Herbivory and trampling by small mammals modify soil properties and plant assemblages

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Abstract

Question: Do trampling and herbivory by small mammals affect salt marsh physical and biological properties?

Location: Upper salt marsh, Mar Chiquita coastal lagoon, Argentina.

Methods: A field experiment was placed from autumn to early summer in runways made by the wild Guinea pig, *Cavia aperea*. Segments of runways were randomly assigned to different treatments: control (herbivory and trampling), total exclusion (without herbivory or trampling) and reduced trampling (herbivory without trampling). After 8 months of experiment, soil hardness, runway depth, maximum plant height, above-ground biomass, plant assemblages, diversity and richness were measured and compared between treatments.

Results: Runways of *C. aperea* covered 14.5% of the area. Through trampling, *C. aperea* compacted the soil, increasing soil hardness and runway depth. Herbivory, in turn, reduced above-ground biomass and plant species richness, and affected species composition. Both herbivory and trampling decreased the maximum plant height.

Conclusion: Our results show how small herbivores, through trampling, are able to drive soil compaction, an effect previously described only for large mammals. Results also show that small mammals can control salt marsh primary production, reduce species richness and modify the composition of plant species through herbivory. Small mammal herbivores, thus, can modify physical and biological properties of salt marsh communities through both trophic and non-trophic mechanisms.

Introduction

Natural systems are affected by biological factors through both trophic and non-trophic mechanisms (Schmitz 2008). Among trophic mechanisms, herbivory can exert important changes on the structure and dynamics of communities (e.g., Milchunas & Noy-Meir 2002) as well as ecosystems (e.g., Augustine & McNaughton 2006). A high proportion of plant biomass may be removed by herbivores (e.g., McNaughton & Georgiadis 1986), affecting the abundance and diversity of plants (e.g., Hillebrand et al. 2007). At the same time, the effects of herbivory on plant diversity vary with the type, size and abundance of consumers. For example, in productive systems, generalist large mammals (e.g., ungulates) may control the abundance of dominant plant species, indirectly increasing light availability (e.g., van der Wal et al. 2000). In those cases, decreased plant above-ground competition favours subordinate species,

increasing plant species diversity (e.g., Borer et al. 2014). Despite the fact that small mammal herbivores remove, in general, less biomass than large mammals (e.g., Olff & Ritchie 1998) they also can modify the structure of the vegetation and affect plant diversity by targeting palatable species (Ritchie & Olff 1999).

Plant diversity can change in accordance with the intermediate disturbance hypothesis (Suzuki et al. 2013). Diversity increases at intermediate densities of herbivores because they create patches with reduced abundance of dominant competitors, providing opportunities for subordinate species (e.g., Bakker et al. 2006). Higher herbivore densities, nevertheless, may increase local extinction, because few species tolerate the intense herbivory (e.g., Milchunas & Lauenroth 1993). However, in stressful environments such as salt marshes, harsh physical conditions limit plant growth (Valiela & Teal 1979). In consequence, salt marsh plants primarily compete for below-ground

resources (e.g., *N*; Valiela & Teal 1979). In those systems, herbivory usually reduces plant richness because few species can tolerate both physical and biological stress (e.g., Crain 2008). While numerous studies have reported the impact of herbivory in salt marshes, most of them showed the effects of large (e.g., cattle Bakker et al. 2003) and medium (e.g., rabbits and nutria: Gough & Grace 1998; geese and hares: van Wijnen et al. 1999) herbivores, resulting in relatively scarce evidence about the effects of small mammal herbivores (but see Crain 2008).

In addition to their direct trophic effects, herbivores usually are also ecosystem engineers (*sensu* Jones et al. 1994), with non-trophic impacts that can modify the abundance and composition of plant communities (e.g., Daleo et al. 2007) and ecosystem functioning (Jones & Lawton 1995). Numerous mechanisms, such as wallowing (e.g., Trager et al. 2004), urine and faecal deposition (e.g., Bardgett & Wardle 2003), as well as changes in the quality of plant debris can modify the mineralization and availability of soil nutrients (e.g., *N*; Bakker et al. 2004). Both earlier and relatively recent studies show that trampling by large herbivores compacts the soil and modifies its physical and chemical properties (e.g., Murphy et al. 1995), affecting the recruitment and survival of plants (e.g., Cumming & Cumming 2003). Similarly, small herbivores such as invertebrates and rodents can also modify the soil structure and nutrient availability through non-trophic mechanisms, such as the creation of runways (e.g., Crain 2008), bioturbation (e.g., Botto et al. 2005) or faecal deposition (e.g., Willot et al. 2001), with impacts on germination, productivity and plant diversity (e.g., Alberti et al. 2010).

Although the role of herbivores on salt marsh structure and function was historically neglected (see Silliman & Bortolus 2003), during the last decades several studies have reported that herbivores may strongly control salt marsh primary production (e.g., Kuijper & Bakker 2005) even generating changes in plant composition (Alberti et al. 2011) and maintaining large areas without vegetation (e.g., Jefferies et al. 2006). In southwest Atlantic salt marshes (southern Brazil to northern Argentinean Patagonia), the main terrestrial herbivore is the wild guinea pig, *Cavia aperea*. Field experiments in these salt marshes have shown that *C. aperea* may control the above-ground biomass, diversity (Alberti et al. 2011) and secondary succession (Daleo et al. 2014). However, these works did not explore trophic and non-trophic effects and their relative importance. In consequence, little is known about the potential non-trophic effects of this small herbivore, such as debris production, faecal deposition or trampling. In this study, we evaluate the effects by *C. aperea* on salt marsh structure and function through trophic and non-trophic mechanisms.

Methods

Study site

The study was conducted at the Mar Chiquita coastal lagoon, Argentina (37°45′ S, 57°23′ W), specifically in the high salt marsh. The climate in the region is sub-humid to humid (76–84% humidity). The mean annual temperature varies between 12.9 and 15.0 °C and the mean annual precipitation oscillates between 578 and 1200 mm, with the rainy season extended during the warm semester (October–March; Reta et al. 2001). The lagoon (a 46-km² body of brackish water affected by low-amplitude tides) is characterized by intertidal mudflats and large surrounding marsh areas dominated by *Spartina densiflora* and *Sarcocornia perennis* (Isacch et al. 2006). In the high marsh, marsh plants (*Sp. densiflora, S. perennis, Juncus acutus*) grow interspersed with typical pampas grassland plant species (e.g., *Cortaderia selloana*), halophytic grasses (e.g., *Distichlis spicata, Paspalum vaginatum, Pa. distichum, Hordeum pusillum*) and other forbs (Pérez et al. 2009), *Sp. densiflora* remaining the dominant species (e.g., Daleo et al. 2014). Plant growing season occurs during spring and summer. Field observations and previous works in the study site (e.g., Alberti et al. 2011) showed that *C. aperea* is more abundant during autumn and winter, with high inter-annual variability, including years with total absence (average number of *C. aperea* droppings, an indirect estimate of its abundance, was 22.37 ± 17.92 ($\pm$SD) droppings day^{-1}·m^{-2} during winter 2012; 46.2 ± 39.01 droppings day^{-1}·m^{-2} during winter 2013, and 0.34 ± 1.06) droppings day^{-1}·m^{-2} during winter 2014; J. Pascual unpublished data). This herbivore limits plant vegetative expansion (e.g., Daleo et al. 2014), creating a complex web of runways through which it moves and forages (e.g., Cassini 1995). This generalist rodent eats all the species in the study site (particularly seedlings and young tissue) across all the microhabitats (i.e., marsh matrix, open areas and runways) and when it feeds on *Sp. densiflora* it consumes the basal meristem, leaving distinctive bevelled marks on stems. In the study site, the width and length of the runways vary between 20–30 and 50–100 m, respectively (J. Pascual personal observation). Plant cover in the runways and other open areas is extremely low (they are covered mostly by bare ground and some seedlings) during autumn and early winter, but plant cover gradually increases until a peak in early summer.

Random samplings were used to estimate the areal cover (%) occupied by runways (summer 2016, $n = 200$, 1 m²) and to compare soil and plant parameters between runways and marsh matrix (summer 2017, $n = 20$, 0.25 m²). Analysed parameters were soil hardness (hand

penetrometer, kg·cm^{-2}), maximum plant height, plant cover and richness. Due to large intra-plot variability, three measurements of runway soil hardness were performed. Then, to evaluate the effects of herbivory and trampling by *C. aperea* on soil structure and plant species composition, a field experiment was conducted. In early autumn (early May 2011), 30 (~1-m long, 30-cm wide) experimental units were randomly placed to include mostly runway bare ground segments and their direct adjacent vegetation (5 cm each side). Experimental units were assigned to one of the following treatments (*n* = 10 each): (1) control (herbivory + runway use), (2) reduced trampling (herbivory + reduced runway use) and (3) total exclusion (no herbivory + no runway use). In "total exclusion", small mammals were completely excluded by surrounding the experimental unit with a fence of plastic mesh. In "reduced trampling", two barriers of plastic mesh (50-cm high, 2 cm × 2 cm mesh size) were placed along the two shorter sides of the experimental unit, allowing grazing by *C. aperea* (lateral access) but reducing the use as a corridor *per se* and then reducing trampling. The assumption that the reduced trampling treatment maintained herbivory was supported by the frequent observation of *C. aperea* grazing traces, such as faeces and bevelled marks in *Sp. densiflora* stems within reduced trampling units. Also, fewer footprints of *C. aperea* were observed in reduced trampling than in control units after rains, and new runway segments (bypass) were created next to reduced trampling, suggesting that this treatment indeed reduced the use of runways as corridors. Total exclusions reflect a transient state that naturally occurs due to the oscillations in *C. aperea* abundances, and to the associated abandonment of runways. Although this transient state will likely end up as the marsh matrix, this is a slow process that might take several years (Daleo et al. 2014). Considering all the above, experimental results were interpreted as follows: (1) if "control" and "reduced trampling" were similar to each other and different from "total exclusion", effects were assigned to herbivory; (2) if "reduced trampling" and "total exclusion" were similar to each other and different from "control", effects were assigned to trampling; (3) if the three treatments were different from each other, effects were assigned to both trampling and herbivory.

Eight months later (late Dec 2011) the depth of runways, soil hardness (see above) and maximum height of plants growing within experimental units were measured. Runway depth was measured using two rulers, one placed horizontally crossing the runway and the other vertically in the centre of the runway. Then, all plants that grew within experimental units were harvested, classified to species and dried in oven (60 °C) to constant weight.

To evaluate whether there were differences between runways and marsh matrix in plant parameters, Student's

t-tests were used. Mixed models (Legendre & Legendre 2012) were used to evaluate differences in soil hardness (log-transformed), considering "treatment" or "microhabitat" as the fixed term and "number of experimental unit or sampling unit" as the random term. Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality. One-way ANOVAs (Zar 1999) were used to evaluate no differences between treatments for runway depth, maximum height, above-ground biomass (square root-transformed), plant richness and Simpson diversity ($D = \sum(ni[ni - 1]) / (N [N - 1])$; ni = abundance of the ith species; N = the total abundance of species; Magurran 2004). Tukey tests were used to evaluate *a posteriori* differences. Finally, dissimilarity in plant assemblages between treatments was evaluated using PERMANOVA, for which the assumption of multivariate homogeneity of group dispersions was tested and met (Anderson 2001). Biomass data (log (x + 1)) were used to construct the dissimilarity matrix (Bray-Curtis index) and NMDS analysis was used to visually evaluate treatment effects (Anderson 2001).

Results

In the study site, runways covered on average 14.5 ± 10.3% of the area. Compared to the marsh matrix, runways showed 113% higher soil hardness (1.33 ± 0.44 vs 0.62 ± 0.17 kg·cm^{-2}; $F_{1,49}$ = 359, P < 0.001), 168% higher plant richness (4.3 ± 1.05 vs 1.6 ± 0.7 species; t_{18} = 6.72, P < 0.001), 51% lower maximum plant height (52.6 ± 13.22 vs 109 ± 13.5 cm; t_{18} = −9.4, P < 0.001) and 64% less plant cover (36 ± 14.8 vs. 100 ± 0%; t_{18} = −13.5, P < 0.001).

Soil hardness in "total exclusion" (1.99 ± 0.77 kg·cm^{-2}) and "reduced trampling" (2 ± 1.07 kg·cm^{-2}) treatments was decreased by 32% with respect to "control" treatment (2.96 ± 1.31 kg·cm^{-2}; $F_{2,78}$ = 5.18, P < 0.01; Fig. 1a). Similarly, runway depth was decreased by 16% in "total exclusion" (2.8 ± 0.55 cm) and by 12% in "reduced trampling" (2.94 ± 0.37 cm) with respect to "control" (3.35 ± 0.48 cm; $F_{2,27}$ = 3.33, P < 0.05; Fig. 1b). Because both soil hardness and runway depth did not differ between "total exclusion" and "reduced trampling", the physical properties of the runways that we measured were more affected by trampling than by herbivory.

Maximum plant height was lowest in the "control", intermediate in "reduced trampling" and highest in "total exclusion" (Table 1, Fig. 2a). Thus, the elimination of both herbivory and trampling in "total exclusion" increased maximum plant height by 75% and 25% compared to "control" and "reduced trampling", respectively. The reduction of runway use in "reduced trampling" increased maximum plant height by 50% compared to "control"
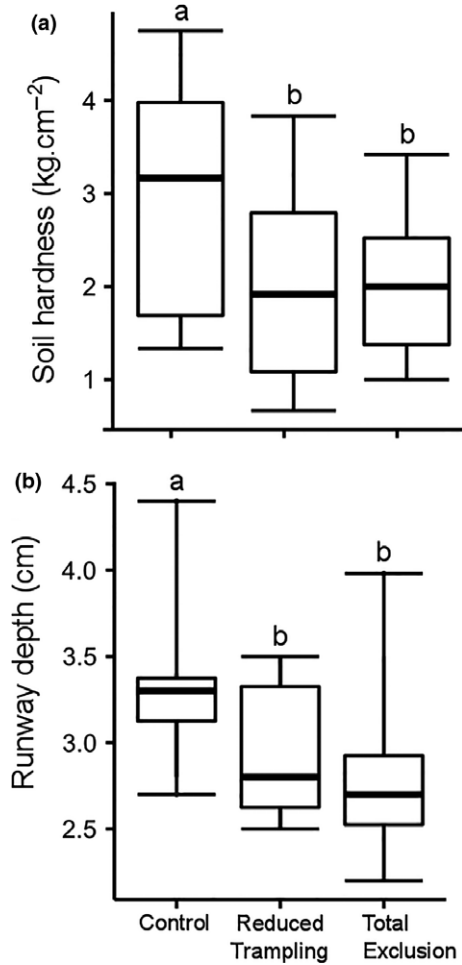
Fig. 1. Herbivory and trampling effects by *C. aperea* on soil hardness (**a**) and runway depth (**b**). Here and thereafter boxes: quartiles, vertical lines: 1st and 95th percentiles, bold horizontal lines: medians. Different letters indicate significant differences between treatments after a posterior Tukey test.
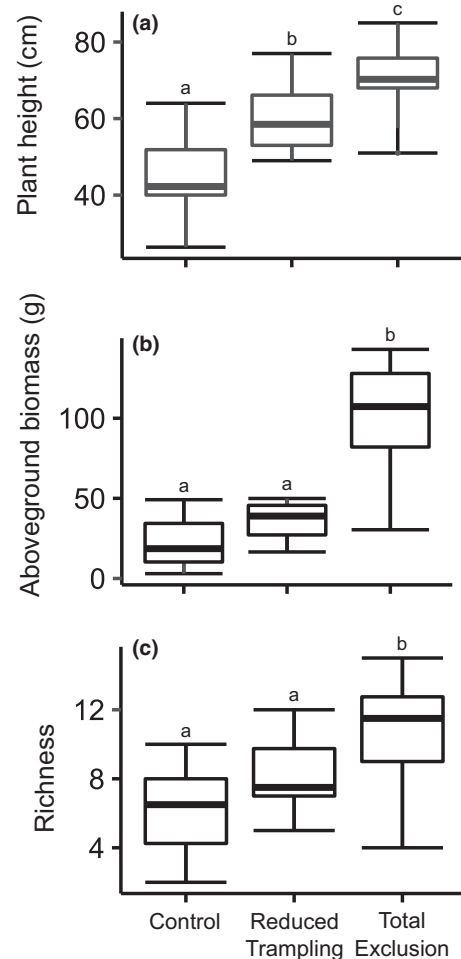
Table 1. One-way ANOVA results of the effects of trampling and herbivory by *Cavia aperea* on runways and their vegetation.

Source	df	SS	MS	F	P
Runway depth					
Factor	2	0.092	0.046	3.33	**0.046**
Residuals	27	0.372	0.014		
Maximum plant height					
Factor	2	13.7	6.83	13.9	**<0.001**
Residuals	27	13.2	0.49		
Above-ground biomass					
Factor	2	139.5	69.7	22.9	**<0.001**
Residuals	27	82.1	3		
Richness					
Factor	2	3.11	1.557	6.72	**0.004**
Residuals	27	6.26	0.232		
Diversity (Simpson)					
Factor	2	0.017	0.008	1.82	0.18
Residuals	27	0.126	0.004		

Significant values are highlighted in **bold**.

(Fig. 2a). In addition, "total exclusion" increased above-ground biomass by 100% over both "control" and "reduced trampling", which were similar (Fig. 2b). Average plant richness was not different between "control" and "reduced trampling" treatments, with seven species on average. However, species richness in the "total exclusion" treatment was 57% higher, with 11 species on average (Fig. 2c). Simpson diversity was similar across all treatments (see Table 1).

As opposed to the physical properties of the runway, the composition of vegetation was modified by herbivory more than by trampling; plant assemblages within "total exclusion" were different from both "reduced trampling" and "control", which were similar between them ($F_{2,27} = 3.35$, $P < 0.001$; Table 2, Fig. 3). We found 33 species across all the experimental plots,

Fig. 2. Effects of *C. aperea* on maximum plant height (**a**), above-ground plant biomass (**b**) and plant species richness (**c**).

**Table 2.** Mean (±SD) biomass of each species in each of the three treatments.

Plant Species	Control	Blocked Runway	Total Exclusion
Acmella decumbens	0.004 (0.009)	0 (0)	0.15 (0.3)
Anagallis arvensis	0.47 (1.48)	0.11 (0.19)	0.003 (0.008)
Apium sellowianum	1.68 (1.55)	4.24 (3.95)	37 (34.5)
Blackstonia perfoliata	0.077 (0.24)	0.014 (0.039)	0 (0)
Carex phalaroides	0 (0)	0.01 (0.027)	0.05 (0.15)
Centaurium pulchellum	3.80 (6.25)	3.07 (2.96)	2.3 (2.7)
Chaetotropis sp.	0.0002 (0.0007)	0.018 (0.047)	0.65 (1.33)
Cirsium vulgare	0 (0)	0 (0)	0.2 (0.6)
Conyza bonariensis	8.87 (12.14)	15 (11.36)	14 (19.3)
Coronopus didymus	0.018 (0.044)	0 (0)	0.086 (0.17)
Cressa truxillensis	0.46 (0.83)	0.69 (1.47)	2.3 (2.6)
Distichlis spicata	0.13 (0.3)	0.74 (1.93)	2.7 (2.83)
Gamochaeta americana	0 (0)	0 (0)	0.035 (0.06)
Isolepis cernua	0 (0)	0.038 (0.07)	0.02 (0.025)
Limonium brasiliense	0.11 (0.33)	0 (0)	0 (0)
Melilotus officinalis	0 (0)	0.015 (0.036)	4 (6.41)
Physalis viscosa	0.22 (0.56)	0.35345	0.3 (0.9)
Picris echioides	0 (0)	0 (0)	0.07 (0.22)
Plantago myosuros	0 (0)	0.005 (0.015)	5.27 (8.44)
Pluchea sagittalis	0.003 (0.011)	0.89 (2.8)	0 (0)
Poa lanigera	0 (0)	0 (0)	0.022 (0.07)
Pseudognaphalium gaudichaudianum	0 (0)	0.24 (0.62)	0.78 (2.46)
Rumex crispus	0 (0)	0 (0)	0.2 (0.76)
Samolus valerandi	0.003 (0.01)	0 (0)	0.065 (0.2)
Sarcocornia perennis	1.37 (4.1)	0.21 (0.26)	7.88 (15)
Senecio selloi	0 (0)	0.0035 (0.011)	0 (0)
Silene antirrhina	0 (0)	0 (0)	1.3 (2.96)
Sonchus asper	0.027 (0.046)	0.008 (0.02)	0 (0)
Spartina densiflora	5 (4)	10.6 (6.91)	17.6 (10)
Spergula laevis	0 (0)	0 (0)	0.014 (0.045)
Unidentifed forb	0.001 (0.003)	0 (0)	0 (0)
Unidentified *Poaceae*	0 (0)	0 (0)	0.37 (1.17)
Vicia setifolia	0 (0)	0 (0)	0.015 (0.034)

The area of each experimental unit was 2500 cm^2.

nine species grew exclusively within "total exclusion", one species only in "reduced trampling" and one species only in "control" (Table 2). Although *Sp. densiflora* (the dominant plant in the marsh matrix) grew in all treatments, its abundance decreased with herbivore access (Table 2). The two dimensions of the NMDS plot showed a high representation of the complete multidimensional space (stress value = 0.0161).

Discussion

Results show that small mammals affect different physical and biological properties of runways through both trophic (herbivory) and non-trophic (trampling) factors. Through herbivory, small mammals removed a significant amount of above-ground plant biomass, reduced plant richness and modified the composition of the vegetation, while through trampling they increased soil compaction and
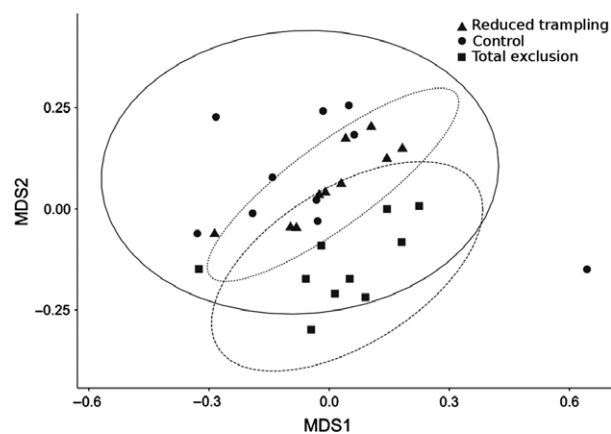
Fig. 3. NMDS ordination based on Bray-Curtis similarities depicting plant assemblages in the different treatments. Stress value = 0.161. Ellipses represent 95% CI around treatment centroids.

runway depth. Finally, both herbivory and trampling changed the structure of vegetation in runways by reducing maximum plant height.

Overwhelming evidence has revealed the importance of herbivores on the structure and dynamic of natural terrestrial systems (e.g., Cebrian & Lartigue 2004). The clearest examples in grasslands show that large herbivores can remove large quantities of above-ground biomass (e.g., Milchunas et al. 1988) and they can promote plant growth through compensatory responses (e.g., Belsky 1986), directly affecting primary production (e.g., McNaughton 1985) and ecosystem functioning (e.g., Augustine & Frank 2001). On the other hand, evidence about the effects of small mammals is limited, however they can reduce plant biomass (e.g., Hulme 1996) and even generate bare soil patches (e.g. Bakker et al. 2003). In contrast, in many cases herbivores do not affect primary producers or their effects are inconsistent (de-Val & Crawley 2005).

In our case, small mammal herbivory strongly affected plant biomass, richness and the composition of species. Indeed, the plant consumption we observed in runways is comparable with that reported for small and medium herbivores in European (Kuijper & Bakker 2005) and North American (Cargill & Jefferies 1984) marshes, and with previous works in our study site (e.g., Alberti et al. 2011). Although, richness in runways was higher (168%) than in marsh matrix (field sampling), our field experiment showed negative effects of herbivory on richness. Likewise, herbivory drove strong changes in plant composition, with 28% of the species only able to grow within "total exclusion" treatment (Table 2). It is worth mentioning that our "total exclusion" does not represent a true marsh matrix state but probably an intermediate successional stage between runway ("control") and marsh matrix. In this context, although the differences in plant height and soil hardness between runways and "total exclusion" were similar to the differences between runways and the (natural) marsh matrix, plant richness was higher in "total exclusion" but lower in marsh matrix compared to runways. However "total exclusion" does resemble a naturally occurring transient state, produced by the oscillations in *C. aperea* abundance and the associated abandonment of runways. Moreover, the process from bare ground to a fully recovered marsh matrix takes several years during which this transient state can be found (Daleo et al. 2014). The dominant marsh grass, *Sp. densiflora* grew in all treatments of our experiment, although it is important to note that its abundance decreased with the access of small mammals (Table 2). These results agree with previous works in the study site, which show that herbivory strongly suppresses the growth of *Sp. densiflora* (Alberti et al. 2011), and can be a key factor during succession dynamics (Daleo et al. 2014).

The effects of large mammal herbivory have been intensively studied in salt marshes. However, despite some previous work with voles and hares in the northern (e.g., Kuijper & Bakker 2005) and small mammals in the southern (e.g., Alberti et al. 2011) hemisphere salt marshes (e.g., Alberti et al. 2011; Daleo et al. 2014), there is still limited knowledge about the impact of herbivory by small mammals on these systems. Even less is known about non-trophic effects of herbivores, although some studies have reported soil bioturbation by burrowing species (e.g., Daleo et al. 2007) and soil compaction by large mammals (e.g., Schrama et al. 2013b). In accordance with this background information, our experiment shows that small mammals can strongly reduce above-ground plant biomass, change the composition of plant assemblages and modify the structure of the vegetation. Those effects were mainly mediated by plant consumption, although other variables analysed (maximum plant height) were affected by both herbivory and trampling.

The direction and magnitude of ecosystem engineering effects vary according to species, ecological process and the environmental context (e.g., Jones et al. 1994). An extensive body of evidence has shown how small herbivores (e.g., mammals: Bakker et al. 2006; invertebrates: Alberti et al. 2010) may affect physical (e.g., erodability, sedimentation and oxygenation), chemical (e.g., nutrient cycling) and biological process in salt marshes. However, most of these effects are usually mediated by burrowing organisms (e.g., Paramor & Hughes 2005). Nevertheless, recent studies show that large herbivores, through trampling and subsequent soil compaction, are able to decelerate nutrient mineralization rates (e.g., N; Schrama et al. 2013a). For example, Schrama et al. (2013a) found that soil compaction from the activity of large mammals can reduce oxygen and water availability in humid and arid soils, respectively, modifying the soil macrofauna and decelerating decomposition and N mineralization rates (e.g., Schrama et al. 2013a), thus affecting plant composition (Veldhuis et al. 2014). In accordance with this model, our results show that through trampling, small mammals can modify physical properties of the system by increasing soil compaction and runway depth. Through both herbivory and trampling, small mammals are able to modify the structure of the vegetation by reducing maximum plant height. This change is not minor, given that reduced plant height and altered canopy architecture can affect photosynthetically active radiation at ground level (Alberti et al. 2017), with consequences for plant competition and diversity, and indirectly for the abundance and diversity of arthropods (Gibson et al. 1992).

In summary, our results show that ecosystem engineers can have profound effects on salt marshes not only

through the widely recognized burrowing activities (e.g., Botto et al. 2005) but also through this recently highlighted mechanism of trampling (Schrama et al. 2013a). Overall, our study reinforces that small mammals can strongly control vegetation, and it reveals that they can also modify the physical environment, something currently expected only for large herbivores.

Acknowledgements

References

Alberti, J., Bakker, E., van Klink, R., Olff, H. & Smit, C. 2017. Herbivore exclusion promotes a more stochastic plant community assembly in a natural grassland. *Ecology* 98: 961–970.

Alberti, J., Casariego, A.M., Daleo, P., Fanjul, E., Silliman, B., Bertness, M. & Iribarne, O. 2010. Abiotic stress mediates top-down and bottom-up control in a Southwestern Atlantic salt marsh. *Oecologia* 163: 181–191.

Alberti, J., Canepuccia, A., Pascual, J., Pérez, C. & Iribarne, O. 2011. Joint control by rodent herbivory and nutrient availability of plant diversity in a salt marsh–salty steppe transition zone. *Journal of Vegetation Science* 22: 216–224.

Anderson, M. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26: 32–46.

Augustine, D.J. & Frank, D.A. 2001. Effects of migratory grazers on spatial heterogeneity of soil nitrogen properties in a grassland ecosystem. *Ecology* 82: 3149–3162.

Augustine, D.J. & McNaughton, S.J. 2006. Interactive effects of ungulate herbivores, soil fertility and variable rainfall on ecosystem processes in a semi-arid savanna. *Ecosystems* 9: 1242–1256.

Bakker, J.P., Bos, D. & de Vries, Y. 2003. To graze or not to graze: that is the question. In: Wolff, W., Essink, K., Kellerman, A. & van Leeuwen, M. (eds.) *Challenges to the Wadden Sea, Proceedings of the 10th International Scientific Wadden Sea Symposium*, pp. 67–88. Dutch Ministry of Agriculture, Nature Management and Fisheries, Groningen, NL.

Bakker, E.S., Olff, H., Boekhoff, M., Gleichman, J.M. & Berendse, F. 2004. Impact of herbivores on nitrogen cycling: contrasting effects of small and large species. *Oecologia* 138: 91–101.

Bakker, E.S., Ritchie, M.E., Olff, H., Milchunas, D.G. & Knops, J.M.H. 2006. Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. *Ecology Letters* 9: 780–788.

Bardgett, R.D. & Wardle, D.A. 2003. Herbivore-mediated linkages between aboveground and belowground communities. *Ecology* 84: 2258–2268.

Belsky, A.J. 1986. Does herbivory benefit plants? A review of the evidence. *The American Naturalist* 127: 870–892.

Borer, E.T., Seabloom, E.W., Gruner, D.S., Harpole, W.S., Hillebrand, H., Lind, E.M., Adler, P.B., Alberti, J., Anderson, T.M., (...) & Yang, L.H. 2014. Herbivores and nutrients control grassland plant diversity via light limitation. *Nature* 508: 517–520.

Botto, F., Valiela, I., Iribarne, O., Martineto, P. & Alberti, J. 2005. Impact of burrowing crabs on C and N sources, control and transformations in sediments and food webs of SW Atlantic estuaries. *Marine Ecology Progress Series* 293: 155–164.

Cabrera, A.L. & Zardini, E.M. 1993. *Manual of the flora of Buenos Aires environs (Manual de la flora de los alrededores de Buenos Aires)*. Editorial Acme, Buenos Aires, AR.

Cargill, S.M. & Jefferies, R.L. 1984. The effects of grazing by lesser snow geese on the vegetation of a sub-Arctic salt marsh. *Journal of Applied Ecology* 21: 669–686.

Cassini, M.H. 1995. Cavia's food ecology: integrating behavioral ecology to the population ecology (Ecologia alimentaria de Cavia: integrando la ecología comportamental a la ecología de poblaciones). *Marmosiana, Acta Teriológica Latinoamericana* 95: 94–103.

Cebrian, J. & Lartigue, J. 2004. Patterns of herbivory and decomposition in aquatic and terrestrial ecosystems. *Ecological Monographs* 74: 237–259.

Crain, C.M. 2008. Interactions between marsh plant species vary in direction and strength depending on environmental and consumer context. *Journal of Ecology* 96: 166–173.

Cumming, D.H.M. & Cumming, G.S. 2003. Ungulate community structure and ecological processes: body size, hoof area and trampling in African savannas. *Oecologia* 134: 560–568.

Daleo, P., Fanjul, E., Casariego, A., Silliman, B., Bertness, M. & Iribarne, O. 2007. Ecosystem engineers activate mycorrhizal mutualism in salt marshes. *Ecology Letters* 10: 902–908.

Daleo, P., Alberti, J., Pascual, J., Canepuccia, A. & Iribarne, O. 2014. Herbivory affects salt marsh succession dynamics by suppressing the recovery of dominant species. *Oecologia* 175: 335–343.

Gibson, C., Hambler, C. & Brown, V.K. 1992. Changes in spider (Araneae) assemblages in relation to succession and grazing management. *Journal of Applied Ecology* 29: 132–142.

Gough, L. & Grace, J.B. 1998. Herbivore effects on plant species density at varying productivity levels. *Ecology* 79: 1586–1594.

Hillebrand, H., Gruner, D.S., Borer, E.T., Bracken, M.E.S., Cleland, E.E., Elser, J.J., Harpole, W.S., Ngai, J.T., Seabloom, E.W., Shurin, J.B. & Smith, J.E. 2007. Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. *Proceedings of the National Academy of Sciences of the United States of America* 104: 10904–10909.

Hulme, E. 1996. Herbivory, plant regeneration, and species coexistence. *Journal of Ecology* 84: 609–615.

Isacch, J.P., Costa, C.S., Rodriguez-Gallego, L., Conde, D., Escapa, M., Gagliardini, D.A. & Iribarne, O. 2006. Distribution of salt marsh plant communities associated with environmental factors along a latitudinal gradient on the south-west Atlantic coast. *Journal of Biogeography* 33: 888–900.

Jefferies, R.L., Jano, A.P. & Abraham, K.F. 2006. A biotic agent promotes large-scale catastrophic change in the coastal marshes of Hudson Bay. *Journal of Ecology* 94: 234–242.

Jones, C.G. & Lawton, J.H. (eds.) 1995. *Linking species and ecosystems*. Chapman and Hall, New York, NY, US.

Jones, C.G., Lawton, J.H. & Shachak, M. 1994. Organisms as ecosystem engineers. *Oikos* 69: 373–386.

Kuijper, D.P.J. & Bakker, J.P. 2005. Top-down control of small herbivores on salt-marsh vegetation along a productivity gradient. *Ecology* 86: 914–923.

Legendre, P. & Legendre, L.F.J. 2012. *Numerical ecology*, 3rd ed. Elsevier, Oxford, UK.

Magurran, A.E. 2004. *Measuring biological diversity*. Blackwell, Oxford, UK.

McNaughton, S.J. 1985. Ecology of a grazing ecosystem: the Serengeti. *Ecological Monographs* 55: 259–294.

McNaughton, S.J. & Georgiadis, N.J. 1986. Ecology of African grazing and browsing mammals. *Annual Review of Ecology and Systematics* 17: 39–65.

Milchunas, D. & Lauenroth, W. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* 63: 327–366.

Milchunas, D.G. & Noy-Meir, I. 2002. Grazing refuges, external avoidance of herbivory and plant diversity. *Oikos* 99: 113–130.

Milchunas, D.G., Sala, O.E. & Lauenroth, W.K. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. *The American Naturalist* 132: 87–106.

Murphy, W.M., Barreto, A.D., Silman, J.P. & Dindal, D.L. 1995. Cattle and sheep grazing effects on soil organisms, fertility and compaction in a smooth-stalked meadowgrass-dominant white clover sward. *Grass and Forage Science* 50: 191–194.

Olff, H. & Ritchie, M.E. 1998. Effects of herbivores on grassland plant diversity. *Trends in Ecology & Evolution* 13: 261–265.

Paramor, O.A.L. & Hughes, R.G. 2005. Effects of vertebrate fauna on early salt marsh plant colonization on managed realignment areas in southeast England. *Marine Ecology Progress Series* 303: 61–71.

Pérez, C.F., Latorre, F., Stutz, S. & Pastorino, S. 2009. A two-year report of pollen influx into Tauber traps in Mar Chiquita coastal lagoon, Buenos Aires, Argentina. *Aerobiologia* 25: 167–181.

Reta, R., Martos, P., Perillo, G., Piccolo, M. & Ferrante, A. 2001. Hydrographic characteristics of the estuary of Mar Chiquita lagoon (Características hidrográficas del estuario de la laguna Mar Chiquita). In: Iribarne, O.O. (ed.) *Mar Chiquita Biosphere Reserve: Physical, biological and ecological characteristics (Reserva de Biosfera Mar Chiquita)*, pp. 31–52. Editorial Martin, Mar del Plata, AR.

Ritchie, M.E. & Olff, H. 1999. Herbivory diversity and plant dynamics: compensatory and additive effects. In: Olff, H., Brown, V.K. & Drent, R.H. (eds.) *Herbivores: between plants and predators*, pp. 175–204. Blackwell Science, Oxford, UK.

Schmitz, O.J. 2008. Effects of predator hunting mode on grassland ecosystem function. *Science* 319: 952–954.

Schrama, M., Heijning, P., Bakker, J.P., van Wijnen, H.J., Berg, H.P. & Olff, H. 2013a. Herbivore trampling as an alternative pathway for explaining differences in nitrogen mineralization in moist grasslands. *Oecologia* 172: 231–243.

Schrama, M., Veen, G.F., Bakker, E.S., Ruifrok, J.L., Bakker, J.P. & Olff, H. 2013b. An integrated perspective to explain nitrogen mineralization in grazed ecosystems. *Perspectives in Plant Ecology, Evolution, and Systematics* 15: 32–44.

Silliman, B.R. & Bortolus, A. 2003. Underestimation of *Spartina* productivity in western Atlantic marshes: marsh invertebrates eat more than just detritus. *Oikos* 101: 549–554.

Suzuki, M., Miyashita, T., Kabaya, H., Ochiai, K., Asada, M. & Kikvidze, Z. 2013. Deer herbivory as an important driver of divergence of ground vegetation communities in temperate forests. *Oikos* 122: 104–110.

Trager, M.D., Wilson, G.W.T. & Hartnett, D.C. 2004. Concurrent effects of fire regime, grazing and bison wallowing on tall grass prairie vegetation. *The American Midland Naturalist* 152: 237–247.

de-Val, E. & Crawley, M.J. 2005. What limits herb biomass in grasslands: Competition or herbivory? *Oecologia* 142: 202–211.

Valiela, I. & Teal, J.M. 1979. The nitrogen budget of a salt marsh ecosystem. *Nature* 280: 652–656.

Veldhuis, M.P., Howison, R.A., Fokkema, R.W., Tielens, E. & Olff, H. 2014. A novel mechanism for grazing lawn formation: large herbivore-induced modification of the plant–soil water balance. *Journal of Ecology* 102: 1506–1517.

van der Wal, R., Egas, M., van der Veen, A. & Bakker, J. 2000. Effects of resource competition and herbivory on plant performance along a natural productivity gradient. *Journal of Ecology* 88: 317–330.

van Wijnen, H.J., van der Wal, R. & Bakker, J.P. 1999. The impact of herbivores on nitrogen mineralization rate: consequences for salt-marsh succession. *Oecologia* 118: 225–231.

Willot, S.J., Miller, A.J., Incoll, L.D. & Compton, S.G.H. 2001. The contribution of rabbits (*Oryctolagus cuniculus* L.) to soil fertility in semi-arid Spain. *Biology and Fertility of Soils* 31: 379–384.

Zar, J.H. 1999. *Biostatistical analysis*, 4th edn. Prentice-Hall, Upper Saddle River, NJ, US.