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An Eltonian proxy for restoring a lost browser-tree interaction

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ABSTRACT

Many South American dry woodlands lack good historical or paleoecological baseline data to inform restoration and conservation. However, functionalist approaches such as those popularized by rewilding suggest that functional interactions producing target ecosystem processes are valid even without data confirming compositionist values such as a long coevolutionary history or known historical range overlaps of target species. In central Chile, the guanaco (*Lama guanicoe*) has been extirpated but is known to browse trees in other regions of South America, and the tree *Vachellia [Acacia] caven* shows adaptations to browsing but has no extant browsers within its Chilean range. Both species are native to Chile but there are no data to assess their historical levels of interaction. Here we test the hypothesis that they can act as mutual “Eltonian proxy” species: interacting species for which we lack sufficient data (the Eltonian shortfall) to prove they are not proxies. Specifically we predict that they have complementary adaptations such that guanacos will browse *Vachellia [Acacia] caven* and the latter will show adaptive responses to their browsing. We introduced five guanacos into an enclosure of *Vachellia [Acacia] caven* “espinal” woodland, and over two years measured the growth responses of individual branches, compared to branches of trees in an area without browsing. We predicted that *Vachellia [Acacia] caven* would show compensatory growth in response to guanaco browsing resulting in an increase in branching. Guanacos browsed throughout the two years. In the presence of guanaco browsing, *Vachellia [Acacia] caven* branches grew longer, grew more sub-branches, and showed more densely streamlined branch architectures. These results indicate that guanacos could be used to substitute anthropogenic pruning as a restoration and management technique in *Vachellia [Acacia] caven* “espinal” woodlands. However, other extinct megaherbivores or extirpated deer may also be key components of a past herbivore community to which *Vachellia [Acacia] caven* was adapted. Further attention to a network of multiple interacting browsers, and their indirect and nontrophic effects, is an area for further research.

1. Introduction

Considerable research attention is currently paid in Europe to

restoring woodland dynamics and functioning by rewilding large mammalian herbivores up to their historical densities (Svenning et al., 2016). Similarly, other continents have lost their faunal diversity in a

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way that most likely affected forest cover and successional trajectories (Soulé and Noss 1998). Although we have data on the likely causes and rates of extinction of megafauna on different continents (e.g., Sandom et al., 2014), our hypotheses and knowledge about prehistorical woodland dynamics before and after these extinctions is not equally well developed for all parts of the globe. Research draws on generalities observed in the present to interpolate to past woodland dynamics for which we have little data (Bakker et al., 2016). A non-uniform but largely shallow temporal depth for ecological data also informs projections of possible future global woodland dynamics (e.g. McDowell et al., 2020). This dependence on the present may induce shifting baseline biases.

The many woodland types of South America, ranging from temperate, semi-arid, and seasonally dry to tropical, have lost a range of large herbivores since the late Pleistocene (Fariña et al., 2013). Trees in these woodlands show adaptations to megaherbivore browsing such as thorns, small leaves and densely branched crowns (Dantas and Pausas 2022). These traits are likely to have been adaptations to currently extinct or extirpated browsers. However, in many cases our knowledge of prehistorical co-evolution and historical landscape dynamics in South American woodlands, especially the less-studied arid and semi-arid woodlands, is insufficient to inform restoration and conservation policy (Newton et al., 2012). This is the case for the two main woodland types of central Chile, which can be connected by succession, the *espinal* and sclerophyllous forest (Root-Bernstein et al., 2017, 2022). Sclerophyllous forest is an open or closed woodland dominated by endemic sclerophyllous tree species, whereas *espinal* is an open silvopastoral pseudo-savanna currently dominated by the native *Vachellia [Acacia] caven*, often in a multi-stemmed or shrub habit due to felling or coppicing (Donoso 1982). In these woodlands, browsing currently does not occur due to the absence of any browsing species, and is considered by many local experts to be inherently harmful for trees (pers. obs. Guerrero-Gatica, Root-Bernstein). Therefore, its reintroduction is not considered as a possible restoration or conservation measure. However, practices that could be considered as analogues to browsing such as intensive pruning or pollarding have been proposed as management strategies for *espinal*, and have been shown to induce cascades of positive effects on productivity and biodiversity (Olivares 2016).

Espinal in fact has considerable regenerative or resilience capacity when faced with varying intensities of pruning, pollarding, coppicing and felling (Root-Bernstein et al., 2017, 2022). Reducing canopy cover from closed-canopy to around 30–40% canopy cover is judged to maximize both tree and understory herbaceous growth (Benedetti, 2012; Olivares 2016). At that level of pruning, regrowth after cutting is maximized in terms of number of stems, length, and speed in trees with a basal diameter over 20 cm, reflected in trees with multiple stems; while total growth biomass is generally reported to be several times greater than in non-pruned trees (Benedetti, 2012). Coppicing and pruning interventions are analogous to very different forms of browsing or herbivory-related disturbance, for example browsing by mesoherbivores vs trunk destruction by large herbivores such as elephants. The level of optimized compensatory growth reported by Benedetti (2012) appears to be analogous to herbivore effects including higher-intensity forms of disturbance, perhaps of a type created by megaherbivores.

The rewilding approach to restoration and conservation has pioneered a “functionalist” rather than “compositionalist” perspective (Gillson et al., 2011). For example, due to the absence of a species that has gone extinct, a related species with similar ecological functions may serve as a functional proxy in rewilding projects, to restore similar ecological processes (Griffiths et al., 2010). Such an approach may also be valuable when the data required for a compositionalist approach, for example data about species interactions implicated in key ecological functions such as seed dispersal, browsing, soil biopedurbation or pollination, is missing or incomplete. Data shortfalls about species interactions (Eltonian shortfalls), even without considering historical or paleoecological data, are not unusual (Strydom et al., 2021).

In the case of central Chilean *espinal* and sclerophyllous woodlands, a combination of around 500 years of land cover change, poor historical records, and missing paleoecological data, makes it difficult to determine which species of trees and large herbivores coevolved, where, and with what temporal depth and interaction intensity, to result in the observed tree traits that appear to be adaptations to herbivory, and their cascading ecological effects. Several large herbivores such as South American horses, deer species, and paleolamas and their descendant guanacos (*Lama guanicoe*), as well as megafauna including various species of giant sloth and gomphothere, existed on both sides of the Andes (Prado et al., 2001; Mendoza et al., 2018). The tree *Vachellia [Acacia] caven* and other Fabaceae are native to both sides of the Andes, while other central Chilean woodland tree species are endemic to Chile (Scherson et al., 2014). Range overlap alone tells us little about species interactions or the potential for coevolution (Tylianakis & Morris, 2017). To what extent the Andes was a barrier for species interactions such as herbivory, potentially leading either to the maintenance, alteration or loss of established interactions (e.g. Hoorn et al., 2022), is hard to assess for the entire potential set of tree-herbivore interactions. Furthermore, most work on coevolution at range frontiers or dispersing across barriers focuses on mutualism or parasitism pairs (e.g. Keeler and Rafferty 2022). By contrast, herbivory is a network of species interactions and may thus show different patterns across biogeographical gradients (Tylianakis and Morris 2017; Stephan et al., 2021). Given these complications, here we adopt a functionalist perspective on questions about herbivory adaptations in *Vachellia [Acacia] caven*. From a functionalist perspective, it is less important to determine which species coevolved when and where to produce the observed traits, and more important to determine contemporary analogues through which the positive benefits of the observed traits can be stimulated.

A number of functional analogues or proxy species could be chosen to recreate the set of potential browsers living in South American open woodlands to which *Vachellia [Acacia] caven* may have been adapted. Most of these would present difficulties for reintroduction into central Chile. Non-native potential proxies for megafauna, such as elephants (Donlan et al., 2006), are very unlikely to be approved for release into the wild, for a combination of cultural and legal reasons. Free-range cattle already represent a kind of unintentional proxy species, but their browsing activity in these habitats appears to be minimal and to be primarily destructive (see Root-Bernstein et al., 2016; Root-Bernstein et al., 2022). The native deer huemul (*Hippocamelus bisulcus*), could hypothetically be translocated to central Chile, where huemuls may have had a historical distribution (Flueck et al., 2022), but their threatened population status mean that *in situ* conservation is likely to be the priority. Guanacos, by contrast, are native wild species that are regionally extirpated but nationally and globally abundant, making them an ideal candidate proxy species for the reintroduction of lost browsing functions.

Guanacos are likely to be one of the browsers coexisting with *Vachellia [Acacia] caven* at least for some prehistorical period on one side of the Andes or both. Nevertheless, we refer to them as a proxy species—an Eltonian proxy—for browsing because we have no data about the temporal depth of coexistence, geographical range overlap at fine scales (e.g., floristic habitat composition and corresponding habitat use), or strength of interaction between the two species at any prehistorical or historical time. Although both species are native to Chile, currently the ranges of guanacos and *Vachellia [Acacia] caven* do not overlap in Chile, and this has been the case for up to 500 years depending on the location (Molina 1782; Falabella, 2016). Guanacos currently live and browse in other semi-arid woodlands in South America (González et al., 2006; Cuéllar Soto et al., 2017), although some authors consider this to be an unnatural or suboptimal behavior in response to anthropogenic pressures (Muñoz and Simonetti 2013). Here, we test the hypothesis that guanacos and *Vachellia [Acacia] caven* can act as Eltonian proxies for one another, such that guanaco browsing behavior can be spontaneously directed at *Vachellia [Acacia] caven* and the adaptations to herbivory of

Vachellia [Acacia] caven will respond positively to browsing by guanacos. If so, by reintroducing guanacos to central Chilean *espinal*s, the demonstrated ecological and agronomic benefits of pollarding and pruning (Olivares 2016) could potentially be stimulated, forming a method of natural woodland restoration (Root-Bernstein et al., 2016). If, however, guanaco browsing does not correspond to the type of browsing to which *Vachellia [Acacia] caven* is adapted (it is a poor functional proxy), we would expect trees to show net damage in the presence of guanaco browsing, giving the *espinal* a degraded character. Specifically, we predict that (1) naïve guanacos spontaneously browse *Vachellia [Acacia] caven* and incorporate it into their diet; (2) *Vachellia [Acacia] caven* shows compensatory growth following browsing by guanacos; (3) *Vachellia [Acacia] caven* shows an increase in branching following browsing by guanacos.

2. Methods

Site and animals. The experimental site was a fenced 0.5 ha area of *espinal* at the entrance to the private Altos de Cantillana Nature Sanctuary, in central Chile (Fig. 1). An electrical fence kept guanacos inside the site and kept out other herbivores and feral dogs. The guanacos used in the experiment were five adult males from the breeding facility of Fauna Australis, a research group of the Pontifical Catholic University of Chile. Approval for the conditions of the experiment was obtained from SAG (Agriculture and Livestock Service).

Central Chile is a mediterranean-climate zone with winter rain and a dry summer, and a hotspot of plant endemism (Myers et al., 2000). Its main habitat type can be described as matorral scrub and sclerophyllous forest, with three subhabitats including *espinal*, shrubland and sclerophyllous forest, with functional and compositional affinities to other semi-arid and seasonally dry South American woodlands, and other mediterranean-climate habitats. These sub-habitats are linked through succession (Root-Bernstein et al., 2017). The majority of woodlands and forests in central Chile are spontaneously recovering from historical clearing for charcoal production or agriculture (Vergara et al., 2013; Schulz et al., 2010; Root-Bernstein et al., 2017). Our control and experimental sites were monospecific stands of *Vachellia [Acacia] caven*, which is common (Root-Bernstein et al., 2017). Between 90 and 100% of canopy cover in the experimental and control areas was *Vachellia [Acacia] caven*.

Our five guanacos had been raised in captivity, derived from stock originally from Tierra del Fuego. They had been castrated for reasons unrelated to our experiment. Housing groups of bachelor males together mimics natural behavior in the wild (Candino et al., 2022). Guanaco

populations in the Southern Cone of South America have been isolated from one another by a modern history of land-use change and hunting, but have not yet sub-specified (Marín et al., 2013). We thus do not believe that the guanacos used in this experiment, bred from Tierra del Fuegian populations, lacked genetic adaptations required to live in central Chile. They were, however, naïve to *espinal* or other central Chilean woodlands, since up until the experiment they had lived together in an open paddock without trees, and were fed alfalfa or hay.

2.1. Experimental design

Individual marked tree branches are the independent unit of analysis in the study. Pseudoreplication is generated due to repeatedly measuring the same branches across the course of the experiment, and due to the nested structure of the experiment (see *Data analysis*). Branches are nested within the tree to which they belong, trees are nested within the sector in which they are found, and the sectors are nested in either the experimental or control area. Further, the guanaco herbivory condition within the experimental area is not applied uniformly, but is divided temporally into pulse and non-pulse phases as described below.

2.2. Experimental conditions and procedure

The *espinal* enclosure was divided into four sections of 0.125 ha each (Fig. 1). We also established a control site of a similar total size (0.5 ha) without guanacos in an adjacent *espinal* area. The control site was also divided into four sections. Characteristics of each experimental section and the control site without guanacos are shown in Appendix A Table A.1.

The sections of the enclosure had gates between them that could be left open or closed to allow circulation between sections or to force a “pulse” of herbivory in just one section. During half the year, the guanacos were rotated through the sections clockwise, creating a series of pulse treatments. These pulse treatments took place in winter and spring (the wet season, June–November); the guanacos spent 4 weeks in each section (reduced to 2 weeks in late spring to prevent over-grazing as seasonal aridity increases). Our rotational plan is based on the expectation that winter herbivory will give the largest compensatory growth response. Several observations support scheduling pulse herbivory during central Chilean winter, as we explain in the following sentences. Firstly, Abate Molina, a Chilean naturalist writing in the 1740s, reported that guanacos spent the summer in the high Andes and the winter in the Chilean central valley (Molina 1782), consisting of flat lowlands, areas



Fig. 1. Map of the experimental and control areas. The experimental enclosure (inset), outlined in red, and shown (right most inset) with the interior gates, the direction in which the guanacos were moved and the electric fence for protecting guanacos mainly from feral or neighboring dogs. The location of the control area, unfenced, is indicated with the yellow line. The hill visible to the left of the two sites is part of the Central Cordillera, and is covered in sclerophyllous vegetation.

now dominated by espinal and agricultural fields. Thus it is likely that the largest pulses of browsing on *Vachellia [Acacia] caven* in central Chile would be during winter (Fig. 2). In addition, Cromsigt and Kuijper (2011) report that early-growth-season pulses of herbivory are associated with adaptations to herbivory in trees: early growth season starts in late winter in central Chile. Our pulse schedule also follows Oba et al. (2000) in implementing more-intense browsing when the trees have no leaves (winter-spring), in the expectation that this will stimulate increased growth during their next growth season (spring-summer). In summer and fall (the dry season December–May) the guanacos were allowed to move freely throughout the enclosure. In addition to simulating historical guanaco movement and foraging patterns, the rotational phase of the experiment also allows us to track the temporal lag of growth following known periods of herbivory. The locations of the guanacos in each time period can be seen in Appendix A Table A.2. The experiment ended in June 2016, and thus included three winter (rainy season) periods and two full summers (dry seasons) across 24 months of sampling.

Our experimental treatment includes only browsing and not mechanical damage (tree tipping, branch ripping, foliage crushing, etc). Although optimal coppicing levels may be equivalent to mechanical damage, as noted in the Introduction, we could not work with a species that creates significant mechanical damage for the reasons reviewed in the Introduction. Due to their size and weight, we did not expect guanacos to create mechanical damage, and none was observed, thus it was not controlled for or measured.

2.3. Data collection

Tree branches. Predictions 1 and 2 are measured by total branch length of sampled branches. This should be reduced if guanacos browse, and should increase if there is compensatory growth (they should grow more than they are browsed, and also net more than control branches). Prediction 3 is measured as branching angles on the same branches. See below for how these were sampled and measured.

In May 2014 we arbitrarily selected about half the trees in each section in both the experimental and control areas, and marked 10 branches per tree <2 m from the ground (see Appendix A Table A.1), by tying a plastic tag 10 cm from the tip of the branch. *Vachellia [Acacia] caven* reproduces vegetatively and can regrow from a coppice stool; trunks that were separated at ground level were treated as separate trees. Prior to introducing the guanacos, we measured tree height, trunk diameter immediately above the ground, area of maximum crown cover, and number of trunks per marked tree, both in the experimental and

control areas.

Prior to each rotation, we collected data from the marked branches from both the section from which the guanacos had previously moved, and the section to which they were about to move (but not the section where they were at the time). For example in Fig. 1 the guanacos are shown in the southern sector, so we would sample the western and eastern sectors. Next, when the guanacos were in the western sector, we would sample the southern and northern sectors. In other words, we sampled immediately before and 1 month after the last pulse of herbivory. The same rotational sampling schedule for the sectors was maintained when the guanacos had access to the entire enclosure. The control section was sampled every three months.

Sampling the branches consisted of photographing each marked branch in front of a white poster with a scale, ensuring that all edges of the photograph were parallel to the poster sides (to avoid distortion of branch dimensions) and that the main branch structure was parallel to the plane of the poster (Fig. 2).

To analyze the photographs we used ImageJ to derive three measures to assess our predictions about *Vachellia [Acacia] caven* growth: total branch length (a measure of growth), median sub-branch angle (a measure of bushiness of branching), and number of sub-branches (a measure of growth and branching strategy) (Fig. 2). We recorded the branch elongation (branch length) using the tag as a reference, and included the lengths of all sub-branches. We recorded the angles between the tag on the main branch and the tip of each sub-branch. Angles around 180° indicate sub-branches aligned with the main branch, and angles around 90° indicate a bushier, more defensive structure. Finally, the length of 50 cm on the background poster was measured to provide a conversion to centimeters.

Guanaco management and behavior. The guanacos were introduced to the enclosure on the June 18, 2014, with prior permission granted by the SAG (No. Exenta 1597). As mandated welfare measures, *ad libitum* water was provided in each sector, supplementary *ad libitum* alfalfa was provided starting at the end of the first month, and between months 2–4 of the experiment a nutritional supplement was added to the alfalfa. During the first month we did not give them supplementary feed. This served as a habituation period similar to soft releases in translocation procedures (Tetzlaff et al., 2019). *Ad libitum*, as in animal behavior studies, means that the alfalfa was freely provided in excess at all times by the resident caretaker, at a rate of approximately 1 bale per week. The alfalfa was dried. Since alfalfa is a high-nutrient feed, and guanacos are adapted to low-nutrient herbivory, it should exceed their tolerance to eat constantly, and we expected them to nevertheless also eat the herbaceous layer and the trees. During the first three months of the experiment we observed that the guanacos spent 39.2–62.7 % of their

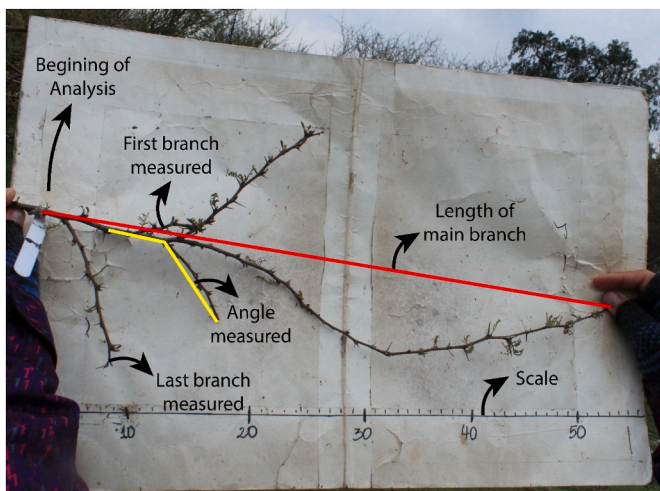


Fig. 2. Example of photograph analysis to derive the three main variables: total length, median sub-branch angle, and number of sub-branches.

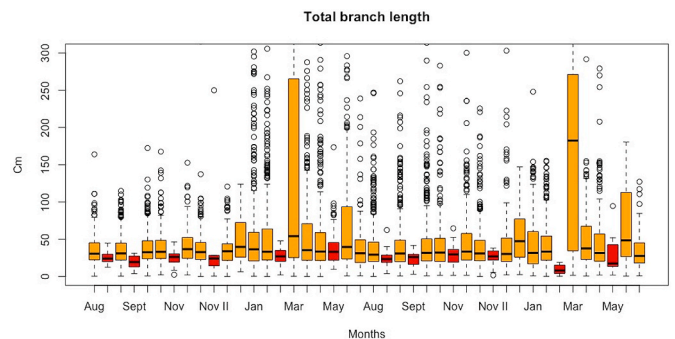


Fig. 3. Time series of total branch length showing box plots (median and quartiles) for each sample. Orange indicates the Experimental condition (with guanaco browsing), red the Control condition (without guanaco browsing). Note that each sample of the Experimental condition includes different combinations of parcels, following the sampling design. This time series is intended to illustrate the main trends, and does not fully represent the nested data structure.

time foraging, of which 1.2–10.6 % of their time browsing; the amount of time browsing was independent of the amount of time eating alfalfa (Root-Bernstein et al., 2016). We were not able to repeat these observations throughout the experiment. Anecdotally, the guanacos ate less alfalfa in spring, and by the end of the 2-year experiment they ate very little alfalfa. According to the resident caretaker, towards the end of the experiment the guanacos were ‘paying little attention’ to the alfalfa. This suggests that the guanacos learned how to mix their diets to depend largely on the available fresh herbs, leaves and branches, although we did not collect systematic data on their diet preferences across the 2 years. We are not aware of any calculations of Animal Units for guanacos which would allow us to calculate the carrying capacity of the enclosure or exactly how much supplementary food was necessary. We monitored the guanacos for signs of stress, injury and weight loss on a daily (informal) and monthly (formal) basis. After signs of stress during the first four months, their condition stabilized and remained good. We also monitored the enclosure for signs of degradation, vegetation trampling, or overgrazing. The lack of cumulative degradation can likely be attributed to four factors: (1) guanacos concentrate their movements along narrow paths (Guerrero-Gatica & Root-Bernstein et al., 2019); (2) guanacos are efficient herbivores adapted to marginal, dry habitats and to eating low-nutrient plants (Lauenroth 1998); (3) the *ad libitum* alfalfa; (4) a combination of pulsed herbivory and adjustment to a shorter rotation period during late spring prior to allowing the guanacos access to the entire enclosure in the dry season. Clearly the experiment does not provide information about historical natural conditions or about the optimal density of guanacos for a given *Vachellia [Acacia] caven* density, but these questions go beyond our goal in this study.

In November 2014, the fourth month of the experiment, we were obliged to separate one of the five guanacos from the other four and keep him in a separate section, due to his emerging agonistic behavior towards the others. Removing him entirely from the experiment was not logistically feasible, so he was placed in the section prior to the others in the rotational order (he advanced ahead of them). This arrangement was continued for the rest of the experiment, and no injuries from fighting were observed.

Proxies for productivity: Herbaceous growth and precipitation data. In each section of the enclosure where branches were being sampled, we also collected herbaceous growth data. We threw a 25 cm × 25 cm quadrat in four random directions to create four random samples (excluding under-canopy space) per section. In each quadrat we cut the vegetation down to ground level, and weighed it on site to obtain fresh weight. The samples were then transported in paper bags to the Ecology Department at the Pontificia Universidad Católica de Chile where they were oven dried at 60 °C for 72 h and weighed to obtain dry weight. Monthly accumulated precipitation data from the nearest weather station (San Antonio de Naltahua) was downloaded from agromet.inia.cl in 2019.

Data analysis. The final data set included 13515 measures of each of the three dependent variables Total length, Median angle, and Number of sub-branches. Including the three dependent variables, we had 18 variables in the dataset (Table 1). The variables were nested spatially and also showed temporal pseudoreplication due to measuring the same branches repeatedly over time. To deal with both of these aspects of the data structure, we used a mixed model with both fixed and random effects (Crawley 2007). We nested the temporal pseudoreplication variable (identifying the sample) inside the spatial nesting. The spatial nesting consisted of branch nested inside tree inside experimental section. See Appendix A for the structure of the code used. We used the *lme* function in RStudio R version 4.1.1. We ran three separate models, one for each dependent variable: Total length, Median angle, and Number of sub-branches. Since these variables undoubtedly influence one another through the overall growth strategy of each tree, we also used each dependent variable as a potential explanatory variable for the other two. We considered the best model to be the model with the largest number of significant variables.

3. Results

Guanaco browsing. Our primary measure of browsing pressure in this study was branch length (see below). We observed guanacos browsing on *Vachellia [Acacia] caven* within the first week of the experiment. During the period without leaves we observed them to eat branches and in the period with leaves they also ate leaves. Few seeds were produced by the trees in the enclosure and we did not directly observe the guanacos eating them. Elsewhere we have reported that four of the guanacos spent more time eating leaves than branches, and spent between 1.2 and 10.6% of their time browsing on leaves and branches combined (Root-Bernstein et al., 2016).

Total branch length. Mean total branch length in the Experimental condition was 55.74 SE 0.72 cm, and in the Control condition was 56.14 SE 1.56 cm. Median total branch length fluctuated from month to month and displayed many outliers in the Experimental condition, but not in the Control condition, which we interpret to mean that guanaco browsing occurred throughout the two years of the experiment (see Fig. 3.) The best model for Total branch length included the significant

Table 1
Variables included in the statistical models.

Variable	Description	Interpretation
Median angle	Dependent variable. Median angle of sub-branches (degrees), per branch, per sample	Branching/bushiness. Dependent variable 1
Number of sub-branches	Dependent variable. Number of sub-branches, per branch, per sample	Branching/growth strategy. Dependent variable 2
Total length	Dependent variable. Sum of lengths of main branch and all sub-branches (cm), per branch, per sample	Net of growth (gain) and herbivory (loss). Dependent variable 3
Treatment	Experimental or Control	With guanaco herbivory or without guanacos
Parcel	Section sampled	Following the rotational schedule for sampling
Date	Date of sample event	Temporal sequence of sampling
Month	Month of sample event	Seasonal effects
Year	Year of sample event (2014, 2015, 2016)	Inter-annual variation effects
Season	Winter, Summer	Pulse (winter) or non-pulse (summer) treatment
Sample	Sample number	Accounts for temporal pseudoreplication of samples
Tree	Tree ID	Individual tree effects
Branch unique name	Branch ID	Individual branch effects
Number of guanacos	Total (during pulse) or mean (during non-pulse) guanacos in the sampled section, per sample	Guanaco herbivory pressure
Number of guanacos t-1	Total or mean guanacos in the sampled section at previous sample date, per sample	Previous guanaco herbivory pressure, accounting for ant lagged response
Precipitation	Accumulated monthly total as registered at San Antonio de Naltahua weather station	Proxy for productivity
Herbaceous dry weight	Dry weight of 0.25 m ² herbaceous cover, per section, per sample	Proxy for productivity
Tree height t0	Height of tree (m) prior to experiment beginning, per tree	Controls for height differences affecting growth strategy
Tree trunk number t0	Number of trunks splitting off above ground level prior to experiment beginning, per tree	Multi-stem trees are a common adaptation to past cutting; controls for architectural differences affecting growth strategy
Tree canopy t0	Area of tree canopy (m ²) prior to experiment beginning, per tree	Controls for canopy size differences affecting growth strategy

variables Number of guanacos, Herbaceous dry weight, Number of sub-branches, and Precipitation (Table 2). From inspection of Fig. 3, it is clear that there is a large growth peak in the month of March. To get a sense of how the variables interacted outside the main growth period in March, we reran the model excluding data from March. In this case, the best model additionally included significant variables Treatment and an interaction between Herbaceous dry weight and Precipitation (Table 3). However, if we run the same model with March data included, Treatment is no longer significant, and the interaction is also no longer significant (Supplementary Material Table A3). Thus, outside the main growth period (March), the Experimental treatment had an overall negative impact on growth, but greater guanaco presence (pulse treatments) was associated with greater branch lengths. Higher rain and greater herbaceous biomass at the same time as guanacos are present resulted in a negative trend in branch lengths. Including the main growth period (March), total branch length is greater the more sub-branches there are, and increased when there was greater herbaceous biomass and greater guanaco presence (pulse treatments), but was negatively associated with precipitation.

Number of sub-branches. The mean number of sub-branches was 2.31 SE 0.03 in the Experimental condition and 2.30 SE 0.08 in the Control condition. We observe some variability in median number of sub-branches over time, especially in the second year (Fig. 4). The significant variables in the best model of Number of sub-branches were Total length, Number of guanacos, Herbaceous dry weight, and Precipitation, and the interaction between Herbaceous dry weight and Number of guanacos (Table 4). The number of sub-branches was greater the longer the total branch length (and vice versa, see above). Guanaco presence, more rain and more herbaceous growth were associated with more sub-branches, although again the number of sub-branches declined when there were simultaneously more guanacos and more herbaceous growth.

Median branch angle. Mean median branch angle was 49.48 SE 11.23° in the Experimental condition, and 63.73 SE 1.82° in the Control condition. Medians of the median branch angle changed over time in the Experimental condition, increasing in late spring in the first year before again decreasing, and then increasing from summer onwards in the second year (Fig. 5). The best model of Median branch angle included the significant variables Number of sub-branches, Year, Treatment, and the interaction between Year and Treatment (Table 5). Median branch angle was higher the greater the number of sub-branches, but narrowed over time, and in the Experimental treatment.

4. Discussion

Guanaco herbivory on *Vachellia [Acacia] caven* continued and showed evidence of impacting growth throughout the experiment. Observations, and the fluctuations and changes in our branch measures in the experimental condition, attest that our naïve guanacos spontaneously included *Vachellia [Acacia] caven* branches and leaves in their diet over the course of the experiment, even when other forage was available *ad libitum* (see also Root-Bernstein et al., 2016). Although we do not

Table 2

Results of the best linear mixed-effects model for Total branch length. The treatment species is the guanaco (*Lama guanicoe*) and the experimental branches are of the tree species espino (*Vachellia [Acacia] caven*). The experiment was conducted at Altos de Cantillana Nature Sanctuary, Chile, between 2014 and 2016. Significant variables are shown with the p value in bold. Alpha is 0.05.

Variable	Estimate	SE	DF	t	p
Intercept	27.12	3.55	12147	7.63	0.0000
Tree trunk number t0	-1.87	1.89	125	-0.99	0.3255
Herbaceous dry weight	0.00	0.00	12147	3.95	0.0001
Number of guanacos	2.67	0.69	12147	3.85	0.0001
Number of sub-branches	12.82	0.20	158	65.48	0.0000
Precipitation	-0.09	0.01	12147	-6.85	0.0000

AIC: 148323.7 BIC: 148406.3 logLik: 74150.83.

Table 3

Results of the best linear mixed-effects model for Total branch length excluding data from the month of March, the main observed growth period. The treatment species is the guanaco (*Lama guanicoe*) and the experimental branches are all of the tree species espino (*Vachellia [Acacia] caven*). The experiment was conducted at Altos de Cantillana Nature Sanctuary, Chile, between 2014 and 2016. Significant variables are shown with the p value in bold. Alpha is 0.05.

Variable	Estimate	SE	DF	t	p
Intercept	28.16	2.62	11272	10.73	0.000
Treatment: Experimental	-5.81	2.77	11272	-2.09	0.0362
Herbaceous dry weight	-0.0001	0.00	11272	-0.95	0.3426
Number of guanacos	1.66	0.57	11272	2.88	0.0039
Number of sub-branches	12.49	0.16	154	77.10	0.0000
Precipitation	-0.06	0.01	11272	-6.17	0.0000
Interaction: Herbaceous dry weight x Number of guanacos	-0.0003	0.00	11272	-4.61	0.0000

AIC: 129908.3 BIC: 129997.6 logLik: 64942.14.

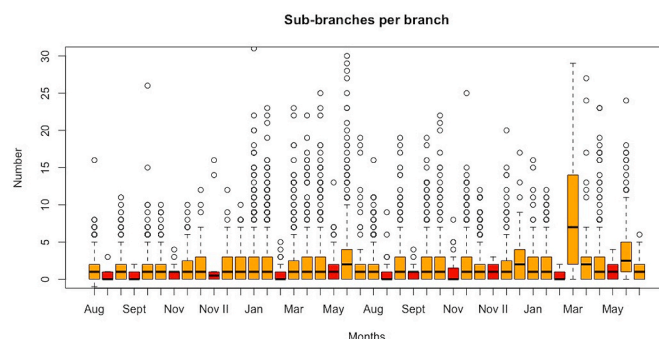


Fig. 4. Time series of number of sub-branches showing box plots (median and quartiles) for each sample. Orange indicates the Experimental condition (with guanaco browsing), red the Control condition (without guanaco browsing). Note that each sample of the Experimental condition includes different combinations of parcels, following the sampling design. This time series is intended to illustrate the main trends, and does not fully represent the nested data structure.

Table 4

Results of the best linear mixed-effects model for Number of sub-branches. The treatment species is the guanaco (*Lama guanicoe*) and the experimental branches are all of the tree species espino (*Vachellia [Acacia] caven*). The experiment was conducted at Altos de Cantillana Nature Sanctuary, Chile, between 2014 and 2016. Significant variables are shown with the p value in bold. Alpha is 0.05.

Variable	Estimate	SE	DF	t	p
Intercept	1.671	0.23	12164	7.21	0.0000
Total branch length	0.009	0.00	158	38.57	0.0000
Herbaceous dry weight	0.000	0.00	12164	2.73	0.0062
Number of guanacos	0.081	0.02	12164	3.49	0.0005
Precipitation	0.002	0.00	12164	5.01	0.0000
Interaction: Herbaceous dry weight x Number of guanacos	-0.000	0.00	12164	-7.95	0.0000

AIC: 54769.47 BIC: 54852.09 logLik: 27373.74.

have direct measures of biomass, we interpret our length measures as providing evidence consistent with compensatory growth. On the whole, both branch lengths and number of sub-branches increase with number of guanacos. However, branch lengths and number of sub-branches both declined when there was simultaneously more herbaceous growth and more guanacos present, suggesting that most browsing on branches occurs during the spring, at the intersection of the pulse treatments (winter and spring) and when herbaceous biomass is highest. Although the herbaceous biomass might be expected to distract the guanacos from browsing, we interpret based on the tree physiology (see below) that new growth on the trees occurs at this time and is also an attractive

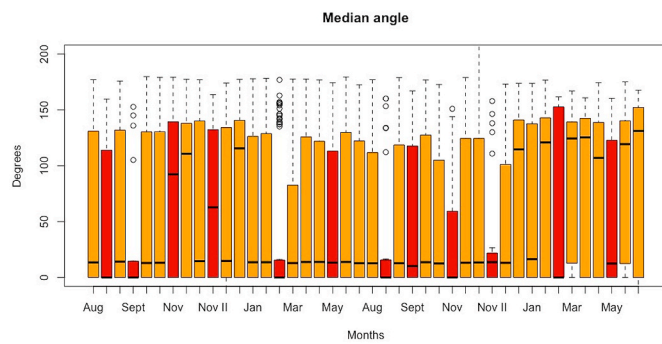


Fig. 5. Time series of median angles showing box plots (median and quartiles) for each sample. Orange indicates the Experimental condition (with guanaco browsing), red the Control condition (without guanaco browsing). Note that each sample of the Experimental condition includes different combinations of parcels, following the sampling design. This time series is intended to illustrate the main trends, and does not fully represent the nested data structure.

Table 5

Results of the best linear mixed-effects model for Median angle. The treatment species is the guanaco (*Lama guanicoe*) and the experimental branches are all of the tree species espino (*Vachellia [Acacia] caven*). The experiment was conducted at Altos de Cantillana Nature Sanctuary, Chile, between 2014 and 2016. Significant variables are shown with the p value in bold. Alpha is 0.05.

Variable	Estimate	SE	DF	t	p
Intercept	12087.00	4741.47	12132	2.55	0.0108
Number of sub-branches	4.61	0.229	157	20.12	0.0000
Year	-5.98	2.35	12132	-2.54	0.0111
Treatment: Experimental	-12611.19	4963.97	12132	-2.54	0.0111
Interaction: Year x Treatment	6.262	2.46	12132	2.54	0.0110

AIC: 147949.2 BIC: 148024.3 logLik: 73964.59.

forage. The negative effects of precipitation are probably due to delayed growth response in *Vachellia [Acacia] caven*, which can grow outside the winter-spring rainy period due to its deep tap roots. This allows the explosive growth period observed in summer (March). Excluding the March growth period from the analysis shows that the experimental guanaco treatment decreases growth. When including the growth period, the experimental condition is not significantly different than the control condition—it becomes nonsignificant when adding March back into the dataset, and is excluded from the best model including March. Thus collectively, our measures suggest net loss to herbivory in spring, and compensatory regrowth in summer. Much of this compensatory growth appears to be immediately eaten, since by visual inspection subsequent months have lower lengths and have lost sub-branches again, but retain altered median angles. Although unfortunately we lack control data from the key month of March (because we did not anticipate that most growth occurred in that month), since there is no herbivory in the control condition, if branches had grown a similar amount in March in the control plots as well, we would expect that growth to be retained in subsequent months and to be cumulative. However we see no evidence of that.

In contrast to our last prediction, we found the apparent contradiction that guanaco herbivory both increased and decreased bushy branching in *Vachellia [Acacia] caven*: the angle of the lateral branches is wider when there are more sub-branches, but also narrower over time in the experimental condition. A bushy wide-angled branch, associated here with having more sub-branches, may be simply an outcome of this tree's branching architecture, where branching is stimulated by browsing. However, a branch architecture with a narrower angle of lateral branching increases the spine density by bringing branches and sub-branches closer together, thus reducing stem browsing and slowing leaf browsing. This can also be a browsing response strategy, associated

with slowing browsing on isolated branches in trees that do not constitutively form a cage to protect interior canopy leaves (Charles-Dominique et al., 2017), which appears consistent with *Vachellia [Acacia] caven* architecture (Supplementary Material Fig. A2). We interpret that both responses were occurring at once. Potentially, these two responses could be related to browsing at different times of year or browsing leaves vs. browsing branch tips (buds) (e.g. Lehtilä et al., 2000), which we cannot distinguish between in this study.

Our herbivory pulse schedule, designed to maximize the chances of observing any potential compensation effect, was based on the interpretation that most *Vachellia [Acacia] caven* growth occurs in winter (the rainy season) before they have leaves, and secondarily in summer when they grow new leaves. Our data confirms this double growth period, but suggests that most compensatory growth is in summer. Total branch growth is likely affected by inputs to productivity, as suggested by the positive relationship between total branch length and herbaceous dry weight. However, monthly precipitation was negatively correlated with branch growth measures, as most growth was not in the rainy season, which is likely explained by an escape from dependence on rainfall due to *Vachellia [Acacia] caven*'s deep taproots (Aljaro et al., 1972). Increases in branch length and sub-branch number can be observed in mid summer, January and February, especially notable in the first year (Figs. 3 and 4), following leaf emergence. However the vast majority of branch length growth was concentrated in March (late summer). Flowers (if present) appear around October or November (spring). Aljaro et al. (1972) found that cambial activity in *Vachellia [Acacia] caven* was present in mid summer (January), declined from March to July (fall to winter), and then reinitiated in August (winter) to peak in November (late spring). Taking into account likely variations in abiotic conditions, this more or less corresponds to what we observe: maximum growth in terms of length at the end of the summer growth period, as well as an early-winter/spring growth period.

Our pulse herbivory condition was designed to coincide with the leafless season (Oba et al., 2000), as well as the early-growth period (Cromsigt and Kuijper, 2011), and is also consistent with the historical description from Abate Molina about the season when guanacos descended into the central valley in the early 1700s. We hypothesize that it may increase the compensatory growth effect to also have pulses of herbivory during the primary period of growth during the leafy period in summer. Since we did observe guanacos eating leaves during the leafy season, which coincides with a loss of most of the understory herbaceous layer due to herbivory and die-back, the leaves could potentially be an important resource for resident, non-migratory guanaco groups (Candino et al., 2022).

We did not have enough information on *Vachellia [Acacia] caven* responses to guanaco browsing across the year (due in part to the Eltonian shortfall) to carry out controlled experiments that would have allowed us to understand the mechanisms behind the observed growth patterns. However, having established that compensatory growth is a response to guanaco browsing, there are obviously several more mechanistic questions that should be addressed. These include, for example, whether and when guanacos eat leaves, stems and buds, and the difference between tree responses to each (e.g. Lehtilä et al., 2000), and the exact lag time or optimal browsing time in the year to produce the large compensatory growth phase in March. In addition, we did not get a strong signal for growth in spring as might be expected, but this is likely to be because the guanacos were actively eating the new growth during this period. While the control data shows some indication of new growth during spring (e.g. Figs. 4 and 5), notably we do not observe the large numbers of outliers found in the experimental data (Figs. 3 and 4); this suggests that the outliers are not branches that have escaped herbivory, but more likely are ones that are showing compensatory growth. This could be verified with closer or more frequent monitoring of individual branches. Considering that there were effects that seemed to emerge only in the second year, there is inherent climate variability due to ENSO, and that we also observe many outliers in all three measures of

branch growth suggesting considerable variability in responses between branches, a study over many more years, and in which browsing can be controlled or directly observed for each branch, may be better able to control for sources of variability and detect tree responses to herbivory.

Another trend that would become clearer over time, and could benefit from controlled study at the branch level, is the bushy and streamlined growth responses of sub-branches, which may protect buds and leaves from herbivory (Charles-Dominique et al., 2017). A possible outcome, over time, is increased under-canopy shadiness. Research on pruning *Vachellia [Acacia] caven* indicates that increasing shade under canopies leads to positive ecological cascades (Olivares 2016). Shady conditions are also required for some germination niches of trees that may be nursed by *Vachellia [Acacia] caven* (Root-Bernstein et al., 2017). We did not measure shadiness under the canopies, and this is unlikely to have changed significantly in two years. However, it seems possible that over decadal scales, increased growth of sub-branches forming dense bunches could lead to significant decreases in light penetration under the canopy.

Our results also do not provide information on the optimal density of guanacos for a given *Vachellia [Acacia] caven* density and herbaceous biomass, or on their diet preferences as a function of available biomass or nutrients. While the addition of *ad libitum* high-nutrient alfalfa may appear to add an unnatural element to the foraging conditions that may have reduced browsing pressure, one of the unexpected outcomes of the experiment was the appearance of zones of distinct high biomass vegetation, including plants typical of high-nutrient zones, around the guanacos' dung middens (Guerrero-Gatica and Root-Bernstein 2019). Further studies are required, but a landscape with (reintroduced) guanacos would be a landscape full of dung middens, which may also be a landscape with many patches of high-nutrient plant material, to which the high-nutrient fodder may have formed an analogue.

These observations suggest that reintroducing guanaco as an Eltonian proxy into *espinal* woodlands is unlikely to lead to *espinal* degradation. Under continuous (but pulsed) browsing, the short-term effect appears to be positive but minimal since essentially all of the compensatory growth appears to have been eaten. However, if, as appears to be the case, browsing in spring leads to significant compensation in summer, guanacos could be removed from areas with recent compensatory growth (in summer), and this growth could potentially accumulate, before forming new buds during the second phase of growth in spring. Thus, with migration or rotation, over the long term it seems possible that guanaco browsing could significantly increase productivity and biodiversity, via shade effects. We were not able to study the impact of guanaco browsing on *Vachellia [Acacia] caven* seedlings or small trees or on survival across the tree lifespan, as no small trees were available. This is not unusual, since *Vachellia [Acacia] caven* under recent land-use patterns tend to form similar-age stands because they are pioneer trees that establish after tree cutting for charcoal or after agricultural abandonment, and reproduce in infrequent pulses (Root-Bernstein et al., 2017). Guanaco browsing might be more damaging to small *Vachellia [Acacia] caven* and retard growth by favoring a bushy, spiny habit as can sometimes be observed in small isolated *Vachellia [Acacia] caven* presumably due to livestock damage. On the other hand, pulses of similar-aged seedlings might effectively dilute browsing pressure or trampling intensity. The interplay between timing and densities of tree establishment and timing and intensities of browsing deserves further study.

Interactions with other species may also be important. First, indirect effects (Pringle et al., 2007; Fox and Potts 2023) may over time lead to a larger effect on *Vachellia [Acacia] caven* growth. Note that pruning or pollarding is tested in the context of silvopastoral management and is thus usually applied in the presence of grazing herbivores, which is not controlled for. In this study, we only studied the direct trophic interaction between guanacos and *Vachellia [Acacia] caven*, although over the course of the experiment it became apparent that indirect effects including non-trophic pulse and disturbance effects and ecosystem

engineering of guanacos are likely to be important (Guerrero-Gatica and Root-Bernstein 2019). A second possibility is that to fully stimulate *Vachellia [Acacia] caven* compensatory growth to the optimum found in pruning and pollarding studies, one would need to also reintroduce native deer and/or proxies for extinct megaherbivores, involving potentially complex alterations to trophic and non-trophic interactions and net outcomes (Goheen et al., 2018; Fox and Potts 2023). For example, although huemuls and guanacos apparently co-foraged extensively in historical periods, we do not know how they interact, or how their joint browsing and grazing might affect central Chilean ecosystems (Flueck et al., 2022).

Another kind of intensive browsing proxy would be manual pruning and pollarding of entire woodlands, which could be paid for through a payment for ecosystem services (PES) scheme, or a government-sponsored scheme in the context of the National Plan for Climate Adaptation, meeting Chile's commitments to the United Nations Convention to Combat Desertification and the Convention on Biological Diversity. Ecological studies could help to devise pruning and pollarding strategies that follow natural dynamics in being irregular or tied to specific environmental events (Rackham 2013), and that mimic natural browsing patterns.

Further studies on the browsing patterns of guanacos, alone and when co-foraging with other browsing proxies, will be a valuable step towards developing landscape restoration plans. Studies of this kind could also pioneer an ecologically validated procedure for the use of Eltonian or regular proxy species, or indeed groups of proxy species, in restoration, an issue which remains relatively controversial, and which when applied is often not previously tested. Such a procedure would be useful for the restoration of the many other woodland types in understudied parts of the world suffering from paleoecological and contemporary Eltonian shortfalls.

CRedit authorship contribution statement

Meredith Root-Bernstein: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Supervision, Writing – original draft, Writing – review & editing, Data curation. **Matias Guerrero-Gatica:** Data curation, Investigation, Project administration, Writing – review & editing. **Andoni Elorrieta Rossle:** Data curation. **Jory Fleming:** Data curation. **Jorge Ramos Aguillar:** Data curation, Investigation. **Benjamín Silva Rochefort:** Data curation. **Tristan Charles-Dominique:** Writing – review & editing. **Juan Armesto:** Funding acquisition, Resources. **Fabián M. Jaksic:** Funding acquisition, Resources, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data are provided on Dryad: <https://datadryad.org/stash/share/6Vp0ySAT6pDpdG-yuiFdl38y6IEpNoLdNQYgaJd0J7A> for peer review and will be archived here upon acceptance.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jaridenv.2024.105228>.

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