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Editorial

Twenty-five years of research in the north-central Chilean semiarid zone: The Fray Jorge Long-Term Socio-Ecological Research (LTSER) site and Norte Chico

This special issue of the *Journal of Arid Environments* includes papers addressing diverse aspects of the abiotic and biotic environment of the Mediterranean semiarid drylands in north-central Chile (29–32°S, the Norte Chico), as well as a review and recent research findings on one of the longest-running field experiments in global drylands, the Fray Jorge Long-Term Socio-Ecological Research site (LTSER), located in Bosque Fray Jorge National Park. The Fray Jorge LTSER started in 1989 and has become a sentinel site for monitoring effects of resource variability, climate change, and extreme climatic events on diverse groups including plants, small mammals, and their predators, and more recently arthropods and songbirds. This special issue takes a multidisciplinary approach that includes reviews, new data, and research ideas grouped into two sections: (i) climate, vegetation and avifauna of the national park and semiarid drylands of north-central Chile, and; (ii) focal papers summarizing some of the research performed in Fray Jorge LTSER. This effort include the long-term monitoring of different aspects and components of the biotic community: e.g., soil microorganisms, shrub and ephemeral plant species, arthropods, native small mammals (including the main herbivores in the system), and their vertebrate predators; analysis of the interactions among these components across trophic levels; and finally, analyses of the biotic responses to rainfall, the main abiotic factor governing these communities. This special issue ends with a review of the research performed over 25 years on biotic interactions including predation, herbivory, and interspecific competition and community dynamics in the semiarid Fray Jorge LTSER (Meserve et al., 2016a).

Drawing on contributors in this special issue, we summarize the main environmental characteristics of these temperate drylands in western South America and Bosque Fray Jorge National Park (BFJNP; Fig. 1). The Norte Chico is an ecotonal region sandwiched between the more mesic Chilean Mediterranean region to the south (a recognized worldwide biodiversity hotspot; Myers et al., 2000) and the hyperarid Atacama Desert (the driest non-polar desert in the world) just to the north (Fig. 1). Longitudinally, Norte Chico is delimited by the Pacific Ocean to the west and the Andean crest to the east, with peaks at this latitude over 5000 m a.s.l. The general climate is Mediterranean semiarid with a mean annual precipitation of 126.8 mm (average values for the last ca. 100 years in the vicinity of the Fray Jorge LTSER, Fig. 2). Rainfall occurs predominantly in winter, between May and October, while the rest of the year it is dry and warm near the coast (e.g., mean temperature range: 12–18 °C at 2 m above ground, Montecinos et al., 2016) with marked variations from the coast to the inland areas (Fig. 3). Rainfall at Fray Jorge LTSER and nearby areas exhibits marked interannual variability (CV > 65%), with very dry years (e.g., 1998; 11 mm) and relatively wet years (e.g., 2002; 359 mm, Fig. 2 and Meserve et al., 2016a). These interannual climatic fluctuations are strongly influenced by El Niño – Southern Oscillation (ENSO) events; irregular oscillations between warm-rainy (El Niño) and cold-dry (La Niña) periods (Aceituno, 1992) induce huge variations in aboveground net primary productivity and plant diversity (Gutiérrez et al., 2010; Jiménez et al., 2011) with cascading effects across trophic levels and ecosystem functions (Acosta-Jamett et al., 2016; Aguilera et al., 2016; Jiménez et al., 2016; Kelt et al., 2016; Madrigal-González et al., 2016; Meserve et al., 2011, 2016a, b).

The climate of the region is influenced mainly by three drivers; these are atmospheric (the southeast Pacific anticyclone), oceanic (the cold Humboldt Current, affecting the values of sea and air temperatures that lower the expected temperature inland), and orographic factors (Montecinos et al., 2016). These features determine thermally-induced wind regimes and the formation of low cloud stratum throughout the year along the coastline. Above 400 m a.s.l. these clouds are intercepted by the N–S oriented Coastal Range leading to frequent fog. These conditions lead to fog formation allowing the presence of a narrow strip of remnant patches of Valdivian temperate rainforest within a broader matrix of semiarid shrublands between 450 and 660 m a.s.l. (Squeo et al., 2016). These fog-forests are relicts of a more widespread forest cover during the Tertiary and Quaternary (Villagrán et al., 2004; Squeo et al., 2016), although these were never contiguous with the more southern forests. Thus, remnant forests in BFJNP are the northern-most of such fog-forest relicts (Squeo et al., 2016) and are subjected to long-term isolation and dispersal filters (Cornelius et al., 2000; Reid et al., 2002).

The ecotonal nature of Norte Chico results in high species diversity (Kelt et al., 2016; Meserve et al., 2016b; Squeo et al., 2016) and belies traditional perceptions of semi-arid systems as being impoverished habitats with low biotic diversity. However, this area has also a multi-century history of anthropogenic influences such as clearing, overgrazing, and neglect, and as a result it has become highly desertified (Bahre, 1979; Kelt et al., 2016; Squeo et al., 2016). In this sense BFJNP (ca. 9000 ha; Fig. 1) is a veritable oasis; it has been protected from grazing and disturbance since its

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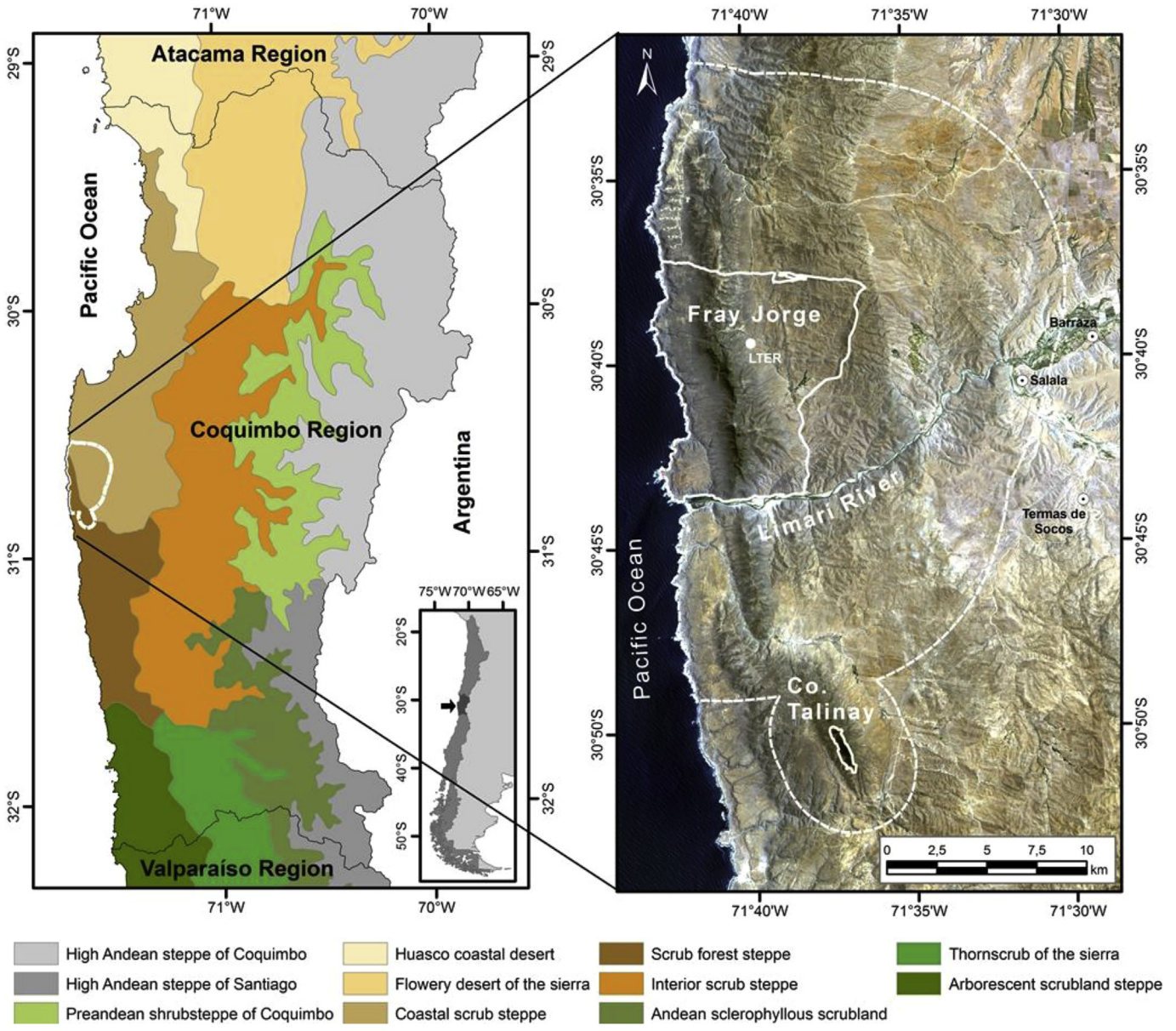

Fig. 1. Location and limits of Bosque Fray Jorge National Park (white solid line, right panel). Both panels include the National Park buffer area (white dashed line, see details in Squeo et al., 2016) and the left panel shows major vegetation types in the region, after Gajardo (1994).

establishment in 1941, and constitutes a remnant of natural vegetation that dominated the Coastal Desert before European Colonization; that is, a natural mosaic of semiarid shrublands that includes thorn scrub (64% of the total park area) and scrub with cacti and other succulents (34%); perennial shrub cover exceeds 40% (Squeo et al., 2016). Additionally, BFJNP includes the previously-noted relict fog forest (2.5%). Its conservation status and this unique combination of xerophytic and temperate rainforest floras partly explain the high plant species richness in BFJNP and surroundings. Squeo et al. (2001, 2016) highlight that BFJNP hosts the highest plant species diversity (i.e., 440 native species, including 266 endemic to Chile, and 17 that are unique to the relict fog forest) and the highest concentration of species with conservation status concern from all north-central Chile. Moreover, the Coquimbo Region, where BFJNP is located, is the most floristically diverse of all of Chile's Regions (Squeo et al., 2012). Summing up other biodiversity characteristics of BFJNP and Norte Chico, Jaksic et al. (2004) estimate the total number of species in this park at 227, including 123 birds (54%), 74 arthropods (33%), 23 mammalian (10%), five reptilian (2%) and two amphibian (1%) species. Preliminary analysis of arthropod collections by Meserve et al. (2016b) suggest a much greater diversity, and underscore the importance of basic scientific investigation here. For example, in 10 years of monitoring terrestrial arthropod abundance and biomass in the Fray Jorge LTSER from 2003 to 2013, members of 5 classes, 22 orders and 81 families were distinguished; among volant arthropods members of 2 classes, 18 orders and 113 families were verified; both terrestrial and volant arthropods exhibited pronounced seasonality in collections. After nearly a decade of avian surveys, Kelt et al. (2016) increase the number of birds known from the park to ca. 130 species, with 123 of them inhabiting the semiarid shrubland. They document 63 terrestrial bird species forming avian

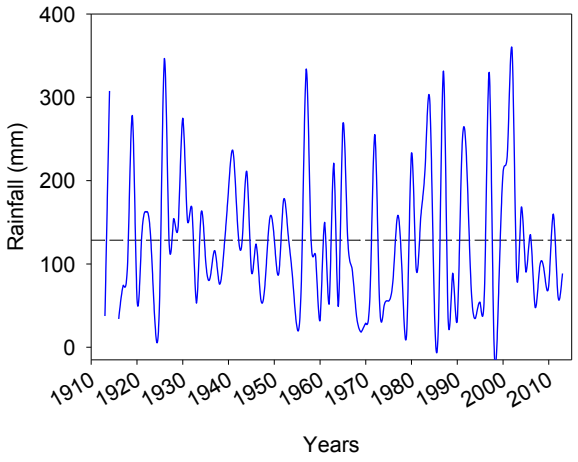

Fig. 2. Annual rainfall from 1913 to 2013 registered in the weather stations of Fray Jorge LTSER, Bosque Fray Jorge National Park (BFJNP; 71°40′ W, 30°38′ S, 230 m a.s.l.) and Ovalle (71°11′ W, 30°36′ S, 292 m a.s.l.), 90 km inland from BFJNP. Data collected from the Anuarios Climatológicos, Dirección Meteorológica de Chile (1913–1988) and from Fray Jorge LTSER weather station since 1989 onwards. The dashed line represents the long-term annual mean (ca. 127 mm).

assemblages with predictable seasonal and interannual structure that fall into 4 occupancy patterns: year-round residents, winter visitors, summer breeders, and transients. They also document a gradual transition of the avifaunal assemblages that may be a response to anthropogenic influence and/or climate change, and provide a comprehensive review of the literature on the natural history and ecology of birds inhabiting the remnant fog-forest and semiarid shrublands in this region. Both Squeo et al. (2016) and Kelt et al. (2016) highlight potential threats to BFJNP undisturbed ecosystems and north-central Chile biodiversity.

The second section of this special issue includes reports on medium-to long-term studies performed in the Fray Jorge LTSER and reflecting different aspects and components of the biotic community and the interactions among them. One conclusion of all these studies is the paramount influence of ENSO-driven oscillations in rainfall on diverse biotic processes. As Meserve et al. (2011, 2016a) note, the implications of such changes in annual rainfall for this semiarid region are diverse. Increased rainfall in El Niño years leads to dramatic changes in ephemeral plant cover (range: 0–80%) while in ensuing dry La Niña years plant cover sharply decreases, promoting changes in species composition and even favoring colonization by exotic species during extreme droughts (Jimenez et al., 2011). In a response that appears to be a consequence of upwardly cascading effects of high rainfall on productivity in regions that are extremely arid (Holmgren et al., 2001, 2006), all animal groups studied exhibit dramatic delayed increases during and following El Niño events, including small mammals and their vertebrate predators (see references in Meserve et al. (2011) and review in Meserve et al. (2016a)), while the opposite occurs during severe droughts. Research on birds has spanned a relatively dry period here, and we look forward to documenting any responses in this group to increased rainfall in the future.

This major control of precipitation on population dynamics appears to dominate the nature of interactions among organisms within and across trophic levels in this system. Starting belowground, Aguilera et al. (2016) show over ten years of contrasting precipitation that root colonization by arbuscular mycorrhizae (AM) is higher in dry compared to wet years. This enhanced AM colonization likely confers the plants some degree of resistance to drought. Meanwhile, free-living soil bacteria and fungi are more abundant during wet years. These responses of the soil microbial community to rainfall are modulated by the spatial and temporal heterogeneity of soil resources, with all soil microorganisms more abundant in the nutrient-rich and milder microhabitat under shrub canopies than in open spaces between shrubs. Interestingly, the activity of small mammals, the main native herbivores in the area, appear to influence the abundance of soil microorganisms as well, locally modifying the distribution of soil microbial resources and likely acting as endo- or epi-zoochorus dispersers of AM spores. Madrigal-González et al. (2016) ask if the three dominant shrub species here – *Porlieria chilensis*, *Adesmia bedwellii* and *Proustia cuneifolia* – serve as nurse shrubs, enhancing ephemeral plant survival and establishment of other plants beneath their canopies, as seen in many other arid environments (Filazzola and Lortie, 2014; Flores and Jurado, 2003). However, across four relatively dry years, ephemeral biomass production and species richness were lower under these dominant shrubs when compared with areas between shrubs, and these negative effects were exacerbated in the driest years. The authors suggest that the combined effects of deep shading and drought impose functional trade-offs to ephemerals that can significantly alter nurse plant effects; that is, the positive effects of shading by nurse plants will exceed negative effects only when sufficient water is available to compensate for increased evaporative demands associated with larger above-ground photosynthetic biomass (Holmgren et al., 1997). Thus, in this system shade actually exacerbates the decline in biomass production and species richness associated with low precipitation in the driest years. Nonetheless, shrubs increased local diversity by favoring some ephemeral plant species that were absent in open areas. These results contrast with those from Molina-Montenegro et al. (2016) who show that one of these potential nurse species, *Porlieria chilensis*, a keystone shrub species in these semiarid shrublands (Gutiérrez et al., 1993; Squeo et al., 2016), does function as a nurse for other native shrub species as *Flourensia thurifera*, *Puya berteroniana* and *Senna cumingii*, enhancing survival or growth of these species beneath *Porlieria* canopy. Interestingly, consistent with Aguilera et al.'s (2016) findings, these facilitative effects of *Porlieria* seem to be mediated by the soil microbial community underneath the shrubs. Revisiting the ephemeral community, Jimenez et al. (2016) worked with changes in the abundance and cover of different native and exotic ephemeral species over 17 years of contrasting precipitation. They showed that while variation in rainfall promotes the evolution of bet-hedging strategies, the nature of these strategies varies across species, presumably to minimize competitive exclusion. They conclude that the success of two exotic ephemeral species in the diverse community of native annual species in Fray Jorge LTSER seems to reflect bet-hedging germination strategies that complement rather than compete with those expressed in dominant natives.

Addressing the effects of rainfall and its high interannual variability on the abundance and dynamics of diverse animal groups, Meserve et al. (2016b) report on monitoring of arthropod abundance and their biomass for 10 years in the Fray Jorge LTSER. Peaks in the abundance and biomass of terrestrial and volant arthropods occur in similar months (spring-early summer; August–November) with time lags of 2–4 months, and they track relatively high rainfall years (above mean annual precipitation values; >123 mm). Large increases in arthropod biomass are due mostly to increases in a few dominant groups, i.e., tenebrionid beetles (Coleoptera) in terrestrial sampling, and moths (Lepidoptera: Nocturidae, Microlepidoptera) in aerial sampling. At a very different scale, Acosta-Jamett et al. (2016) analyze the interaction between wild carnivores, native herbivores and livestock as mediated by interannual rainfall variability. Over 15 years they analyzed if native prey abundance (small mammals) in this area influence domestic livestock

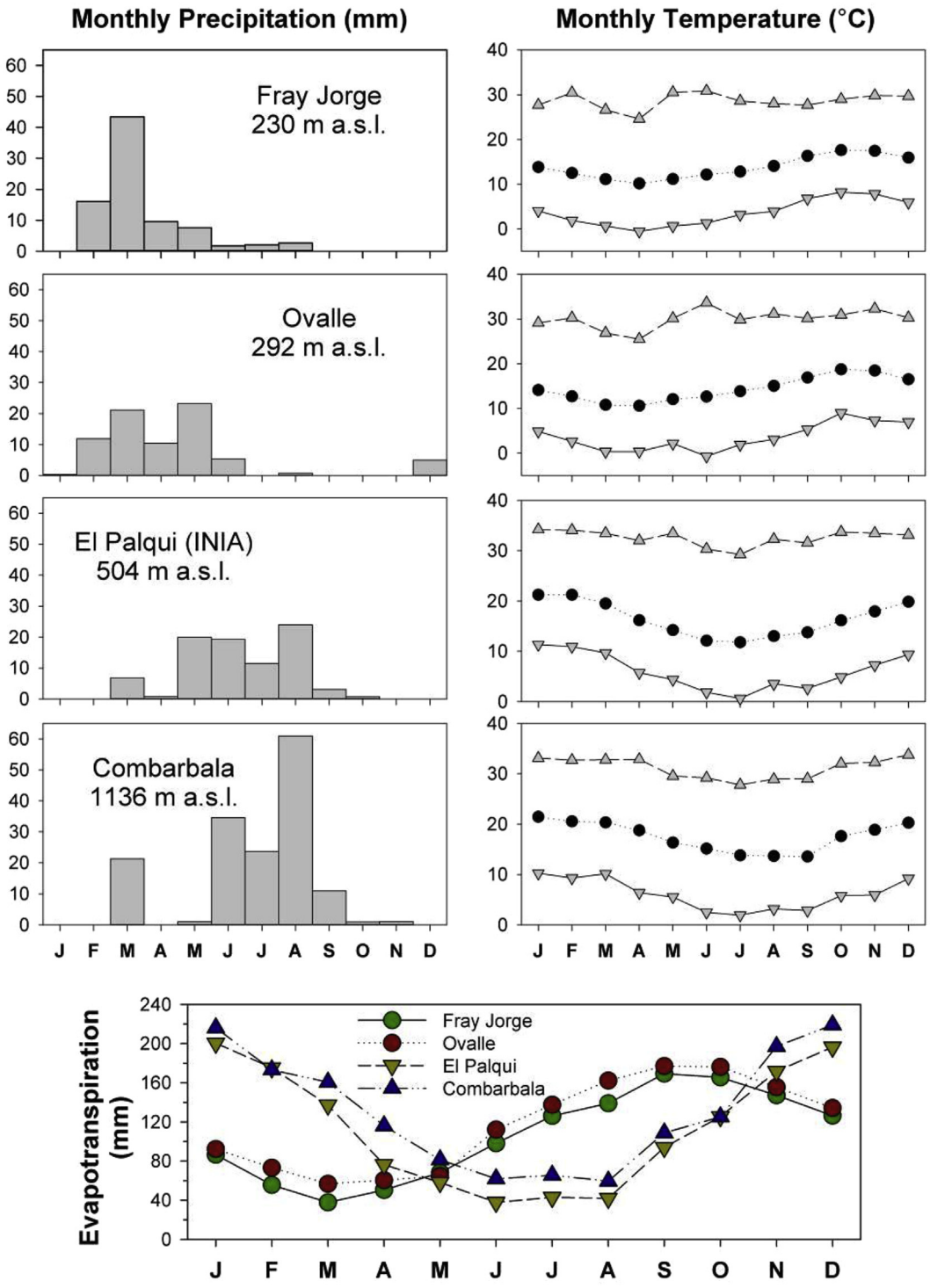

Fig. 3. Climatic data from four sites representing variation across the Coquimbo Region. Note that patterns and total annual amount of rainfall varies greatly across the region, as do monthly temperatures. Evapotranspiration (mm) at two lowland sites (Fray Jorge, Ovalle) exhibit very different patterns from that at two sites further inland and at higher elevation (El Palqui, Combarbala). All data from www.ceazamet.cl but these differ in duration as follows: Fray Jorge (Jan 2010–Dec 2014), Ovalle (Jan 2013–Aug 2015), El Palqui (Oct 2010–Aug 2015), Combarbala (Oct 2013–Aug 2015).

predation rates by wild foxes, one of the main predators of the native small mammals. Small mammal density correlates positively with rainfall from the previous year (see also Previtali et al., 2009), and when small mammal populations decline livestock predation by foxes increases, but only after two years of low rainfall. It seems that, again, rainfall modulates this interaction and wild carnivores employ functional responses in response to varying prey availability, shifting from wild to domestic prey during periods of drought.

Finally, Meserve et al. (2016a) ends this special issue with an overview of the 25 years of investigations into the role of biotic

interactions including predation, herbivory, interspecific competition, and community dynamics in the semiarid shrubland of the Fray Jorge LTSER. They describe a large-scale multi-factorial field manipulation where they selectively excluded vertebrate predators and small mammals, most of which are herbivorous or omnivorous (and hence partly herbivorous). They document important "top-down" effects of predation on some small mammal species and of small mammals on some plant species. However, populations of plants and small mammals are strongly influenced by rainfall fluctuations driven by ENSO events; high rainfall episodes result in large "bottom-up" increases in both plants and animals, whereas in dry years populations are controlled mainly by resource limitation.

Superimposed on evidence for the role of biotic interactions has been a major shift in the composition of the small mammal assemblage. After a prolonged high rainfall event in 2000–2003, the abundance and biomass proportions of an herbivorous rodent, the degu (*Octodon degus*), began to increase, such they now dominate the small mammal assemblage. In addition, temporal changes in their numbers and biomass have decreased. We posit that although mean rainfall has only increased slightly since 2003, annual variation in seasonal rainfall has declined dramatically. This has enabled the longer-lived degu to survive relatively short drought periods, and to increase cumulatively in the assemblage despite the higher fecundity and immigration rates of short-lived (but fluctuating) sigmodontines that were formerly dominant (e.g., *Abrothrix olivacea* and *Phyllotis darwini*; Meserve et al., 2011, 2016a). Since degus are important herbivores, their potential effects on both native and exotic ephemerals may lead to larger scale changes in the plant community. Additionally, changes in the rainfall regime from strong interannual fluctuations due to aperiodic ENSO-events, to one with a more equitable pattern of annual rainfall may ultimately lead to other larger scale changes in the system. This may one of the first examples of the biotic consequences of long-term climatic change in this region. Continued monitoring of changes in important biotic components of this system may reveal other long-term changes over time.

Overall, research reviewed in this Special Issue shows that because intervals between ENSO events are long, and the effects long-lasting, whereas bottom-up and top-down biotic responses to rainfall fluctuation range from fast to slow, long-term studies are essential for understanding the community dynamics and functions of these semiarid ecosystems. With the hyperarid Atacama Desert just to the north, and the more mesic Chilean Mediterranean biodiversity hotspot to the south, this region presents an unusually interesting fauna and flora juxtaposed within the context of potentially sweeping climatic and environmental changes. Indeed, placed within the broader perspective of long-term research on ephemeral and perennial plants, small mammals, and predators, we believe that BFJNP and Fray Jorge LTSER is poised to become a global focal point for research on the impacts of climate change in ecotonal regions, and hope that this compilation of multidisciplinary long-term ecological studies in this special issue will contribute to a better understanding of the functioning of global arid systems. Certainly the Fray Jorge LTSER has already assumed an important role as a sentinel site for monitoring effects of resource variability, climate change, and extreme climatic events in aridlands.

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