NON-NATIVE UNGULATES INDIRECTLY IMPACT FOLIAR ARTHROPODS BUT NOT SOIL FUNCTION

Mariano A. Rodriguez-Cabal[1*], M. Noelia Barrios-Garcia[2], Christopher J. Greyson-Gaito[3], Heather L. Slinn[3], M. Paz Tapella[4], Agustín Vitali[1], Gregory M. Crutsinger[5]

[1] Grupo de Ecología de Invasiones, INIBIOMA - CONICET, Universidad Nacional del Comahue - Av. de los Pioneros 2350, Bariloche, CP. 8400, Rio Negro – Argentina.

[2] CONICET, CENAC - APN - Fagnano 244, Bariloche, CP. 8400, Rio Negro - Argentina.

[3] Department of Integrative Biology, University of Guelph, Summerlee Science Complex, Guelph, N1G 2W1, Ontario - Canada.

[4] Facultad de Ciencias Exactas, Físicas y Naturales - Universidad Nacional de Córdoba, CP. 5000, Córdoba - Argentina.

[5] Scholar Farms, El Cerrito, CA – USA.

*Author for correspondence, email: rodriguezcabal@gmail.com

ABSTRACT

One of the greatest challenges in contemporary ecology is to understand how the homogenization of biodiversity at all levels of organization and spatial scales will influence the assembly of communities and the functioning of ecosystems. Such homogenization can occur through the gain of non-native species and the loss of native species. Here, we show that by disrupting a keystone mutualistic interaction, non-native ungulates indirectly impact foliar arthropod abundance and richness, but not soil properties (soil respiration, temperature and humidity), in a temperate forest of Patagonia. The results of this study show that the gain of non-native ungulates and the loss of a key interaction can trigger unnoticed cascading effects. Our findings highlight the importance of assessing biodiversity not only as the sum of different components but also through the direct and indirect interactions among them.

Keywords: Arthropod community; indirect effects; introduced herbivores; keystone interactions; soil microbes

INTRODUCTION

Species interactions, both direct and indirect, are the main drivers of community assembly (Holt 1977; Gross 2008, Cavieres & Badano 2009, Schöb et al. 2013). Many studies on the impact of global change overlook indirect interactions, the effects of one species on another mediated by a third (Strauss 1991; Wotton 1994), due to the complexity in quantifying their extent (Traveset and Richardson 2006; White et al. 2006; but see Stireman et al. 2005). However, in many cases indirect interactions can have greater impacts on community structure than direct interactions. The great majority of studies of indirect effects have addressed the impacts of predators (Crooks and Soule 1999; Terborgh et al. 2001; Borer et al. 2005; Mooney et al. 2010; Schmitz et al. 2000; Shurin et al. 2002; Estes et al. 2011). For example, Fukami et al. (2006) showed that predation of seabirds by introduced rats in islands of New Zealand, increased aboveground plant biomass and nutrients, and in turn altered the belowground food web. Yet, herbivores can induce strong cascading effects within food webs by altering vegetation quantity and quality (Williamson 1996; Nuttle et al. 2011; Vanbergen et al. 2006), shifting nutrient cycles, changing disturbance regimes (Williamson 1996; Mack and D’Antonio 1998) and disrupting other plant-animal interactions (Vázquez and Simberloff 2004; Pringle et al. 2007; Rodriguez-Cabal et al. 2013).

Terrestrial ecosystems consist of above- and below-ground components whose interaction influences the structuring of above- and below-ground communities (Wardle et al. 2004; Fukami et al. 2006; Peay et al. 2012, Van der Putten 2012) and ecosystem-level processes (Bardgett and

Wardle 2010). For example, aboveground herbivores can alter the quantity and quality of resources that plants produces (Bardgett and Wardle 2010). These plants in turn support two distinct food webs, the green and brown food webs. The green food web is comprised of animals exploiting the above-ground components of plants, such as flowers, leaves, fruits and shoots. However, almost 90% of the carbon fixed by plants is consumed by detritivores in the brown food web (Allison 2006; Kaspari and Yanoviak 2009) when returning to the litter and soil (Moore et al. 2004). These two food webs are closely linked at the community level with positive and negative feedbacks through direct and indirect interactions. For example, in unproductive ecosystems herbivory causes a shift of vegetation composition to well defended plants that produces poorer litter quality for associated aboveground arthropods and belowground decomposers (Wardle et al 2001, Bardgett and Wardle 2010). These herbivore-mediated changes can in turn alter soil processes by decreasing litter decomposition rate (Findlay et al 1996, Wardle et al. 2002) and soil respiration (Pastor et al. 1993, Persson et al. 2009). Similarly, by decreasing plant cover and trampling, herbivores can alter the soil microclimate conditions thereby increasing soil temperature and decreasing soil moisture (Chen et al. 2004, van der Wal et al. 2001). Therefore, these changes in above- and belowground components can influence how communities are structured and ecosystem function (Wardle et al. 2004).

In the temperate forest of Patagonia more than 70% of the woody plants depend on animals for their reproduction and seed dispersal (Armesto and Rozzi 1989; Aizen and Ezcurra 1998). In the northern portion of this temperate forest there is a keystone interaction involving a hummingbird (*Sephanoides sephaniodes*), a mistletoe (*Tristerix corymbosus*), a dominant understory shrub and mistletoe host (*Aristotelia chilensis*), and an endemic marsupial (*Dromiciops gliroides*) (Rodriguez-Cabal et al. 2013). This southern-most hummingbird relies on mistletoe nectar to survive the Patagonian winter. During the Patagonian spring the hummingbird pollinates approximately 20% of the woody plant genera in the Patagonian forests (Aizen 2003). The endemic and nocturnal marsupial (*D. gliroides*) is the only seed disperser of mistletoe in these forests; mistletoe seeds have to pass though the marsupial's gut to germinate (Amico and Aizen 2000). This marsupial also disperses seeds of at least other 16 fleshy-fruited species (Amico et al. 2009).

Non-native ungulates are the main source of anthropogenic disturbance in the temperate forest of Patagonia, decreasing the abundance and changing the physiognomy of seedlings and recruits of plant species (Veblen et al. 1992, Vazquez 2002, Barrios-Garcia 2005). Livestock (*Bos taurus*) was introduced by Europeans in the late eighteenth century (Veblen et al. 1992), and game animals, red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) were introduced around 1904 (Jacksic et al. 2002). There are no large native ungulates in the forest, and currently non-native ungulates occupy 56% of the forest (Jacksic et al. 2002). Here, we examine the potential indirect effects of the disruption of this keystone interaction induced by the invasion of non-native ungulates on foliar arthropods and on soil function in Patagonia, Argentina. Previous work showed a 16-fold reduction in *A. chilensis* abundance in sites invaded by non-native ungulates relative to uninvaded (intact) sites (Rodriguez-Cabal et al. 2013). This reduction in *A. chilensis* abundance indirectly affected the other species in the keystone mutualistic interaction: mistletoe abundance was 83× lower in invaded versus intact sites (Rodriguez-Cabal et al. 2013). Although previous work showed that non-native ungulates disrupted a key mutualistic web and indirectly affected other vertebrates, it is unknown whether these indirect effects also impact the amount and quality of plant resources that enter the aboveground food web and influence below-ground function (Figure 1). Based on previews studies we expect to find that ungulate herbivory will alter the aboveground arthropod community by decreasing richness and abundance; and alter soil function by decreasing soil respiration and moisture, and increasing soil temperature.

MATERIAL AND METHODS

Study area and natural history

We conducted our research in Los Arrayanes National Park (1,753 ha; 40.7839° S, 71.6605° W), in northwestern Patagonia, Argentina. The vegetation in the study area belongs to the Sub-Antarctic biogeographical region (Cabrera 1976). The forest is dominated by the evergreen southern beech (*Nothofagus dombeyi*), with a dense understory of the native shrub *A. chilensis* and bamboo (*Chusquea culeou*). Within the Los Arrayanes National Park, we selected two sites for this study 10 km apart. Non-native ungulates are present at one site (invaded site hereafter), while the other site has not been invaded by these non-native ungulates (intact site). In the Austral summer of 2014 we examined the indirect effect of non-native ungulates on the above- and below-ground components of the system. We measured the following variables on 34 *A. chilensis* individuals in the invaded site, and 60 *A. chilensis* individuals (30 with mistletoe and 30 without mistletoe) in the intact site. Due to the indirect effect of non-native ungulates on mistletoes (see Rodriguez-Cabal et al. 2013), we could not find *A. chilensis* infested by mistletoes at the invaded site.

Plant traits - we examined a suite of *A. chilensis* traits that varied across invaded and intact sites and could potentially account for variation in foliage arthropod community structure and soil function (Cornelissen et al. 2003). Specifically, we measured the height (m), diameter at breast height (DBH, cm), and the crown diameter (m) of each *A. chilensis*. To assess plant quality we measured chlorophyll content in five fully-expanded *A. chilensis* leaves per individual using a chlorophyll meter (atLEAF CHL PLUS meter).

Foliar arthropods - we used a combination of techniques to assess the foliar arthropod community on all sampled *A. chilensis* individuals. First, we visually surveyed each shrub for sessile arthropod species (e.g. galls). We then vacuum-sampled the entire crown of each *A. chilensis* using a modified leaf blower/vacuum (Craftsman 25cc 2-cycle) with a fine insect net attached. Vacuum samples were taken to the laboratory, stored in 70% ethanol, and identified to species or morphospecies. In total, we collected 2845 individuals.

Soil function - we measured soil respiration (CO_2), temperature, and moisture on invaded and intact sites. *In situ* soil CO_2 emissions were measured using an EGM-4 Environmental Gas Monitor with a closed system soil respiration chamber (PP Systems, USA). For each measurement the soil chamber (15 cm high; 10 cm diameter) was placed under the canopy of each *A. chilensis.* Soil respiration measurements were made at the end of summer, when re-wetted soils with fall precipitation enhances soil activity.

Statistical analysis - to analyze plant traits, foliar arthropods, and soil function response to non-native ungulates, we used separate one-way ANOVAs. We accounted for variation in *A. chilensis* size by converting foliar arthropod abundance to foliar arthropod density (total foliar arthropod abundance / crown size (m) of each tree). We log-transformed the response variables to meet normality assumptions. When transformation did not improve normality, we used a Kruskal-Wallis test. For clarity, we show the untransformed values in all figures. Next, we used PERMANOVA in PRIMER v. 6 (Clark 1993, 9999 permutations) on a Bray-Curtis dissimilarity matrix with log transformed abundance data to test for differences in arthropod community composition between sites. We analyzed the results using a non-parametric multidimensional scaling analysis (NMDS) in PRIMER v.6 (Clarke and Gorley 2006).

RESULTS AND DISCUSSION

Non-native ungulates are known to modify native plant communities by directly affecting plant survival, growth, reproduction, and recruitment through browsing, grazing, and trampling (McNaughton 1983, Crawley 1986, Gill 1992, Martinsen et al. 1998, Cotê et al. 2004). In our study, non-native ungulates' herbivory resulted in *Aristotelia chilensis* plants with 50% larger DBH (*Chi-square* = 16.887, *df* = 2, *P* = 0.0002; Figure 2a), and ~40% larger crown size (*Chi-square* = 9.604, *df* = 2, *P* = 0.0082; Figure 2b) in the invaded compared to the intact site. In contrast, plant height ($F_{2,91} = 0.926$, $P = 0.399$) and chlorophyll content ($F_{2,61} = 0.249$, $P = 0.780$; Figure 2c) was similar in both sites. We did not find differences in DBH, crown size, height, or chlorophyll content among unbrowsed *A. chilensis* with and without mistletoes at intact sites (Figure 2a, b, c). These results are consistent with previous studies in the area showing that selective browsing reduces the regeneration and abundance of *A. chilensis* saplings, where only large established individuals survive (Veblen et al 1989; Barrios-Garcia et al. 2012; Rodriguez-Cabal et al. 2013).

Mammalian herbivory modifies foliar arthropod communities by affecting the abundance and distribution of their host plants; this can occur via changes in plant chemistry, architecture, and phenology (Karban and Baldwin 1997; Bailey and Whitman 2002; Ohgushi 2005, van Klink et al. 2015). Some studies have found positive effects of mammalian herbivory on foliar arthropods. For example, Martinsen et al. (1998) showed that beaver (*Castor canadensis*) browsing of cottonwoods (*Populus fremontii* x *P. angustifolia*) increased the distribution and abundance of a beetle (*Chrysomela confluens*). Similarly, Danell and Huss-Danell (1985) found that herbivorous insects were more abundant on birch trees (*Betula pendula* and *B. pubescence*) previously browsed by moose (*Alces alces*) than on unbrowsed birch trees. On the other hand, Bailey and Whitham (2002) showed that high-severity fire and high levels of elk browsing resulted in 69% lower arthropod richness and 72% lower abundance on aspens (*Populus tremuloides*). We found that browsed *A. chilensis* plants supported ~24% fewer foliar arthropod species ($F_{2,91} = 5.202$, $P = 0.0073$; Figure 2d) and had ~25% fewer foliar arthropod individuals

($F_{2,91} = 4.617$, $P = 0.0123$; Figure 2e) than unbrowsed plants. We also found that arthropod community composition was similar on unbrowsed *A. chilensis* with and without mistletoe, but differed from the community on browsed *A. chilensis* (ANOSIM, $R = 0.18$, $P = 0.05$ and $R = 0.26$, $P = 0.01$ respectively, Figure 3). We propose four possible mechanisms by which non-native ungulates might reduce foliar arthropod diversity. First, non-native ungulates can decrease plant abundance for foliar arthropods. Indeed, a previous study (Rodriguez-Cabal et al. 2013) found that the total abundance of *A. chilensis* and mistletoes was greatly reduced in invaded versus intact sites. Second, changes in plant community structure and diversity can also impact foliar arthropods. The same study by Rodriguez Cabal et al. (2013) showed that total plant cover in the understory was 35× lower, habitat complexity was 20× lower, and the density of fruiting plants was 3× lower in invaded sites compared to intact sites. Third, herbivory by introduced ungulates can alter the quality of remaining tissues as a source of food and shelter for other organisms via the induction of (or selection for) traits that give resistance or tolerance to herbivory (e.g. Nuñez et al. 2010). Fourth, mammalian herbivores can also alter foliar arthropod community by accidentally ingesting them while browsing (Gish et al. 2017). In our study, we did not examine the unintentional predation of foliar arthropods by the non-native ungulates, or interactions between the four proposed mechanisms. More studies are needed to tease apart the contribution of each of the proposed mechanisms to the reduction of *A. chilensis*-associated foliar arthropod communities.

We did not detect any differences in soil function. Soil respiration was similar beneath the canopy of browsed and unbrowsed *A. chilensis* ($F_{2,61} = 0.249$, $P = 0.780$; Figure 2f). Similarly, we did not find a difference in soil temperature ($F_{2,61} = 1.369$, $P = 0.262$; Figure 2g) or soil humidity ($F_{2,61} = 0.835$, $P = 0.439$; Figure 2h). Based on previous studies showing better litter quality and faster decomposition rates of hemiparasitic plants (Quested et al. 2003; Press and Phoenix 2005), we expected to find higher CO_2 flux under unbrowsed *A. chilensis* with mistletoe, intermediate values under unbrowsed *A. chilensis*, and lowest respiration under browsed *A. chilensis*. However, we did not find any effect on soil respiration nor on abiotic properties. This finding could be a result of antagonist effects of litter quality and arthropod herbivory. While unbrowsed plants and mistletoe litter could have better nutrient quality, a larger and richer arthropod community could increase herbivory rates and in turn reduce litter quality and slow decomposition (Findlay et al. 1996; Karban and Baldwin 1997). Additionally, mistletoe infection triggers the production of defense compounds by the host plant (Cuevas-Reyes et al. 2017). Consequently, hosts weakened by a parasitic plant are more susceptible to insect attack (Press and Phoenix 2005; Cuevas-Reyes et al. 2017). All of these factors might result in similar litter quality with no consequences on overall soil respiration rates.

Understanding the indirect consequences of invasive non-native species is crucial for quantifying the real effects of global change. Taken together, our results reveal that by disrupting a keystone interaction in the temperate forest of Patagonia, non-native ungulates indirectly impact foliar arthropod abundance and richness but not soil properties (soil respiration, temperature and humidity). We propose that these results are not limited to this special case in which non-native ungulates disrupted a keystone interaction. Community structure and ecosystem process maintenance are supported by direct and indirect interactions between species, and all ecosystems are threatened by a combination of climate change, habitat disturbance and invasive species. Our study highlights the importance of indirect interactions beyond the classic examples of pair-wise interactions. Finally, our findings emphasize how long-term plans to conserve biodiversity must not only focus on maintaining the elements that form biodiversity but also on the interactions among these elements, such as interspecific interactions, trophic webs and ecological networks.

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FIGURE LEGENDS

FIG. 1. The potential cascading effects induced by non-native ungulates on foliar arthropods and soil function interactions (Drawings by Ezequiel Rodriguez-Cabal and Greg Crutsinger).

FIG. 2. Direct and indirect effects of non-native ungulates on plant traits, foliar arthropod communities and soil function. We found that: **a.** *Aristotelia chilensis* plants had 50% larger DBH in the invaded versus the intact site. **b.** Similarly, crown size was ~40% larger in the invaded versus the intact site. **c.** Chlorophyll content in relative units (Chl index) was similar in both sites. **d.** We found that browsed *A. chilensis* plants supported fewer foliar arthropod species. **e.** The abundance of foliage arthropods was also lower in browsed *A. chilensis* plants. **f.** Soil respiration, **g.** soil temperature and **h.** soil humidity were similar beneath the canopy of browsed and unbrowsed *A. chilensis*. Bars represent means (± SE); pairwise differences ($P < 0.05$) are indicated by uppercase letters.

FIG. 3. Foliar arthropod community composition was similar for *A. chilensis* with and without mistletoe in intact sites, but differed from the foliar arthropod community on browsed *A. chilensis* (NMDS ordination of community composition based on Bray-Curtis dissimilarity); grey triangles = intact site (*A. chilensis*), grey circles = intact site (*A. chilensis* + mistletoe) and black squares = invaded site.

FIGURE 1.

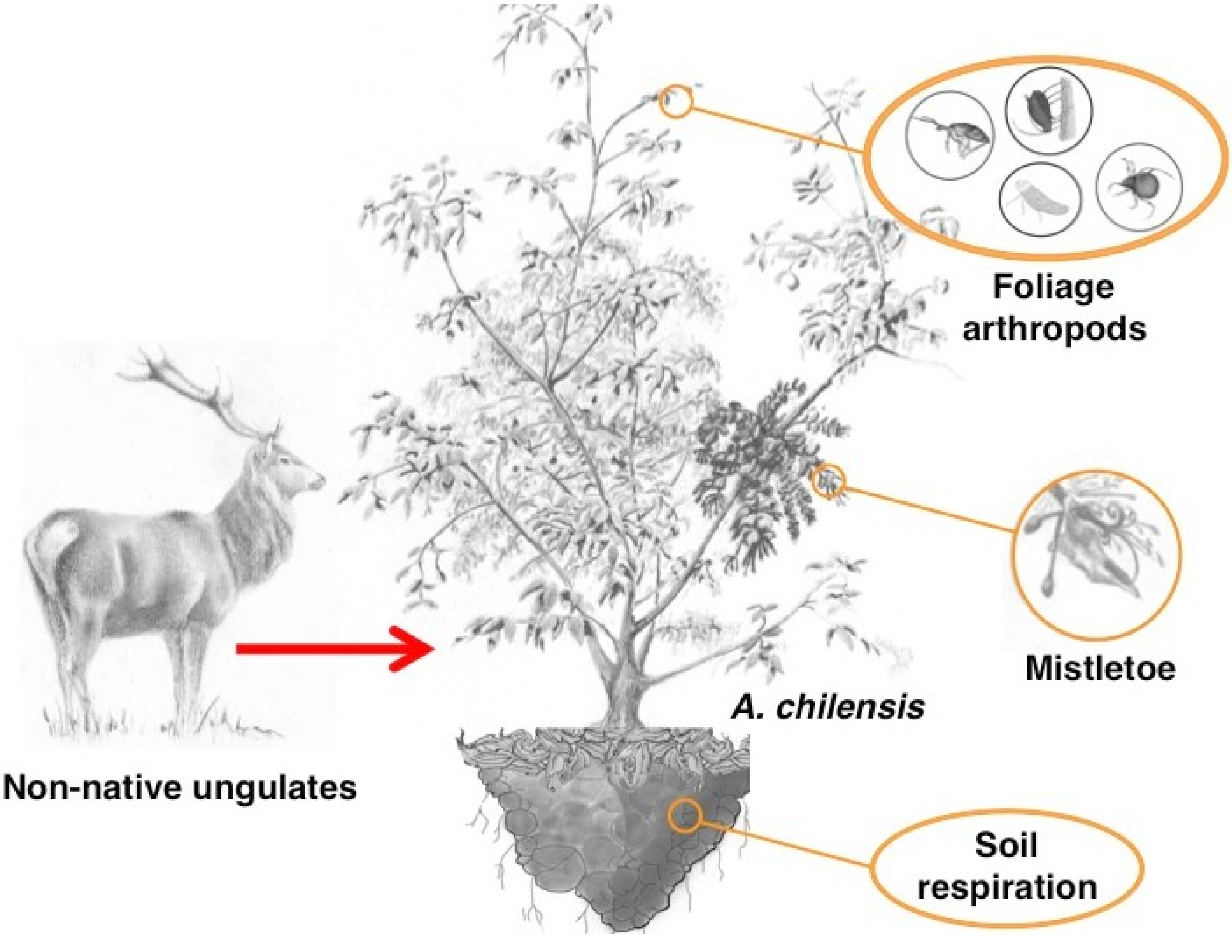
Foliage arthropods
Non-native ungulates
Mistletoe
A. chilensis
Soil respiration

FIGURE 2.

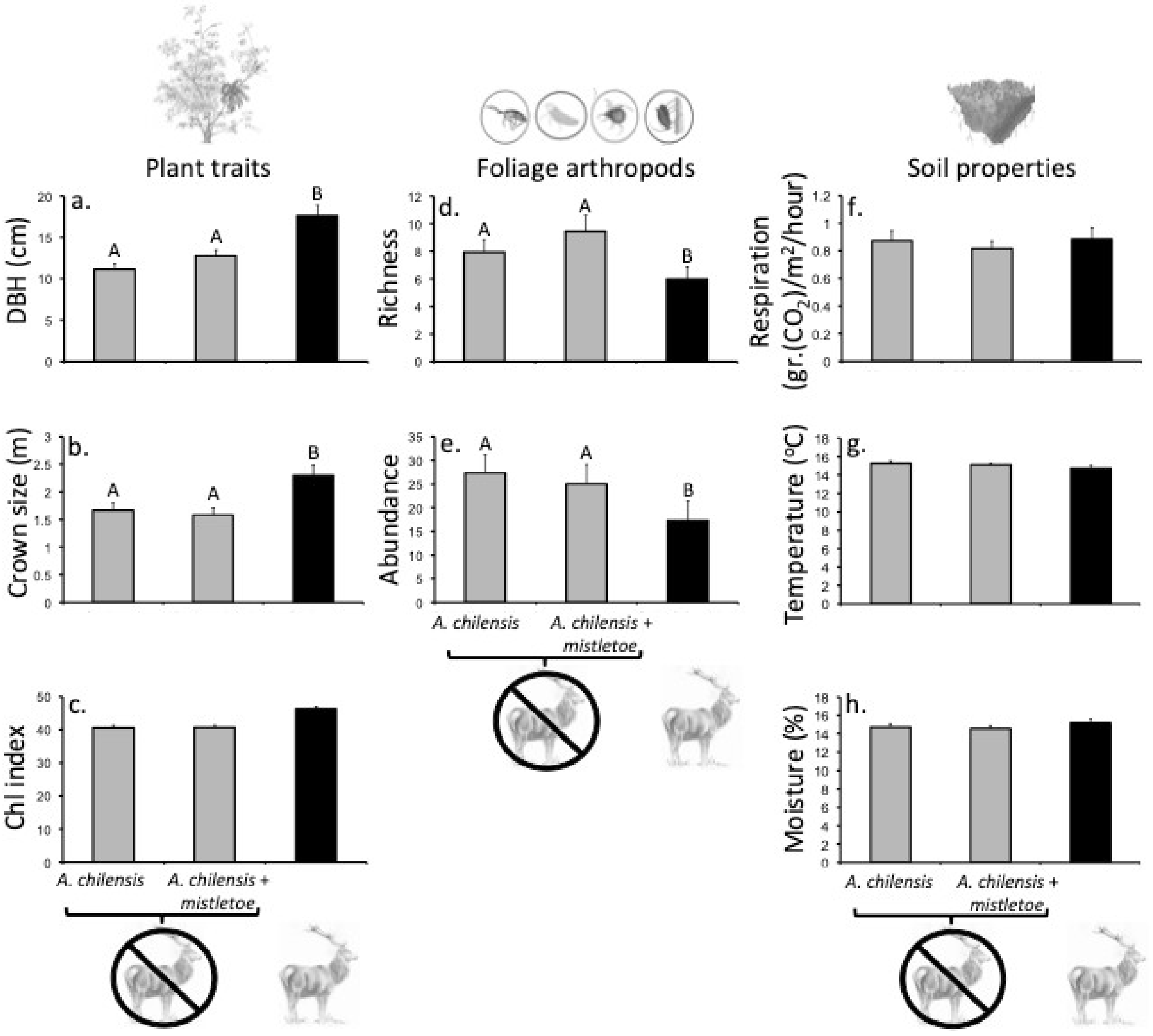
Plant traits
Foliage arthropods
Soil properties
a.
DBH (cm)
0
5
10
15
20
A
A
B
d.
Richness
0
2
4
6
8
10
12
A
A
B
f.
Respiration (gr.(CO$_2$)/m^2/hour)
0
0.2
0.4
0.6
0.8
1
1.2
b.
Crown size (m)
0
0.5
1
1.5
2
2.5
3
A
A
B
e.
Abundance
0
5
10
15
20
25
30
35
A
A
B
g.
Temperature (ºC)
0
2
4
6
8
10
12
14
16
18
c.
Chl index
0
10
20
30
40
50
h.
Moisture (%)
0
2
4
6
8
10
12
14
16
18
A. chilensis
A. chilensis + mistletoe

FIGURE 3.