Received: 22 April 2024 | Revised: 13 September 2024 | Accepted: 18 October 2024

DOI: 10.1111/jvs.70001

Journal of Vegetation Science IAVS

RESEARCH ARTICLE

Mammalian herbivory alters structure, composition and edaphic conditions of a grey-dune community

Sandra Francés Alcántara[1] | Rubén Retuerto[1] | Julia Sánchez Vilas[1,2]

[1]Departamento de Bioloxía Funcional (Área de Ecoloxía), Facultade de Bioloxía, Universidade de Santiago de Compostela, Santiago de Compostela, Spain

[2]School of Biosciences, Cardiff University, Cardiff, United Kingdom

Correspondence
Julia Sánchez Vilas, Departamento de Bioloxía Funcional (Área de Ecoloxía), Facultade de Bioloxía, Universidade de Santiago de Compostela, c/Lope Gómez de Marzoa s/n, 15782 Santiago de Compostela, Spain.
Email: julia.sanchez.vilas@usc.es

Funding information
NextGenEU, Grant/Award Number: PRTR-2022-CE106

Co-ordinating Editor: Stephen Roxburgh

Abstract

Question: Mammalian herbivory affects the structure and composition of plant communities, soil characteristics and intraspecific leaf traits. Understanding the effects of this type of herbivory is particularly relevant in grey dunes, a priority habitat type of the European Union Habitats Directive.

Location: Sálvora island (NW Spain).

Methods: Vegetation surveys and sampling were carried out in a coastal grey-dune community, comparing the structure and composition of plant communities and soil characteristics in plots with herbivory exclusion and plots with herbivore activity, in autumn and spring. Changes in the specific leaf area (SLA), C/N ratio, δ^{13}C and δ^{15}N of two main plant species were also analysed.

Results: The differentiation between treatments was low in autumn, in contrast to spring results, which demonstrated seasonal variation in the plant community and herbivore behaviour. Spring results showed lower above-ground dry mass in plots with herbivory due to defoliation, but greater richness and diversity, indicating that intermediate levels of disturbance reduced competition from dominant species. Herbivory treatments were different in terms of species composition, highlighting the positive effects of herbivory on the development of the threatened species *Linaria arenaria*. Soil temperature and moisture content were higher in herbivory plots because of the suppression of vegetation cover and the effect of trampling, respectively. No differences were detected in the chemical composition of the soil or the SLA, although the variability of these traits was greater in herbivory plots, indicating spatial heterogeneity generated by the activity of herbivores. No differences between treatments were obtained for % C and δ^{13}C, whereas herbivory plots showed lower values of N content and δ^{15}N as an adaptive response to herbivory pressure at the leaf and root level.

Conclusion: Our findings show that herbivory effects on plant communities vary by season—stronger in spring and weaker in autumn—emphasising the need for seasonal analysis and highlighting disturbance as a driver of spatial heterogeneity.

KEYWORDS
Atlantic coast, coastal dunes, defoliation, exclusion experiment, plant community

1 | INTRODUCTION

Herbivores have a high potential for the transformation of plant communities, which has been widely documented in the scientific literature for decades (Crawley, 1997; Maron & Crone, 2006; Agrawal & Maron, 2022). Herbivores can directly alter the survival, growth and fecundity rates of plant species by selective consumption and by trampling (Cole, 1995; Crawley, 1997; Warner & Cushman, 2002; Schädler et al., 2003). In the long term, these effects can have major impacts on the functioning of natural ecosystems, leading to changes in the structure, composition and productivity of plant communities (Collins et al., 1998; Maron & Crone, 2006; Millett & Edmondson, 2013; Enquist et al., 2020). In the case of medium-sized mammals (such as rabbits) and large-sized mammals (such as deer or horses) herbivory can result in reduced above-ground dry mass of plant communities associated with defoliation losses (Jessen et al., 2020). Herbivory by medium- and large-sized mammals can also increase biodiversity by exerting direct control over the abundance of certain dominant plant species, favouring other species that would otherwise remain subordinate due to the competition regime (Pascual et al., 2017). The impact of herbivores at the community level can also be exerted indirectly, through changes in the physicochemical characteristics of soils and by influencing nutrient cycling (Schädler et al., 2003; Feeley & Terborgh, 2005). Soil fertilisation associated with animal excrements can cause important changes in ecosystem biochemistry (Kielland & Bryant, 1998; Kristensen et al., 2022) and soil biota (Li et al., 2024), and consequently in the plant communities established on them, their structure and productivity (Bardgett et al., 1998; Forbes et al., 2019). Trampling by herbivores may also have substantial indirect effects on plant communities by changing the physical conditions of the soil. Trampling causes an erosive effect that prevents the development of certain species of flora (Vilas et al., 2005), creating characteristic plant communities dominated by life forms that are relatively tolerant of trampling (Cole, 1995). Trampling by large ungulates increases soil compaction which can modify the local water balance by reducing infiltration and water retention capacity and increasing surface runoff losses, influencing plant community composition (Veldhuis et al., 2014).

At the individual level, herbivore pressure can significantly modify important functional traits of plants (Salgado-Luarte & Gianoli, 2012). For example, Jessen et al. (2020) reported that species subjected to herbivory show a reduction in specific leaf area (SLA), as an adaptive response associated with reduced visibility and palatability by predators. Herbivores may also spatially redistribute important nutrients within ecosystems, altering the uptake, assimilation, and allocation of nutrients in plant tissues. Thus, changes in C/N ratios may have consequences for the palatability and nutritional value of plant tissues (Poorter et al., 2004; Agrawal & Fishbein, 2006). Herbivores can even change the C and N isotopic signatures of plant tissues (Dawson et al., 2002) by improving the water use efficiency of browsed plants (Alstad et al., 1999), and by increasing N inputs in soil (Frank et al., 2000).

The study of the effects of herbivory on coastal dune ecosystems is particularly relevant because these ecosystems are under threat due to ongoing global climate change and increasing anthropogenic pressure (Brown & McLachlan, 2002; Feagin et al., 2005). Fixed coastal dunes with herbaceous vegetation, also known as grey dunes, are classified as a priority habitat type by the European Union Habitats Directive, demanding special attention for conservation and management (Directorate-General for Environment et al., 2016). In grey dunes, vegetation cover plays a crucial role in stabilising the substrate and preventing erosion by wind and storms (Delgado-Fernández et al., 2019). However, the impact of mammalian herbivory on grey-dune vegetation has been little studied to date (but see El-Keblawy et al., 2009), even though the effect of herbivores may be accentuated in low-nutrient plant communities, due to a reduced ability of plants to tolerate or compensate for herbivore damage (Gianoli & Salgado-Luarte, 2017).

The aims of this study are: (1) to analyse the effects of herbivory by medium- and large-sized mammals (rabbits, horses and deer) on the structure and plant composition of a grey-dune community; (2) to study the impact of herbivores at the individual plant level on plant functional traits putatively adaptive in defence against herbivores; and (3) to study the changes in edaphic characteristics caused by herbivores. Based on previous studies, we expect that: (1) herbivory pressure exerted by mammal species would lead to a decrease in above-ground dry mass, and a change in specific composition with increased richness and diversity; (2) at the intraspecific level, individuals subjected to herbivory would have tougher leaves, with lower SLA and higher C/N ratios, than those in the exclusion zone; and (3) these changes at the community and plant level would be related to soil physicochemical characteristics altered by the presence of herbivores.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was carried out on Sálvora island, belonging to the Maritime-Terrestrial National Park of the Atlantic Islands of Galicia, northwest Spain (Fernández Bouzas, 2017) (Figure 1). The climate is described as subhumid Mediterranean with an Atlantic tendency. The average annual rainfall is 1193 l/m^2, while the average monthly temperature throughout the year ranges from 20°C in August to 10°C in December (Campoy et al., 2021). This island preserves a good representation of dune ecosystems (Fernández Bouzas, 2017), hosting endangered species of flora, such as *Rumex rupestris*, or critically endangered species, such as *Linaria arenaria* or *Erodium maritimum* (Bañares et al., 2004).

Sálvora is currently inhabited by 17 individuals of *Cervus elaphus* and 10 of *Equus ferus* (Fernández-Bouzas, personal communication, 24 April 2023). Exact population data for *Oryctolagus cuniculus* L. are not available, although the estimated average density between 2008 and 2010 was 55.88 individuals/ha (Santamaría et al., 2012).

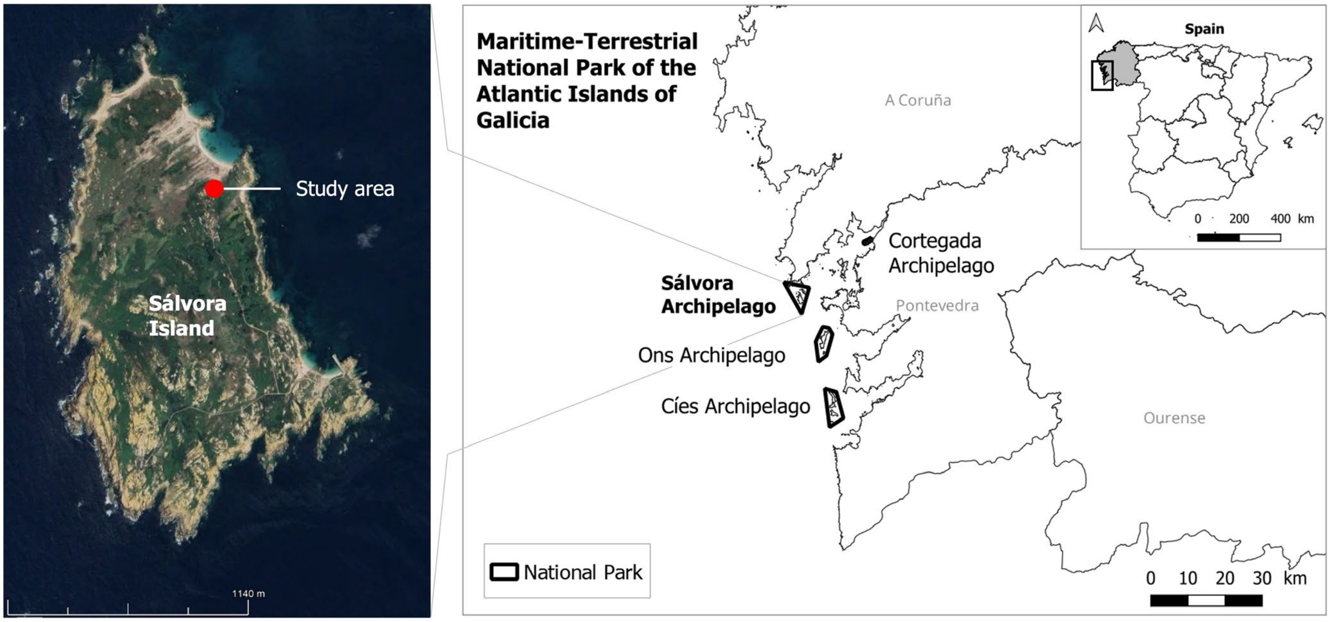


FIGURE 1 Location of the study area in the northeast of the island of Sálvora within the Atlantic Islands National Park (Galicia), in the northwest of the Iberian Peninsula, in Spain.

The experimental plots were located in an area of secondary dune with herbivore activity, demonstrated through the observation of tracks and the capture of photo-trapping images. The plots were situated in the northeast of the island (42°28′44″ N, 9°0′34″ W), at 6 m a.s.l. (Campoy et al., 2021).

2.2 | Experimental design

This study focused on comparing the effects of herbivory by establishing two treatments: a treatment without herbivore exclusion (herbivory) and a treatment with herbivore exclusion (no-herbivory). To minimise the impact of the experimental design on the dune ecosystem, considering that the study area is protected for biodiversity conservation, the replicate plots corresponding to the no-herbivory treatment were within a single exclusion fence installed in June 2015. The fence has a rectangular perimeter of 21 m × 12 m and has a height of 1.15 m above-ground that prevents access to horses and deer and extends 1 m underground to prevent the entry of rabbits. The central point of the herbivore exclusion zone is 75 m from the coastline (Campoy et al., 2021).

Within the exclusion zone, eight 1.27 m^2 hexagonal plots were marked at regular intervals using wooden stakes (Appendix S1). Outside and all around the exclusion zone, the no-herbivory plots were paired with herbivory plots of equal size and shape, each of them at a distance of no more than 4.5 m from the exclusion zone to minimise edaphic or climatic differences between the two groups of experimental plots.

In each of the 16 plots (eight for each treatment), we harvested the above-ground plant mass and measured soil characteristics at the end of autumn (2/12/2022), and in the following spring (2/5/2023). In the autumn of 2022—after a seven-year herbivore exclusion period—a 50 cm × 50 cm square was fitted into one side within each plot (randomly chosen), so that vegetation on another 50 cm × 50 cm square on the other side of the plot was left untouched until the next sampling date in the spring (Appendix S1). At each sampling date, the above-ground biomass harvested was taken to the lab and identified to species, and their dry mass was measured by drying in an oven at 40°C until constant weight. With these data we calculated the above-ground dry mass (g), which was used as a measure of abundance, the species richness (number of species), and the Simpson's ($D=\Sigma[n_i(n_i-1)/N(N-1)]$; n_i is the above-ground dry mass of each species and N is the total above-ground dry mass of all species) and Shannon's diversity indices ($H'=-\Sigma p_i \ln p_i$; p is the proportion of above-ground dry mass of each species in the whole sample).

At each sampling date, soil temperature and soil moisture content were measured by taking three readings at 5-cm depth for each plot with a Testo-925 thermometer (Testo SE & Co. KGaA, Lenzkirch, Germany) and a Theta Probe ML2× hygrometer (Delta-T Devices Ltd., Cambridge, England), respectively. Soil samples were also taken from each plot, by sampling at 10-cm depth. The soil samples were transported in a cool box (4°C) to the laboratory, in hermetically sealed containers, and dried to constant weight at 40°C. Dried subsamples (approximately 2 mg) of each sample were ground to a fine powder (<2 mm) and encapsulated for elemental analysis. The contents (%) of carbon, nitrogen and sulphur were analysed via dry combustion at high temperature using a LECO CHNS-932 elemental analyser (LECO Corporation, St. Joseph, Michingan, USA). The contents (mg/kg) of Al, Ca, Cu, Fe, K, Mg, Na, P were measured after digestion of the samples with nitric acid, using induced coupled plasma-mass spectrometry, in an Agilent 7700x ICP-MS (Agilent Technologies Inc., Santa Clara, California, USA).

We also analysed possible intraspecific differences in specific leaf area (SLA) between individuals growing with and without herbivory. For this purpose, two species that were present in every plot for both treatments during spring sampling were selected: *Cistus salviifolius* (Cistaceae) and *Echium rosulatum* (Boraginaceae). Samples were collected and analysed according to the sampling protocol described in Pérez-Harguindeguy et al. (2013). For each species, two individuals were randomly chosen within each of the 16 plots and two leaves were collected from each individual, resulting in a total of four leaves per species per plot. Young and fully expanded leaves from adult plants were selected, avoiding leaves affected by pathogens or herbivores. Leaves were immediately stored in zip-lock plastic bags and placed in a cool box (4°C) for transport to the laboratory, where their SLA was calculated by dividing their fresh leaf area (measured using a leaf area scanner LI-3100 Area Meter (LI-COR, Inc. Lincoln, Nebraska, USA)) by their dry mass (obtained after drying in an oven at 40°C until constant weight). After weighing, the leaves were ground for analysis of carbon (% C) and nitrogen (% N) content, and their isotopic composition ($\delta^{15}N = {}^{15}N/{}^{14}N$; $\delta^{13}C = {}^{13}C/{}^{12}C$), following the protocol described in Roiloa et al. (2014).

2.3 | Data analysis

To examine whether the plant community composition differed between the herbivory treatments (herbivory, no-9herbivory), we carried out multivariate statistical analyses using Primer v. 7 (Clarke & Gorley, 2015). The order of distances between replicates was represented in a two-dimensional ordination space using NMDS (Non-Metric Multidimensional Scaling) with above-ground dry mass as a measure of abundance. Next, an ANOSIM (Analysis of Similarities) test was applied to determine whether the communities were statistically different. SIMPER (Similarity Percentage) analysis, which is based on testing the Bray–Curtis similarities between samples, was used to identify the species that contributed most to the similarities within each treatment and to the differences between the two treatments.

A principal components analysis (PCA) was carried out using Primer v. 7 to summarise the variation in the soil chemical composition in relation to the herbivory treatments.

To test for differences between the herbivory treatments (herbivory, no-herbivory) in terms of ecological and edaphic variables we carried out two-sample *t*-tests, except for the Simpson's diversity index in autumn, and the C/N ratio for *E. rosulatum* where the non-parametric Wilcoxon signed-rank test was performed. The normality of the data was checked using the Shapiro–Wilk test and the homogeneity of variance using *F*-tests. All these analyses were performed in R.

Specific leaf area (SLA) was analysed using linear mixed models (LMM) with the 'lmer' function from the *lme4* package in R (Bates et al., 2011). Treatment was included as a fixed factor and plot as a random factor to include the structure of the experimental design and avoid pseudoreplication problems associated with sampling several individuals per plot. Residual plots were examined to check for normality and homoscedasticity of the residuals and found adequate (Zuur et al., 2009). The *p*-values were obtained with the 'anova' function of the *lmerTest* package (Kuznetsova et al., 2014), using the Satterthwaite method. Boxplot figures were produced using *ggplot2* (Wickham, 2016). All R analyses were performed in R v.4.2.2. (R Core Team, 2022).

3 | RESULTS

3.1 | Effects at the community level

3.1.1 | Above-ground dry mass, species richness and diversity indices

From the autumn sampling data, no statistically significant differences were detected between treatments for any of the ecological variables analysed: above-ground dry mass, richness, Shannon's index and Simpson's index (Appendix S2). However, statistical differences between the treatments were found in the spring for these variables. In spring, the total above-ground dry mass was higher in the no-herbivory than in the herbivory plots (Figure 2a). This result is consistent with the visual differences observed during spring sampling between the appearance of the vegetation in herbivory and no-herbivory plots. The vegetation in no-herbivory plots was higher in height, density and cover. In contrast, in the herbivory plots large patches of bare ground and lower vegetation cover were observed. Species richness and Shannon's and Simpson's diversity indices were higher in the herbivory plots (Figure 2b–d).

3.1.2 | Community composition

In terms of community composition, taking above-ground dry mass as a measure of abundance for each species, the NMDS analysis for the autumn sampling shows a slight spatial clustering of herbivory plots (Figure 3a), although the separation between treatments is not conclusive. By contrast, in the spring sampling this clustering is evident (Figure 3b). In this season, the herbivory and no-herbivory plots are clearly differentiated along the first axis of the ordination plane. The NMDS ordination analyses provided a stress value below 0.20, indicating a good ordination pattern (Dexter et al., 2018). The ANOSIM test found significant differences between treatments which are greater in spring ($R = 0.438$; p-value$= 0.001$) than in autumn ($R = 0.193$; p-value$= 0.013$). SIMPER analyses enabled a further test of species composition differences between herbivory and no-herbivory treatments (Table 1). The SIMPER analysis identified that similarities within no-herbivory and within herbivory in autumn are almost exclusively determined by the presence of *Arisarum vulgare* (Appendix S3). Dissimilarities between both treatments in this season are mostly related to lichens, *Euphorbia* spp. and *Sedum* spp. (Appendix S4). In spring, the species contributing most to the similarities between no-herbivory plots are *Echium rosulatum*, *Vulpia membranacea*, *Scolymus hispanicus* and *Rumex bucephalophorus*,

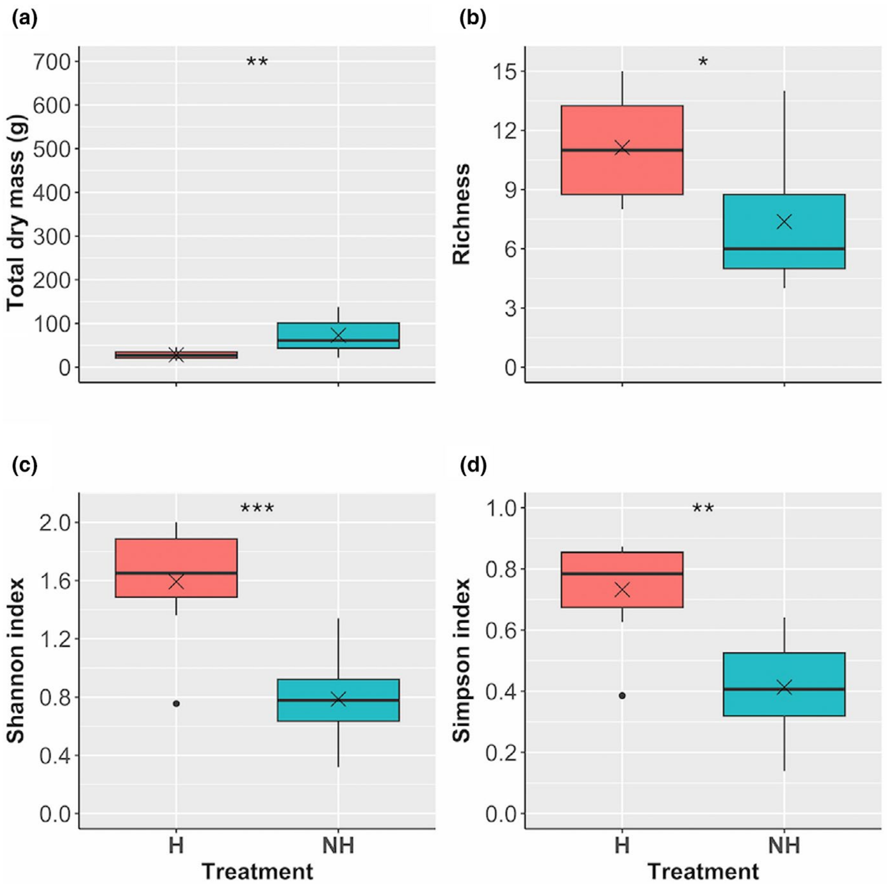


FIGURE 2 Boxplots of the distribution of (a) total above-ground dry mass; (b) species richness; (c) Shannon's diversity index; and (d) Simpson's diversity index in the no-herbivory (NH) and herbivory (H) treatments for the spring sampling. Replicates for each treatment encompassed eight plots. For each treatment, the thick horizontal line represents the median of the distribution, the box includes 50% of the data, and the whiskers reach the highest and lowest value within 95% of the distribution. Solid circles represent single values outside 95% of the distribution. Crosses represent the mean value. Significant effects are indicated with asterisks above the boxplots (*, $p \le 0.05$; **, $p \le 0.01$; ***, $p \le 0.001$).

while the species contributing most to the similarities within herbivory plots are *Linaria arenaria*, *Sedum* spp., *Xolantha guttata* and *Urtica membranacea* (Appendix S5). The high percentage of dissimilarity between treatments in spring is mainly determined by *Linaria arenaria*, *Xolantha guttata*, *Sedum* spp., *Urtica membranacea* and *Echium rosulatum* (Appendix S6).

3.2 | Soil variables

The *t*-test analyses between treatments showed no significant differences in soil chemical composition for any of the studied elements (N, C, Al, Ca, Cu, Fe, K, Mg, Na, P and S) for both autumn and spring data (Appendix S7).

The PCA does not show much separation in the soil chemical composition of the two treatments, neither for autumn nor for spring data. However, in the case of autumn data, the plots belonging to the no-herbivory treatment are slightly clustered around the origin of the vectors, indicating that these plots do not stand out as being characterised by any particular chemical element (Appendix S8). The herbivory plots, in contrast, are generally more dispersed with respect to the origin of the vectors, indicating a greater variability in their characterisation based on these edaphic variables. This distribution becomes less evident in the case of spring data, where only four of the eight plots of no-herbivory are clustered around the origin of vectors (Appendix S8).

Soil temperature and soil moisture content were not significantly different between the treatments during the autumn sampling (Appendix S9). However, significant differences were found during the spring sampling (soil temperature: $p = 0.012$, soil moisture content: $p = 0.004$). In particular, temperature and moisture values were higher for herbivory plots in spring (Appendix S9).

3.3 | Effects at the individual level

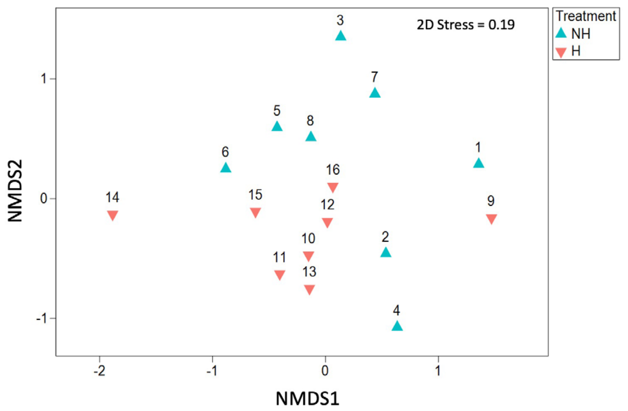
3.3.1 | Specific leaf area

There were no significant differences in SLA between the two treatments for either of the two species studied (*Echium rosulatum*: LMM: $F_{1,16} = 1.685$, $p = 0.213$, and *Cistus salviifolius*: LMM: $F_{1,16} = 0.561$, $p = 0.465$; Appendix S10). However, in the case of *Echium rosulatum*, the data showed greater variability between plots in the herbivory treatment than in the no-herbivory treatment (Appendix S10).

3.3.2 | Carbon and nitrogen isotope composition and leaf content

No significant differences were obtained for any of the studied variables (% N, δ^{15}N, % C, δ^{13}C and C/N) for *Echium rosulatum* (Appendix S11). In the case of *Cistus salviifolius*, the analysis did

(a) Autumn



(b) Spring

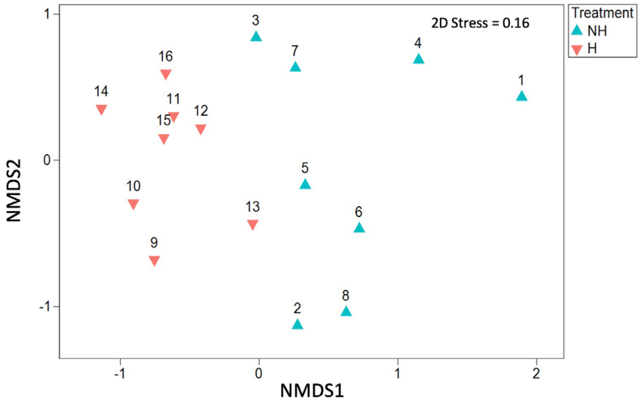


FIGURE 3 Two-dimensional non-metric multidimensional scaling (NMDS) plots based on Bray–Curtis distance similarities using above-ground dry mass as a measure of abundance and illustrating experimental plots (1–16) and herbivory treatment (NH = no-herbivory, H = herbivory) at the (a) autumn and (b) spring sampling. Replicates for each treatment encompassed $n = 8$ plots. Points closer to one another in the ordination space are more similar to those farther apart. Stress values indicate how well the multivariate data are represented in two dimensions. Analysis of Similarities (ANOSIM) tests showed significant differences between the groups based on the herbivory treatment. (a) $R = 0.193$, $p = 0.013$; (b) $R = 0.438$, $p = 0.001$.

TABLE 1 Percentages of similarity for each treatment and percentage of dissimilarity between treatments. Values obtained from SIMPER analysis. H: Herbivory treatment, NH: No-Herbivory treatment.

	Autumn	Spring
Average similarity NH (%)	26.04	6.47
Average similarity H (%)	35.95	23.19
Average dissimilarity between NH & H (%)	74.36	94.64

not show significant differences for % C and δ^{13}C (Appendix S11). However, leaves of *Cistus salviifolius* had significantly higher values of % N and δ^{15}N in the no-herbivory than in the herbivory plots, whilst they had a greater C/N proportion in the herbivory than in the no-herbivory plots (Appendix S11).

4 | DISCUSSION

Our findings show that mammalian herbivory impacts grey-dune ecosystems both at the community level and at the individual level, with important seasonal variations. We discuss these results in depth, emphasising their relevance for the conservation of dune flora.

4.1 | Effects at the community level

No differences in above-ground dry mass, species richness and Shannon and Simpson's diversity indices were detected between the two treatments in the autumn sampling, which can be explained by two factors. The first is that many of the species were probably not developed in autumn because of their phenological cycle, which attenuated possible differences associated with herbivory. The second factor is that at the time of the autumn sampling the study area (including both herbivory and no-herbivory plots) was dominated by *Arisarum vulgare*, which covered the surface with its horizontal growth, preventing the development of other species and homogenising the plant communities of both treatments. In addition, *Arisarum vulgare* is known to contain alkaloids that are toxic for fresh consumption, causing severe effects ranging from mucosal irritation to allergic reactions, gastroenteritis, liver damage and even death (Rakba et al., 1999). It is therefore to be expected that the impact of herbivory was low in the area at that time of year and that mammal species chose to feed elsewhere on the island. Differences in the level of herbivory between spring and autumn have been detected previously and have also been related to the palatability of species (Miranda et al., 2011). In contrast to the above, significant differences in these parameters were detected in the spring sampling that will be discussed in the sections below.

4.1.1 | Above-ground dry mass

Above-ground dry mass sampled in spring was lower in those plots exposed to herbivory than in those where herbivores were excluded. This may be explained as the result of direct control exerted by herbivores through browsing on the vegetation, removing a large proportion of the above-ground dry mass (Pascual et al., 2017). Other factors that may influence these differences are the mechanical action of trampling and substrate mobilisation by herbivores, which interfere with plant growth. As .a result, this can determine the appearance of areas with soil devoid of vegetation in the herbivory treatment. Moreover, in the long term, exposure to herbivory may lead to the prevalence of species that adopt a horizontal occupation of the space, in contrast to the area without herbivory, in which formations with a vertical structure and high occupation in volume are common (Gómez Sal et al., 1986).

4.1.2 | Species richness and diversity indices

In contrast to dry mass, higher species richness and diversity, as expressed by Shannon's and Simpson's indices, were observed in spring in the plots exposed to herbivory. This result can be associated with the so-called intermediate disturbance hypothesis (Connell, 1978). According to this hypothesis, when herbivore density reaches intermediate values, richness and diversity indices increase, as herbivory generates spatial heterogeneity resulting in areas with a reduction of dominant competing species. This allows access to limiting resources by other plant species that would remain subordinate in the absence of herbivory (Pascual et al., 2017).

4.1.3 | Community composition

In the community analysis for the autumn sampling, a certain clustering of the herbivory plots in terms of composition and above-ground dry mass for each species can be found, which is clearly accentuated in the spring sampling (see NMDS representation, Figure 3a,b) because of the change in plant composition and herbivory behaviour. In spring, no-herbivory plots appear spatially separated from herbivory plots, indicating that both treatments differ in composition and above-ground dry mass. However, it should be noted that the no-herbivory plots show greater variability, which translates into a greater dispersion of points in the NMDS plot.

The greater similarity between the herbivory plots during spring is due to the fact that all plots have a similar specific composition and very low levels of above-ground dry mass for all species. This can be explained by the high number of species with very low above-ground dry mass (e.g. *Linaria arenaria*, *Sedum* spp., *Xolantha guttata*, *Urtica membranacea*) that are represented in most or all of the plots, although they are not dominant in any case. In the no-herbivory plots, on the other hand, species with a larger volume develop and reach a higher degree of dominance, so each plot tends to have a greater above-ground dry mass that corresponds to one or two clearly dominant species that differ between plots (e.g., *Echium rosulatum*, *Vulpia membranacea*, *Scolymus hispanicus*, *Rumex bucephalophorus*). In other words, the species that dominate in one plot are different from those that dominate in another, all presenting higher above-ground dry mass than in the herbivory treatment.

From the species unique to each treatment, the case of *Linaria arenaria* stands out because it is a critically endangered species according to the Atlas and Red Book of vascular flora in Spain (Bañares et al., 2004). The presence of this species was only detected in the herbivory plots, so predation seems to be favouring the conservation of this species. This phenomenon could again be linked to the afore-mentioned hypothesis of intermediate disturbance, allowing the development of this small-sized species in a less severe competition regime. Coastal sand dunes are dynamic ecosystems where vegetation has evolved to withstand recurrent disturbances (Brunbjerg et al., 2012). As a result, disturbance plays a key role in the conservation of dune vegetation and in promoting plant diversity (Brunbjerg et al., 2014, 2015). In this context, disturbances may facilitate the persistence of endemic species by increasing their recruitment rates, as observed for the endangered plants *Lupinus tidestromii* and *Layia carnosa* in coastal sand dunes of northern California, USA (Pardini et al., 2015). Consequently, grazing by large herbivores can help maintain the necessary level of disturbance, and has been proposed as a management tool for the conservation of dune vegetation (Plassmann et al., 2010).

4.2 | Soil variables

Regarding the analysis of the edaphic variables, no statistically significant differences were detected between treatments for any of the chemical elements analysed (C, N, Al, Ca, Cu, Fe, K, Mg, Na, P and S). However, in the case of the autumn sampling, the PCA allows us to observe a greater variability between herbivory plots than between no-herbivory plots. The lower variability of no-herbivory plots may be due to the zero-disturbance regime in the lack of herbivores, which results in a more homogeneous soil. In contrast, the herbivory regime is linked to greater variability at the local level associated with the interaction of herbivores with the substrate (burrows, paths, latrines, trampling, grazing areas). The reason for observing this greater variability in the herbivory treatment in autumn and not in spring (as found for most of the other traits measured in the study) could be due to a delayed effect of herbivory activity on soil composition (Brown & Allen, 1989). Soil inputs from faeces, for example, would be expected to be higher at the end of autumn/winter (after peak season for herbivory activity) than in early spring (after a period of low herbivory activity).

Regarding soil temperature and soil moisture content, no differences were detected in the autumn sampling. In the spring sampling, significantly higher values for both variables were obtained in the herbivory treatment. The increase in soil temperature in the herbivory plots may be related to the suppression of above-ground dry mass caused by herbivory, which would lead to increased exposure of the soil to solar radiation, resulting in increased soil temperature (Veldhuis et al., 2014). Regarding soil moisture content, the results obtained seem a priori contradictory (higher in herbivory than in no-herbivory), because at higher temperatures (as found), a higher evaporation rate could also be expected, and hence also a lower moisture content. However, the soil in plots exposed to herbivory has a greater compaction caused by trampling. Previous studies suggest that long-term trampling leads to soil compaction, which results in increased water content due to an increase in water retention in the soil pores (Liddle & Greig-Smith, 1975). Therefore, in dry periods (with no rain for several consecutive days), it is possible that soil compaction helps to retain the scarce water present in the soil pores. This mechanism may be particularly important in sandy soils, as pressing sand particles closer together reduces pore size, thereby increasing the water-holding capacity of the soil (Huang & Hartemink, 2020). Another plausible explanation for the lower soil moisture content in plots exposed to herbivory may relate to a reduced plant cover/biomass. Some studies suggest that losses of soil water through transpiration by plant species (evapotranspiration) can be as much as double the losses through physical evaporation (Stan et al., 2016). Therefore, the higher vegetation cover present in the no-herbivory plots would imply higher losses of soil moisture through evapotranspiration than in the herbivory plots.

4.3 | Effects at the individual level

4.3.1 | Specific leaf area

Specific leaf area (SLA) can be considered an indicator of thickness or density and tends to be lower in individuals subjected to resource scarcity (Pérez-Harguindeguy et al., 2013). Leaves with a lower SLA are typically thick and suffer lower levels of herbivory (Schädler et al., 2003). In the same line, Jessen et al. (2020) have interpreted low SLA as an adaptation to lower visibility and palatability by herbivorous species. For this reason, SLA has been considered a putative defence trait against herbivores (Agrawal & Fishbein, 2006). Contrary to expectations, in this study no significant differences were detected between the two treatments for either of the two species studied (*Cistus salviifolius* and *Echium rosulatum*). A greater between-replicate variability inherent to this trait compared to other leaf traits may help explain the lack of significant differences (Wilson et al., 1999). However, in the case of *Echium rosulatum*, a higher variability was obtained between the herbivory plots than between the no-herbivory plots. Therefore, individuals with higher and lower SLA developed in the herbivory treatment, even though the mean value was similar to that of the no-herbivory plots. This may again be because in the herbivory zone there is more variability of conditions at the local level, while the no-herbivory zone is subject to more homogeneous conditions that determine a similar development of the individuals grown there.

4.3.2 | Carbon and nitrogen isotope composition and leaf content

Carbon and nitrogen isotopic composition, leaf C and N content and C/N ratio of individuals of *E. rosulatum* were not affected by the herbivory treatment. However, for *C. salviifolius*, lower % N and δ^{15}N values were detected in the herbivory treatment, as well as a higher C/N ratio in the herbivory treatment. A lower % N in the herbivory treatment is expected, as plants under herbivory pressure tend to withdraw nitrogen from their leaves in order to conserve it, thus increasing the C/N ratio of the leaves. The C/N ratio of leaves reflects their fibre/protein proportion. Thus, leaves with higher fibre-to-protein ratios in the herbivory treatment indicate lower palatability and lower nutritional quality, which is an adaptive mechanism to deter predators (Hartley & Jones, 1997; Schädler et al., 2003). Variation in δ^{15}N in plants is driven by complex mechanisms (Evans, 2001; Dawson et al., 2002), and there is still limited information on how foliar δ^{15}N changes in response to herbivory. Previous research on a grassland ecosystem has reported lower δ^{15}N values in response to ungulate grazing, with various mechanisms, such as root depth or use of different N pools from the soil, invoked to explain this phenomenon (Frank & Evans, 1997). A decrease in root length may occur in response to herbivory (Frew, 2021), which would reduce the proportion of ^{15}N available for plant assimilation, as shorter roots are limited to accessing nitrogen from the upper soil layers, where ^{15}N levels are typically lower compared to deeper soil layers (Dawson et al., 2002). Nitrification, a process that discriminates against ^{15}N, has been found to increase as a result of grazing (Le Roux et al., 2003). Therefore, grazing can alter the nitrogen sources available to plants, leading to lighter isotopic compositions in plant tissues within grazed areas compared to areas without herbivores (Frank & Evans, 1997; Frank et al., 2004). However, other factors, such as changes in mycorrhizal associations may also be at play. Light or moderate grazing has been found to increase mycorrhizal associations (Dudinszky et al., 2019), which could cause a reduction in foliar δ^{15}N (Hobbie & Högberg, 2012).

In contrast, regarding the C composition of the leaves, no significant differences in % C and δ^{13}C values were detected. On the one hand, the % C results indicate that, in this scenario, herbivory pressure is not modifying the fibre content of the leaves (Hartley & Jones, 1997). On the other hand, the absence of differences in δ^{13}C values indicates that predation pressure is not altering the water use efficiency of the plants (Lambers & Oliveira, 2019). This result could reflect that the effects of herbivory do not affect the shoot-to-root ratio, the gas exchange, the leaf temperature or the CO_2 sources (atmospheric vs soil respired) (Alstad et al., 1999).

5 | CONCLUSIONS

Herbivory by medium to large mammals influences the composition and structure of the grey-dune plant community, causing a decrease in above-ground dry mass and an increase in species richness, Shannon's index and Simpson's index. At the individual plant level, this predation altered C/N ratio and N isotopic composition reducing % N and δ^{15}N content. Herbivory also alters soil conditions, increasing soil temperature and soil moisture content. Overall, our findings have a strong seasonal component, with effects being noticeable in spring and limited in autumn, which highlights the need to analyse the plant communities on a seasonal basis in order to draw real conclusions about the effects of herbivory by medium to large mammals. Our study also highlights the role of disturbance as a potential mechanism contributing to spatial heterogeneity. Ultimately, these results demonstrate the influence of herbivory on grey-dune vegetation and suggest the need to take these effects into account when developing management plans, particularly those considering the introduction of large herbivore species in coastal and island ecosystems.

ACKNOWLEDGEMENTS

The authors thank the staff at Parque Nacional Illas Atlánticas (Atlantic Islands National Park) for granting access to the site.

FUNDING INFORMATION

Sandra Francés Alcántara was funded by a contract within the action 'Conservation and improvement of biodiversity in the Atlantic Islands National Maritime Terrestrial Park, under the Recovery, Transformation and Resilience Plan (PRTR-2022-CE106)'. Funding for Open Access: Universidade de Santiago de Compostela/CISUG.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in Appendix S12.

ORCID

Rubén Retuerto https://orcid.org/0000-0002-9879-5512
Julia Sánchez Vilas https://orcid.org/0000-0002-4049-8443

REFERENCES

Agrawal, A.A. & Fishbein, M. (2006) Plant defense syndromes. *Ecology*, 87(7), 132–149. Available from: https://doi.org/10.1890/0012-9658

Agrawal, A.A. & Maron, J.L. (2022) Long-term impacts of insect herbivores on plant populations and communities. *Journal of Ecology*, 110(12), 2800–2811. Available from: https://doi.org/10.1111/1365-2745.13996

Alstad, K.P., Welker, J.M., Williams, S.A. & Trlica, M.J. (1999) Carbon and water relations of *Salix monticola* in response to winter browsing and changes in surface water hydrology: an isotopic study using δ13C and δ18O. *Oecologia*, 120(3), 375–385. Available from: https://doi.org/10.1007/S004420050870

Bañares, Á., Blanca, G., Güemes, J., Moreno, J.C. & Ortiz, S. (2004) *Atlas y libro de rojo de la flora vascular amenazada de España*. Madrid: Dirección General de Conservación de la Naturaleza.

Bardgett, R.D., Wardle, D.A. & Yeates, G.W. (1998) Linking above-ground and below-ground interactions: how plant responses to foliar herbivory influence soil organisms. *Soil Biology and Biochemistry*, 30(14), 1867–1878.

Bates, D., Maechler, M. & Bolker, B. (2011) lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-39. http://CRAN.R-project.org/package=lme4

Brown, A.C. & McLachlan, A. (2002) Sandy shore ecosystems and the threats facing them: some predictions for the year 2025. *Environmental Conservation*, 29(1), 62–77. Available from: https://doi.org/10.1017/S037689290200005X

Brown, B.J. & Allen, T.F.H. (1989) The importance of scale in evaluating herbivory impacts. *Oikos*, 54(2), 189–194. Available from: https://doi.org/10.2307/3565265

Brunbjerg, A.K., Borchsenius, F., Eiserhardt, W.L., Ejrnæs, R. & Svenning, J.C. (2012) Disturbance drives phylogenetic community structure in coastal dune vegetation. *Journal of Vegetation Science*, 23(6), 1082–1094. Available from: https://doi.org/10.1111/J.1654-1103.2012.01433.X

Brunbjerg, A.K., Jørgensen, G.P., Nielsen, K.M., Pedersen, M.L., Svenning, J.C. & Ejrnæs, R. (2015) Disturbance in dry coastal dunes in Denmark promotes diversity of plants and arthropods. *Biological Conservation*, 182, 243–253. Available from: https://doi.org/10.1016/J.BIOCON.2014.12.013

Brunbjerg, A.K., Svenning, J.C. & Ejrnæs, R. (2014) Experimental evidence for disturbance as key to the conservation of dune grassland. *Biological Conservation*, 174, 101–110. Available from: https://doi.org/10.1016/J.BIOCON.2014.04.002

Campoy, J., Lema, M., Fenollosa, E., Munné-Bosch, S. & Retuerto, R. (2021) Functional responses to climate change may increase invasive potential of *Carpobrotus edulis*. *American Journal of Botany*, 108(10), 1902–1916. Available from: https://doi.org/10.1002/AJB2.1745

Clarke, K.R. & Gorley, R.N. (2015) *PRIMER v7: User Manual/Tutorial*.

Cole, D.N. (1995) Experimental trampling of vegetation. II. Predictors of resistance and resilience. *The Journal of Applied Ecology*, 32(1), 215–224. Available from: https://doi.org/10.2307/2404430

Collins, S.L., Knapp, A.K., Briggs, J.M., Blair, J.M. & Steinauer, E.M. (1998) Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science (New York, N.Y.)*, 280(5364), 745–747. Available from: https://doi.org/10.1126/SCIENCE.280.5364.745

Connell, J.H. (1978) Diversity in tropical rain forests and coral reefs. *Science*, 199(4335), 1302–1310. Available from: https://doi.org/10.1126/SCIENCE.199.4335.1302

Crawley, M.J. (1997) Plant-herbivory dynamics. In: Crawley, M.J. (Ed.) *Plant ecology*. Oxford: Blackwell Scientific Publications.

Dawson, T.E., Mambelli, S., Plamboeck, A.H., Templer, P.H. & Tu, K.P. (2002) Stable isotopes in plant ecology. *Annual Review of Ecology and Systematics*, 33, 507–559. Available from: https://doi.org/10.1146/ANNUREV.ECOLSYS.33.020602.095451

Delgado-Fernández, I., O'Keeffe, N. & Davidson-Arnott, R.G.D. (2019) Natural and human controls on dune vegetation cover and disturbance. *Science of the Total Environment*, 672, 643–656. Available from: https://doi.org/10.1016/J.SCITOTENV.2019.03.494

Dexter, E., Rollwagen-Bollens, G. & Bollens, S.M. (2018) The trouble with stress: a flexible method for the evaluation of nonmetric multidimensional scaling. *Limnology and Oceanography: Methods*, 16(7), 434–443. Available from: https://doi.org/10.1002/LOM3.10257

Directorate-General for Environment, E.C, Tsiripidis, I., Piernik, A., Janssen, J.A., Tahvanainen, T., Molina, J. et al. (2016) European red list of habitats. Part 2, *Terrestrial and freshwater habitats*.

Dudinszky, N., Cabello, M.N., Grimoldi, A.A., Schalamuk, S. & Golluscio, R.A. (2019) Role of grazing intensity on shaping arbuscular mycorrhizal fungi communities in Patagonian semiarid steppes. *Rangeland Ecology & Management*, 72(4), 692–699. Available from: https://doi.org/10.1016/J.RAMA.2019.02.007

El-Keblawy, A., Ksiksi, T. & El Alqamy, H. (2009) Camel grazing affects species diversity and community structure in the deserts of the UAE. *Journal of Arid Environments*, 73(3), 347–354. Available from: https://doi.org/10.1016/J.JARIDENV.2008.10.004

Enquist, B.J., Abraham, A.J., Harfoot, M.B.J., Malhi, Y. & Doughty, C.E. (2020) The megabiota are disproportionately important for biosphere functioning. *Nature Communications*, 11, 699. Available from: https://doi.org/10.1038/s41467-020-14369-y

Evans, R.D. (2001) Physiological mechanisms influencing plant nitrogen isotope composition. *Trends in Plant Science*, 6(3), 121–126.

Feagin, R.A., Sherman, D.J. & Grant, W.E. (2005) Coastal erosion, global sea-level rise, and the loss of sand dune plant habitats. *Frontiers in Ecology and the Environment*, 3(7), 359–364.

Feeley, K.J. & Terborgh, J.W. (2005) The effects of herbivore density on soil nutrients and tree growth in thropical forest fragments. *Ecology*, 86(1), 116–124. Available from: https://doi.org/10.1890/03-0657

Fernández Bouzas, J.A. (2017) Gestión ambiental y desarrollo en el Parque Nacional de las Islas Atlánticas de Galicia. *Boletín de la Sociedad de Ciencias de Galicia*, 17, 7–26.

Forbes, E.S., Cushman, J.H., Burkepile, D.E., Young, T.P., Klope, M. & Young, H.S. (2019) Synthesizing the effects of large, wild herbivore exclusion on ecosystem function. *Functional Ecology*, 33(9), 1597–1610. Available from: https://doi.org/10.1111/1365-2435.13376

Frank, D.A. & Evans, R.D. (1997) Effects of native grazers on grassland N cycling in Yellowstone National Park. *Ecology*, 78(7), 2238–2248. Available from: https://doi.org/10.2307/2265959

Frank, D.A., Evans, R.D. & Tracy, B.F. (2004) The role of ammonia volatilization in controlling the natural ^{15}N abundance of a grazed grassland. *Biogeochemistry*, 68(2), 169–178. Available from: https://doi.org/10.1023/B:BIOG.0000025736.19381.91

Frank, D.A., Groffman, P.M., Evans, R.D. & Tracy, B.F. (2000) Ungulate stimulation of nitrogen cycling and retention in Yellowstone Park grasslands. *Oecologia*, 123(1), 116–121. Available from: https://doi.org/10.1007/S004420050996/METRICS

Frew, A. (2021) Aboveground herbivory suppresses the arbuscular mycorrhizal symbiosis, reducing plant phosphorus uptake. *Applied Soil Ecology*, 168, 104133. Available from: https://doi.org/10.1016/J.APSOIL.2021.104133

Gianoli, E. & Salgado-Luarte, C. (2017) Tolerance to herbivory and the resource availability hypothesis. *Biology Letters*, 13(5), 20170120. Available from: https://doi.org/10.1098/RSBL.2017.0120

Gómez Sal, A., De Miguel, J.M., Casado, M.A. & Pineda, F.D. (1986) Successional changes in the morphology and ecological responses of a grazed pasture ecosystem in Central Spain. *Vegetatio*, 67(1), 33–44. Available from: https://doi.org/10.1007/BF00040316

Hartley, S.E. & Jones, C.G. (1997) Plant chemistry and herbivory, or why is the world green. In: Crawley, M.J. (Ed.) *Plant ecology*. Oxford: Blackwell Scientific Publications, pp. 284–324.

Hobbie, E.A. & Högberg, P. (2012) Nitrogen isotopes link mycorrhizal fungi and plants to nitrogen dynamics. *New Phytologist*, 196(2), 367–382. Available from: https://doi.org/10.1111/J.1469-8137.2012.04300.X

Huang, J. & Hartemink, A.E. (2020) Soil and environmental issues in sandy soils. *Earth-Science Reviews*, 208, 103295. Available from: https://doi.org/10.1016/J.EARSCIREV.2020.103295

Jessen, M.T., Kaarlejärvi, E., Olofsson, J. & Eskelinen, A. (2020) Mammalian herbivory shapes intraspecific trait responses to warmer climate and nutrient enrichment. *Global Change Biology*, 26(12), 6742–6752. Available from: https://doi.org/10.1111/GCB.15378

Kielland, K. & Bryant, J.P. (1998) Moose herbivory in taiga: effects on biogeochemistry and vegetation dynamics in primary succession. *Oikos*, 82(2), 377–383. Available from: https://doi.org/10.2307/3546979

Kristensen, J.A., Svenning, J.C., Georgiou, K. & Malhi, Y. (2022) Can large herbivores enhance ecosystem carbon persistence? *Trends in Ecology & Evolution*, 37(2), 117–128. Available from: https://doi.org/10.1016/J.TREE.2021.09.006

Kuznetsova, A., Brockhoff, P.B. & Christensen, R.H.B. (2014) lmerTest: Tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package) *R package version* R package version 2.0-6. http://CRAN.R-project.org/package=lmerTest

Lambers, H. & Oliveira, R. (2019) *Plant physiological ecology*. Switzerland: Springer.

Le Roux, X., Bardy, M., Loiseau, P. & Louault, F. (2003) Stimulation of soil nitrification and denitrification by grazing in grasslands: do changes in plant species composition matter? *Oecologia*, 137(3), 417–425. Available from: https://doi.org/10.1007/S00442-003-1367-4/FIGURES/5

Li, L., He, X.Z., Wang, M., Huang, L., Wang, Z., Zhang, X. et al. (2024) Grazing-driven shifts in soil bacterial community structure and function in a typical steppe are mediated by additional N inputs. *Science of the Total Environment*, 912, 169488. Available from: https://doi.org/10.1016/J.SCITOTENV.2023.169488

Liddle, M.J. & Greig-Smith, P. (1975) A survey of tracks and paths in a sand dune ecosystem I. Soils. *Journal of Applied Ecology*, 12(3), 893–908. Available from: https://doi.org/10.2307/2402097

Maron, J.L. & Crone, E. (2006) Herbivory: effects on plant abundance, distribution and population growth. *Proceedings of the Royal Society B: Biological Sciences*, 273(1601), 2575–2584. Available from: https://doi.org/10.1098/RSPB.2006.3587

Millett, J. & Edmondson, S. (2013) The impact of 36 years of grazing management on vegetation dynamics in dune slacks. *Journal of Applied Ecology*, 50(6), 1367–1376. Available from: https://doi.org/10.1111/1365-2664.12113

Miranda, M., Díaz, L., Sicilia, M., Cristóbal, I. & Cassinello, J. (2011) Seasonality and edge effect determine herbivory risk according to different plant association models. *Plant Biology*, 13(1), 160–168. Available from: https://doi.org/10.1111/J.1438-8677.2009.00316.X

Pardini, E.A., Vickstrom, K.E. & Knight, T.M. (2015) Early successional microhabitats allow the persistence of endangered plants in coastal sand dunes. *PLoS One*, 10(4), e0119567. Available from: https://doi.org/10.1371/JOURNAL.PONE.0119567

Pascual, J., Alberti, J., Daleo, P. & Iribarne, O. (2017) Herbivory and trampling by small mammals modify soil properties and plant assemblages. *Journal of Vegetation Science*, 28(5), 1028–1035. Available from: https://doi.org/10.1111/JVS.12562

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P. et al. (2013) New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, 61(3), 167–234. Available from: https://doi.org/10.1071/BT12225

Plassmann, K., Laurence, M., Jones, M. & Edwards-Jones, G. (2010) Effects of long-term grazing management on sand dune vegetation of high conservation interest. *Applied Vegetation Science*, 13(1), 100–112. Available from: https://doi.org/10.1111/J.1654-109X.2009.01052.X

Poorter, L., Van De Plassche, M., Willems, S. & Boot, R.G.A. (2004) Leaf traits and herbivory rates of tropical tree species differing in successional status. *Plant Biology*, 6(6), 746–754. Available from: https://doi.org/10.1055/S-2004-821269

R Core Team. (2022) R: A language and environment for statistical computing.

Rakba, N., Melhaoui, A., Loyer, P., Guy Delcros, J., Morel, I. & Lescoat, G. (1999) Bgugaine, a pyrrolidine alkaloid from *Arisarum vulgare*, is a strong hepatotoxin in rat and human liver cell cultures. *Toxicology Letters*, 104(3), 239–248.

Roiloa, S.R., Antelo, B. & Retuerto, R. (2014) Physiological integration modifies δ15N in the clonal plant *Fragaria vesca*, suggesting preferential transport of nitrogen to water-stressed offspring. *Annals of Botany*, 114(2), 399–411. Available from: https://doi.org/10.1093/AOB/MCU064

Salgado-Luarte, C. & Gianoli, E. (2012) Herbivores modify selection on plant functional traits in a temperate rainforest understory. *The American Naturalist*, 180(2), E42–E53. Available from: https://doi.org/10.1086/666612

Santamaría, L., Latorre-Piñeiro, L. & Larrinaga, A. (2012) Control integrado de complejos de invasión en el Parque Nacional Marítimo-Terrestre de las Islas Atlánticas de Galicia. In: Ramírez, L. & Asensio, B. (Eds.) *Proyectos de investigación en Parques Nacionales*, Madrid, España: Organismo Autónomode Parques Nacionales. pp. 183–205.

Schädler, M., Jung, G., Auge, H., Brandl Schädler, R., Schädler, M., Jung, G. et al. (2003) Palatability, decomposition and insect herbivory: patterns in a successional old-field plant community. *Oikos*, 103(1), 121–132. Available from: https://doi.org/10.1034/J.1600-0706.2003.12659.X

Stan, F.-I., Neculau, G., Zaharia, L., Ioana-Toroimac, G. & Mihalache, S. (2016) Study on the evaporation and evapotranspiration measured on the Căldăruşani Lake (Romania). *Procedia Environmental Sciences*, 32, 281–289. Available from: https://doi.org/10.1016/J.PROENV.2016.03.033

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(6), 1506–1517. Available from: https://doi.org/10.1111/1365-2745.12322

Vilas, A., Gamallo, B., Framil, J., Fernández, J.A., Sanz, K., Lois, M. et al. (2005) Guía de visita Parque Nacional Marítimo-Terrestre de las islas Atlánticas de Galicia.

Warner, P.J. & Cushman, J.H. (2002) Influence of herbivores on a perennial plant: variation with life history stage and herbivore species. *Oecologia*, 132(1), 77–85. Available from: https://doi.org/10.1007/S00442-002-0955-Z

Wickham, H. (2016) *ggplot2: elegant graphics for data analysis*. Cham, Switzerland: Springer International Publishing. Available from: https://doi.org/10.1007/978-3-319-24277-4

Wilson, P.J., Thompson, K. & Hodgson, J.G. (1999) Specific leaf area and leaf dry matter content as alternative predictors of plant strategies. *New Phytologist*, 143(1), 155–162. Available from: https://doi.org/10.1046/J.1469-8137.1999.00427.X

Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A. & Smith, G.M. (2009) *Mixed effects models and extensions in ecology with R*. New York: Springer Science.

SUPPORTING INFORMATION

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

Appendix S1. Photo of experimental plot.

Appendix S2. Boxplots of total above-ground dry mass and diversity indices.

Appendix S3. Similarity values obtained via SIMPER analysis from autumn data.

Appendix S4. Dissimilarity values obtained via SIMPER analysis from autumn data.

Appendix S5. Similarity values obtained via SIMPER analysis from spring data.

Appendix S6. Dissimilarity values obtained via SIMPER analysis from spring data.

Appendix S7. Summary statistics of soil variables for autumn and spring data.

Appendix S8. Principal component analysis of soil chemical variables.

Appendix S9. Boxplots of soil temperature and soil moisture content.

Appendix S10. Specific Leaf Area (mean ± SE) of *Echium rosulatum* and *Cistus salviifolius*.

Appendix S11. Boxplots of C and N leaf content and C and N leaf isotopic composition.

Appendix S12. Data set.

How to cite this article: Francés Alcántara, S., Retuerto, R. & Sánchez Vilas, J. (2024) Mammalian herbivory alters structure, composition and edaphic conditions of a grey-dune community. *Journal of Vegetation Science*, 35, e70001. Available from: https://doi.org/10.1111/jvs.70001