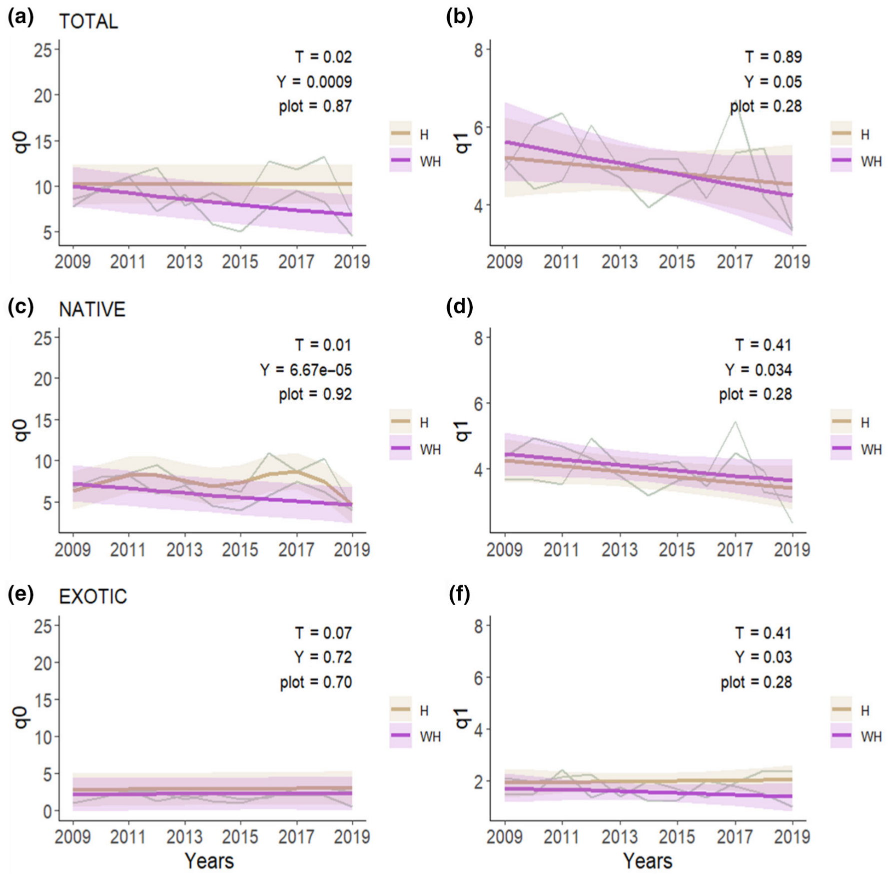

FIGURE 3 Variation in species diversity of the seed bank over time in a semi-arid ecosystem in central Chile in which herbivores are experimentally excluded; the treatment without herbivores is represented by WH and with herbivores by H. Seed bank diversity was quantified using Hill numbers; q_0 represents the effective number of species, which indicates species richness, and q_1 represents Hill–Shannon diversity. (a, c, e) Total, native, and exotic species richness (q_0) of the ephemeral plant community, respectively. (b, d, f) Total, native, and exotic Hill–Shannon diversity of the ephemeral plant community, respectively. Each figure presents *p*-values for the generalized additive mixed model (GAMM), year (*Y*), treatment (*T*), and random factor (plot). The gray lines indicate the mean plot per treatment, the colored lines indicate the mean of the smoothed GAMM model for each treatment, and the shaded area indicates the variance.

TABLE 1 Summary of analysis of variance comparing coverage of ephemeral plants and seed abundance for the total community, dominant species (*Oxalis micrantha*, *Plantago hispidula*, and *Bromus berteroanus*), and functional groups (native and exotic) between treatments, years, and plot.

	Seed bank			Ephemeral plant community		
Groups	Treat	Year	Plot	Treat	Year	Plot
Oxalis micrantha	**0.0006**	**0.0020**	0.314	**$1.08e^{-06}$**	**$<2e^{-16}$**	0.115
Plantago hispidula	**$2.01e^{-06}$**	**0.0003**	0.733	**$5.97e^{-07}$**	**$<2e^{-16}$**	0.992
Bromus berteroanus	0.764	**0.0006**	0.912	0.503	**$<2e^{-16}$**	0.445
Natives	0.073	**0.0001**	0.652	**0.013**	**$<2e^{-16}$**	0.913
Exotics	0.102	**0.0020**	0.917	**0.024**	**$3.61e^{-06}$**	0.495
Total	**0.013**	$<2e^{-16}$	0.686	**0.015**	**$<2e^{-16}$**	0.804

Note: Bold values indicate statistically significant differences.

3.3 | Joint impacts of herbivore and variation in precipitation on ephemeral plant community and seed bank dynamics

Our structural equation modeling (SEM) reveals distinct effects of interannual variation in precipitation and herbivory on the dynamics of the ephemeral plant community and the soil seed bank (Figure 5a,b). In both treatments, interannual variation in precipitation positively impacted *Plantago hispidula* cover and exotic plant species richness. Only in the absence of herbivores did precipitation positively affect native plant richness, while precipitation positively impacted native seed species richness where herbivores were present. As expected, no significant relationship was observed between small mammals and other variables without herbivory.

The SEM model for the ephemeral plant community and soil seed bank with herbivores fit the data well ($\chi^2 = 0.535$ with $p = 0.997$ and six degrees of freedom, and Fisher's $C = 18.021$ with $p = 0.115$ and 12 degrees of freedom). This model indicates that native plant richness is positively and strongly influenced by *Plantago hispidula* cover, but is negatively affected by small mammals (Figure 5a). Finally, we found that native plant richness increases exotic plant species richness, while exotic plant richness increases native seed species richness (Appendices S6–S8).

The SEM model for the ephemeral plant community and soil seed bank without herbivores also fit the data well ($\chi^2 = 0.863$ with $p = 0.649$ and two degrees of freedom and Fisher's $C = 3.727$ with $p = 0.444$ and four degrees of freedom). In contrast, this SEM model shows a loss of the regulatory effect of *Plantago hispidula* on

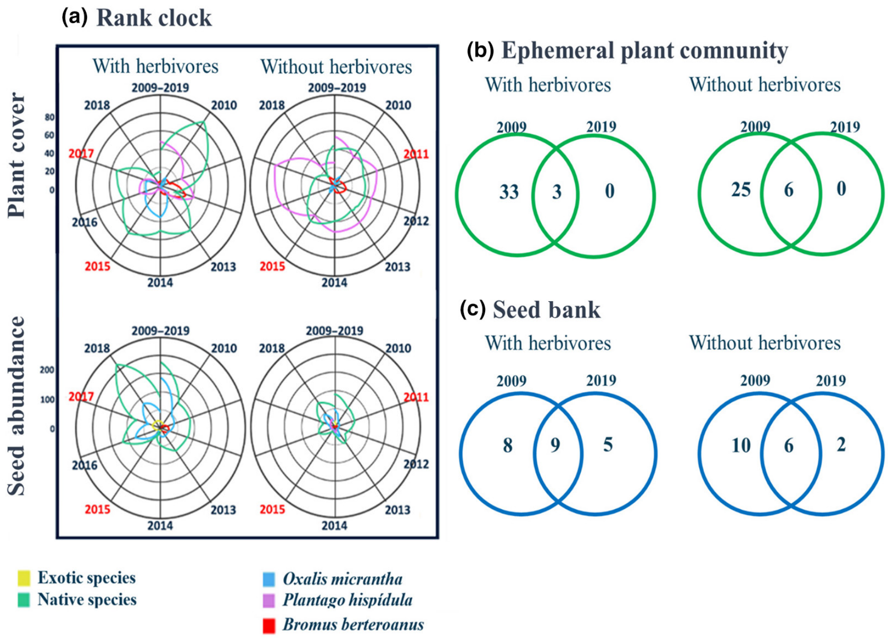

FIGURE 4 (a) Range clocks showing temporal shifts in the abundance of three dominant native ephemeral plant species, *Bromus berteroanus* (red), *Oxalis micrantha* (light blue), and *Plantago hispidula* (magenta), and two functional groups, native (green) and exotic (yellow), with and without herbivores in terms of plant cover and seed abundance. Vertical black lines represent study years (2009–2019). Years with high precipitation are represented in red. (b, c) Venn diagram analysis of ephemeral plant species (green) and seed bank (blue), respectively, for each treatment (with and without herbivores). Each circle represents the number of species in the first (2009) and last (2019) sampling year; where circles overlap, species that occur in both years are shown, and non-overlapping parts of the circles show unique species. Numbers in each section of the Venn diagram represent the number of species.

native plant species richness, while *Plantago hispidula* reduced exotic plant species richness and increased native seed species richness (Figure 5b). Finally, *Plantago hispidula* and exotic species richness of seeds jointly and directly increased native species richness of seeds (Appendices S6, S9, S10).

4 | DISCUSSION

Native herbivores are essential for regulating plant communities and soil seed banks (Koerner et al., 2014; Roy et al., 2020). However, climatic variability in arid and semi-arid ecosystems can mask the real effect of herbivores (Jia et al., 2018). In this study, we attempted to elucidate the impacts of small mammals on plant and seed dynamics of annual plants. Here, we found that the absence of herbivores alters ephemeral plant community dynamics more strongly than that of the soil seed bank, suggesting that either buffering effects or bet-hedging are dominant strategies in this ecosystem (Plue et al., 2021). Our SEM indicated that herbivory directly and negatively regulates native plant richness, which were largely canceled out by the indirect effects of precipitation, which acted upon native plant species richness via the abundance of *Plantago hispidula*, the dominant species in the experiment. Our results suggest, therefore, that abiotic conditions regulate ephemeral plant community and seed bank dynamics both directly and indirectly to a greater extent than herbivores.

4.1 | Dominant species as regulators of ephemeral plant and soil seed bank dynamics

In our SEM models, we initially hypothesized that *Plantago hispidula* would mediate the effects of small mammals on plant richness and, consequently, affect native and exotic seed richness. However, we found that micromammals do not directly regulate the abundance of dominant species. Rather, we find that precipitation impacts positively on native plant species richness through its effects on *Plantago hispidula* and directly on exotic plant richness in communities with herbivores, whereas in communities without herbivores the effect of precipitation is direct and positive for both native and exotic plant richness. Interestingly, in the absence of herbivores, there was a higher abundance of *Plantago hispidula*, which—depending on the context—may limit the species richness of exotic plant species. These results are consistent with previous studies showing that dominant species can be good competitors and prevent the spread of exotic species (e.g., Fargione et al., 2003). This result is also partially consistent with what other authors have postulated, that is, that dominant species often monopolize resources and influence community structure, including species diversity (Sasaki & Lauenroth, 2011; Koerner et al., 2018). Therefore, reduced dominance (or higher evenness) may be directly related to an increased availability of limiting resources such as light, nutrients and water and may lead to an increased abundance of less common species, colonization of new species, and reduced local extinctions (Kigel et al., 2021). We

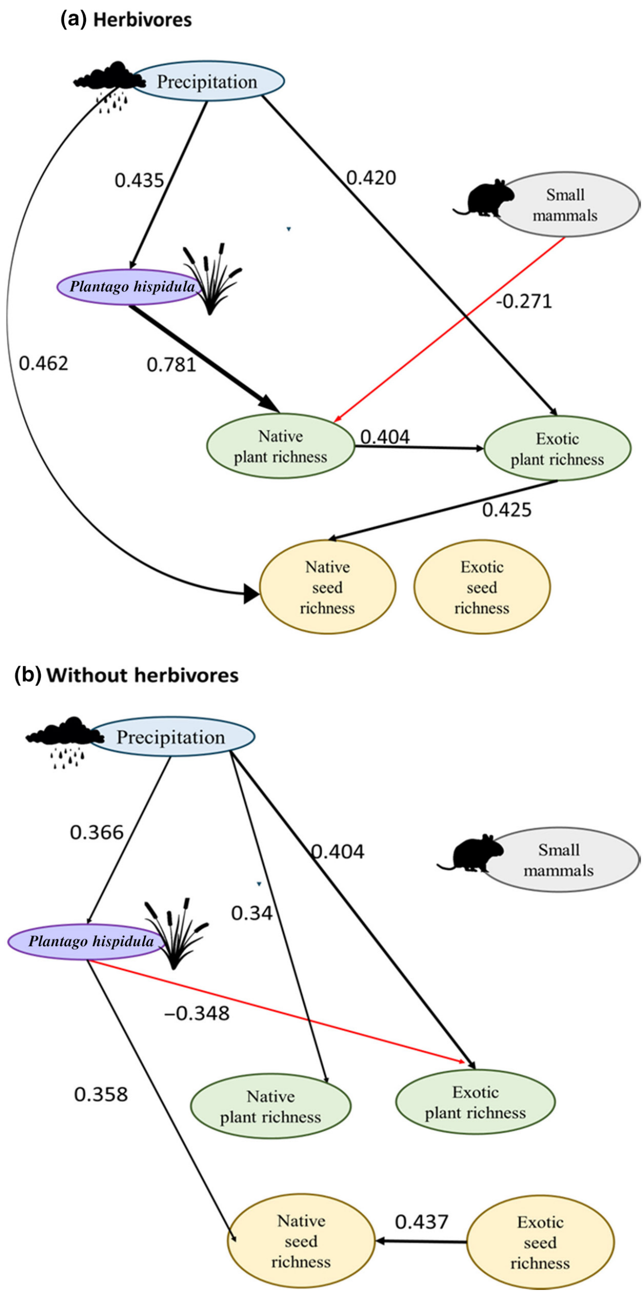

FIGURE 5 Direct and indirect effects of interannual variation in precipitation and herbivore abundance on the dynamics of native and exotic ephemeral plants and the seed bank. (a) Here, we evaluate these effects in communities with herbivores and, in (b), in communities without herbivores using structural equation models (SEM). Arrows indicate the relationship between variables and are proportional to the strength of the standardized coefficients. Solid black lines indicate positive relationships and solid red lines indicate negative relationships. The numbers adjacent to the arrows are standardized path coefficients and indicate the effect size of the relationship. The model fit with herbivores has the following parameters $\chi^2=0.535$ with $p=0.997$ and six degrees of freedom, and Fisher's $C=18.021$ with $p=0.115$ and 12 degrees of freedom. The model fit without herbivores has the following values: $\chi^2=0.863$ with $p=0.649$ and two degrees of freedom and Fisher's $C=3.727$ with $p=0.444$ and four degrees of freedom (more information on the model in Appendices S6–S10).

did not find a direct link between herbivory and the abundance of *Plantago hispidula*, although its abundance is higher in plots without herbivory. This finding suggests that the effects of small herbivores may reflect that they tend to be more selective in their diet and consume less plant biomass due to their lower body mass, which has a similar effect on the abundance of most ephemeral plant species and the maintenance of community structure (Jia et al., 2018), unlike the effects expected from large herbivores that mainly consume dominant plants (Gutiérrez et al., 1997; Maron et al., 2012; Larios et al., 2017).

4.2 | Temporal patterns of ephemeral plant communities and the soil seed bank

While our structural equation modeling (SEM) analyses indicate that precipitation plays a central role in regulating the richness of ephemeral plant communities, as expected in the context of an arid study, these patterns do not hold consistently when examining herbivore impact. In particular, this discrepancy occurs despite the fact that precipitation levels are uniform in both herbivore presence and absence scenarios. In the presence of herbivores, our results show a clear trend. Here we observe a decrease in the cover and diversity of the total plant community, including native species. In contrast, the cover of exotic species shows an increase (Table 1 and Figure 2). Our SEM suggests that, compared to the positive effect of *Plantago hispidula* abundance, herbivore abundance has a negative effect on native plant richness, albeit of a smaller magnitude. This effect indirectly extends to exotic plant species. Conversely, in the absence of herbivores, we observed a direct negative effect of *Plantago hispidula* abundance on exotic plant richness. Together, these results suggest that herbivory increases the diversity of ephemeral plant communities. This may occur by reducing competition between plants or by increasing resource availability (Tilman & Pacala, 1993). In addition, short periods of restricted species dominance caused by herbivores may increase the abundance of exotic plant species, which are often more opportunistic and more readily established than native species (Hillebrand et al., 2008; Hooper et al., 2012; Mortensen et al., 2018). Furthermore, the presence of small herbivores can contribute to an increase in ephemeral plant species richness through mechanisms such as burrow construction (Hillebrand et al., 2008; Hooper et al., 2012). This activity can create favorable conditions for germination, facilitate the redistribution of nutrients and even aid in the dispersal of seeds (Maron & Vilà, 2001; Escobedo et al., 2017).

We found that ephemeral plant community dynamics are markedly different from soil seed bank dynamics (Figures 2 and 3). Our results support the idea that the structure of seed banks is more resilient to long-term changes than that of ephemeral plant communities (DeMalach et al., 2021; Plue et al., 2021). First, our analysis showed that, although seed abundance in the presence of herbivory is low, seed bank structure was similar over time, in contrast to the greater interannual fluctuations in plant community structure

(Figure 4). Secondly, we found that seed turnover rates did not vary between years or treatments, in contrast to that of plants, which only differed between years (Appendix S4). This interannual variation is indirectly associated with interannual variation in rainfall, the main limiting factor in our study system (Figure 5). This finding is consistent with the idea of the ability of some species to hold out until better conditions allow germination and thus remain in the seed bank until the next season, a mechanism known as the storage effect (Facelli et al., 2005; Chesson et al., 2012).

Our results indicate that ephemeral plant community and soil seed bank dynamics are influenced by interannual rainfall variability, in addition to the presence of small herbivores. We found that the diversity of the ephemeral plant community, the cover of native species, and the cover of *Plantago hispidula* increased in wet years (Figure 2). This agrees with previous research at the study site (Gutiérrez et al., 1993a, 1993b; Gutiérrez et al., 1997). In addition, there was an increase in the abundance of seeds in the soil bank in wet years (Figure 4). These results confirm that the seed bank has a delayed but positive response to increased rainfall, as reported in a previous study (Gutiérrez & Meserve 2000, 2003). Our results show changing patterns of plant and seed abundance (Figure 4). High-rainfall years had higher plant cover and lower seed abundance, with opposite patterns in dry years. For example, in 2017, native plant cover in communities with herbivory averaged 54.86%, while seed abundance was 91 seeds per cm^3, equivalent to 10% of the abundance in a high-rainfall year. In contrast, in 2018, one year after the rainfall event and coincidentally a dry year, native plant cover was 15%, and seed abundance was 274 seeds per cm^3. Annual plants depend on the storage effect to persist, especially in semi-arid and arid ecosystems (Chesson et al., 2012; Sotomayor & Gutiérrez, 2015). In years with favorable conditions, e.g., high rainfall, germination rates often increase, leading to a decrease in seeds in the soil, but in the following season, they also produce more seeds (Funes et al., 1999; Clauss & Venable, 2000; Fenner et al., 2005; Ooi, 2012). Records indicate that extreme ENSO-related precipitation events may act as periods of seed bank replenishment, resulting in years with less precipitation in which decreases in seed density are not substantial (Holmgren et al., 2006). There is increasing empirical evidence that soil seed banks are a vital component in maintaining plant biodiversity under climate change through mechanisms such as rescue and storage effects (Chesson, 2000; Royo & Ristau, 2013; Vandvik et al., 2016; Plue et al., 2021), gene pool enhancement (Honnay et al., 2008), and demographic buffering capacity (Piessens et al., 2004).

Our results show that the abundance of *Plantago hispidula* and interannual variation in precipitation, plays a key role in regulating plant richness. In the presence of herbivores, there is a clear positive impact on the richness of native plant species. This positive effect is direct and operates indirectly through the enhancement of native plant richness, subsequently influencing the richness of exotic plant species. On the contrary, when herbivores are absent, their influence takes a negative turn, directly affecting the richness of exotic species. On the other hand, our results highlight the role of the seed bank as a possible buffer for changes associated with interannual variation in rainfall, which indirectly mediates ephemeral plant community dynamics. Although the ephemeral plant community shows a response to climatic variation in semi-arid ecosystems, long-term experiments are a crucial tool to determine the potential effects of other drivers of global change that may only become apparent over longer time periods.

AUTHOR CONTRIBUTIONS

María del Pilar Fernández conceived the research questions and collected the data; María del Pilar Fernández, Dylan Craven, and Fernando Alfaro compiled the data set and contributed to its analysis and interpretation; Douglas Kelt, Julio Gutierrez and Peter Meserve are the designers of the Fray Jorge Long-Term Socio-Ecological Research (LTSER) and gave permission to use the cover plants, abundance seed, and precipitation data. Alejandra Troncoso is the current LTSER project manager and contributed to the revision of the manuscript. All authors contributed critically to the manuscript and gave final approval for publication.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Loss-Herbivores_JVS at https://github.com/fernandezmayor/LOSS-OF-NATIVE-HERBIVORES.git.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. List of ephemeral species categorized by scientific name, their respective acronyms, origin (native and exotic), and life form (annuals or geophytes)

Appendix S2. Rank abundance curve of the seed bank and ephemeral plant community for two treatments (with and without herbivores)

Appendix S3. A priori SEM conceptual model, including all expected effects and their signs

Appendix S4. Total turnover by appearances and disappearances for plant communities and the seed bank with and without herbivores

Appendix S5. Table of probability values of the generalized additive mixed model (GAMM) of species turnover for plants and seeds

Appendix S6. Model with and without herbivores

Appendix S7. Coefficients of the model with herbivores

Appendix S8. Individual R^2 of model with herbivores

Appendix S9. Coefficients of the model without herbivores

Appendix S10. Individual R^2 of model without herbivores

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