Effects of an Ecological Replacement Herbivore on Cactus Recruitment on an Arid Island

Raquel Aviles

University of Hawaiʻi at Mānoa Mentor:
Dr. Creighton Litton

Charles Darwin Foundation Mentor:
Dr. Miriam San José

Contributions from:
Dr. James Fumo

This study was conducted under Galapagos National Park Directorate research permit No. PC-38-25. We thank the Galapagos National Park and the Charles Darwin Foundation for their institutional support.

This document is a final student research paper from the University of Hawaiʻi at Mānoa - Charles Darwin Foundation National Science Foundation International Research Experiences for Students program, and is not peer reviewed

Abstract

Recognized for their high biodiversity and endemism, island ecosystems are particularly vulnerable to anthropogenic factors such as invasive species and extinction of endemic keystone species. The Galápagos Islands, with some of the highest endemism rates in the world, are an important case study of these challenges. Native herbivores are increasingly at risk of extinction worldwide, leading to the loss of vital ecological functions such as seed dispersal and nutrient cycling. On Santa Fé Island, human-driven extinction of the giant tortoise is a prime example of this, while the introduction of feral goats (*Capra hircus*) further degraded island plant communities. Together, these changes altered the distribution and regeneration of endemic species like *Opuntia echios* var. *barringtonensis*, a dominant species and keystone resource for native herbivores. Recent conservation efforts have eradicated goats and reintroduced a related tortoise species, *Chelonoidis hoodensis*, to restore ecological functions and support ecosystem recovery. This study aimed to examine the role of *C. hoodensis* introduction in influencing the distribution and density of *O. echios* seedlings and saplings on Santa Fé Island that is recovering from more than a century of heavy feral goat degradation. I hypothesized that the presence of *C. hoodensis* would positively correlate with higher densities of *O. echios* seedlings and saplings; I hypothesize this because giant tortoises were historically one of the primary seed dispersers of *O. echios*. To examine the relationship between tortoise activity and *O. echios* demographics on Santa Fé Island, nine 50 × 50 m plots were established across varying tortoise activity zones and subdivided into 25 10 × 10 m subplots. Adult cactus height and DBH were recorded in large plots, while seedling and sapling densities and tortoise activity (via direct observation and scat) were documented in smaller subplots. Higher tortoise activity correlated with higher seedling density, suggesting a positive effect of ecological replacements on *Opuntia* regeneration. Continued monitoring is needed to assess long-term vegetation impacts given that the island vegetation is still recovering from feral goats and tortoises are still expanding. Ecological replacements, like the introduction of *C. hoodensis* on Santa Fé Island, offer a promising strategy for restoring lost functions in degraded ecosystems.

Keywords: ecologic replacement, Galapagos Islands, seedling recruitment, giant tortoise introduction, conservation ecology, *Opuntia echios* var. *barringtonensis*, herbivory, *Chelonoidis hoodensis, Capra hircus*

Introduction

Island ecosystems are among the most biodiverse on Earth, yet they are particularly vulnerable to environmental change and human activities (Matthews & Triantis, 2021). Although islands cover only 3.5% of the Earth's land area, they are home to 15-20% of all terrestrial species–with a disproportionate number of endemic species–and represent a critical component of global biodiversity (Matthews & Triantis, 2021). This high level of endemism, where species evolve uniquely due to geographic isolation, makes islands key to understanding and conserving biodiversity and ecological processes (Kier et al., 2009). While many of these ecosystems have been historically neglected in terms of conservation efforts (Nori et al., 2022), island ecosystems often experience rapid biodiversity loss and irreversible ecological changes in the face of invasive species and other anthropogenic factors.

The Galápagos Islands, situated ~1,000 km off the western coast of Ecuador, are home to some of the world's most unique ecosystems containing some of the highest levels of endemism globally (Charles Darwin Foundation, 2005). Many terrestrial plants and animals of the Galápagos have evolved in the islands' predominantly semi-arid environment, with species like cacti and drought-deciduous shrubs adapted to survive extended periods of little to no rainfall (Charles Darwin Foundation, 2005). One of the most arid islands in the Galápagos archipelago is Sante Fé Island–an unpopulated, small island ~30 km to the southeast of Santa Cruz Island. While many island communities lack the policy, regulation and resources to protect biodiversity, the Galápagos Islands are famous for having implemented and enforced strict biosecurity measures. Despite these measures, human activity—particularly the introduction of invasive species—has disrupted the ecological balance of the Galápagos islands (Hamann, 2003).

Feral goats *(Capra hircus)* are among the most ecologically damaging invasive herbivores introduced to island ecosystems worldwide (Chynoweth et al., 2013). First brought to oceanic islands in the 16th century by sailors as a portable food source, goats quickly spread due to their adaptability, high reproductive rates, and ability to survive in harsh, arid environments

(Chynoweth et al., 2013). As generalist feeders, they consume a wide variety of native plants and require minimal water, allowing them to thrive in arid environments and outcompete native herbivores. Their indiscriminate grazing, trampling of vegetation, and contribution to soil erosion have caused widespread ecological degradation across islands globally (Campbell & Donlan, 2005).

The effects of feral goats are particularly severe in island ecosystems, where high levels of endemism, limited gene flow, and low ecological redundancy make native species especially vulnerable (Russell et al., 2017). In the Galápagos Islands, goats were introduced in the 19th century, where they quickly established large populations and caused lasting ecological damage. On Santa Fé Island in particular, feral goats nearly eliminated seedling recruitment of native trees and drastically altered plant community structure (Nogales et al., 2017). Overgrazing and trampling led to habitat degradation, loss of plant diversity, and disruption of critical ecosystem processes (Tye, 2006). These impacts, compounded over many decades, prompted large-scale restoration interventions, including a successful goat eradication campaign in the late 1960s and early 1970s. However, the long-term recovery of native vegetation and ecological function continues to depend on passive restoration and monitoring.

Historically, the Galápagos Islands supported keystone herbivores such as the giant tortoise (*Chelonoidis* spp.) and land iguana (*Conolophus pallidus*). These species played a central role in shaping these arid island ecosystems through herbivory, trampling, nutrient cycling, and especially seed dispersal (Blake et al., 2012). One notable example of this ecological interdependency is the relationship between these herbivores and the endemic giant cactus *Opuntia echios*, whose seeds rely on animal dispersal for successful germination and recruitment (Nogales et al., 2017). However, overexploitation of tortoises and the introduction of invasive goats disrupted these ecological processes, leading to the extinction of tortoises on several islands and a marked decline in *Opuntia* recruitment due to reduced seed dispersal (Hamann, 2001; Tapia & Gibbs, 2023). Understanding the ecological consequences of these disruptions remains a priority for conservation and island restoration efforts (Tapia et al., 2021).

To address such losses, in addition to removal of invasive species, conservationists have increasingly turned to ecological replacements—the introduction of functionally similar species to restore ecosystem function and biodiversity (Sanders & Frago, 2024). This approach has been particularly effective on islands, where native herbivores are often highly vulnerable to extinction (Tapia & Gibbs, 2023; Tapia et al., 2021). Strong evidence suggests that giant tortoises were once native to Santa Fé with genetic analyses of bone fragments suggesting the Santa Fé giant tortoise was a unique tortoise taxon, most closely related to the Española giant tortoise (*Chelonoidis hoodensis*) (Jensen et al., 2022). As a result, the genetically similar *C. hoodensis* was introduced to Santa Fé Island as an ecological replacement for the extinct native tortoise. Between 2015 and 2025, 742 juvenile Española tortoises aged 4–10 years, were introduced to restore essential ecological roles such as seed dispersal and habitat structuring. As generalist herbivores, these tortoises contribute to ecosystem function by promoting plant diversity and limiting dominance by any one species (Blake et al., 2012). Long-term monitoring is critical to evaluate how fully these introduced tortoises replicate the ecological roles of their extinct counterparts, particularly on an island such as Santa Fé that is recovering from heavy feral goat degradation.

On Santa Fé Island, *O. echios* var. *barringtonensis* is the dominant woody species that comprises the majority of the diet of the introduced *C. hoodensis* (Hunter at al., 2021). However, little is known about the long-term effects of the replacement of ecosystem engineers. This study evaluates the impact of the introduction of replacement ecosystem engineers on native plant populations and restoration of ecological functions during the recovery from long-term feral goat disturbance by observing the relationship between *O. echios* var. *barringtonensis* seedlings and saplings and presence/activity of the introduced *C. hoodensis*. By addressing these knowledge gaps, this study supports conservation practitioners, policymakers, and stakeholders in making informed decisions regarding island ecosystem management and biodiversity conservation strategies.

Study Objective and Hypothesis

The main objective of this study is to understand what role the introduced giant tortoise (*Chelonoidis hoodensis*) as an ecological replacement has in influencing the recruitment of the dominant endemic woody species *(Opuntia echios* var *barringtonensis)* on Santa Fé Island, Galapagos. To do this I: (a) identified tortoise activity areas on Santa Fe; (b) sampled the density and demography (i.e., height classifications of seedlings, saplings, adults) of *Opuntia echios* across a gradient of tortoise presence/activity; and (c) assessed the relationship between tortoise presence/activity and the density of adult *O. echios* on the density of *Opuntia* seedlings and saplings. I hypothesize that the presence of adult *O. echios* and activity level of *Chelonoidis hoodensis* would be positively correlated with seedling and sapling density of *O. echios*.

Methods

Study Site

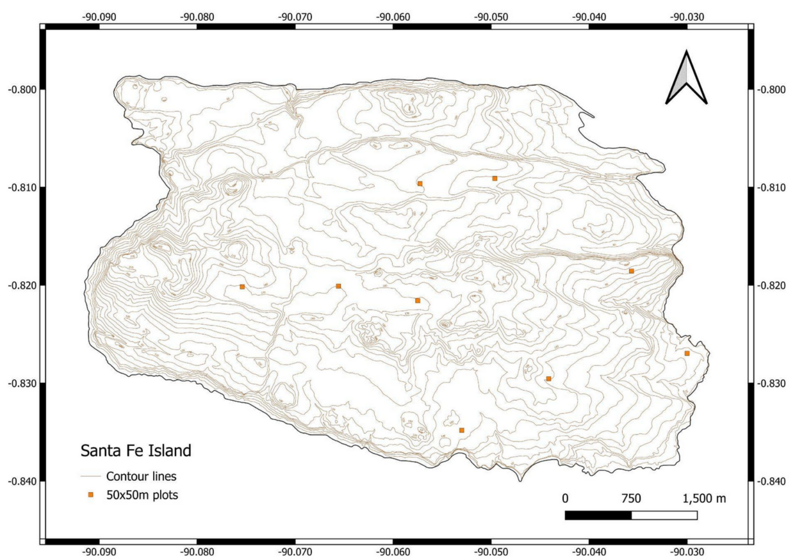

Fig. 1. Santa Fé Island.

The study was conducted on Santa Fé Island, a small, unpopulated, and relatively flat island in the Galápagos archipelago. With an arid climate averaging 200 mm of rainfall per year and ancient geological origins, the island contains one of the oldest volcanic formations in the region, featuring submerged rock layers estimated to be around 3.9 million years old. The island's dominant vegetation includes the Giant Prickly Pear cactus (*Opuntia echios* var. *barringtonensis*), *Bursera graveolens* (Palo Santo), and *Scalesia helleri*. Notable endemic fauna include the Santa Fé Land Iguana (*Conolophus pallidus*) and the Santa Fé Rice Rat (*Oryzomys bauri*). Historically, the island also supported a population of endemic giant tortoises.

The island's endemic giant tortoise was driven to extinction in the 19th century by whalers and pirates, who harvested tortoises for long sea voyages. In the 20th century, the introduction of feral goats caused further degradation, as these invasive herbivores overgrazed native vegetation, reduced plant diversity, and altered the island's plant community composition and overall ecosystem structure (Tye, 2006). In response to these impacts, a major restoration effort was undertaken in the late 1960s and early 1970s, resulting in the successful eradication of goats from Santa Fé Island. This effort laid the groundwork for ongoing ecological restoration initiatives aimed at recovering native species and ecosystem functions. *Chelonoidis hoodensis* has been introduced to Santa Fé as part of a long-term ecological restoration effort, given its similarity to the original taxon and its role as a key seed disperser and herbivore within these arid island ecosystems.

Study Species

Opuntia echios var. *barringtonensis* is an endemic tree cactus found in the Galápagos Islands, primarily within the arid and transition zones. This foundational species plays a critical role in these island ecosystems, providing food and habitat for native herbivores, including giant tortoises and land iguanas. The cactus is characterized by flat, spiny pads and bright yellow flowers, with mature individuals developing thick, orange-brown trunks with flaking bark. Seedlings are typically composed of stacked pads, while saplings exhibit full spination and begin to branch. Individuals are classified as adults once they develop bark along the trunk; those with remaining trunk spines are still considered adults if they exhibit flowering or fruiting. *Opuntia echios* is long-lived, with individuals potentially reaching over 100 years of age.

The introduced herbivore in this study, *Chelonoidis hoodensis* or the Española giant tortoise, serves as an ecological proxy for the extinct Santa Fé giant tortoise. Strong evidence, including genetic analyses of fossil bone fragments, suggests that a now-extinct tortoise species was once native to Santa Fé Island and was closely related to the Española tortoise both genetically and morphologically.

Data Collection

To examine the relationship between tortoise activity and the density and distribution of *Opuntia echios* var. *barringtonensis*, data were collected across nine 50 m × 50 m plots strategically distributed across a gradient of tortoise activity zones on Santa Fé Island. Tortoise sightings collected through direct observation using handheld GPS devices, recording latitude and longitude coordinates beginning in June 2024. The nine plots were not equally distributed amongst the activity zones and plots were situated throughout the northern and southern regions of the island, respectively. Within the larger 50 x 50 m plots, adult *Opuntia* individuals were identified and measured for height and diameter at breast height (DBH), and live tortoises were counted by direct observation. Each large plot was then subdivided into twenty-five 10 m × 10 m subplots to enable fine-scale sampling of seedlings and saplings. Five of the 25 subplots within each larger plot were randomly chosen using the sample command in R without replacement (R Core Team, 2024). In the selected 10 x 10m subplots, *Opuntia* seedlings and saplings were counted and measured for height. This design allowed for spatial comparisons of cactus demographics and tortoise presence across varying levels of tortoise activity.

Statistical analysis

To visualize tortoise activity areas on Santa Fé a heatmap was created using tortoise sightings collected through direct observation. These data were imported into QGIS and processed using kernel density estimation (KDE) to create a heat map of tortoise activity across Santa Fé Island. A 2km bandwidth was applied to reflect the estimated home range of the tortoises. The resulting raster surface represented the relative activity intensity, with higher values indicating greater sighting densities. Raster values were extracted at the centroid of each 50 × 50 m vegetation plot and used to quantify the tortoise activity level in order to assess the relationship between tortoise presence and *O. echios* across the island.

To visualize the distribution of *O. echios* var. *barringtonensis* across developmental stages, a stacked barplot was generated in R to compare cactus height (grouped by 1-meter increments) against the count of individuals classified as seedlings, saplings, or adults. Classification was based on morphological traits discussed in the site species section. Density of seedlings and saplings (individuals/m^2) were conducted using stratified random sampling within the 10 × 10 m subplots, while adults were measured across the entire 50 × 50 m plot, allowing for consistent comparison across size classes.

A scatter plot and correlation test were used to assess the relationship between tortoise activity and *Opuntia* adults on seedling and sapling density overall, and separately for seedlings <50 cm height. This threshold of <50 cm height was chosen because these individuals are the most likely to have been established since the giant tortoise introduction in 2015 based on the growth rate of the species (Tapia et al., 2021). The density of seedlings and saplings as a dependent variable was assessed using the number of adults or the tortoise activity index as interactive explanatory variables using the GLM function in R (R Core Team 2024).

Results

The heat map revealed a central zone of high tortoise activity (Figure 1), with the highest intensity values concentrated near the initial tortoise release site, gradually decreasing toward the island's edges. Activity levels were quantified by extracting raster values from the heat map at the centroid of each 50 × 50 m plot. These categories were subsequently used to assess the relationship between tortoise presence and *Opuntia echios* demography across the island.

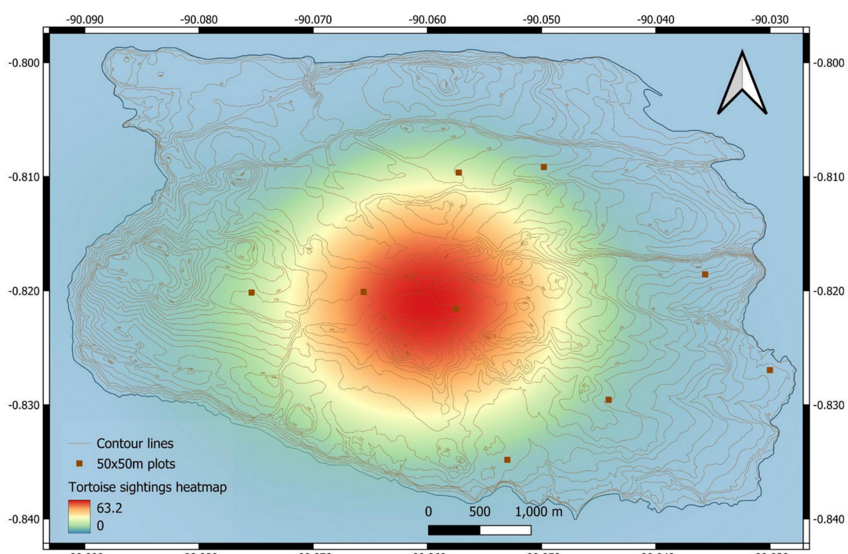

Figure 1. Heat map of tortoise activity on Santa Fé Island, Galápagos, based on compiled tortoise sightings. Warmer colors (red) indicate higher tortoise activity, with sighting values ranging from 0 to 63.2 tortoises per m^2. Contour lines illustrate the island's topography, and brown squares mark the locations of the nine 50 × 50 m vegetation plots used for demographic surveys. Tortoise activity was estimated using spatial kernel density estimation of sighting data, with intensity values later extracted for each plot to quantify tortoise influence across activity zones.

The height distribution of *Opuntia echios* individuals across all sampled plots revealed a reverse-J shaped distribution, or a pronounced skew toward younger, shorter plants, with seedlings (0–1 m) representing the largest portion of the population (Figure 2). Seedlings were estimated at 0.4 seedlings/m^2. Saplings (1–2 m) also showed relatively high abundance, but lower than seedlings. In contrast, adult cacti (2 m and taller) were progressively less common with increasing height. The tallest height classes (6–7 m and 7–8 m) had very few individuals, suggesting limited representation of the oldest individuals in the population.

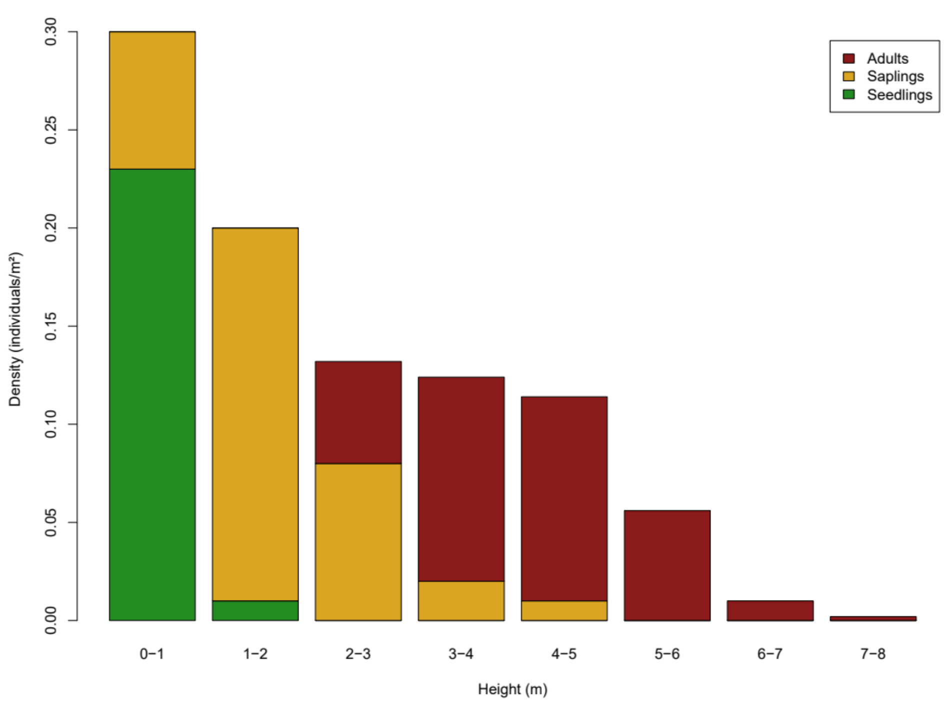

Figure 2. Height distribution of *Opuntia echios* var. *barringtonensis* densities (individuals/m^2) categorized by life stage within 1-meter height intervals. Bars represent the estimated number of individuals per meter^2 across three height-based classes: seedlings (green), saplings (yellow), and adults (red). Seedling and sapling counts were estimated using random subplot sampling and scaled up to match the full plot area.

The estimated density of *Opuntia* seedlings and saplings did not vary significantly with adult *Opuntia* density (Figure 3A; $p = 0.19$) or tortoise activity index (Figure 3B; $p = 0.14$). The interactive effect of these two variables was marginally significant ($p = 0.08$). When considering only *Opuntia* individuals under 50 cm in height, seedling and sapling density again showed no significant relationship with adult *Opuntia* density (Figure 3C; $p = 0.59$) or tortoise activity (Figure 3D; $p = 0.64$), and the interaction remained non-significant ($p = 0.48$).

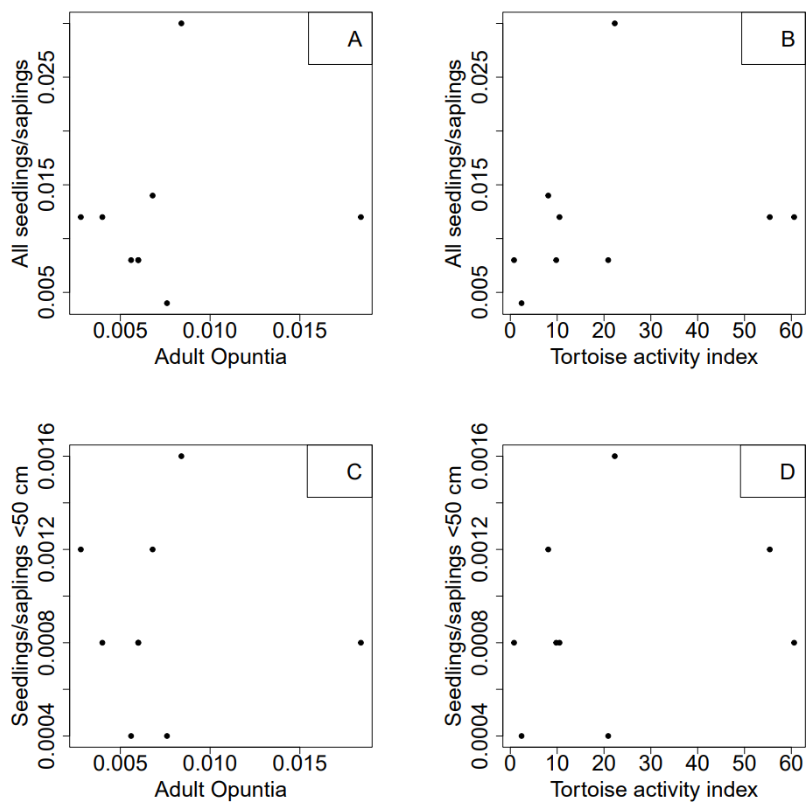

Figure 3. Figure 3. Relationships between *Opuntia echios* seedling and sapling density (individuals/m^2) and adult *Opuntia* density (A, C) and tortoise activity index (B, D) across 50 × 50 m plots on Santa Fé Island. Panels A and B show all seedlings and saplings combined; panels C and D show only individuals <50 cm in height. None of the relationships were statistically significant.

Discussion

These results did not show statistically significant relationships between tortoise activity, adult *Opuntia* density, and *Opuntia* seedling or sapling density. However, the relationship between overall seedling/sapling density and the combined effect of tortoise activity and adult cactus density was of marginal significance ($p = 0.08$), suggesting a potential interactive effect between tortoises and adult *Opuntia* that may become clearer with longer-term monitoring or larger sample sizes. The reverse-J shaped height distribution of *O. echios* indicates a healthy population structure dominated by younger individuals (Tsheboeng et al., 2024) which may reflect successful recruitment following the removal of goats and early effects of tortoise reintroduction.

Although no statistically significant patterns were detected, the observed trends—such as higher seedling estimates in plots with elevated tortoise activity—align with other studies showing positive impacts of giant tortoises on seed dispersal and recruitment (Tapia & Gibbs, 2023; Blake et al., 2012). It is important to mention that the sample size of this study was relatively small, however these patterns suggest that ecological replacements may be starting to replicate lost herbivory and dispersal functions. With longer term studying on a larger sample size, the results may have revealed layers that can't quite be understood with a small sample size on a small timeframe. Previous work has shown that seed dispersal by tortoises increases both germination rates and spatial distribution of *O. echios*, allowing recruitment in microsites not accessible via passive seed fall alone (Nogales et al., 2017, Hunter et al., 2021). Our findings complement these studies by examining a site in the early stages of rewilding.

Globally, the decline and extinction of large-bodied herbivores—often termed "ecosystem engineers" for the outsized roles they play in ecosystem structure and function—has contributed to profound structural and functional shifts in ecosystems. The Galápagos Islands, like many other insular ecosystems, have experienced both the loss of native megafauna and invasions of non-native herbivores that further degraded habitats (Chynoweth et al., 2013; Russell et al., 2017). On Santa Fé, decades of goat overgrazing slowed cactus recruitment (Tye, 2006; Hamann, 2003), while tortoise extinction removed a key seed disperser. Ecological replacements like *Chelonoidis hoodensis* provide a rare opportunity to restore lost functions in the absence of the original species.

As climate change and human pressures intensify, biodiversity loss continues to accelerate. Many scientists argue that we are currently undergoing a sixth mass extinction event, driven primarily by anthropogenic causes such as habitat loss, overexploitation, and climate change (Cowie et al, 2022). Islands, with their high rates of endemism and limited redundancy, are among the most vulnerable ecosystems (Veron et al., 2019). In this context, ecological replacements offer a promising, although sometimes controversial, strategy for mitigating functional losses when native species can no longer be recovered (Sanders & Frago, 2024; Tapia et al., 2021). The case of Santa Fe Island contributes to a growing body of evidence supporting carefully planned rewilding efforts as a viable conservation tool to build ecosystem resilience under global change scenarios (Jaramillo et al, 2024).

Conclusion

This study offers one of the first ecological assessments of Santa Fe Island in the early years following feral goat eradication and the reintroduction of a native ecosystem engineer, the Española giant tortoise. By building on prior research and integrating both field data and historical insights, this work provides a foundation for understanding how ecological recovery unfolds in an insular, arid system with limited direct human presence but increasing vulnerability to climate change. The findings highlight the importance of long-term monitoring and adaptive management strategies to guide restoration goals and ensure the resilience of Santa Fe's unique biota. As the island continues to recover, it will serve as a valuable reference point for ecosystem restoration efforts across the Galápagos Archipelago and other arid islands worldwide.

References

Biodiversity. (n.d.). *Galápagos Conservancy*. Retrieved March 5, 2025, from https://www.galapagos.org/about_galapagos/biodiversity/

Campbell, K., & Donlan, C. J. (2005). Feral goat eradication on islands. Conservation Biology, 19(5), 1362–1374.

Charles Darwin Foundation. (2005). Action plan for the conservation of giant tortoises in the Galapagos Islands. Charles Darwin Foundation. https://www.darwinfoundation.org/en/documents/662/051124-plan-accion-ing.pdf

Chynoweth, M. W., Litton, C. M., Lepczyk, C. A., Hess, S. C., & Cordell, S. (2013). Biology and impacts of Pacific island invasive species. 9.*Capra Hircus*, the feral goat (mammalia: Bovidae). *Pacific Science*, 67(2), 141–156. https://doi.org/10.2984/67.2.1

Cowie, R. H., Bouchet, P., & Fontaine, B. (2022). The Sixth Mass Extinction: Fact, fiction or speculation? Biological Reviews, 97(2), 640–663. https://doi.org/10.1111/brv.12816

Escobar-Camacho, D., Rosero, P., Castrejón, M., Mena, C. F., & Cuesta, F. (2021). Oceanic islands and climate: Using a multi-criteria model of drivers of change to select key conservation areas in Galapagos. *Regional Environmental Change*, 21(2), 47. https://doi.org/10.1007/s10113-021-01768-0

Godbehere, A. (2024). Exploring the impact of reintroduced *Chelonoidis hoodensis* on *Opuntia echios* on Santa Fé Island, Galápagos. University of Hawai'i at Mānoa, Department of Natural Resources and Environmental Management.

Hamann, Ole. (2001). Demographic studies of three indigenous stand-forming plant taxa (*Scalesia*, *Opuntia*, and *Bursera*) in the Galápagos Islands, Ecuador. Biodiversity and Conservation. 10. 223-250. 10.1023/A:1008952319105.

Hamann, O. (2003). Vegetation changes over three decades on Santa Fe Island, Galápagos, Ecuador. *Nordic Journal of Botany* 23 (1): 1-10. https://doi.org/10.1111/J.1756-1051.2003.TB00375.X

Hunter, E. A., Blake, S., Cayot, L. J., & Gibbs, J. P. (2021). Role in ecosystems. In Galapagos giant tortoises (pp. 299–315). Elsevier. https://doi.org/10.1016/B978-0-12-817554-5.00006-X

Jäger, H., Kowarik, I., & Tye, A. (2009). Destruction without extinction: Long-term impacts of an invasive tree species on Galápagos highland vegetation. *Journal of Ecology*, 97(6), 1252–1263. https://doi.org/10.1111/j.1365-2745.2009.01578.x

Jaramillo Díaz, P., Velasco, N., Chirman, D., & Calle-Loor, A. (2024). Ecological restoration and species recovery plan for Baltra, South Plaza, Española, and North Isabela 2025–2029. Charles Darwin Foundation for the Galapagos Islands. https://www.darwinfoundation.org/en/documents/662/051124-plan-accion-ing.pdf

Jensen, E. L., Quinzin, M. C., Miller, J. M., Russello, M. A., Garrick, R. C., Edwards, D. L., Glaberman, S., Chiari, Y., Poulakakis, N., Tapia, W., Gibbs, J. P., & Caccone, A. (2022). A new lineage of Galapagos giant tortoises identified from museum samples. *Heredity*, 128(4), 261–270. https://doi.org/10.1038/s41437-022-00510-8

Kier, G., Kreft, H., Lee, T. M., Jetz, W., Ibisch, P. L., Nowicki, C., Mutke, J., & Barthlott, W. (2009). A global assessment of endemism and species richness across island and mainland regions. Proceedings of the National Academy of Sciences, 106(23), 9322–9327. https://doi.org/10.1073/pnas.0810306106

Matthews, T. J., & Triantis, K. (2021). Island biogeography. Current Biology, 31(19), R1201–R1207. https://doi.org/10.1016/j.cub.2021.07.033

Moorhouse-Gann, R. J., Vaughan, I. P., Cole, N. C., Goder, M., Tatayah, V., Jones, C. G., Mike, D., Young, R. P., Bruford, M. W., Rivers, M. C., Hipperson, H., Russo, I.-R. M., Stanton, D. W. G., & Symondson, W. O. C. (2022). Impacts of herbivory by ecological replacements on an island ecosystem. *Journal of Applied Ecology,* 59(9), 2245–2261. https://doi.org/10.1111/1365-2664.14096

Nogales, M., González-Castro, A., Rumeu, B., Traveset, A., Vargas, P., Jaramillo, P., Olesen, J. M., & Heleno, R. H. (2017). Contribution by vertebrates to seed dispersal effectiveness in the Galápagos Islands: A community-wide approach. *Ecology*, 98(8), 2049–2058. https://doi.org/10.1002/ecy.1816

Nori, J., Villalobos, F., Osorio-Olvera, L., & Loyola, R. (2022). Insufficient protection and intense human pressure threaten islands worldwide. *Perspectives in Ecology and Conservation*, 20(3), 223–230. https://doi.org/10.1016/j.pecon.2022.06.003

Russell, J. C., Meyer, J.-Y., Holmes, N. D., & Pagad, S. (2017). Invasive alien species on islands: Impacts, distribution, interactions and management. Environmental Conservation, 44(4), 359–370. https://doi.org/10.1017/S0376892917000297

Sanders, D., & Frago, E. (2024). Ecosystem engineers shape ecological network structure and stability: A framework and literature review. *Functional Ecology*, *38*(8), 1683–1696. https://doi.org/10.1111/1365-2435.14608

San-José, M., Arroyo-Rodríguez, V., Jordano, P., Meave, J. A., & Martínez-Ramos, M. (2019). The scale of landscape effect on seed dispersal depends on both response variables and landscape predictor. *Landscape Ecology*, 34(5), 1069–1080. https://doi.org/10.1007/s10980-019-00821-y

Tapia Aguilera, W., & Gibbs, J. P. (2023). Rewilding giant tortoises engineers plant communities at local to landscape scales. *Conservation Letters*, *16*(4), e12968. https://doi.org/10.1111/conl.12968

Tapia, W., Goldspiel, Harrison & Gibbs, James. (2021). Introduction of giant tortoises as a replacement “ecosystem engineer” to facilitate restoration of Santa Fe Island, Galapagos. *Restoration Ecology*. 30. https://doi.org/10.1111/rec.13476

Tsheboeng, G., Teketay, D., Murray-Hudson, M., Kashe, K., Mmusi, M., & Madome, J. (2024). Diversity, stand and population structure of riparian woody species in two contrasting land use types in the distal Okavango Delta, Northwestern Botswana. Tropical Ecology, 65(4), 664–676. https://doi.org/10.1007/s42965-024-00364-7

Tye, A. (2006, January). (PDF) restoration of the vegetation of the dry zone in Galapagos. *Research Gate*. https://www.researchgate.net/publication/258927384_Restoration_of_the_vegetation_of_the_Dry_Zone_in_Galapagos

Veron, S., Haevermans, T., Govaerts, R., Mouchet, M., & Pellens, R. (2019). Distribution and relative age of endemism across islands worldwide. *Scientific Reports*, *9*(1), 11693. https://doi.org/10.1038/s41598-019-47951-6