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Feral goats shift keystone cacti communities in Caribbean Islands

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ABSTRACT

Vegetation on islands is particularly vulnerable to overgrazing by introduced herbivores as plants have evolved under lower herbivore pressure than on the mainland. We conducted a combination of field experiments and surveys to study the foraging behavior of feral goats and their impact on the composition, abundance and condition of keystone columnar cactus species. On the goat-browsed Caribbean island of Bonaire, 76.6 % of the adult cacti showed bark damage. The degree of bark damage on individual cacti was negatively correlated with the probability of bearing fruits and the number of fruits carried. Foraging experiments, in both field and enclosure settings, showed that goats preferentially consume the *Subpilocereus repandus* cacti. Experimental spine removal did not change goat foraging preference for this species. Overgrazing by feral goats reduced recruitment and increased mortality, shifting species relative abundance and population structure of columnar cacti species. *S. repandus* had a population structure characterized by a large proportion of adults, and low proportion of juveniles and resprouting individuals. We subsequently show that cactus communities have largely recovered from such impacts on the nearby island of Klein Bonaire where goats have been controlled for about half a century. Our findings reveal how overgrazing by feral goats shapes the community structure of columnar cactus species and imply that goat eradication is an essential step for the recovery and conservation of the original columnar cacti communities of Caribbean dry seasonal forests.

1. Introduction

Biological invasions are a major driver of ecological degradation worldwide. Islands have proven particularly sensitive and provided some of the best documented cases of how non-native species can cause biological extinctions and alter, directly and indirectly, the functioning of whole ecosystems (Lenzner et al., 2020). The introduction of exotic herbivores has been very destructive on islands as insular vegetation often lacks defensive traits (Bowen and Van Vuren, 1997; Parker et al., 2006). The introduction of goats (*Capra hircus*) on islands worldwide resulted in overgrazing of vegetation and soil erosion with cascading effects for the composition, structure and functioning of terrestrial ecosystems and their interconnected marine systems (Coblentz, 1978; Roberts et al., 2017; Gizicki et al., 2018; Debrot et al., 2019). On Caribbean islands, goats were introduced in the 16th century to support European colonizing expeditions. Large feral populations established locally, especially in regions with arid and semiarid climate, where alternative productive land uses were less attractive (Terpstra et al., 1948). As a result, Caribbean seasonally dry tropical forests became less dense and diverse, and likely also less resilient to other perturbations (Rojas-Sandoval et al., 2014). Today, these dry forests are considered the most threatened tropical biome (Dryflor et al., 2016).

Columnar cacti are conspicuous species in the overstory of neotropical deserts and seasonally dry tropical forests where they are considered keystone species (Drezner, 2014) forming strong mutualistic networks with birds and bats (Fleming and Valiente-Banuet, 2002; Fleming and Holland, 2018). The entire Cactaceae family has a vulnerable conservation status due to overharvesting, land clearance, invasive species and increased fire regimes (Hultine et al., 2023). These factors, coupled with intrinsically slow plant growth rates, hinder the recovery of cactus populations. About 30 % of all cactus species are currently threatened with extinction (Goettsch et al., 2015) and 60 % are likely to face deteriorating environmental conditions as climate change progresses (Pillet et al., 2022). Understanding how cacti respond to local disturbances, such as browsing by exotic herbivores, is important to anticipate bottlenecks in regeneration that could affect cactus resilience

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to climate perturbations with cascading impacts on the ecological networks they form (Scheffer et al., 2015). This knowledge can inform more effective conservation and ecological restoration actions as current protected areas fail to represent the evolutionary diversity of the Cactaceae family (Amaral et al., 2022).

Recent reviews have highlighted the notorious scarcity of studies that quantify the effects of herbivores on cactus populations and analyze the potential mechanisms of plant defense (Bravo-Avilez et al., 2019; Aliscioni et al., 2021). Current native herbivores of cacti include mostly insects, nematodes, birds, and rodents (Bravo-Avilez et al., 2019). The most common large mammals that consume cacti are exotic livestock (Malo et al., 2011; Peco et al., 2011) and people (Jiménez-Sierra and Eguiarte, 2010; Bravo-Avilez et al., 2019). Goat browsing has been sporadically reported for several cactus species but there is no comprehensive analysis of how goat dietary preferences impact columnar cactus abundance, population structure, and distribution. Although goats are generalist herbivores, their foraging behavior is influenced by an array of factors including their breeds, learning behavior, environmental contexts, and local plant communities (Solanki, 2000). Goats feed on a large diversity of herbaceous and woody species partly depending on their seasonal availability (Ramírez-Orduña et al., 2008). In overgrazed drylands, moisture-rich stems of cacti can represent vital sources of water for feral goat populations (Vieira et al., 2008). On the other hand, plant defenses could potentially prevent or reduce goat browsing. Spinescence is the most conspicuous morphological trait among cacti and likely evolved primarily as an anti-herbivory physical defense mechanism, yet assessing this defense function has remained poorly explored compared to evaluating the role of spines on thermoregulation, water retention, and plant dispersal (Aliscioni et al., 2021).

Goat browsing can affect columnar cactus populations, directly and indirectly, through different mechanisms. Columnar cacti store water and other resources in their stems and rely on these reserves for photosynthesis, growth, and reproduction during dry seasons (Williams et al., 2014). Browsing can therefore affect performance, growth, and survival rates of established cactus individuals. Goats can also limit cactus recruitment by reducing flower and fruit production (Peco et al., 2011), by predating on fruits (Meléndez-Ackerman et al., 2008), or by reducing germination rates of digested seeds (Baraza and Fernández-Osores, 2013). Because cactus recruitment is often facilitated under the canopy of established trees and shrubs (Drezner, 2006; Larrea-Alcazar and Soriano, 2006; Munguía-Rosas and Sosa, 2008; Conver et al., 2017; Miranda-Jácome et al., 2023), excessive browsing on these nurse plants can diminish the availability of safe microsites, with lower abiotic stress and herbivore damage, needed for successful cactus seedling establishment (Holmgren et al., 1997; Holland and Molina-Freaner, 2013).

In this study, we assess the population structure, distribution and bark damage on the three columnar cactus species *Stenocereus griseus*, *Subpilocereus repandus* and *Pilosocereus lanuginosus* in Bonaire, where feral goats are abundant, and Klein Bonaire, where goats have been eradicated for several decades. Understanding the impacts of goats foraging behavior on columnar cactus populations can inform management plans for the control of exotic herbivores and identify priorities and opportunities for the conservation and restoration of these keystone plant species. We conducted a combination of field surveys and experiments to assess goat foraging behavior and consumption of these three native columnar cactus species. We hypothesised that spinescence could influence goat preference and conducted foraging experiments with and without spine removal. We further hypothesised that goat dietary preference would be mirrored in the relative abundance of the cactus species, the size structure of their populations and the likelihood of cacti forming associations with nurse plants. Specifically, we anticipated that in areas with feral goats, the cactus species preferentially consumed would exhibit natural populations characterized by 1) a higher proportion of individuals bearing goat browsing scars, 2) reduced seedling and juvenile recruitment, and 3) a higher proportion of juveniles associated to thorny nurse plants.

2. Methods

2.1. Study area and species

The study was conducted within the Washington Slagbaai National Park (WSNP; 12°16′ 2″ N, 68° 22′ 58″ W), in the northern part of the island of Bonaire and on the satellite island of Klein Bonaire (12°09′20″ N, 68°18′27″ W). All field surveys and experiments were conducted between February–May 2015. Bonaire is located 80 km north off the coast of Venezuela within the Caribbean Lesser Antilles (Fig. 1). The climate is tropical semiarid, with mean annual temperature of 28 °C, mean annual rainfall of 463 mm and seasonal rains concentrated between October–January. Large interannual variation in precipitation is strongly associated to El Niño Southern Oscillation (Martis et al., 2002). Substrates have a limestone and volcanic origin and are covered with distinct vegetation types (De Freitas et al., 2005). The vegetation is xerophytic, dominated by columnar cacti and thorny shrublands in the overstory and an understory of mostly *Opuntia* cacti (i.e., *O. curassavica*, *O. elatior* and *O. wentiana*). Trees are very scarce after a long history of severe logging. Goats were introduced in 1700 and established feral populations. Although the WSNP is fenced, feral goats are abundant within the park. Other feral livestock (sheep, pigs, donkeys) are less abundant. The island of Klein Bonaire is a 6 km^2 coral-limestone island, located 1-km off the central west coast of Bonaire. After a long tradition of goat keeping, eradication efforts drastically reduced goat numbers in Klein Bonaire by 1963 (Wagenaar Hummelinck, 1981), practically eradicating them by 1966 (Great Goat Round Up) and with certainty fully eradicating them by the mid 80's (Eric Newton personal communication, see Debrot (1997).

We studied the effects of goat browsing on three columnar cactus species *Stenocereus griseus* (Yatu), *Subpilocereus repandus* (Kadushi), and *Pilosocereus lanuginosus* (Kadushi di Pushi) with sympatric distributions in semiarid Caribbean islands and northern South America (Petit, 2001). The three species have an erect growing habit, with stems branching in a candelabra form. Stems are cylindrical, succulent, ribbed, and leafless. They produce a woody skeleton surrounded by succulent tissue (Gibson, 1978; Gibson and Horak, 1978). *S. griseus* can reach up to 9 m tall, trunk is generally missing or short (<30 cm tall and <20 cm width), stems are thick, green-grayish and bear white thorns (Alvarado-Sizzo et al., 2018). *S. repandus* can reach up to 12 m high and develops a strong, 40-cm thick woody trunk as it ages. *S. repandus* has been traditionally used as staple food, medicine, for the making of household items (Morton, 1967) and, as also is the case with *S. griseus*, used for building living fences in production systems (Debrot, 2009). *P. lanuginosus* can reach 6 m high and has slender stems with many long, yellow spines (Franck et al., 2019). Interestingly, climate can induce variations to morphological and branching patterns (Cornejo and Simpson, 1997). These cacti are pollinated by nocturnal nectar-feeding bats (Nassar et al., 1997) and dispersed by several bat and bird species feeding on their fruits during the dry season (Ruiz et al., 2000; Naranjo et al., 2003). The three species do not face a significant risk of extinction and have been classified as "Least Concern" by the International Union for Conservation of Nature (IUCN; https://www.iucnredlist.org/). However, locally, the populations of these cactus species can be strongly impaired by land conversion and over harvesting (Petit, 2001).

2.2. Field sampling design

We established five sampling strata based on the landscape units defined by De Freitas et al. (2005), following their original classification between parentheses: four strata within the WSNP (including its two sections, Washington and Slagbaai), and the adjacent Labra-Brasil area, outside the WSNP, as a separate stratum. The four strata were recognized as: Stratum 1: Most barren slopes of Washikemba volcanic hills

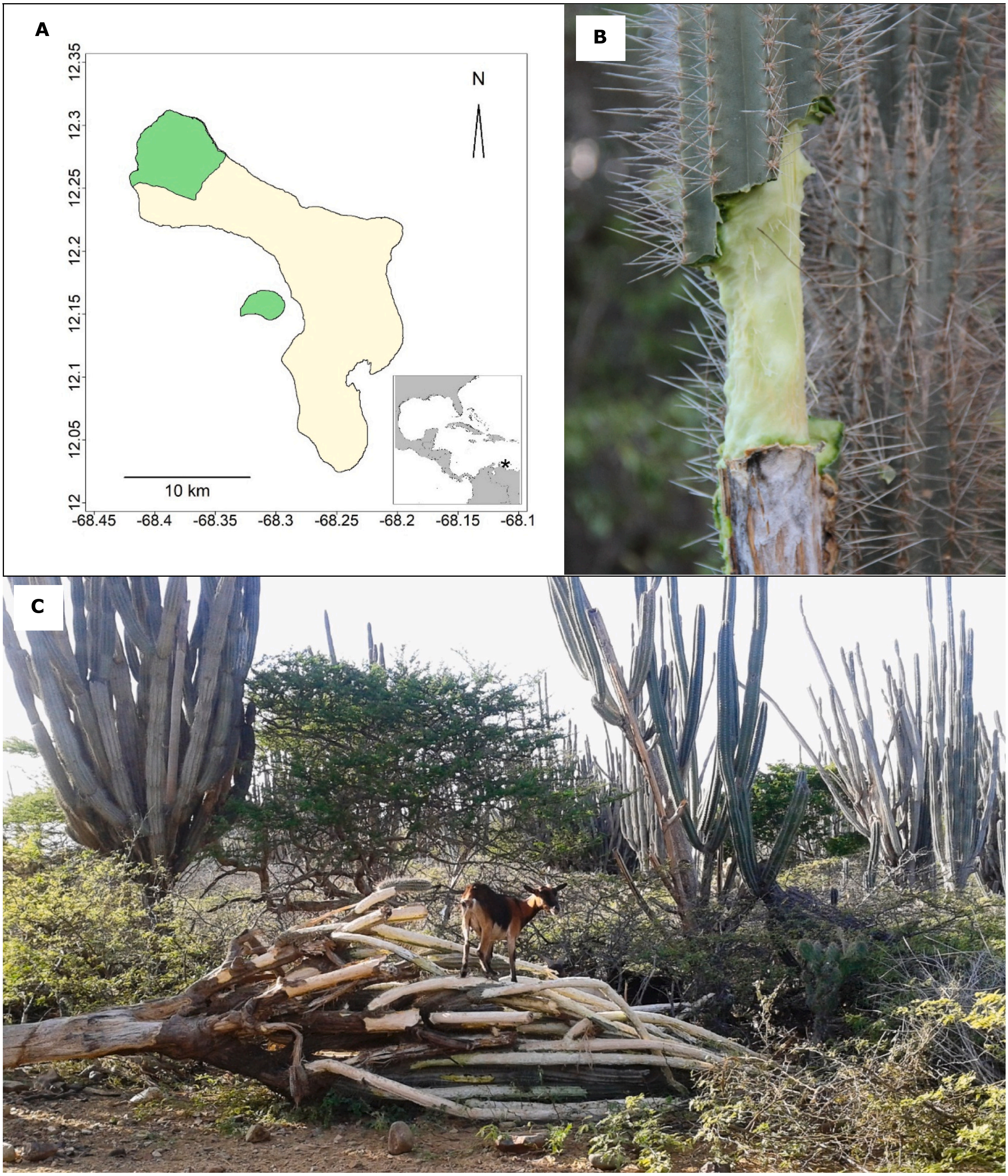

Fig. 1. The study was conducted within Washington Slagbaai National Park in northern Bonaire and Klein Bonaire (A; shaded green) in the Southern Caribbean (see star in lower right corner). Feral goats are abundant in Bonaire but were eradicated from Klein Bonaire. Goats browse on columnar cacti leaving injuries (B) and killing individuals (C) (Photos by M. Holmgren and P. Bertuol). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

with practically no trees (fully D1 sub-landscape); Stratum 2: Degraded Washikemba hills dominated by *Haematoxylon* and *Casearia* trees, followed by *Prosopis* (fully D2 sub-landscape); Stratum 3: Mix of mainly more-wooded Washikemba and co-occurring middle-terrace limestone vegetation with mainly *Prosopis* trees, followed by *Casearia* and then *Subpilocereus* (mostly D3 sub landscape, but with some D4, TM9 and its co-occurring TM1); Stratum 4: Very degraded and scantly-wooded lower-terrace limestone vegetation, with mostly bushes and few trees of *Prosopis*, *Acacia*, *Haematoxylon*, *Caesalpinia* (TL1 and TL7 sub landscapes). Klein Bonaire had only lower terraces of limestone substrate with plant communities comparable to Stratum 4 of Bonaire.

2.3. Goat density estimation

We used a stratified sampling design to estimate the density of feral goats within the five strata previously defined. We distributed 250 line transects, 100 m-long (Fig. S1.1). Strata were sampled with similar sampling effort of 0.5 km/km^2, which is the mean effort that has been used in comparable studies (Table S1.2). Transects were distributed systematically to cover an entire landscape unit without overlap between transect lines. We used all small roads and systematically assigned transects perpendicularly to the road. This design facilitated accessibility despite the thick understory of prickly pears (*Opuntia* spp). Transects started between 15 and 25 m from the edge of the roads into the bush to avoid the primary effect of the roads on vegetation and were GPS-mapped (Garmin GPSMAP 62) to allow sampling goat density and cactus populations in the same locations (Fig. S1.1).

We used the distance method (Buckland et al., 2001) to estimate goat density along the preselected line transects. We used a Leica CRF 1000-R rangefinder to record the distance and angle of detection of every detected goat (and other feral livestock). The transect surveys were done while silently walking at approximately 1 km/h, between 8:00–16:30, when goats are most actively foraging. We recorded all goats, left and right from the transect line and also recorded sex (i.e. female, male or unknown) and rough age-class categories (i.e. young, sub adult, adult). When using the distance method, the observer records the animals, the distance to the detected animal (i.e. observer-animal distance) and the angle from the line of detection with the transect line. With this information we calculated the perpendicular distance between the detected animal and the transect line and used it to estimate a detection function (i.e. the probability an animal is detected as a function of the distance to the transect line), and subsequently animal density. We also assessed dung depositions as a proxy of goat density. We counted fresh dung (i.e. brown or black) in two circular 12.6 m^2 plots, positioned at the start and end of each transect (i.e. 2 m radius).

2.4. Cactus abundance, distribution, and condition

We counted all columnar cacti along 200 transects (100 m long, 5 m wide) distributed across the four strata within the WSNP where goat density was estimated. Along each transect, we counted all cacti and measured height, volume, bark damage and number of fruits (i.e. 0; 1–25; 26–50; 51–75). We distinguished cactus stadia as seedling, round globose-shaped (young juveniles), club-shaped (older juveniles), adult not ramified, adult ramified, dead, and dead with resprouts based on Steenbergh and Lowe (1983) (Fig. S2.1).

We used an extendible 7 m-long marked stick to measure plant height and estimated cactus volume using the method described by Petit (2001). To estimate the volume of each cactus, we assessed the relationship between number of branches and volume using a subsample of 50 individuals of each cactus species. For each cactus, we noted the height and diameter below which 50 % of the branch tips were located to calculate the volume as a cone: $1/3\ \pi * radius^2 * height$ (Fig. S2.2).

We recorded browsing damage caused by feral livestock (i.e. mostly large scars at low heights) and by parrots or bats (i.e. small and on top of the cactus branches). If a browsing scar was present, both length and width were measured. To estimate the proportion of the cactus trunk browsed, we measured the height and diameter of the trunk (at its widest point) and calculated the total surface area of the trunk. We then estimated the proportion of the browsed surface area by summing the areas of all the scars on the trunk and dividing it by the total area of the trunk. This approach is a refinement of the method previously used by (Malo et al., 2011) since we measured both width and length of all scars instead of only width. The cactus surface area foraged by birds and bats, on unreachable top branches, was estimated visually and a total surface area (cm^2) was calculated.

We defined as overall bark damage the percentage of the cactus bark covered by brownish coloration as an indicator of unhealthy tissue. Brownish coloration has been described in stressed individuals and in cacti affected by opportunistic bacterial infections after direct bark injuries. Epidermal browning in stressed individuals has been associated with impaired physiological performance (Evans et al., 1994) whereas bacterial necrosis is often associated with cactus death (Chamberland, 2021).

We recorded the type of microsites where all juvenile cacti were growing: open and sheltered (i.e. rock, dead shrub, living shrub). We considered as juveniles all unramified cacti lower than 100 cm including the categories seedling, round shape, and club shape (Fig. S2.1). Living nurse plants were identified and measured. We measured soil temperature, air temperature and soil moisture inside and outside the microsite, as paired measurements, in 25 replicates of each type of microsite. Soil moisture and soil temperature were recorded using a Time Domain Reflectometer (Trime Pico 64) at a depth of 10 cm. Air temperature was measured using a Fisher Scientific Traceable thermometer. Data was collected between 10:00–14:00 on two subsequent days with similar weather conditions.

2.5. Goat foraging experiments

We used a combination of field and in-enclosure experiments to investigate the foraging behavior and dietary preferences of goats for the three columnar cactus species, namely *S. griseus, S. repandus* and *P. lanuginosus* (Fig. S3.1). The experiments were designed to assess goat diet preference (Experiment I); effect of spiny *Opuntia* cactus nurse plants on columnar cactus consumption (Experiment II); and effect of spine morphology on cactus consumption (Experiment III). All goats and plant material used in these experiments were sourced, ensuring ethical collection practices, by authorized personnel from STINAPA (i.e. Stichting Nationale Parken), the non-governmental organization that manages nature parks on the island of Bonaire on behalf of the Public Entity of Bonaire. Feral goats were captured inside the WSNP and removed from the park after the experiments by the park management team as part of their goat culling program. Plant material was collected outside the park from branched adult cactus.

2.5.1. Field experiments

2.5.1.1. Experiment I: goat diet preference for columnar cacti. We used a completely randomized one-factorial experimental design to assess goat diet preference for the three cactus species. We selected 12 locations within the Washington Slagbaai National Park with comparable vegetation cover (Fig. S3.2). At each experimental location, we placed two 3 × 3 m plots: an accessible plot where animals could freely enter and a fenced control plot. The two plots were marked with iron poles and positioned approximately 5 m from each other. The control plot was enclosed with chicken wire (1.2 m high) on each side and on top, preventing goats and green iguanas (*Iguana iguana*), from entering. Although there are no published observations that green iguana consume any of the three columnar cacti studied, field observations from nearby Curaçao island have demonstrated that green iguanas feed on flowers and leaves of a large variety of plant species, including some cactus species (van Marken Lichtenbelt, 1993).

At each plot, we placed three 50 cm-long pieces of cactus, one of each columnar cactus species. The response variable was the amount of cactus biomass consumed by goats within 48 h in the open plot. The biomass consumption was calculated by weighing the cacti before and after each experimental trial. We corrected for plant biomass loss by water evaporation by measuring the weight loss per cactus in the fenced control plots and subtracting this from the biomass loss measured from the pieces of cacti exposed to goat browsing in the open plots.

2.5.1.2. Experiment II: effect of Opuntia on goat consumption of columnar cacti. We used a factorial experimental design to assess if the presence of

Opuntia affects goat consumption of the three columnar cacti. *Opuntia* forms a thick understory layer in the dry forests of Bonaire and could potentially provide associational resistance against browsing to recruiting columnar cactus. The experimental factors were columnar cacti (i.e. *P. lanuginosus*, *S. repandus* and *S. griseus*) and *Opuntia* (i.e. presence, absence). The treatment with *Opuntia* presence consisted of surrounding 50 cm-long pieces of columnar cacti with a 15-cm thick cover of *Opuntia* plants (Fig. S3.3). We used a combination of *Opuntia wentiana* and *Opuntia elatior* because of their high abundance. We replicated the experiment across the same 12 locations, following the same protocols described previously for Experiment I. The response variable was the amount of biomass of the three columnar cactus species consumed by goats within 48 h after correcting for losses due to water evaporation as previously described.

2.5.2. Enclosure experiments

Parallel to the field foraging experiments, we conducted experiments with goats in captivity under more controlled conditions. We replicated the foraging Experiments I and II, following the protocols previously described, with individual goats kept in captivity ($n = 10$ replicates). During the enclosure experiments, goats were individually placed in test pens (3 × 3 m). All goats had ad libitum access to 1.5 m^2 shade, 10 l of water and 5 kg of cacti.

2.5.2.1. Experiment III: influence of spine morphology on cactus consumption by goats. We evaluated if spine morphology could affect goats' consumption preferences using a factorial experimental design with the three columnar cacti (i.e. *P. lanuginosus*, *S. repandus* and *S. griseus*) and spine occurrence (i.e. presence, absence) as factors (n = 10 replicates). Before the experimental trials, we measured spine morphology of all 50 cm-long pieces of cactus (Figs. S3.4 and S3.5). Cacti receiving the treatment of 'spines absent', were completely stripped of their spines. To account for the effect of bark damage, cacti receiving the treatment of 'spines present', were also partially stripped of their bark, while keeping the spines as much as possible, to ensure an equal amount and type of bark injury between the two treatments (Fig. S3.6). The response variable was the cactus biomass consumed by goats in 24 h correcting for water loss as previously described for Experiments I and II.

In all field and enclosure experiments, we installed camera traps (Relux) in each experimental plot to monitor goat behavior. For the field experiments, we programmed the settings to take 10 s videos when triggered and one picture every 12 h. For the enclosure experiments, we took one picture every 5 min.

2.6. Statistical analysis

We used the Distance Software (Thomas et al., 2010) to calculate the detection function and goat density for every stratum. We selected for conventional distance sampling (CDS) and comparable settings as in previous pilot studies (Lagerveld et al., 2015). We selected the model with the lowest AIC (Akaike Information Criterion). The effective strip width for goat detections turned out to be 15.6 m. The model output also included 95 % CIs of the goat densities.

We used non-parametric tests when data significantly deviated from normality and could not be transformed, variances significantly deviated from equality or when sample sizes were too small to test the distribution. We used χ^2 tests based on the raw count data of the transects, using the chisq.test function in base R, to compare goat abundances and cactus numbers between different groups (e.g. areas, landscape units or plant stages). We applied the Kruskal-Wallis test, using the kruskal.test function in base R, to compare mean percentage of bark damage between cactus species. We applied pairwise Fisher's exact tests, using the fisher.test function in base R, to compare the fraction of individuals with a high degree of bark damage (i.e. ≥ 35 %) across species with manual Holm–Bonferroni corrections as post-hoc tests. Comparisons between WSNP (goats present) and Klein Bonaire (goats absent) were based only on data collected on limestone (T) since this is the only substrate type present on Klein Bonaire.

The number of fruits produced per cactus was estimated in the field in three broad classes, namely no fruits, 1–25 fruits and 25–75 fruits (other categories were pooled because of low numbers). Therefore, we used logistic regressions to assess the relationships between fruiting on the one hand, i.e. probability of fruiting (no fruits vs. fruits) and number of fruits produced (1–25 fruits vs. 25–75 fruits) as response variables, and different indicators of bark damage on the other. These indicators included overall bark damage, goat browsing damage on cactus trunk and parrot and/or bat foraging damage. Logistic models were applied separately for *S. repandus* and *S. griseus* and for both cactus species combined. The final model was obtained by backward selection and lowest AIC value.

We applied non-parametric Kruskal-Wallis tests, using the *coin* (version 1.4.2) R package with 10,000,000 resampling, to compare the amount of biomass of the three cactus species consumed by goats in both field and enclosure experiments (Experiment I). We used resampling because of the small sample sizes involved. We applied the non-parametric Exact Wilcoxon test, using the *exactRankTests* (version 0.8.35) R package, for pairwise comparisons with manually calculated Holm–Bonferroni corrections as post-hoc tests. We used a Friedman non-parametric test to assess the effects of *Opuntia* (presence vs. absence) and spines (presence vs. absence) on goat consumption across the three cactus species (Experiments II and III). We applied Wilson score 95 % CIs for proportions and sex ratio's, using the *binom* R (version 1.1.1.1) package. The 95 % CI interval for ratios of proportions was estimated with the delta method using the prop.test function in base R.

3. Results

3.1. Goat density

Approximately 11,064 goats roamed freely (95 % CI: 8513–14,378) through WSNP and Labra-Brasil areas. Goat density in the Labra-Brasil area was significantly lower (0.45 ind./ha, 95 % CI: 0.14–1.40) than in the Washington (2.65 ind./ha, 95 % CI: 1.92–3.67) and Slagbaai (2.69 ind./ha, 95 % CI: 1.79–4.05) sectors of the WSNP ($\chi^2 \geq 27.7$, df = 1, $p <$ 0.0001). Other feral livestock species were considerably less abundant (total density: 0.26 ind./ha, Table S1.3). We found no significant differences in goat abundance across landscape units within WSNP ($\chi^2 =$ 2.34, df = 3, $p = 0.51$; Table S1.4). Comparable results were found when using dung counts as dung and goat counts per transect were positively correlated (Linear regression, adj. $R^2 = 0.05$, $N = 250$, $p = 0.0002$) (Fig. S1.5). About 20.6 % (95 % CI: 15.3–27.0 %, $n = 37$) of the goat population was composed of young individuals, 30.6 % (95 % CI: 24.3–37.6 %, $n = 55$) by sub-adults and 48.9 % (95 % CI: 41.7–56.1 %, $n = 88$) by adults. The sex ratio (female/male) for all goats was 2.23 (95 % CI: 1.53–3.25, $n = 126$), while for adult goats, in particular, it was 1.96:1 (95 % CI: 1.25–3.08, $n = 83$).

3.2. Cactus abundance, distribution and condition

In the WSNP, we counted 10,094 cacti along the sampling transects. The most abundant columnar cactus was *S. griseus* (88.9 %), followed by *S. repandus* (9.5 %) and *P. lanuginosus* (1.6 %) (Fig. 2). The relative abundance of plant stages differed significantly across species ($\chi^2 =$ 1533.0; $n = 9914$; df = 4; p < 0.0001). *S. repandus* had a large proportion of adults (54.2 %) and low proportions of juveniles and resprouting individuals (14.7 % and 24.9 % respectively). In contrast, *S. griseus* and *P. lanuginosus* had a much lower proportion of adults (13.9 % and 10.4 %, respectively) and abundant regeneration by either juveniles (5.9 % and 40.2 % respectively) or resprouting individuals (78.8 % and 49.4 % respectively; Fig. 2). *S. repandus* had the largest proportion of dead individuals (6.2 % compared to ≤1.3 % for the other two species).

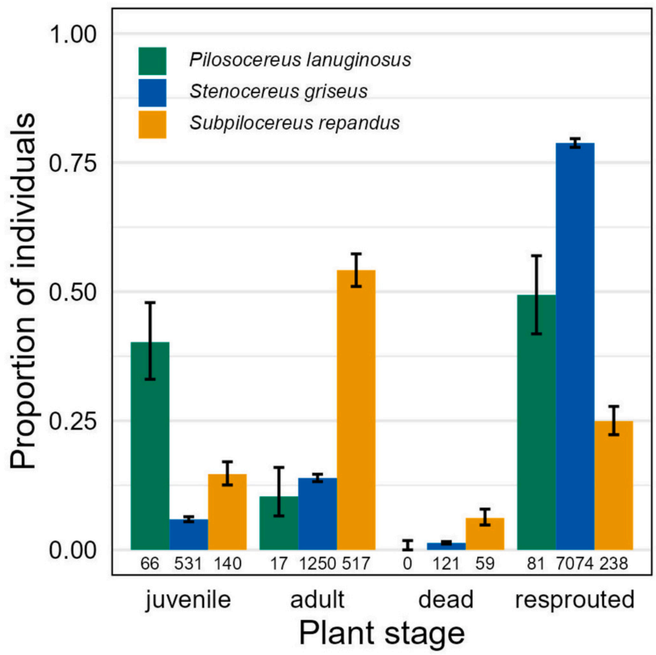

Fig. 2. Population structure of *Subpilocereus repandus*, *Stenocereus griseus*, and *Pilosocereus lanuginosus* growing within the Washington Slagbaai National Park (Bonaire). Data shows proportion of individuals (Mean ± Wilson score 95 % CI). Number of individuals are presented below every bar. The population of *S. repandus* has high proportion of adults and low proportion of juveniles and resprouting individuals compared to the population structure of the other two cacti species.

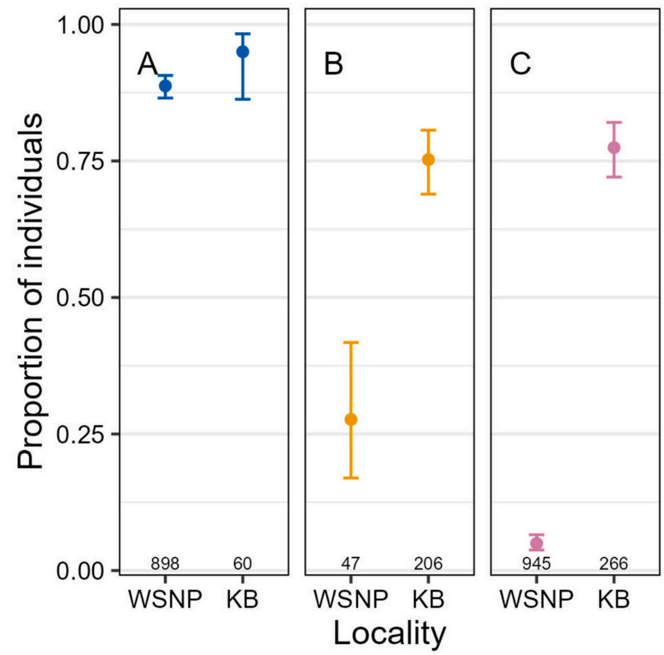

Fig. 3. Species relative abundance and population structure under goat presence (WSNP, Bonaire) and absence (KB, Klein Bonaire) under comparable limestone substrates. Data shows proportion of individuals (Mean ± Wilson score 95 % CI). Number of individuals are presented below every bar. The recruitment of *S. griseus* was slightly higher (Fisher's exact test: $p = 0.19$) under absence of goats (A: proportion juveniles vs. adults for *S. griseus*). In contrast, goat removal resulted in large recruitment success of *S. repandus*, the cacti species preferentially browsed, increasing the proportion of juveniles vs. adults in Klein Bonaire (B: proportion juveniles vs. adults for *S. repandus*) and increasing also the abundance of *S. repandus* vs. *S. griseus* (C: proportion *S. repandus* vs. *S. griseus*). We found no individuals of *P. lanuginosus* in Klein Bonaire.

On goat-free Klein Bonaire, we counted 266 cacti along the sampling transects. The relative abundance of cactus species and their population structure was very different from that of Bonaire. In Klein Bonaire, we found that *S. repandus* accounted for 77.4 % of all living columnar cacti followed by *S. griseus* (22.6 %). We found no individuals of *P. lanuginosus* (Table S2.3). To compare the abundance of cacti between goat-free Klein Bonaire and goat-present WSNP on Bonaire, we used only the stratum with limestone substrates since this is the only type of substrate present in the small island of Klein Bonaire. *S repandus* more than doubled (ratio 2.7, 95 % CI: 1.4–4.0) its proportion of juveniles on Klein Bonaire (75.2 %) compared to WSNP (27.7 %) on comparable limestone substrates (Fig. 3). Except for one individual of *S. repandus*, no dead cacti were observed on Klein Bonaire.

We found signs of bark damage in 76.6 % of the adult cacti growing in the WSNP compared to 13 % of the adult individuals on Klein Bonaire (Table S2.4). The proportion of individuals with browsed trunks was 31 % in WSNP (no browsing on Klein Bonaire due to absence of goats). The species most affected was *S. repandus* with 52 % of the individuals browsed compared to 21 % of the *S. griseus* cacti growing on WSNP (Fig. 4). *S. repandus* showed the highest proportion of browse damage both on trunks (7.6 % vs. 5.1 %) and on top branches (672 cm^2 vs. 346 cm^2) compared to *S. griseus* indicating a preference by both feral livestock and birds and bats for this species. Positive correlations between bark damage and browsing scars on the cactus trunk indicate that injuries by foraging goats may ultimately result in overall bark damage (*S. repandus*: Spearman rho = 0.40, $p < 0.001$, $n = 460$; *S. griseus*: Spearman rho = 0.16, $p < 0.001$, $n = 986$).

Logistic regression analyses showed that the degree of bark damage on an individual cactus reduced the probability of bearing fruits in both *S. repandus* and *S. griseus* (Fig. 6, Table S2.5). Furthermore, the degree of bark damage in *S. repandus* was negatively associated with the probability of carrying many fruits (Fig. S2.6; Table S2.7). Interestingly, according to these regressions, direct browsing damage was positively associated with fruiting. The degree of browsing scars, by birds and bats, was positively associated with the probability of carrying fruits in both cactus species ($p < 0.01$) and near-significantly with the number of fruits produced by *S. griseus* ($p = 0.06$; *S. repandus* $p = 0.20$). Also, the degree of goat browsing damage tended to be positively associated with the probability of carrying fruits in *S. repandus* ($p = 0.09$), but not in *S. griseus* ($p = 0.44$). These patterns suggest that foraging birds, bats, and goats are attracted by fruiting cacti.

S. repandus juveniles were more often growing in sheltered microsites than juveniles of other cactus species. In WSNP, excluding the limestone substrates, 14.5 % ($n = 365$) of *S. repandus* juveniles was found in sheltered microsites compared to 4.8 % ($n = 6808$) of *S. griseus* and 0.7 % ($n = 147$) of *P. lanuginosus*. This proportion increased on limestone substrates of WSNP and Klein Bonaire, where respectively 53.8 % ($n = 13$) and 47.7 % ($n = 155$) of the juveniles of *S. repandus* were found in sheltered microsites. Overall, living shrubs (mostly *Prosopis* and *Opuntia*) were the more common sheltered microsite in WSNP (83 % of the sheltered sites, $n = 384$) while rocks were the more common sheltered microsite in the limestone areas (96 % of the sheltered sites, $n = 89$) of WSNP and Klein Bonaire. In WSNP (excluding the limestone areas), *S. griseus* was predominantly associated with living shrubs (90.6 %, $n = 330$) while *S. repandus* was more evenly associated across different types of sheltered microsites (i.e. 35.8 % living shrubs, 17 % dead shrubs, 47.2 % rocks, $n = 53$). Both, living shrubs and rocks ameliorated air temperatures compared to adjacent open areas (Fig. S2.8).

3.3. Goat preference for columnar cacti

In both field and enclosure experiments, goats showed a notorious

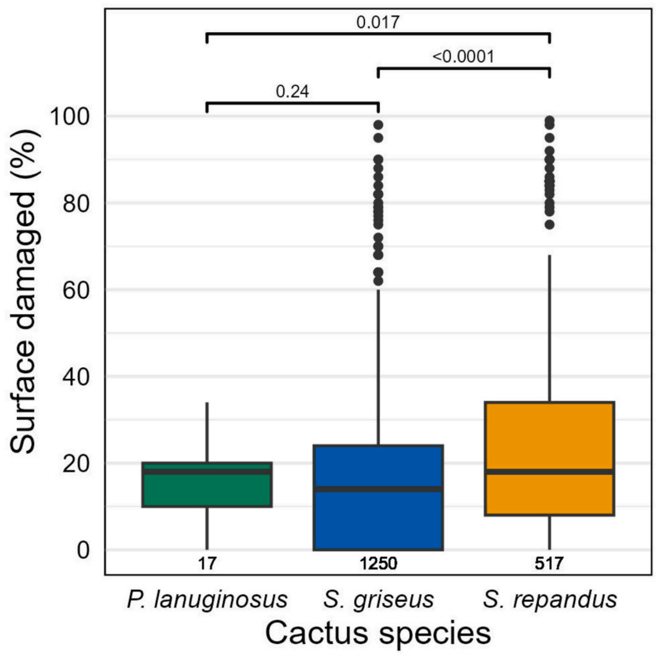

Fig. 4. Browsing damage on *Pilosocereus lanuginosus*, *Stenocereus griseus*, and *Subpilocereus repandus* individuals growing within Washington Slagbaai National Park. *S. repandus* cacti have a larger percentage of their surface with browsing scars (χ^2 test = 46.70, df = 2, $p < 0.0001$). Pairwise comparisons were conducted using Fisher's Exact test with *p*-values shown in figure (Holm-Bonferroni correction of *S. repandus* vs. *P. lanuginosus*: $p = 0.034$).

preference for *S. repandus* as reflected by their first foraging choice and the greater amount of biomass consumed compared to the other two cactus species (Kruskal-Wallis tests: $p \leq 0.024$, Fig. 5). The consumption rates of *S. griseus* and *P. lanuginosus* cacti did not differ significantly (Kruskal-Wallis tests: $p \geq 0.39$). While goats in the enclosure experiments ingested more biomass overall, the relative preference for *S. repandus* over the other cactus species remained consistent with the field findings (Fig. 5). Spine removal and the presence of Opuntia around the columnar cacti did not alter the strong goat foraging preference for *S. repandus* (Figs. S3.7 and S3.8 respectively).

4. Discussion

Our findings demonstrate that goat browsing is a major bottleneck for the conservation of columnar cacti in Caribbean dry seasonal tropical forests. Browsing by feral goats shapes the patterns of abundance, distribution, and population structure in columnar cacti and hence also vegetation composition. More than 76 % of the adult cacti growing in Washington Slagbaai National Park had signs of bark damage and 31 % had trunks browsed by goats. This is roughly six times higher than the bark damage recorded on goat-free Klein Bonaire (13 % of adults), where we did not record any signs of browsing on cactus trunks. Goat browsing has been sporadically reported for several cactus species, as highlighted in recent reviews (Bravo-Avilez et al., 2019; Aliscioni et al., 2021), yet our results are the first comprehensive analysis of how goat dietary preferences impact columnar cactus abundance, population structure, and distribution.

S. repandus is the most susceptible species to herbivory as evidenced by a population dominated by adults, with lower capacity to regenerate and the most extensive bark and browsing damage found among the three columnar cactus species. Consistently, during all our experiments, goats showed a strong predilection for *S. repandus*. This preference was not influenced by the experimental removal of spines or an association with *Opuntia*. Although plant spinescence reduces bite sizes and limits intake rates, it does not deter goats from feeding on spiny plants (Cooper and Owen-Smith, 1986; Wilson and Kerley, 2003). Spinescence is a physical defense mechanism against predation but did not reduce herbivore damage and cannot explain the strong preference of goats for *S. repandus*.

Our results suggest that birds, bats and goats are attracted by fruiting cactus, browsing heavily on both the upper cactus branches and the trunk. We found that the probability of fruiting (and fruit abundance) was negatively correlated with the proportion of cactus bark damage when accounting, not only for the surface of browsing scars, but also for the proportion of dead tissue. Lower number of flowers and fruits have been reported in columnar cacti predated by livestock (Peco et al., 2011) and rodents (Hayes et al., 2013). The relationships between bark damage and reproductive success in columnar cacti are complex as bark damage can be produced by different agents and has contrasting effects on fruiting depending on the interspecific interactions between different herbivores and pathogens (Callejas-Chavero et al., 2020; Bravo-Avilez et al., 2023). Fruit consumption by birds and bats can produce stem damage, but it contributes to seed dispersal and increases germination rates of these cacti species (Naranjo et al., 2003). Although goats have been reported as potential seed dispersers of some cactus species, the digested seeds have lower germination rates (Baraza and Fernández-Osores, 2013).

Our combination of field vegetation patterns and variety of experiments assessing goat foraging behavior clearly demonstrated the susceptibility of native columnar cactus to exotic mammalian herbivores and revealed the cause of the current population structure of these cactus populations on Bonaire. The comparison of columnar cactus communities between goat-free Klein Bonaire and goat-present Bonaire offered the opportunity to assess the resilience of vegetation after 50 years of strong herbivore control and 30 years of complete goat eradication. The eradication of goats on Klein Bonaire resulted in significant vegetation shifts illustrated by a dominance of *S. repandus* cacti and a population with increased regeneration and reduced mortality underscoring the potential for vegetation recovery after goat removal. We did not find any individual of *P. lanuginosus* on Klein Bonaire. Neither was the species recorded in the inventories dating back to 1930s (Wagenaar Hummelinck, 1981), 1960s (Stoffers, 1962) and 1996 (Debrot, 1997). The species is not frequently found in comparable degraded and saline limestone terraces of Bonaire and Curaçao. However, its seed dispersers, such as bats and birds, do cross the short distances between nearby islands and could potentially introduce seeds from Bonaire (Simal et al., 2015). The eradication of goats from Klein Bonaire is a “natural experiment” that allows assessing the resilience of these plant communities at landscape scales. But is of course a “pseudo-replicated” natural experiment. Despite the unavoidable shortcomings of natural experiments at whole ecosystem scales, their combination with field patterns and controlled experiments, as the ones we have presented here, has proven a successful strategy to understand complex phenomena in ecological systems at relevant spatial and temporal scales (Schindler, 1998; Underwood et al., 2000; Donlan et al., 2002).

The strong goat browsing effects we report for columnar cacti may indirectly facilitate the expansion of less palatable plant species with cascading effects on animal diversity as the loss of columnar cacti impacts the mutualist networks they form with birds and bats (Fleming and Valiente-Banuet, 2002; Fleming and Holland, 2018). Our results echo those found on nearby arid Curaçao island where livestock grazing has reduced plant cover and changed vegetation composition (Debrot and de Freitas, 1993).

The management efforts led by STINAPA since 2014 to eradicate goats and other exotic herbivores from the Washington Slagbaai National Park are a priority for ecological restoration and biodiversity conservation. Monitoring the long-term effects of eradication programs is essential to assess the direct and indirect effects of exotic herbivores on ecological communities and ecosystem functioning. Goat removal from islands is often associated with increases in vegetation cover and

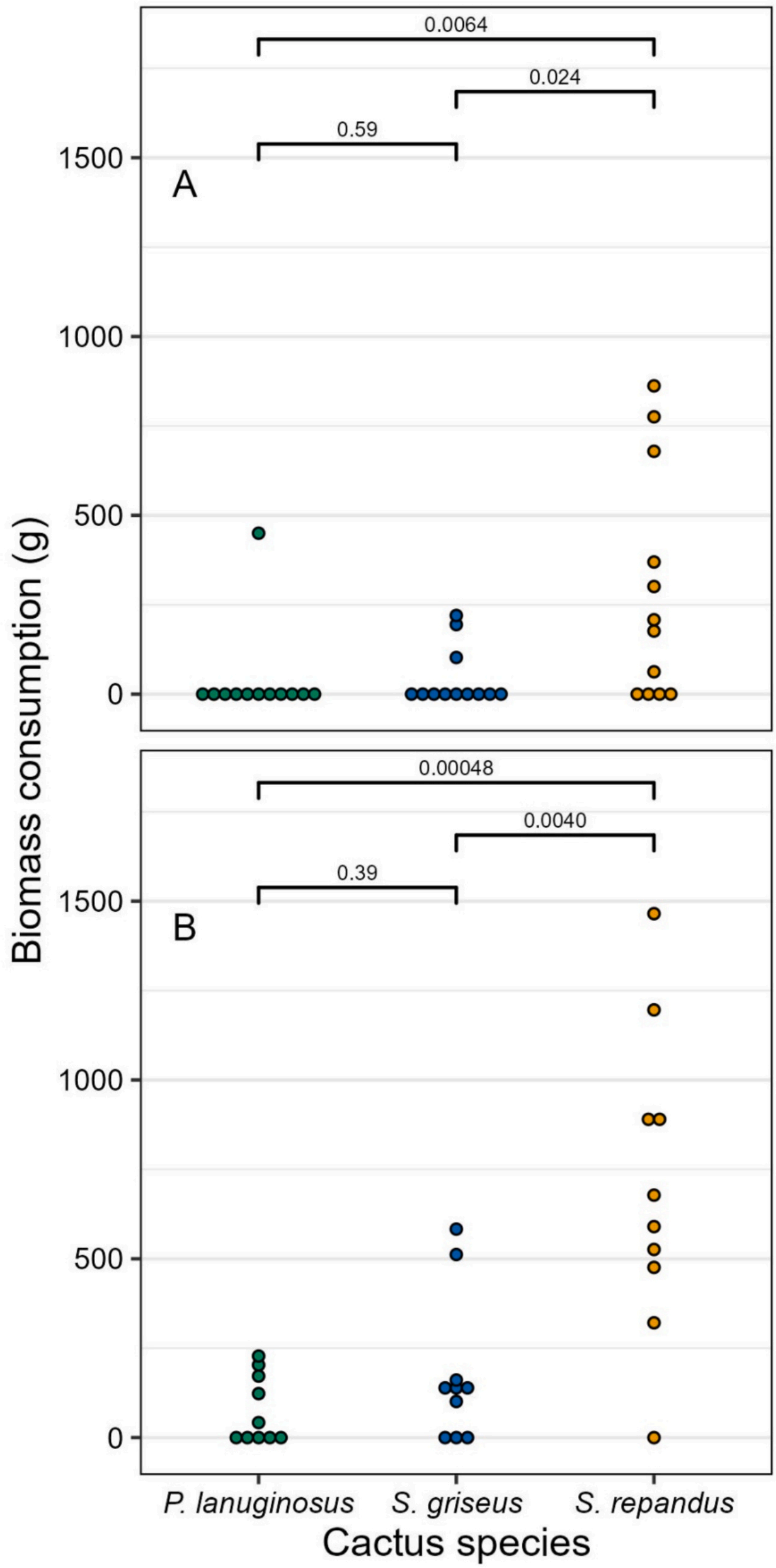

Fig. 5. Foraging experiments on goat preference for three columnar cacti species in field experiments (A) and enclosure experiments (B). Goats preferentially consume *Subpilocereus repandus* compared to *Stenocereus griseus* and *Pilosocereus lanuginosus* cacti. Kruskal-Wallis test, $\chi^2 = 9.85$, p-value $= 0.0049$ (field experiment; $n = 12$), $\chi^2 = 12.97$, p-value $= 0.00059$ (enclosure experiment; $n = 10$). Pairwise comparisons were conducted using exact Wilcoxon Rank Sum test with p-values shown in figure. Holm-Bonferroni correction of *S. repandus* vs. *S. griseus*: experiment A: $p = 0.049$, experiment B: $p = 0.0080$.

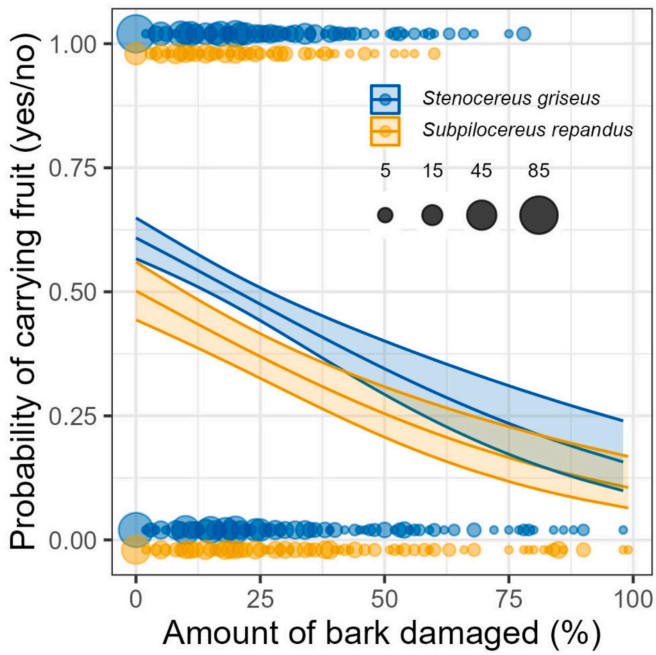

Fig. 6. Relationships between fructification and bark damage. The probability of carrying fruits decreases as the percentage of bark damage increases in individuals of both *S. griseus* and *S. repandus*. Logistic regression: $p < 0.0001$, difference between species: $p < 0.0001$. *S. repandus*: Nind_yes = 176, Nind_no = 284; *S. griseus*: Nind_yes = 503, N_no = 486). The abundance of *P. lanuginosus* was too small to conduct this statistical analysis.

species richness (Schweizer et al., 2016), including endemic and rare native species (Thomson et al., 2022). However, passive recovery of plant species composition and soils is often incomplete (Gizicki et al., 2018; Luna-Mendoza et al., 2019). Also, eradication of exotic herbivores can lead to unexpected ecological surprises (Zavaleta et al., 2001). For example, rapid recovery of exotic plants from released herbivore control may hinder the regeneration of native plants (Donlan et al., 2003) and increase the probabilities of fire occurrence (Mack and D'Antonio, 1998). Resource competition with invasive grasses, for instance, can threaten the persistence of Caribbean cactus populations by reducing growth, survival and reproduction (Rojas-Sandoval et al., 2016). Assessing the response of fast growing native and exotic herbaceous plants and vines to goat herbivory release, and how they may interact with the regeneration of native tree and cactus species should be part of the monitoring efforts of the goat eradication program. Using an ecosystem perspective to assess the ecological changes after eradicating exotic herbivores is essential to identify bottlenecks of resilience and adapt management actions to accelerate recovery. For example, reforestation, erosion control, and fire prevention after goat eradication can further facilitate the recovery of insular ecosystems (Luna-Mendoza et al., 2019) and accelerate a transition to alternative ecosystem states maintained by a new set of positive feedbacks (Oro et al., 2022; Maes et al., 2024).

As demonstrated by the positive response of cactus populations on Klein Bonaire, goat eradication is a fundamental step for vegetation recovery on these Caribbean islands. Because columnar cactus regeneration is highly episodic during wet periods (Arroyo-Cosultchi et al., 2016; Félix-Burruel et al., 2021), coupling restoration efforts to rainy La Niña events could accelerate the recovery of these Caribbean cactus populations. Reducing herbivore pressure during rainy ENSO events can certainly facilitate vegetation recovery as demonstrated in other drylands (Holmgren and Scheffer, 2001; Holmgren et al., 2006; Sitters et al., 2012). Such strategic timing is crucial, especially as climate models predict a drier future with more frequent El Niño events (Martis et al., 2002), potentially narrowing the windows of opportunity for effective cacti population restoration. The strong cultural ties with goats across the Caribbean (Wallman, 2020) requires developing sensitive conservation and management strategies that prevent feral browsing to protect and restore vegetation and soils in priority sites of high conservation importance while allowing sustainable small-scale pastoral farming systems in other areas. Such a combined strategy could facilitate building social acceptance and long-term recovery of Caribbean ecosystems at island scales.

CRediT authorship contribution statement

Milena Holmgren: Supervision, Project administration, Methodology, Formal analysis, Conceptualization, Writing – original draft. **Adolphe O. Debrot:** Project administration, Funding acquisition, Conceptualization, Writing – review & editing. **Barry van den Ende:** Visualization, Methodology, Investigation, Formal analysis, Writing – review & editing. **Kevin Geurts:** Visualization, Methodology, Investigation, Formal analysis, Writing – review & editing. **Nikkie van Grinsven:** Visualization, Methodology, Investigation, Formal analysis, Writing – review & editing. **Pim van Hooft:** Visualization, Validation, Supervision, Project administration, Methodology, Formal analysis, Conceptualization, Writing – review & editing.

Declaration of competing interest

Authors declare no conflicts of interests

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111270.

Data availability

Data will be available at a public repository.

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