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# Capybaras (Rodentia: Cavidae) in highlands: environmental variables related to distribution, and herbivory effects on a common plant species

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## ABSTRACT

The capybara *Hydrochoerus hydrochaeris* is one of the largest and most widely distributed herbivores in the Neotropical lowlands. However, as yet, there are no records of its occurrence in highland environments. Our aim was to evaluate the environmental variables related to the capybara's distribution and monitor the effects of its herbivory on the individuals and on the reproductive phenology of *A. polyanthus*, a common and important plant species of the high-altitude grasslands. Our results show that capybaras frequently occur in the high-altitude grasslands along the Campo Belo River, but they avoid waterlogged areas, occurring more frequently on the dry rocky areas. Capybara herbivory affected the number of *A. polyanthus* rosettes in flower, leading to the presence of inflorescence formation anomalies. High-altitude grasslands apparently provide capybaras with the three main components (food, shelter and water) required for their occurrence. However, although they seem to present a seasonal feeding strategy, which also happens in lowlands, their avoidance of the waterlogged areas suggests that in highlands the species may present different environmental preferences from those presented in lowlands. In addition, the impact of capybaras' herbivory on *A. polyanthus* individuals indicates the potential impact that capybaras can represent on the plant community of the high-altitude grasslands. This appears to be a great opportunity to study the effect of the arrival of a large herbivore in a new environment and possible impacts on plant assemblages.

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## Introduction

The plant-animal relationship includes a diverse array of interactions that can be mutualistic (e.g. pollination and seed dispersion) or antagonistic (e.g. herbivory), or can represent other, undefined kinds of interactions (Lewinsohn et al. 2006), with consequences for both animals and plants. Herbivory, one of the most studied plant-animal interactions (e.g. Coley 1983; Maron and Crone 2006; Ghyselen et al. 2015), can directly and indirectly affect the quantity and quality of flowers, fruits and seeds (Poveda et al. 2003; Puentes and Ågren 2012; Santos et al.

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2012), thereby influencing the growth, reproduction and survival of consumed plants (Strauss and Agrawal 1999; Puentes and Ågren 2012). Moreover, it can also cause changes in the composition of the plant community (increasing the abundance of non-palatable species and reducing the primary productivity; Augustine and McNaughton 1998; Maron and Crone 2006) and alter other multispecies animal-plant interactions (e.g. pollination and seed dispersion; Strauss and Irwin 2004). In return, the quantity and nutritional quality of plants as food resources have direct effects on an herbivore's diet and, consequently, on its feeding strategies and habitat selection at both individual and population levels (van Beest et al. 2011; Bjørneraas et al. 2012). According to the optimal foraging theory, herbivores may maximise their feeding efficiency by preferring more profitable species. The more abundant a plant species is, the more selective an herbivore's feeding behaviour can be (Pyke et al. 1977).

The capybara (*Hydrochoerus hydrochaeris*, Linnaeus, 1766) is the largest living rodent species in the world and one of the largest herbivores of the Neotropics. The species is widespread in South America, occurring from Venezuela to Argentina, with the exception of Chile (Macdonald 1981; Moreira et al. 2012a). They are easily found in seasonally flooded savannas and lowlands (Alho and Rondon 1987; Barreto and Herrera 1998; Quintana et al. 1998), but they also inhabit forest galleries along rivers (Arteaga and Jorgenson 2007), coastal plains (Borges and Colares 2007), and anthropogenic environments, where the species reportedly causes damage to agricultural fields (Verdade and Ferraz 2006). Capybaras often use grasslands to feed and patches of bushes or forested areas to rest (Alho and Rondon 1987; Herrera and Macdonald 1989; Corriale and Herrera 2014). They also require habitats with permanent water bodies (streams, rivers, lakes, swamps and marshes), which are used mainly for mating, temperature regulation and escape from predators (Macdonald 1981; Corriale and Herrera 2014; Schivo et al. 2015).

Despite the wide distribution of capybaras across different Brazilian ecosystems (Paglia et al. 2012), there is still no record of their occurrence on high-altitude grasslands or at greater than 1500 m above sea level (asl; Moreira et al. 2012a). However, since 2010, park rangers, tourists and researchers have often reported seeing capybara tracks in the high-altitude grasslands (2000 m asl) of the Itatiaia National Park (INP) – the first Brazilian Protected Area, which is located in a mountain massif in the rainforest of south-eastern Brazil and is currently considered an area of global importance for biodiversity conservation (Myers et al. 2000; Le Saout et al. 2013). Little is known about the capybara in the INP, with only two published records of its occurrence in lower areas of the park (500 m asl, Geise et al. 2004; Aximoff et al. 2015). Therefore, the causes that could have driven the capybara towards the high-altitude grasslands are not known.

Capybaras feed mainly on grasses and Cyperacea, adapting their feeding strategies seasonally with a preference for the more profitable resources during the wet season, as this period offers greater availability of such resources compared to the dry season (Barreto and Herrera 1998; Arteaga and Jorgenson 2007; Borges and Colares 2007; Barreto and Quintana 2012). Since first appearing in the high-altitude grasslands of INP, the capybara has used *Actinocephalus polyanthus* (Bong.) Sano (Eriocaulaceae) rosettes as a feeding resource (Aximoff and Rosa, personal observation), with unknown effects on plant individuals. *Actinocephalus polyanthus* is a monocarpic herb widespread and abundant in the INP's high-altitude grasslands (Aximoff and Ribeiro 2012). It is characterised by a basal rosette that sends out an inflorescence with a central axis and lateral branches (paraclades), which serve as support for their floral structures (see

Figure 2) (Castellani et al. 2001; Sano 2004; Trovó et al. 2008). This species is resistant to fire, a common event in the high-altitude grasslands; thus, it is important in this environment as it facilitates the return of other plant species by providing shade and protection (Aximoff 2011; Aximoff et al. 2016).

Several studies have documented the habits and environmental preferences of capybaras in lowlands, especially in the seasonally flooding savannas, where they reach the highest densities (e.g. Alho and Rondon 1987; Barreto and Herrera 1998; Quintana and Rabinovich 1993; Moreira et al. 2012b). However, no study has focused on capybara biology in the highlands or the possible impacts of its interaction with the plant species of the high-altitude grasslands. It is known that the interactions between non-native grazers and plants (which have not co-evolved together) can be either negative or positive, depending on whether it is direct (consumptive effect) or indirect (disturbance) interaction (Maron and Crone 2006). Thus, to better understand the recent occurrence of the capybara in the high-altitude grasslands of the INP and the effect of its presence, we attempted to evaluate the environmental variables related to the capybara's distribution based on its tracks, and we monitored the effects of its herbivory on the individuals and on the reproductive phenology of *A. polyanthus* in this habitat.

## Material and methods

### Study area

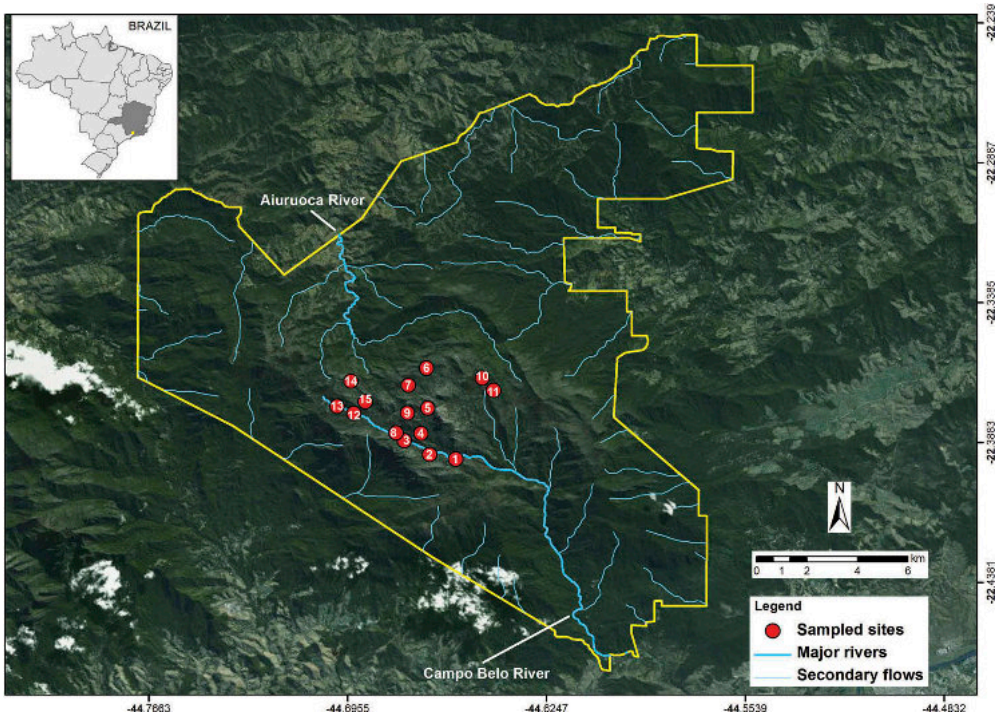
Itatiaia National Park (INP) is located between the states of Rio de Janeiro and Minas Gerais. The park currently covers 28,084 hectares that range in altitude from 540 m to 2791 m, with extensive areas around 2000 m. Due to variation in altitude, INP presents two distinct forest formations: montane forest (between 500 and 1500 m) and upper montane forest (above 1500 m). Situated within the latter are the high-altitude grasslands (above the tree line, over 1800 m asl) (Veloso et al. 1991). INP creates a boundary between two important hydrographic basins in Brazil – the Rio Grande River and the Paraíba do Sul River – with, respectively, the Aiuruoca River and the Campo Belo River as their main tributaries within the park (Figure 1).

We conducted our work in the high-altitude grasslands of INP between 2200 and 2500 m asl (22.378° S, 44.674° W). This region presents a Cwb mesothermal climate type (Köppen 1948), with rainy seasons during the spring and summer. Mean annual temperature and precipitation are around 11.5°C and 2150 mm, respectively (Barreto et al. 2013). A grassland matrix with herbaceous plants, shrubs, and small trees that reach 4 m in height is predominant at the highest altitudes. Freshwater marshes are common in the landscape (Figure 2a), forming permanent wetlands that expand the flooded area during the summer rainy season. The various rocky outcrops scattered throughout the landscape harbour islands of vegetation of different shapes and sizes, composed of herbaceous plants and shrub species, including endemic and endangered species that typically reach up to 1 m in height (Martinelli 1996; Aximoff 2011; Aximoff and Ribeiro 2012). The most representative plant families are Asteraceae, Cyperaceae and Poaceae (Aximoff and Ribeiro 2012), but the Eriocaulaceae *A. polyanthus* is abundant in the area (Aximoff and Ribeiro 2012).

## Data collection

To assess the environmental variables related to the occurrence of capybara in high-altitude grasslands, we sampled 15 sites, spaced 600 to 1000 m apart, located in valleys with permanent water bodies, between 2280 and 2520 m altitude along the Aiuruoca and Campo Belo river basins (Figure 1). We conducted six bimonthly sampling campaigns between July 2014 and June 2015. In each sampling site, one observer performed an active search for 30 minutes for evidence of capybara presence, seeking to register capybara 'tracks' (e.g. footprint, faeces; Figure 2b and c). We choose 30 minutes of search because it is the average time spent to cover the entire valley of each sampling point (~3 ha). We chose to evaluate capybara occurrence using indirect tracks, and standardised by time, because our sampling sites were difficult to access and seasonally flooded, which did not allow us to set a fixed radius or transect. We did not perform direct counts because we believe the species presents a low density in our study area and individuals are rarely observed. In fact, we did not observe any capybara individuals.

We evaluated three environmental variables that may influence capybara distribution: the river basin (Aiuruoca and Campo Belo rivers), soil cover and vegetation structure. We categorised the soil cover and vegetation structure of each sampled site in the field, according to the method of Sanguinetti and Kitzberger (2010). We divided the soil cover into three categories: (1) dry rocky areas (high-altitude grasslands with rocky and dry areas); (2) waterlogged rocky areas (high-altitude grasslands with rocky areas and flooded at least 8 months per year); (3) waterlogged areas (high-altitude grasslands without rocky areas and flooded during at least 8 months per year). We divided the vegetation structure into two categories: (1) low (forbs and grasses); and (2) medium (shrubs and bamboo thickets).



**Figure 1.** Study area showing the sampled sites (red circles) for capybara occurrence. The yellow line indicates the perimeter of Itatiaia National Park, located in the south-eastern region of Brazil.



**Figure 2.** (a) The high-altitude grasslands of the Itatiaia National Park, surrounding the studied marsh; (b) footprints and (c) faeces of *Hydrochoerus hydrochaeris* at the study site; (d) herbivory on the rosette of the *Actinocephalus polyanthus* by *Hydrochoerus hydrochaeris*; (e) normal rosette of the *A. polyanthus*; (f) normal flowering of *A. polyanthus*; and (g) anomalous flowering in rosettes of *A. polyanthus* that underwent foliar damage by capybara herbivory.

From July 2013 to June 2014, we evaluated the effects of capybara herbivory on all reproductive stages of *A. polyanthus* in one of the largest marshes in the region, with around 2 ha of flooded area in the summer, situated at 2500 m asl. In a previous visit to the sampling area, we noticed that capybara herbivory was restricted to the vicinity of the flooded area. We therefore restricted our sampling to a 50-m radius around the freshwater marsh, where we recorded the number of rosettes of *A. polyanthus*, the proportion of those that underwent herbivory (we considered damaged rosettes those having at least 1/3 of the leaves with damage suffered by herbivory; [Figure 2d](#)), and the proportion of those that had not undergone herbivory (intact rosettes; [Figure 2e](#)). To assess the reproductive phenology of *A. polyanthus*, we counted the number of flowering and fruiting rosettes during 1 year ([Figure 2f](#); [Freitas and Sazima 2006](#)) during the monthly sampling. To study the effects of herbivory on reproductive phenology of *A. polyanthus*, we counted the number of damaged and intact rosettes that were in flower. Each rosette of *A. polyanthus* has 33 umbels on average ([Trovó et al. 2008](#)); however, we discovered during field sampling that some damaged rosettes had only one umbel ([Figure 2g](#)). We classified this as anomalous and counted the number of damaged rosettes with anomalies.

### **Data analysis**

We used generalised linear mixed models (GLMM) with a binomial distribution ([Bolker et al. 2008](#); [Zuur et al. 2009](#)) to evaluate the environmental variables that affect capybara occurrence in the high-altitude grasslands of INP. We considered each site a sample unit, and the response variable was the presence/absence of capybaras during each field campaign. To define the candidate models, we used environmental variables as fixed factors and the field campaigns (seasonal variation) as random effects to control pseudoreplication ([Millar and Anderson 2004](#)). Since the seasonal variation of capybaras is not the focus of our study, the control of these random effects is important because we lack of knowledge of the history of the sampled areas. In addition, capybaras can alter their habitat use throughout the year ([Corriale and Herrera 2014](#)). We considered the models with small Akaike's Information Criterion ( $\Delta AIC \leq 2$ ) to have the best descriptive capacity ([Burnham and Anderson 2002](#)) regarding capybara habitat use. We averaged the values of the variables that comprised the best models in terms of the Akaike's Information Criterion weight (AIC $\omega$ ) values of each model. Modelling was performed using the function 'glmer' in the 'lme4' suite of the R software environment ([R Development Core Team 2009](#); [Bates 2010](#)).

To evaluate the effects of capybara herbivory on *A. polyanthus* individuals, we calculated the proportions of damaged and intact rosettes and compared them using a chi-square test. To evaluate the effects of capybara herbivory on the reproductive stages of *A. polyanthus*, we tested two approaches using chi-square: (1) we compared the proportions of both damaged and intact rosettes that flourished and those that did not flourish; (2) for damaged rosettes, we compared the proportions of anomalous rosettes and non-anomalous rosettes. We performed the analysis in the Bioestat program ([Ayres et al. 2007](#)).

**Table 1.** Generalised linear mixed models (GLMM) parameters of the best models ( $\Delta\text{AIC} \leq 2$ ) describing habitat use of *Hydrochoerus hydrochaeris* in high-altitude grasslands of Itatiaia National Park, Brazil: AIC (Akaike information criterion),  $\Delta\text{AIC}$  ( $\text{AIC}_i - \min\text{AIC}$ ),  $\text{AIC}_w$  (Akaike weight).

Candidate models	AIC parameters		
	AIC	$\Delta\text{AIC}$	$\text{AIC}_w$
Microhabitat + river	104.0	0	0.297
River	104.1	0.10	0.282
Microhabitat + river + vegetation	104.8	0.84	0.195
River + vegetation	105.5	1.50	0.140

## Results

We found 24 records of capybara presence and 66 records of available sites, with no record of capybara presence in more than half (53%) of the sampling sites during our study. We recorded capybara presence between 2300 and 2500 m elevation. The best model for capybara occurrence includes soil cover and river basin variables (Table 1). Capybara presence was positively related to Campo Belo River basin, but negatively related to waterlogged areas, showing predominant use of dry rocky areas (Table 2; Figure 3).

In the sampled area, we recorded 88 *A. polyanthus* rosettes, of which 70.4% ( $N = 62$ ) were flowering. Flowering occurred from October to April, with the largest number of simultaneously flourishing rosettes occurring in January. The fruiting began in January and peaked in May. Capybara herbivory in *A. polyanthus* occurred for four consecutive months, from July to October, and affected around half of *A. polyanthus* rosettes ( $N = 48$ ;  $X^2 = 0.727$ ,  $p = 0.455$ ). We did not identify herbivory by capybaras during the flowering or fruiting seasons, and we did not observe mortality of *A. polyanthus* individuals. However, capybara herbivory negatively affected the number of rosettes in flower; while all intact rosettes flourished, only 46% of damaged rosettes flourished ( $X^2 = 30.753$ ,  $p < 0.0001$ ). Furthermore, we observe a high proportion of inflorescence formation anomalies in damaged rosettes ( $N = 35$ , 73%,  $X^2 = 10.083$ ,  $p = 0.0024$ ). We did not find anomalies in rosettes that were not subjected to herbivory.

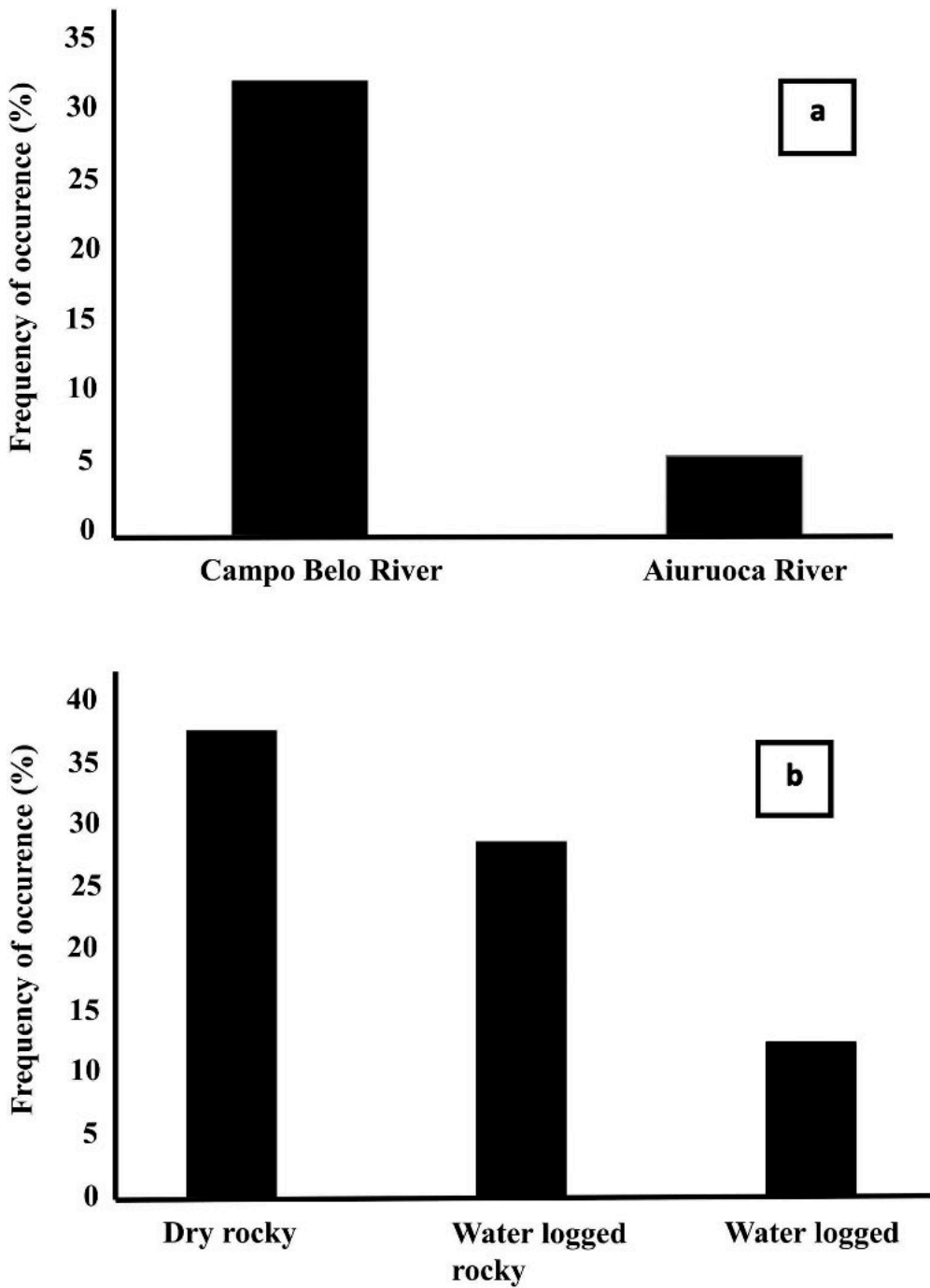
## Discussion

Our study encompasses the first record of capybaras in high-altitude grasslands. Our results suggest that the capybaras are using the wetlands of Campo Belo River basin to disperse and reach the high-altitude grasslands. Once they reach the high-altitude grassland, capybaras seem to avoid the waterlogged areas, preferring dry rocky areas, which was not expected as they have a close relationship with water (Moreira et al. 2012a). In addition, in

**Table 2.** Weighted parameters of the variables included in the best generalised linear mixed models (GLMM) model explaining habitat use of *Hydrochoerus hydrochaeris* in high-altitude grasslands of Itatiaia National Park, Brazil:  $\beta$  = regression coefficient; SE = standard error, Z value = Z test, p value = significance in the Z test.

Variables	$\beta$	SE	Z value	p value
Intercept	-2.3209	1.0834	-2.142	0.0322
Wet rocky areas	-0.6247	0.5808	-1.076	0.2821
Waterlogged areas	-1.5714	0.7842	-2.004	0.0451
Campo Belo River	2.1929	1.0848	2.022	0.0432





**Figure 3.** Frequency of capybara occurrence between July 2014 and June 2015 (a) in the Campo Belo and Aiuruoca rivers and (b) along the three types of soil cover in the Itatiaia National Park, Brazil.

accordance with Barreto and Herrera (1998), we found that capybaras feed on *A. polyanthus* only in the dry and coldest season, suggesting that the capybara presents a seasonal adaptation to its feeding strategy. Also, capybaras reduced the photosynthetic and reproductive capability of this Eriocaulaceae species, which has the potential to affect its local population.

Previous research shows the capybara occurring up to 1500 m asl (Moreira et al. 2012a). Our work presents the highest altitude yet recorded for the capybara range (up to 2500 m asl). In our study area, a long-term monitoring survey registered capybaras only up to 500 m asl (Geise et al. 2004; Aximoff et al. 2015), and more recently single individuals have been registered by camera-traps in montane forest formations in the INP massif up to 1300 m asl (Rosa, unpublished data). Mammals associated with water bodies tend to use drainage basins to reach high altitudes (Andrade-Ponce and Angarita-Sierra 2017) and form populations according to the distribution of water sources (Herrera 1992; Herrera et al. 2011; Byrne et al. 2015). So, the most likely scenario is that capybaras are dispersing along the Campo Belo River basin, which varies in altitude, and the connected water bodies allow the species to colonise the grasslands at higher elevations.

Capybaras seem to have found the three main requirements (water, food and shelter) for their occurrence in the high-altitude grasslands. The permanent water bodies associated with grasslands could be used for feeding and reproduction (Alho and Rondon 1987; Herrera and Macdonald 1989; Herrera et al. 2011). Shelter – which is provided by the forest in lower areas (Alho and Rondon 1987; Herrera and Macdonald 1989; Herrera et al. 2011) – may be found in the small remnants of upper montane forest or dense formations of shrubs and bamboo thickets scattered throughout the high-altitude grasslands, or even in the forested areas of the INP massif below 1800 m asl. On the other hand, our results show that capybaras seem to avoid waterlogged areas, preferring dry rocky areas, differently from what we would expect based on its lowland behaviour (Moreira et al. 2012a). In highlands, mammals, and more specifically rodents, may present differences in their physiology in response to the harsh conditions they find in these environments, and that may be reflected in their behaviour and ecology (Hammond et al. 2001; Broekman et al. 2006). In INP, both waterlogged and dry rocky areas have the resources (permanent water bodies and grassland) that capybaras require (Aximoff and Ribeiro 2012; Corriale and Herrera 2014), and although these areas consist of an association of flooded reeds and sedges (Safford 1999), lacking a sufficiently firm surface for an animal of the capybara's size (35–65 kg; Paglia et al. 2012), we would expect that capybaras use the waterlogged areas more, since they easily move through the water (Quintana 1999). Thus, it is possible that capybaras exhibit different habits from those in lowland areas and avoid these areas in higher lands. However, we have to consider that this result may be negatively biased because it was difficult to walk on this type of soil cover during our survey and we may have failed to detect some of the capybara's tracks.

Capybaras presented a seasonal exploitation of *A. polyanthus* in our study area, as previously observed in lowlands (Barreto and Herrera 1998). As a commonly observed strategy of herbivores to increase energy and nutritional intake (Pyke et al. 1977; Kneigt et al. 2007), capybaras may change their foraging strategy according to the availability of certain plant species in a specific microhabitat or season (Barreto and Herrera 1998; Arteaga and Jorgenson 2007, Borges and Colares 2007), which is part of a strategy to maximise nutritional intake as predicted by the optimal foraging theory (Pyke et al.

1977). Our results suggest that they feed on this plant species only in the driest and coldest period of the year (July to October), when the temperature can reach a low of  $-10^{\circ}\text{C}$  (Barreto et al. 2013). Because *A. polyanthus* has high resistance to hoar frost (Trovó et al. 2008), which is common in INP in the coldest months when other resources are either not available or scarce in the high-altitude grasslands, this plant species may be used by capybaras to optimise their feeding strategy. To confirm this hypothesis, it would be interesting for future studies to assess the diet of capybara and resource availability throughout the year.

Until recently, high-altitude grasslands were considered a poor ecosystem for providing food and shelter for medium and large mammals (Geise et al. 2004). However, it has been suggested that highlands may present higher abundance of resources than previously thought (Raboy et al. 2013). Also, they have less human pressure (e.g. habitat fragmentation and poaching) than lower lands do (Ribeiro et al. 2009; Treves and Bruskotter 2014), which can represent a potential refuge for wildlife. Therefore, these factors may be contributing to the dispersion of capybaras to high-altitude environments. Capybara presence shows that this environment can support prey as big as the capybara, and therefore may also eventually support populations of large felines, which are extinct in many areas of the Atlantic Forest, but are known to occur in this area (Geise et al. 2004; Haag et al. 2010; Beisiegel et al. 2012; Aximoff et al. 2015). In addition, our results supplement those obtained for other medium and large mammal species (e.g. Aximoff et al. 2015; Abreu et al. 2016; Aximoff and Rosa 2016; Aximoff and Vaz 2016; Passos et al. 2016) that are using areas at higher altitudes than previously known. The recent occurrence of capybara and other mammals in the high-altitude grasslands of INP highlights the importance of large remnants of continuous forest and its highland areas within the domains of the Atlantic Forest in maintaining the species population in southern Brazil's protected areas.

Despite the apparent conservational advantages of large mammals occurring in the high-altitude grasslands, capybara herbivory may present a new impact on plants in an environment for which no modern record of occurrence of medium and large herbivores exists, to our knowledge. Although herbivory is considered one of the most frequent interactions tolerated by many plants (Turley et al. 2013), non-native grazers are known to impact an environment whose plant community has not co-evolved with them (Bastrenta et al. 1995). We did not identify mortality in *A. polyanthus* individuals that underwent herbivory. However, we did observe a decrease in photosynthetic area in individuals that underwent herbivory. Reduced photosynthetic area can change the rosette leaf architecture important for plant growth (Zangerl et al. 2002), meristem protection (Leon 2013) and fire resistance, which is fundamental to species regrowth in high-altitude grasslands (Aximoff and Ribeiro 2012).

Plant resistance reflects the degree to which a plant can regenerate and reproduce after sustaining damage by herbivores (Strauss and Agrawal 1999). Tolerance to herbivory alters resource allocations, leading to changes in the development of the plants at the individual level, including reduced fruit and seed production (Boege and Marquis 2005). In our study area, the reproduction of *A. polyanthus* is also affected by herbivory. We found reduced flowering in rosettes that underwent herbivory and at least a 30-fold reduction in their number of umbels (anomalies), in comparison to intact rosettes. This drastic reduction in

the number of flowers lowers the availability of seed production, decreasing the population and gene flow (Ghyselen et al. 2015; Tadey 2015). With this in mind and considering the importance and relevance of *A. polyanthus* in the high-altitude grasslands, we consider this species a good model to assess the potential changes in population and community levels caused by the impacts of capybara herbivory.

The presence of a large herbivore in an environment as fragile and important for biodiversity conservation as the INP's high-altitude grasslands (Myers et al. 2000; Le Saout et al. 2013) summons great concern, as grazing can affect not only individuals, as shown in our work, but also population, community and ecosystem levels (Pringle et al. 2011; Smit and Prins 2015; Zeng et al. 2015; Schrautzer et al. 2016).

Because most of the ecological and biological requirements of capybaras are available in lower lands, more studies must be done to understand the role of the capybara in our study area. Future studies should focus on the diet and foraging strategies of the capybara in high-altitude grasslands, and should evaluate the effects of its grazing on the plant community.

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## Disclosure statement

No potential conflict of interest was reported by the authors.

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