

## Invasive species appear to disrupt the top-down control of herbivory on a Mexican oceanic island

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### Abstract

Oceanic islands are simplified ecosystems, which are very useful for understanding the processes related to the structuring of natural communities and for assessing cascade effects after perturbations. Socorro Island in the Pacific Ocean reaches up to 1040 m in elevation, and the northeastern side that faces trade winds is more humid than the leeward southwestern side. Apparently, the lack of freshwater throughout most of the island has prevented the spread of invasive cats and sheep to the north, but these species have severely impacted land bird communities on the southern side, where they have potentially disrupted functions such as the top-down control of herbivory. We tested the relative importance of bottom-up (soil and foliage nutrient availability) and top-down (predation of insect herbivores) drivers of herbivory in three endemic tree species. By experimentally excluding birds, we assessed changes in herbivory when top-down control was disrupted, and we also evaluated herbivore predation rates using artificial caterpillars. Our findings suggest that the herbivory patterns on Socorro Island are driven by the top-down control of herbivores by land birds, because their exclusion resulted in higher herbivory (12%) despite low nitrogen content (bottom-up control) of leaves on the north side, whereas the leaves were richer in nitrogen on the south side but no change in herbivory was observed when birds were excluded, and overall, herbivory was 30% higher than in the north, suggesting release of herbivores from top down control on the south side, probably due to effects of invasive predators (cats) or sheep, which may have reduced suitable bird habitats. A better understanding of how drivers of ecological interactions operate on Socorro Island may increase the likelihood of success of future restoration programs.

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## **Introduction**

Herbivory is one of the most widely distributed interactions in all ecosystems, in which over half of the currently described species participate either directly (plants and herbivorous insects) or indirectly when natural enemies of herbivores are considered (predators and parasitoids) (Novotny and Basset 2005). A large body of theoretical and empirical evidence supports the effects of herbivory on plant performance and its consequences for other levels of organization, but much less is known about the mechanisms that control herbivore populations and their consumption rates. The abundance of plants, the nutritional quality of their tissues, and the distributions of antiherbivore defenses (chemical and physical) are considered bottom-up determinants of the consumption rates of plant tissues by herbivores, and these determinants ultimately control insect herbivore abundance and diversity (Elton 1927, White 1978, McQueen et al. 1986, Leroux-Loreau 2015). Bottom-up determinants are the foundation of resource-based hypotheses, which briefly state that herbivores are resource (plant tissue) limited when either plant tissues are unavailable or heavily defended. In addition, components of the third trophic level (predators and parasitoids of herbivores) are key drivers of herbivore populations, and thus can regulate the amount of damage caused to plants (Walker and Jones 2001, Mooney et al. 2010, Maas et al. 2015, Vidal et al. 2018.). At present, it is acknowledged that bottom-up and top-down controls of herbivory both contribute to dynamics at the population, community, and ecosystem levels (Leroux-Loreau 2015), but either can prevail over the other depending on the prevalent local conditions. However, very little is known about the balance between these two processes in natural systems (Walker and Jones 2001, Vidal et al. 2018).

A major limitation that hinders advances in our knowledge of this subject is the complexity of mainland ecosystems. By contrast, oceanic islands that harbor simplified ecosystems are suitable model sites for testing the ecological responses of biota to specific environmental conditions, thereby facilitating the investigation of trophic cascades in great detail

(Scatena and Lugo 1995, Austin and Vitousek 1998, Vitousek 2002, McCain and Grytnes 2010, Schoener and Spiller 2010, 2016, Warren et al. 2015). Oceanic islands that reach high elevations often have contrasting environmental conditions on opposite sides and are thus ideal for natural experiments. Islands in the Pacific Ocean are influenced by trade winds, where the windward areas receive more humidity and rain, and have greater biodiversity and higher primary productivity, than leeward areas (Scatena and Lugo 1995, McCain and Grytnes 2010). Thus, the northern forests of Socorro Island, which is the largest island in the Revillagigedo Archipelago in the Mexican Pacific Ocean, have a greater basal area, higher species richness, and more diverse understory community than the southern forests (Levin and Moran 1989, Aguilar-Chama et al. *in prep*), and presumably greater productivity due to the high precipitation on this side of the island compared with the southern side (Miranda 1960, León de la Luz et al. 1996).

Introductions of merino sheep (*Ovis aries*) and cats (*Felis silvestris catus*) on Socorro Island have impacted the vegetation, increased soil erosion rates, and drastically reduced land bird populations to the extent that they are considered key drivers of the extinction of some endemic species (Arnaud et al. 1993, 1994, León de la Luz et al. 1994, Maya-Delgado et al. 1994, Ortega-Rubio and Castellanos-Vera 1995, Rodríguez-Estrella et al. 1996, Martínez-Gómez and Jacobsen 2004, Walter and Levin 2008, Ortiz-Alcaraz et al. 2016a). Most of the effects of sheep and cats are concentrated on the central-southern part of the island below an elevation of 400 m (Ortiz-Alcaraz et al. 2016a, b), although considerable activity has also occurred in the forest ecosystems above 600 m and up to 850 m. The northern part of the island has been mostly free of the influence of these introduced species (Arnaud et al. 1994, Walter and Levin 2008, Ortiz-Alcaraz et al. 2016a, b). Three main components determine the restricted distribution of introduced species: a) the only human settlement (military base) on the island is located in the lowlands of the southern side, b) the lack of long lasting freshwater sources in the northern side

of the island; this despite the more rain and humidity in this side of the island, and c) the wide craggy consolidated lava flow that run across the island east to west.

In this study, considering that the different environmental conditions on the northern and southern sides of Socorro Island should support plant communities that differ in terms of their diversity and productivity, as well as the biased distribution of feral cats (common in the south but absent or scarcely distributed in the north), we conducted an experiment to test the relative strengths of top-down and bottom-up forces as drivers of herbivory in Socorro Island. We hypothesized that the northern forest with higher precipitation should have a more dynamic microbial soil community than that in the southern forest, thereby resulting in higher mineralization rates for key elements such as nitrogen and phosphorus, and that resulting higher nutrient contents of plant tissues may increase herbivory rates. However, feral cats are mostly absent from the northern forest, and thus the large populations of land birds there may exert strong control of herbivore populations, thereby reducing the overall damage to plants. By contrast, in the southern forests, we expected soil with lower nutritional quality and plant tissues with low nutrient contents and predicted bottom-up forces would be the key drivers of herbivory because cats have diminished the land bird populations. We predicted that excluding birds would increase herbivory in the north, but expected no change in the south.

We aimed to address the following three questions. (i) What are the differences in the soil nutrient concentrations and mineralization rates between the southwestern and northeastern sides of the island? (ii) Does insect herbivory differ between these two sides of the island? (iii) Are herbivory levels governed by foliar nutrient concentrations (bottom up forces) or herbivore predation (top down forces)?

## MATERIALS AND METHODS

### *Study site*

Socorro Island (18° 42'28" N, 111° 02'49" W) is located 460 km south of the tip of the Baja California Peninsula and 700 km west of the port of Manzanillo in Colima State. It is the largest (140 km<sup>2</sup>) of the four islands in the Revillagigedo Archipelago and reaches an elevation of 1040 m. The climate is arid-tropical with mean annual temperatures and annual accumulated precipitation ranging from 25 °C to 21 °C and 300 to 500 mm, respectively. Most of the rainfall occurs during the hurricane season from July to October. The northern side of the island is notably more humid, and the high areas are frequently covered by fog (Miranda 1960, León de la Luz et al. 1996). The southern side of the island has deeper soils and flatter terrain, and hosts extensive woodlands. On the northern side, most of the woodlands are confined to narrow ravines that shield the trees from hurricane winds and provide sufficient soil moisture (Walter and Levin 2008). The vascular flora of the island includes 117 species (Levin and Moran 1989) and the main plant associations are: (1) mixed scrub mainly comprising perennial herbaceous shrubs (*Dodonaea viscosa*) and stocky trees (*Guettarda insularis* and *Prunus serotina*); (2) forest where the arboreal communities are represented by associations of *Sideroxylon socorrense*, *Psidium galapagaeum*, and *Ficus cotinifolia*; and (3) deciduous scrub dominated by *Croton masonii* (Flores-Palacios et al. 2009). The native vertebrates of Socorro Island are restricted to one endemic lizard species (*Urosaurus auriculatus*) and eight species of land birds, five of which include invertebrates in their diets (*Parula pitiayumi graysoni*, *Pipilo maculatus socorrensis*, *Troglodytes sissonii*, *Mimus graysoni*, and *Mimus polyglottos*). Little is known about the invertebrate fauna on the island (Brattstrom 2015), but similar to the mainland, Aranae, Orthoptera, Hemiptera, Coleoptera, Lepidoptera, and Diptera are well represented orders, together with an abundant population of the crab *Gecarcinus planatus*. The archipelago is

protected by Mexican laws as part of the Deep Mexican Pacific Biosphere Reserve (DOF 2016) and as a National Park (DOF 2017), and the archipelago was declared a World Heritage Site (UNESCO 2016) at the international level.

In 1869, sheep were introduced to Socorro Island where they readily became feral and occupied the central-southern side of the island up to an elevation of around 500 m, although they frequently visited higher forest ecosystems (Brattstrom 2015). Cats and sheep were effectively confined to the south-central section of the island because of the rough, jagged, and generally rugged bare surfaces of consolidated lava flows (aa-type) running across the island from west to east, as well as the lack of freshwater sources throughout most of the island (Walter and Levin 2008, Ortíz-Alcaráz et al. 2016a). The sheep caused major damage to the soil and vegetation in 30% of the central-southern side of the island, mainly at elevations below 400 m. This damage also affected the nest sites of land birds (León de la Luz et al. 1996, Ortíz-Alcaráz et al. 2016b). After intense campaigns over a period of five years (2008–2012), sheep were eradicated from the island and the recovery of vegetation has been documented (Ortíz-Alcaráz et al. 2016a).

In 1957, the Mexican government deployed a contingent of the army to Socorro Island to build a formal settlement on the southernmost portion of the island, including over 6 km of paved road and an airstrip with the capacity to handle C-130 aircraft. These activities resulted in considerable levels of quarrying, bulldozing, hilly terrain leveling, logging of trees, and subsequent erosion of exposed soil surfaces (Walter and Levin 2008). As a consequence of the settlement, exotic animals such as the house mouse (*Mus musculus*) and house cat (*Felis silvestris catus*) were introduced to the island (Brattstrom 1990). Predation by cats threatens the survival of native bird species and the Socorro tree lizard, *Urosaurus auriculatus* (Arnaud et al. 1994, Ortíz-Alcaraz et al. 2016b).

Our study was conducted in the forest ecosystems of Socorro Island between elevations of 600 and 900 m in 2012 and 2013. According to a recent report by Ortíz-Alcaraz et al. (2016a), the study sites were only slightly affected by sheep on the southern side, whereas sheep had no effects in the northern forests. However, feral cats are not uncommon in the southern forests, whereas no cat activity has been reported in the northern forests (Ortíz-Alcaraz et al. 2016b). Thus, the effects of cats are expected to differ significantly on the northern and southern sides, but the effects of sheep are likely to be minimal on both sides, of Socorro Island.

### *Study species*

We selected three tree species from among those with the highest importance values (IVs), which were calculated as:  $IV_i = RF_i + RA_i$ , where  $RF_i$  is the relative frequency of the  $i^{\text{th}}$  species and  $RA_i$  is the relative abundance of the  $i^{\text{th}}$  species estimated in a previous study (Aguilar-Chama *in prep*).  $RF_i$  is the ratio between the number of plots where the  $i^{\text{th}}$  species was recorded and the total number of plots surveyed, and  $RA_i$  is the ratio between the number of individuals of the  $i^{\text{th}}$  species and the total number of individuals counted in all plots. The selected species occurred on both sides of the island and belonged to different families, in order to minimize the effects of confounding phylogenetic factors. The species that met these criteria were: *Ilex socorroensis* (Aquifoliaceae), *S. socorrense* (Sapotaceae), and *G. insularis* (Rubiaceae). The foliar nutrient traits, herbivory estimates, and experiments based on the exclusion of birds, were restricted to saplings (30-50 cm in height) because the performance of small plants is more likely to be affected by herbivory than that of adult trees (Marquis 1984). We haphazardly located 20 pairs of saplings of each species on both sides of the island, distributed in four and three sites on the southern and northern sides of the island, respectively (Figure 1). The number of sites surveyed varied according to their accessibility. «Figure 1 near here»

### *Soil traits*

We collected three soil samples from each site, with a total of 15 soil samples from the northern side and 20 from the southern side. Each sample comprised 200 g from the top 10 cm of the soil layer. Soil samples were packed and stored at 4°C, before they were transported for analysis in a specialized laboratory at Instituto de Ecología A.C. We quantified the total carbon and nitrogen contents, readily available phosphorus, and carbon and nitrogen mineralization rates.

The soil pH was measured using a Corning Model 320 potentiometer at a soil:water volumetric ratio of 1:2. The soil water content was estimated based on the gravimetric difference between the fresh soil and oven-dried soil (dried for three days at 105°C). The total carbon and nitrogen contents were measured with an automatic soil analyzer (Truspec, LECO; Michigan, USA). Total soil phosphorus was extracted as described by Bray-Kurtz (1945) and colorimetrically quantified using a spectrophotometer based on the procedure presented by Murphy and Riley (1962).

Soil biogeochemical properties were estimated based on the carbon and nitrogen mineralization rates. The carbon mineralization rate was estimated in soil incubated for 30 days in a hermetic flask containing a CO<sub>2</sub> trap with NaOH solution, where the quantity of CO<sub>2</sub> captured in the NaOH solution was directly proportional to the amount of carbon mineralized in the soil sample. Nitrogen mineralization rates were estimated by measuring the ammonia (NH<sub>4</sub><sup>+</sup>) and nitrate (NO<sub>3</sub><sup>-</sup>) contents before and after incubating the soil samples for 27 days. The analyses were based on nitrogen extraction with KCl, as described by Etchevers et al. (1971), with a further vapor extraction step in the presence of MgO. Devarda's alloy was used to facilitate the extraction of nitrates. One-way analysis of variance was conducted to compare the effects of island location (south vs. north) on the soil variables.



### *Nutrient contents of leaves*

The nutrient contents of the leaves were estimated based on the nitrogen and carbon contents, and the nitrogen/carbon ratio. For each of the tree species analyzed, we collected three to five intact leaves from each of the 20 individual trees on each side of the island (the same individual trees used to estimate herbivory) in April 2013. Leaf nitrogen and carbon contents were estimated with an automatic analyzer (TruSpec CN, LECO; Michigan, USA). We used mixed effects models to analyze the effects of the location and species identity on plant nutrient traits. The fixed factor comprising the side of the island had two levels (north and south) and the random component was defined as an individual tree from each species on each side of the island.

### *Bird counts*

We employed a fixed point-count procedure for bird surveys, where we recorded all birds detected on sight within a 25-m radius. We sampled 30 points on each side of the island over six consecutive days in April 2013. Each count lasted 30 min. We conducted all bird counts between 9:00–11:30 and 15:00–17:45. Our records excluded individual birds that we considered to be flying across the landscape above the canopy. We identified birds to species level according to Howell and Webb (2007). Of the six land bird species reported to be on the island, our records were limited to five species because the parrot *Aratinga holochlora* has not been reported to consume arthropods, whereas the other five species consume arthropods, seeds, and fruits (Cervantes 2013). To test the overall abundance of birds on the two sides of the island we used a t-test with the Welch correction on the degree of freedom to account for the lack of

homocedasticity. The distribution of the abundance of birds species on each side of the island was visualized as a contingency table. The expected frequencies were estimated as the product of the partial probabilities (side of the island and bird species) and the overall frequency, and we used the Pearson chi-square goodness of fit to test departures from independent occurrence of the observed frequencies (Person 1900, Cochran 1937).

### *Predation of artificial caterpillars*

We excluded birds from the saplings by caging the entire plant. Exclosures were constructed using agricultural wire netting (mesh size = 2 x 2 cm). These cages effectively excluded birds and tree lizards, whereas arthropods could move freely in and out. We used a paired design comprising excluded and exposed (experimental control) plants where the members of any given pair were separated by no more than 150 cm. We used a total of 20 pairs of plants of each species, on each side of the island. We placed three artificial caterpillars on the leaves of each of the exposed plants, with a total of 60 caterpillars on each plant species on each side of the island. We constructed the artificial caterpillars by combining a 3-cm long brown modeling clay segment with a 0.5-cm long red modeling clay segment, both with a diameter of 4.08 mm, in order to simulate the body and head of an actual caterpillar, respectively. Modeling clay segments were obtained by squeezing the kneaded clay through a lemon squeezer. One end of a 10-cm long monofilament fishing line was embedded in each artificial caterpillar, and the other end was used to tie the artificial caterpillar to its host plant. The artificial caterpillars did not resemble any known caterpillar at the study site because no appropriate information was available. However, artificial caterpillars have been used widely, including in worldwide-scale studies with the same model (Roslin et al. 2017). After seven days, we collected all the artificial caterpillars and recorded those with marks due to predation by birds, tree lizards, or other

arthropods. We used a generalized linear model with binomial error distribution and the logit link function to test the effects of island side (two levels: south vs. north) and plant species (three levels) and their interaction.

### *Herbivory damage*

We estimated the level of herbivory (the percentage of the leaf area consumed by herbivores) on each species on both sides of the island, by considering all leaves on the excluded and control plants. Measurements of herbivory were obtained in April 2012 when the exclusion experiment was conducted, and again one year later (April 2013). Types of leaf damage (parts of the leaf lamina absent) included holes, scraped off areas, and incomplete leaf margins. Each leaf was scored according to the protocol described by Domínguez and Dirzo (1995): zero (leaf intact), one (leaf with damage that is barely perceptible, up to 6% of the leaf area damaged), two (leaf with 6–12% damage), three (12–25% damage), four (25–50% damage), or five (over 50% damage). The calculated score for each leaf was used to construct an index of damage (ID) as:

$$ID = \frac{1}{N} \sum_{k=0}^5 X_i n_i$$

where  $X_i$  is the  $i$  score for damage (0–5),  $n_i$  is the number of leaves with score  $X_i$ , and  $N$  is the total number of scored leaves. ID was then expressed as the percentage of herbivory (denoted as herbivory in the following) based on a simple cubic linear model, where the intercept was set to zero as described by Jimenez-Reyes (2013).

$$\text{Herbivory (\%)} = 5.6131 ID - 2.4505 ID^2 + 0.8691 ID^3$$

To analyze the effects of the side of the island and species identity on herbivory levels, we used a linear mixed model (lme function in the nlme package in R). As we have a paired design, the

herbivory response variable was defined as the difference in herbivory between the excluded and control plants of each pair; in this way we controlled the spatial heterogeneity across experimental units. The fixed factors included side (two levels: north and south), plant species (three levels), and their interactions. The random component was forest site where each pair was located (three in northern side of the island and four in the southern side). In addition, we modeled the variance with an exponential function to meet the model assumptions. All analyses were performed in R 2.1.5.2 (R Core Team, 2012).

## RESULTS

### *Soil traits*

The concentrations of total phosphorus (P), nitrogen (N), carbon (C), and nitrates, as well as the C/N, N/P, and C/P ratios varied significantly between the northern and southern sides of the island (Table 1). The concentrations of phosphorus were 6.3 times higher on the northern side, whereas the nitrogen, carbon, and nitrite concentrations, and the C/N, N/P, and C/P ratios were higher on the southern side (Table 1). Other differences in the soil characteristics included a higher soil pH on the northern side. Nitrogen and carbon mineralization, as well as levels of inorganic  $\text{NH}_4$ , did not differ significantly between the northern and southern sides (Table 1).

«Table 1 near here»

### *Leaf nutrient contents*

There were significant differences in the nitrogen content of leaves between northern and southern sites of the island ( $F = 13.65$ ,  $df = 2, 53$ ,  $P < 0.001$ ), between species ( $F = 10.15$ ,  $df = 2, 38$ ,  $P < 0.001$ ), and there was a significant interaction of these factors ( $F = 7.32$ ,  $df = 2, 53$ ,  $P =$

0.001). The three study species had higher nitrogen concentrations on the southern side of the island than those on the northern side ( $t > 2.4$ ,  $df = 53$ ,  $P < 0.002$ ). *G. insularis*, *I. socorroensis*, and *S. socorrense* had 16%, 37%, and 10% higher nitrogen concentrations on the southern side than the northern side of the island, respectively (Figure 2A). On the southern side, there were significant differences among species: *I. socorroensis* had higher nitrogen concentrations than *G. insularis* ( $t = 2.3$ ,  $df = 38$ ,  $P = 0.023$ ), but there were no significant differences between *G. insularis* and *S. socorrense* ( $t = 1.5$ ,  $df = 38$ ,  $P = 0.133$ ), or between *I. socorroensis* and *S. socorrense* ( $t = 0.85$ ,  $df = 38$ ,  $P = 0.405$ ). By contrast, *S. socorrense* had higher nitrogen concentrations than *G. insularis* and *I. socorroensis* on the northern side ( $t > 2.83$ ,  $df = 38$ ,  $P = 0.007$ ).

There were significant differences in the carbon concentrations between northern and southern sites of the island ( $F = 32.84$ ,  $df = 1, 53$ ,  $P < 0.001$ ), between species ( $F = 49.81$ ,  $df = 2, 38$ ,  $P < 0.0001$ ), and there was a significant interaction between these factors ( $F = 11.60$ ,  $df = 1, 53$ ,  $P < 0.001$ ) (Figure 2B). *G. insularis* and *S. socorrense* had 4% and 2% higher carbon content, respectively, on the southern side of the island ( $t > 5.73$ ,  $df = 53$ ,  $P < 0.0001$ ), whereas the carbon content of *I. socorroensis* did not differ significantly between sides ( $t = 0.2$ ,  $df = 53$ ,  $P = 0.849$ ). On both sides of the island, *G. insularis* had the lowest carbon content compared with the other species ( $t > 2.04$ ,  $df = 38$ ,  $P = 0.04$ ).

There were significant differences in the C/N ratio among species ( $F = 9.4$ ,  $df = 2, 38$ ;  $P < 0.001$ ) as well as a significant interaction between species and side of the island ( $F = 7.4$ ,  $df = 2, 53$ ,  $P = 0.001$ ), but no main effect of side of the island ( $F = 1.1$ ,  $df = 1, 53$ ;  $P = 0.29$ ) (Figure 2C). The C/N ratio for *I. socorroensis* was 37% higher on the northern side compared with the southern side ( $t = 5.87$ ,  $df = 53$ ,  $P < 0.0001$ ), whereas there were no significant differences between sides for *G. insularis* and *S. socorrense* ( $t = 1.06$ ,  $df = 53$ ,  $P = 0.29$ ;  $t = 1.32$ ,  $df = 53$ ,  $P = 0.18$ ).

= 0.19; respectively). On the southern side of the island, there were no significant differences in the C/N ratios among species ( $t < 1.93$ ,  $df = 38$ ,  $P = 0.06$ ) (Figure 2C). «Figure 2 near here»

### *Bird counts*

We recorded 515 individual birds comprising five species and four families: Socorro Mockingbird, *M. graysoni* (Mimidae); Northern Mockingbird, *M. polyglottos* (Mimidae); Tropical Parula, *Parula pitiayumi graysoni* (Parulidae); Rufous-Sided Towhee, *Pipilo maculatus socorroensis* (Emberizidae); and Socorro Wren, *Troglodytes sissonni* (Troglodytidae). Four species are endemic to the island, one arrived only recently (*Mimus polyglottos*), and all include small invertebrates in their diet. *Pipilo maculatus socorroensis* was recorded only on the northern side. We recorded 1.6 times more birds on the northern side than the southern side of the island ( $t = 3.20$ ,  $df = 48$ ,  $P = 0.002$ ). The Person's goodness of fit on the contingency table showed an overall significant effect ( $X^2 = 17.9$ ,  $df = 4$ ,  $P = 0.001$ ) and when the residuals were analyzed the difference was attributable to the null abundance of *P. maculatus socorroensis* in the south and the corresponding over representation of this species in the north side of the island ( $Z > 2.4$ ,  $P < 0.014$ ).

### *Predation of artificial caterpillars*

Attacks on the artificial caterpillars differed significantly between plant species and island sides ( $F = 3.6$ ,  $df = 2, 38$ ,  $P = 0.037$ ;  $F = 9.8$ ,  $df = 1, 54$ ,  $P = 0.002$ ; respectively). The interaction between species and side was borderline nonsignificant ( $F = 3.09$ ,  $df = 1, 54$ ,  $P = 0.054$ ). Predation of artificial caterpillars was two times higher on the northern side than the southern side of the island ( $t = 1.95$ ,  $df = 18$ ,  $P = 0.060$ ) (Figure 3). *G. insularis* had the highest rate of

artificial caterpillar predation, followed by *S. socorrense* and *I. socorroensis*. «Figure 3 near here»

### *Herbivory damage*

The overall herbivory values for the three study species ranged from 2% to 20% when we considered both years (2012, 2013). The herbivory rate was 30% higher on the southern side (9.1%) than the northern side of the island (7.0%), mainly due to changes in the herbivory of *G. insularis*. In 2012, herbivory damage differed significantly between species ( $F = 13.60$ ,  $df = 2$ ,  $233$ ,  $P < 0.0001$ ), but the response varied depending on the side of the island ( $F = 7.13$ ,  $df = 3$ ,  $233$ ,  $P < 0.001$ ). *G. insularis* had higher herbivory levels on the southern side of the island ( $t = 2.79$ ,  $P = 0.005$ ), whereas *S. socorrense* showed an inverse pattern ( $t = 3.09$ ,  $P = 0.002$ ). By contrast, there were no differences in herbivory of *I. socorroensis* between the two sides of the island ( $t = 1.1$ ,  $P = 0.269$ ; Figure 4A).

In the exclusion experiment, the difference in herbivory between caged and exposed plants did not vary significantly between sides of the island ( $F = 5.4$ ,  $df = 1$ ,  $5$ ,  $P = 0.068$ ) or between plant species ( $F = 0.09$ ,  $df = 1$ ,  $79$ ,  $P = 0.919$ ) but the interaction of these factors was significant ( $F = 3.4$ ,  $df = 2$ ,  $79$ ,  $P = 0.038$ ). In *G. insularis* the delta in herbivory between caged and exposed plants was not significantly different from zero, while in the northern side caged plants had around 20% more herbivory than exposed plants ( $t = 2.3$ ,  $df = 79$ ,  $P = 0.023$ ). In the same way no differences were observed for *S. socorrense* in the south while in the north caged plants had 14% more herbivory than exposed plants ( $t = 3.1$ ,  $df = 79$ ,  $P = 0.002$ ). There was no significant difference for *I. socorroensis* on either side of the island (Figure 4B). «Figure 4 near here»

## DISCUSSION

In terrestrial systems, vertebrate predators can have large impacts on arthropod communities and indirect effects may be propagated to primary producers (Gruner 2004). However, plants can limit the abundance of arthropods via their nutritional and defensive traits. Numerous studies have documented the biota of Socorro Island, but to our knowledge, only limited information is available about its trophic interactions (Brattstron 2015). In this study, we explored the relative influences of bottom-up and top-down forces in three tree plant species via herbivory. We showed that the herbivory patterns in Socorro Island are driven by both top-down and bottom-up controls. The N content of the soil was higher on the southern side of the island, and thus the leaves of the three studied plant species on that side had higher nitrogen content. In 2012, *G. insularis* experienced higher herbivory on the southern side, whereas *S. socorrense* had the inverse pattern, and there were no differences in herbivory for *I. socorroensis* on different sides of the island. When we excluded predators, herbivory levels increased on the northern side by up to 14–20%, depending on the plant species identity. By contrast, in the southern forest, the exclusion of birds had no effects on herbivory levels. As expected, herbivory was greater on the southern side where the leaf nutrient contents (nitrogen) were high, but the exclusion of herbivore predators had no effects on herbivory. These results suggest that herbivory levels in *G. insularis* are determined by bottom-up forces on the southern side, whereas herbivory levels in *S. socorrense* are determined by top-down forces on the northern side.



### *Soil traits*

We found marked differences in some soil traits between the northern and southern sides of the island, which may be related to the geomorphology of the island. The northern side of the island is mountainous with multiple gorges, where the transport of sediment produces micro-sites with considerable variation in terms of nutrient deposition and soil biogeochemistry, similar to variation observed on some Hawaiian Islands (Vitousek et al. 2003). The higher phosphorus content on the northern side of the island may be explained by different processes, as follows. (1) Weathering of relatively young loose volcanic deposits on top of Evermann volcano and consolidated lava flows has occurred, similar to those documented on other oceanic islands (Vitousek 2004, Kertesz and Frossard 2015, Aguirre-Muñoz et al. 2016). By contrast, the basaltic lava flows at the southwestern side of the island are older and thus the weathering of rock is considerably slower and the nutrients are mostly contained within the biomass (Vitousek 2004, Kertesz and Frossard 2015). (2) Nesting colonies of large populations of seabirds, such as Townsend's shearwater (*Puffinus auricularis*), which occur at elevations between 850–750 m (CONANP-SEMARNAT 2004). The diet of Townsend's shearwater mainly comprises fish, and on other oceanic islands and atolls, it has been demonstrated that allochthonous marine subsidies that enter terrestrial ecosystems via the guano of these seabirds considerably enrich the pool of nutrients (mainly nitrogen and phosphorus) in the soil, which are readily available for assimilation by soil microbes and plants (Anderson and Polis 1998, Piovia-Scott et al. 2013) with potential effects on higher trophic levels, as discussed in the following.

The lack of differences in soil humidity, as well as nitrogen and carbon mineralization, between the two sides of the island can be explained by the fact that our soil samples were collected during the dry season, and thus we may have missed potential differences associated with the wet season. For instance, Rivas et al. (2009) showed that the carbon mineralization rates

could change seasonally, increasing with greater precipitation and soil moisture content. In addition to soil moisture content, one of the most important factors that affects nitrogen mineralization is the quality of the litter. The differences in dominant tree species between the two sides of the island mean that the rate of nitrogen mineralization is likely to differ in the wet season (Austin and Vitousek 1998), during which it is expected to be higher on the northern side of the island.

### *Herbivory and predation of herbivores*

The amount and quality of plant tissue available for herbivores may have crucial effects on populations of phytophagous organisms (Price 1992). Changes in the microclimate associated with vegetation coverage and soil fertility (phosphorus and nitrates) can affect the nutritional quality of plant tissues as well as the levels of herbivory (Spiller and Agrawal 2003, Piovia-Scott et al. 2013). In the present study, the nitrogen contents of the plant tissues were higher on the southern side of the island, probably due to higher nitrate concentrations in the soil. In general, plants with higher nitrogen content are consumed more frequently by herbivores because of their greater nutritional value (Spiller and Agrawal 2003). Compared with the levels of damage before the exclusion experiment, we found that *G. insularis* suffered higher levels of herbivory on the southern side of the island, where nitrogen availability was higher and the abundance of herbivore predators was lower. By contrast, *S. socorrense* exhibited the opposite pattern, and there was no difference in levels of herbivory of *I. socorroensis* between the two sides. These differences between species may be explained by their traits and by the abundance of herbivorous insects. For instance, *S. socorrense* is consumed exclusively by what appears to be a specialist leaf miner, the performance of which may be affected by the high temperatures and low humidity prevalent on the southern side of the island (Valladares et al. 2006), whereas

environmental conditions in the ravines on the northern side are less stressful. *I. socorroensis* has very tough leaves with an abundance of latex, so it experiences little herbivory, and this was reflected by the lack of significant difference in herbivory between the two sides of the island.

The density of birds is directly related to the vegetation coverage, plant density, and vertical stratification. In areas with more vegetation, there are greater numbers of nesting sites and higher availability of food and shelter (Álvarez-Cárdenas et al. 2000, Martínez-Gómez et al. 2001). Walter and Levin (2008) reported a decline in the number of endemic birds on Socorro Island, especially those that forage in the lower strata (e.g., *Parula pitayoni graysoni* and *Pipilo maculatus socorrensis*). This decline was related to the predation risk imposed by feral cats on the island (Rodríguez-Estrella et al. 1996, Ortega-Rubio and Castellanos-Vera 1995, Martínez-Gómez and Jacobsen 2004, Nogales et al. 2004). Similarly, we showed that the diversity and abundance of insectivorous birds were greater on the northern side than the southern side, where *Pipilo maculatus socorrensis* (one of the main arthropod predators on Socorro Island) was the most abundant species (Cervantes 2013). *Pipilo maculatus socorrensis* spends considerable time foraging for food, by turning over leaf litter and scratching the soil surface to catch crawling arthropods, as well as foraging on plants in the lower stratum. These habits could make it more vulnerable to feline predation. In addition, we detected greater predation of artificial caterpillars on the northern side, where herbivory levels increased in the bird-excluded plants, thereby suggesting the presence of top-down control. In this study, we focused on birds because they are main predators of herbivorous insects. Another potential insect predator on the island is the blue lizard, *Urosaurus auriculatus*; however, its population has also been reduced due to predation by feral cats, and the exclusions impeded their access to the plants (Arnaud et al. 1993). Our results are similar to those obtained by Spiller and Schoener (1997) and Schoener and Spiller (2010) on the Bahamas islands, where they demonstrated that excluding the predator *Anolis sagrei*

increased levels of herbivory of *Coccoloba uvifera* (also see Pacala and Roughgarden 1984, Polis et al. 1998, Mäntylä et al. 2011).

Changes in herbivory can have severe long-term impacts on the distribution, composition, and structure of vegetation. For example, herbivores that lack top-down control on the islands of Lake Guri in Venezuela can transform a highly diverse forest into a site with low plant diversity (Terborgh et al. 2006). It has also been suggested that the development and abundance of highly defended plant species can be promoted in areas with increased herbivory (McNaughton 1979, Howe et al. 2006, see also Bowen and Van Vuren 1997). According to Brattström (2015), birds are among the more important components of food webs on Socorro Island, and changes in their populations are likely to disrupt the functionality of the ecosystem, particularly herbivory, as well as other biotic interactions such as seed dispersal. For instance, it has been reported that *M. polyglottos* and *M. graysoni* are potential dispersal agents of *I. socorroensis*, *G. insularis*, and *S. socorrense* (Cervantes 2013).

#### *Implications for conservation and management*

Socorro Island is home to endemic and threatened species, including recently extinct species, and introduced species with great impacts, *i.e.*, cats and sheep, which have moved freely for decades but are now under control. Sheep were eradicated in 2012 and there are currently strong campaigns underway to free the island of cats (Ortíz-Alcaráz et al. 2016b). Therefore, it is necessary to encourage research to support conservation and restoration efforts on the island. Considering the fragility of oceanic island ecosystems, all these efforts need to consider the ecological and evolutionary history of the island. In addition to knowing the identity and relative abundances of the species present, it is essential to understand the processes and mechanisms that drive their ecological interactions.

The loss of insectivorous birds can have cascading impacts that change ecosystem dynamics. In this study, we showed that a reduction in the abundance of land birds south of the island disrupts the top-down control of herbivory. Similarly, reductions in bird populations could affect the dispersal of seeds from tree species, such as *G. insularis*, *S. socorroensis*, *Psidium*, and *Prunus*, as well as other plant species with fleshy fruits, which may affect the natural regeneration of forest ecosystems. Sheep and cats have caused major transformations in the central-southern part of the island, so intensive restoration processes are urgently required and better understanding of how drivers of ecological interactions operate may increase the likelihood of success of future restoration programs.

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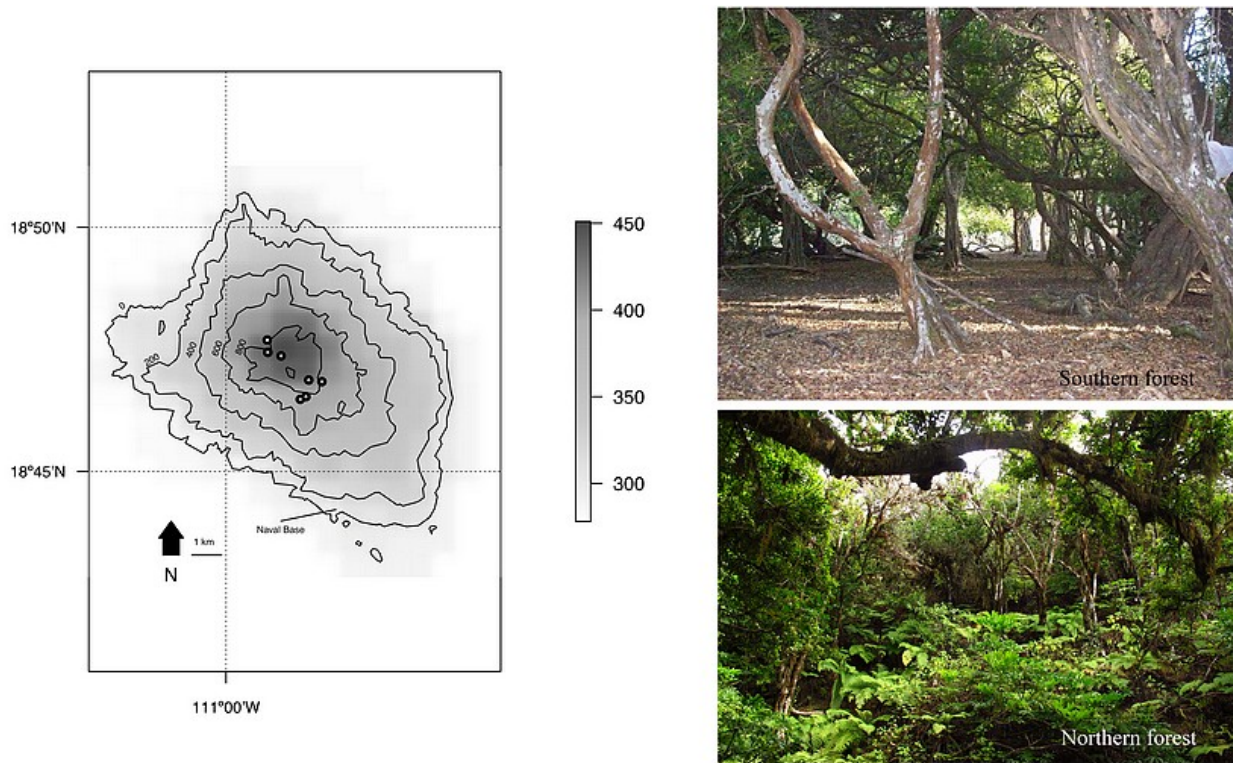
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TABLE 1

ANOVA one-way table of soil traits and Carbon and Nitrogen mineralization at the Northern and Southern sides of Socorro Island. Values are mean  $\pm$  standard error.

<b>Soil</b>	<b>South-Side</b>	<b>North-Side</b>	<b>F</b>	<b>P</b>
pH	5.61 $\pm$ 0.08	5.88 $\pm$ 0.07	5.39	0.026
Humidity (%)	20.29 $\pm$ 1.02	17.83 $\pm$ 1.14	2.50	0.120
P (mg/g)	0.047 $\pm$ 0.01	0.249 $\pm$ 0.01	34.12	< 0.001
N (mg/g)	16.4 $\pm$ 1.13	11.86 $\pm$ 1.00	8.32	0.007
C (mg/g)	196.8 $\pm$ 17.73	120.00 $\pm$ 14.13	10.33	0.003
CMR ( $\mu\text{gC}\cdot\text{soil g}^{-1}\cdot\text{day}^{-1}$ )	94.6 $\pm$ 14.50	86.62 $\pm$ 12.45	0.16	0.690
NMR ( $\mu\text{gN}\cdot\text{soil g}^{-1}\cdot\text{day}^{-1}$ )	-0.55 $\pm$ 1.15	-1.25 $\pm$ 0.06	0.26	0.610
NO <sub>3</sub> (mg/g)	0.11 $\pm$ 0.01	0.03 $\pm$ 0.003	105.8	< 0.001
NH <sub>4</sub> (mg/g)	0.40 $\pm$ 0.01	0.46 $\pm$ 0.003	0.53	0.473
C/N	11.77 $\pm$ 0.40	9.86 $\pm$ 0.28	13.00	0.001
N/P	2027.0 $\pm$ 575.15	97.99 $\pm$ 35.50	8.35	0.007
C/P	7570.1 $\pm$ 845.11	1040 $\pm$ 975.50	25.6	< 0.001



**Figure 1.** Schematic map of Socorro island showing the sample sites (dots) and mean annual precipitation according to Worldclim-Bio12 (grey shadows) and photographs illustrating general views of the forests sites in the southern and northern sides of Socorro Island.

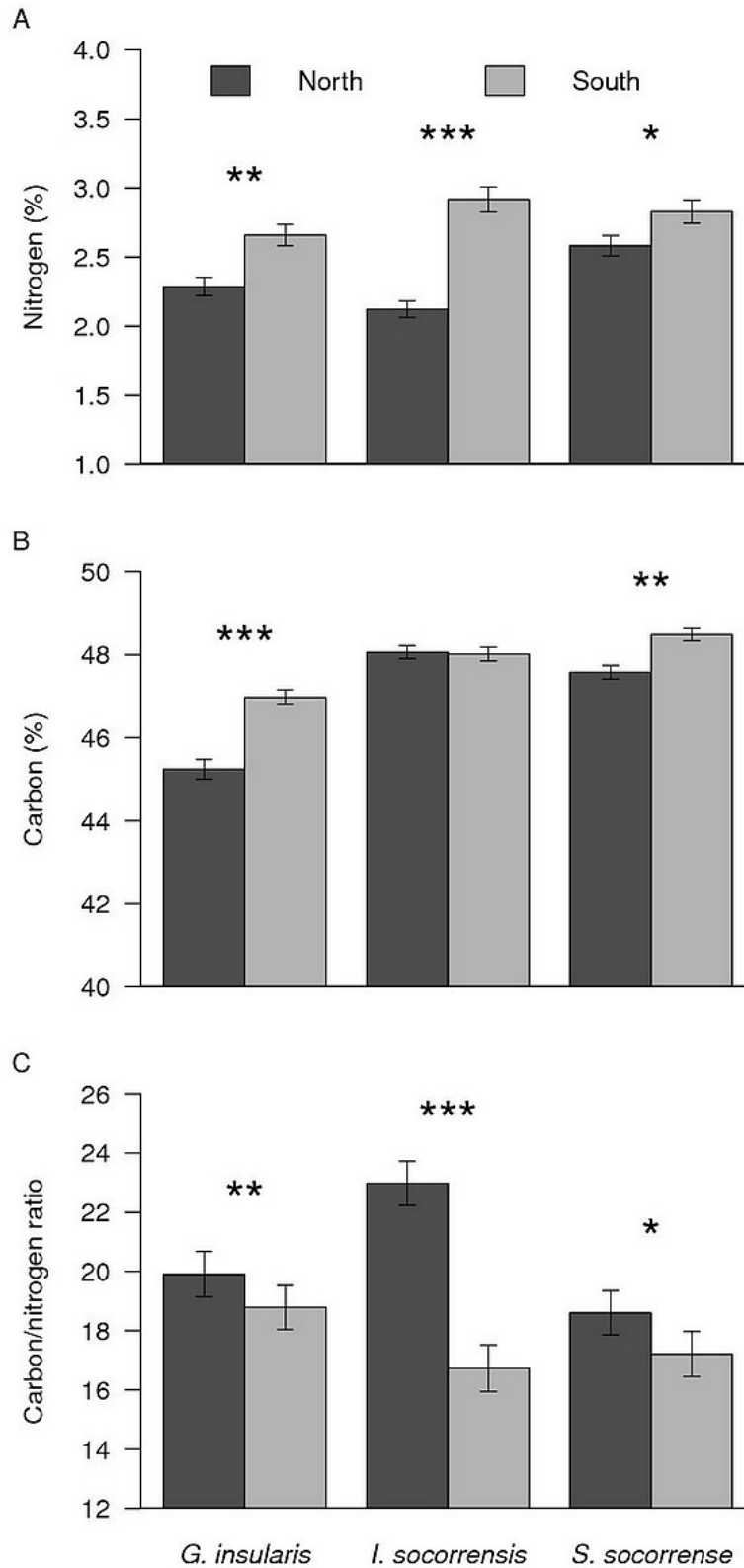
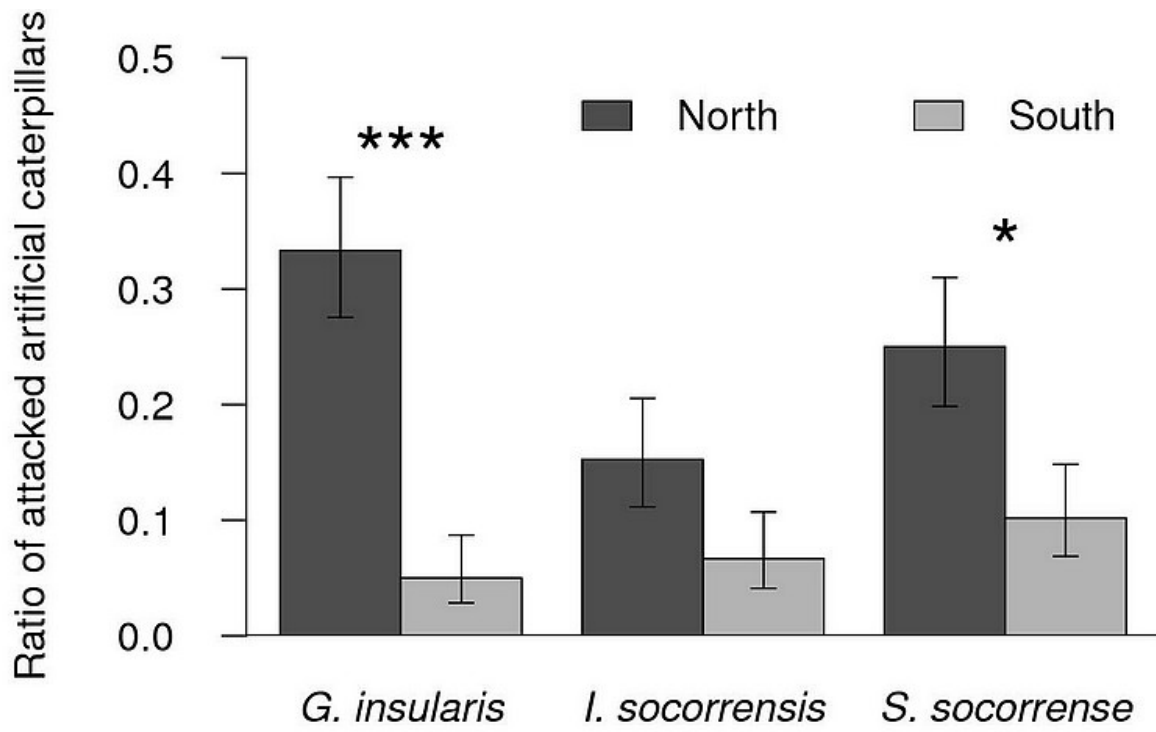
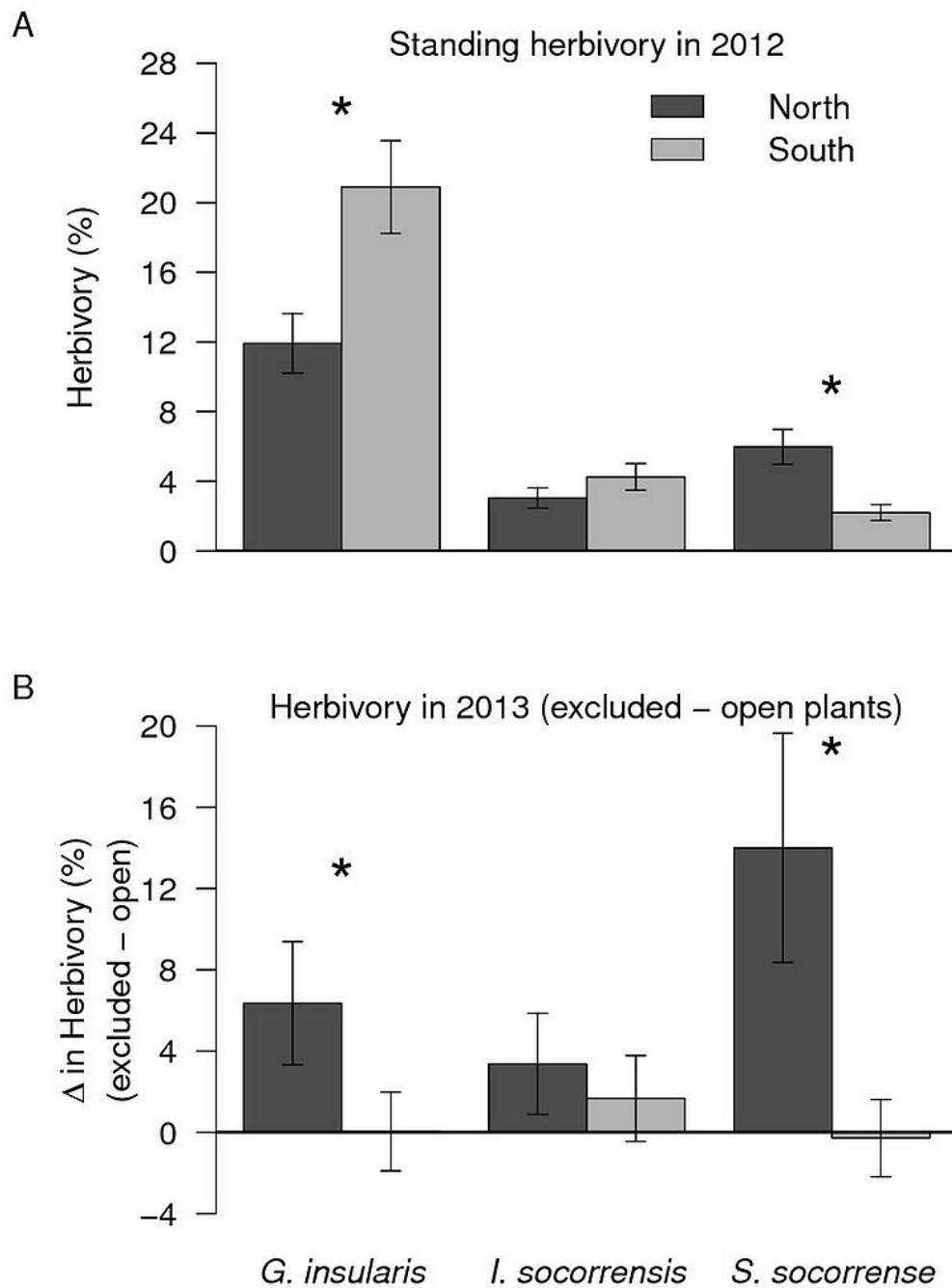


Figure 2. Nutrient content of leaves (mean  $\pm$  SE) estimated in three species, in northern and southern sides of Socorro Island. A) Nitrogen, B) Carbon and C) Carbon over nitrogen ratio. \*P < 0.05, \*\*P < 0.01, \*\*\*P < 0.001.



**Figure 3.** Ratio of attacked to artificial caterpillars in northern and southern sides of Socorro Island. \*\*P < 0.01.





**Figure 4.** Herbivory (mean  $\pm$  SE) in three species of woody plants comparing the southern northern forests of Socorro Island. A) Standing herbivory in 2012. B) Difference in the observed herbivory in paired plants (excluded - open) after a year of experimental exclusion. \*P < 0.05.