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Exclusion of small mammals and lagomorphs invasion interact with human-trampling to drive changes in topsoil microbial community structure and function in semiarid Chile

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ABSTRACT

Species losses and additions can disrupt the relationship between resident species and the structure and functioning of ecosystems. Persistent human-trampling, on the other hand, can have similar effects through the disruption of biocrusts on surface soils of semiarid systems, affecting soil stability and fixation of carbon and nitrogen. Here, we tested the interactive and synergistic impacts of the exclusion of native mammalian herbivores and the effects of introduced lagomorphs in a semiarid thorn scrub ecosystem, where soils were subjected to two different trampling intensities (i.e., trampled and non-trampled). We postulated that because of their differential habitat use and fossorial activities, with respect to native small mammals, lagomorphs would have strong negative effects on soil structure, biocrust cover, and biocrust bacterial community structure. Our expectations were that changes in biocrust cover in response to trampling where native mammals were excluded, but exotic lagomorphs were present, will spread their impacts on soil chemical and physical features. To test our hypotheses, we measured changes in soil biogeochemical properties in four experimental plots where lagomorphs (L)/small mammals (SM) were experimentally manipulated to exclude them from the plots (−), or let them be present (+). The experimental combinations monitored were: -L/+SM, -L/-SM, +L/+SM, and +L/-SM. Results showed that human-trampling disturbance interacted with the loss of native small mammals and the presence of non-native lagomorphs to cause large changes on biological (i.e., biocrust cover, bacterial and *nifH* genes abundance), physical (i.e., soil moisture and soil stability) and chemical (i.e., TC and TN) soil features. The relative impacts of trampling disturbance on biological and physicochemical features were strongly influenced by the presence of non-native lagomorphs. For example, larger decreases in biocrust cover and bacterial abundance were observed in treatments without lagomorphs (-L/+SM; -L/-SM). In turn, losses of biocrust cover, in addition to trampling, determined decreases in soil stability in all treatments. These results suggest that non-native lagomorphs surpass the effects of the loss of native small mammals in reducing soil quality and productivity. Therefore, human-trampling has the potential to convert low disturbed soils, as those observed in non-trampled soils in treatments -L/+SM, -L/-SM into poor soils with low biocrusts cover and concomitant low stability, as observed in +L/+SM; +L/-SM treatments. These findings agree with previous observations that different components of global change act in synergic ways in fragile, water-limited environments. Because

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biological invasions and soil surface disturbance are becoming widespread in dryland regions globally, understanding the long-term consequences of these interactions is essential.

1. Introduction

Above and belowground processes in ecosystems are often integrated by the activities of vertebrate herbivores and this integration can become decoupled when dominant native herbivores are excluded (Bardgett and Wardle, 2003; Harrison and Bardgett, 2008). Accordingly, the loss of native herbivores is often accompanied by a decline in native functional diversity, which can substantially impact soil ecosystem processes (Neely et al., 2009; IPCC, 2013; Fleming et al., 2014; Eldridge et al., 2017). This loss, in turn, can accelerate the effect of other forms of environmental degradation, such as global warming, through altering soil carbon (C) and nitrogen (N) cycling, in addition to enhancing soil erosion (Stavi et al., 2008; Hooper et al., 2012; Fleming et al., 2014). Drylands are expected to undergo critical environmental transformations as a consequence of climate change drivers, as well as through the intense disturbances caused by exotic animal grazing and trampling (Eldridge et al., 2016; Maestre et al., 2016). Many dryland soils are thin and oligotrophic, with low C and N contents, and hence recovery rates after physical disturbances can be exceedingly slow (Barger et al., 2006; Housman et al., 2006; Ferrenberg et al., 2015). Also, soil surface disruption by trampling and digging decreases soil stability and accelerates fertility loss via wind and water erosion (Eldridge and Myers, 2001; Neff et al., 2005; Eldridge and Koen, 2008). Despite increasing evidence for soil disruption due to the loss of native herbivores, and concomitant increases in exotic species activities and trampling (Eldridge and Myers, 2001; Reid et al., 2005; Eldridge and Koen, 2008; Kuske et al., 2012; Ferrenberg et al., 2015), the interactive effects of these three critical factors upon soil structure and function remain poorly understood.

In water-limited ecosystems, vascular plant cover is sparse and soils between vegetation patches are often occupied by a biotic consortium of cyanobacteria, lichens, heterotrophic bacteria and fungi, algae, and mosses, known collectively as biological soil crusts or biocrusts (Belnap and Lange, 2003; Belnap, 2006). This multi-trophic assembly of microorganisms often represents the functional interface between the soil and the atmosphere in these semiarid ecosystems, driving the cycles of resources (e.g., soil water) and elements (e.g., C, N, and phosphorus) (Chamizo et al., 2012; Elbert et al., 2012). As biocrusts become dominated by lichens or mosses, C and N fixation increase in tandem, along with soil aggregation and stability that prevents erosion (Eldridge and Leys, 2003; Elbert et al., 2012; Delgado-Baquerizo et al., 2013). As digging and trampling by exotic animals increases, cover and connectivity between biocrust patches decreases substantially (Eldridge et al., 2016).

Physical soil disturbance can modify the functional structure of biocrusts by transforming late successional assemblages dominated by lichens and mosses into early successional ones dominated by cyanobacteria; these early successional communities are both less productive and have limited ability to stabilize soils (Ferrenberg et al., 2015; Belnap et al., 2016). In semiarid environments of central Chile, under a Mediterranean-type climate, with a pronounced summer drought, late-successional biocrusts are naturally absent or only occur in low abundance; therefore, most soils are often covered by cyanobacterial-dominated biocrusts (Castillo-Monroy and Maestre, 2011). The dominant native small mammals in these sites graze on annual herbs and preferentially excavate burrows beneath shrubs, cactus, and rocks. In contrast to native herbivores, the introduced European hare (*Lepus europaeus*) and the European rabbit (*Oryctolagus cuniculus*) have a marked preference for burrowing in open areas between shrubs (Jaksic et al., 1979; Fuentes et al., 1983); often resulting in soil disruption between bushes (Jaksic et al., 1979). In addition, introduced lagomorphs facilitate invasion by exotic grasses as they forage heavily on the native perennial species (Gutierrez et al., 2010). As in other semiarid environments, in semiarid Chile, mammals and other native species of vertebrates (e.g., reptiles and birds) are affected by habitat fragmentation (Araya et al., 1992), species invasion (Jimenez et al., 2011; Meserve et al., 2016), livestock grazing and changes in land use (Acosta-Jamett et al., 2016).

In this research, we assessed the effects of a 10-year exclusion of native and introduced herbivores on soil physical and chemical features, as well as on the structure and function of the bacterial biocrust community in a Chilean semiarid thorn scrub. Specifically, we hypothesized that (i) the presence and activities of invasive lagomorphs and exclusion of native herbivores, combined with human trampling, will reduce biocrust cover and bacterial abundance, in turn driving changes in community structure and composition, and (ii) changes in bacterial community organization will have a cascading effect on edaphic physicochemical properties, such as nutrient cycling processes and soil stability. Further, we hypothesize that soil fertility will decline in parallel with biocrust cover loss and decreasing bacterial abundance across the disturbance gradient of trampling intensity and mammal burrowing.

2. Materials and methods

2.1. Study site

The study site was located in the Fray Jorge Forest National Park (FJ henceforth), near the southern border of the Atacama Desert in central Chile (71°39′W, 30°39′S). The prevailing climate is semiarid, with a strong Mediterranean influence, with 90% of precipitation concentrated in the winter months (May through September) and large inter-annual variability in total rainfall. The mean annual temperature (MAT) is ~18 °C, with maximum temperatures during the warm and dry summers (~27 °C) and minimum temperatures during cold winters (~4 °C) (Jimenez et al., 2011; Aguilera et al., 2016). Mean annual precipitation over the last two decades is 127 mm (Armas et al., 2016), although El Niño–Southern Oscillation (ENSO) events promote strong variation in precipitation among years.

Soils across the study area are highly heterogeneous, with large differences in physical and chemical features between open patches without shrub cover and sites beneath the crown of dominant shrubs (Gutiérrez et al., 1993). Whereas, soil pH remained similar between these two micro-environments, electric conductivity is 5.5 fold lower in open areas. Soil texture in open areas and below shrub cover is characterized as loamy sand, with low values of silt and clay. Soil nutrients (i.e., N and P) and organic matter contents in open areas are significantly lower than in the soil underneath shrubs, and these differences are greater during the wet season (Gutiérrez et al., 1993; Aguilera et al., 1999).

The local plant community is characterized by a scattered population of drought-deciduous and evergreen spiny shrubs, 2–3 m tall, established over an ephemeral carpet of herbaceous plants on a primarily sandy substrate (Gutierrez et al., 1993). The dominant shrub species are the evergreen *Porlieria chilensis* I.M. Johnst. (Zygophyllaceae, ca. 31% cover), the drought-deciduous *Proustia cuneifolia* D. Don (Asteraceae, ca. 9% cover), the drought-semidecidous *Adesmia bedwellii* Skottsb. (Fabaceae, ca. 5% cover), and the sub-shrub *Chenopodium petiolare* Kunth (Chenopodiaceae, ca. 16% cover) (Gutierrez et al., 1997, 2004). Mean cover of all other shrub species combined was lower than 1.5%.