

**Assessing Plant Diversity After Giant Tortoise Reintroduction on Santa Fé Island,
Galápagos**

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Abstract

Invasive species pose significant threats to island ecosystems, often leading to the loss of native biodiversity and altered ecosystem functions. On Santa Fé Island (SFI) in the Galápagos, the eradication of invasive goats has been followed by the introduction of the giant tortoise species *Chelonoidis hoodensis* from Española Island as an ecological replacement for the extinct native tortoise species. This study investigated the impact of this introduction on plant diversity since giant tortoise reintroduction in 2015. We established 20 permanent quadrats (PQs) along gradients of tortoise activity on SFI and conducted vegetation surveys using the line-intercept method, along with observations of tortoise presence and scat. We used Shannon's diversity index to measure plant diversity and performed non-metric multidimensional scaling (NMDS) with Bray-Curtis dissimilarity to compare plant diversity. An activity index was created from tortoise and scat counts to estimate tortoise activity in each plot. Our results, revealed no significant correlation between tortoise activity and plant diversity ($r = 0.0406$, $p = 0.9$). Our findings suggest that the introduction of *C. hoodensis* has not yet significantly influenced plant diversity on SFI. The lack of observed impact could be due to the relatively short timescale since introduction, the predominance of juvenile tortoises, and the prior recovery of vegetation post-goat eradication. This study highlights the complexity of ecological replacement strategies and underscores the need for long-term monitoring and adaptive management to fully understand and enhance their effectiveness in conservation efforts.

Introduction

Invasive species are species not native to an environment where they were introduced (Carlton & Schwindt 2023) and negatively impact ecosystem functions (Brewington et al., 2023) and native biodiversity via predation and herbivory, competition for resources, and altering native habitats (Clout 2002). This is especially true for islands (Simberloff 2000), where invasive species are known to exacerbate the loss of native biodiversity alongside anthropogenic influences and climate change (Fernández-Palacios et al., 2021; Russell & Kueffer, 2019). More specifically, large mammals such as goats (*Capra hircus*) and wild boars (*Sus scrofa*) are especially harmful invasive species on islands, as they're able to acclimatize to various environmental conditions, reproduce rapidly, and feed opportunistically (Nogueira-Filho et al., 2009; Chynoweth et al., 2013; Coblenz 1977; Wehr et al., 2018).

Eradication of invasive species from native island ecosystems has shown to be a viable method to aid in recovering both native and non-native vegetation (Simberloff 2000; Cole et al., 2012; Cole & Litton 2014; Hamann 2004; Jones et al. 2016). In the Galápagos, goats have been present since the 17th century, and have been one of the largest drivers of vegetation loss across several islands in the archipelago (Eliasson 1968; Hamann 2004). This loss is substantial, as the Galápagos Islands hosts some of the highest levels of endemism on the planet (McMullen 1999; Kricher & Loughlin 2022). Since the inception of the Galápagos National Park Directorate and Charles Darwin Foundation, initiatives in the 1960s to eliminate goats from these islands have been successful, exemplified by the eradication of goats on Santa Fé Island (SFI) in 1971 (Cruz

et al., 2009; Hamann 1975, 2004; Desender et al., 1999; Carrion et al., 2011; Kricher & Loughlin 2022). SFI is an uninhabited island located near the center of the Galápagos Archipelago. Geological studies estimate an age between 2.8 to 4.6 million years old, making it one of the oldest in the archipelago (Geist et al., 1985; Geist 1996). Recorded plant taxa on the island include 95 species—44 endemic, 47 indigenous, and 4 introduced (Hamann 2004). Notable plant taxa include two dominant native tree species and one shrub species: *Opuntia echios* var. *barringtonensis*, *Bursera graveolens* (Burseraceae), and *Cordia lutea* (Malvaceae), respectively (Hamann 2004). Following goat eradication on SFI, the island's vegetation recovered significantly but slowly over three decades (Hamann 2001, 2004).

To further facilitate ecosystem restoration on SFI, the giant tortoise species *Chelonoidis hoodensis* from Española Island was introduced to serve as an ecological replacement for an extinct giant tortoise species (*Chelonoidis* sp. undescribed) possibly endemic to SFI (Poulakakis et al., 2008; Blake et al., 2012; Hunter et al., 2013; Tapia et al., 2021, 2022). Giant tortoises are the main native herbivores of the Galápagos and contribute to seed dispersal, nutrient cycling, and spatial distributions for many native plant taxa (Hansen et al., 2010; Blake et al., 2012). While *C. hoodensis* is not native to SFI, genetic analyses and morphological observations have shown that *C. hoodensis* is closely related to the SFI species (Hunter et al., 2013; Tapia et al., 2021, 2022). In addition, similarities in geological history, climate, and arid-adapted vegetation between SFI and Española Island suggest that both species may have provided similar ecological functions in their native ranges (Blake et al., 2012; Hunter et al., 2013; Tapia et al., 2021, 2022).

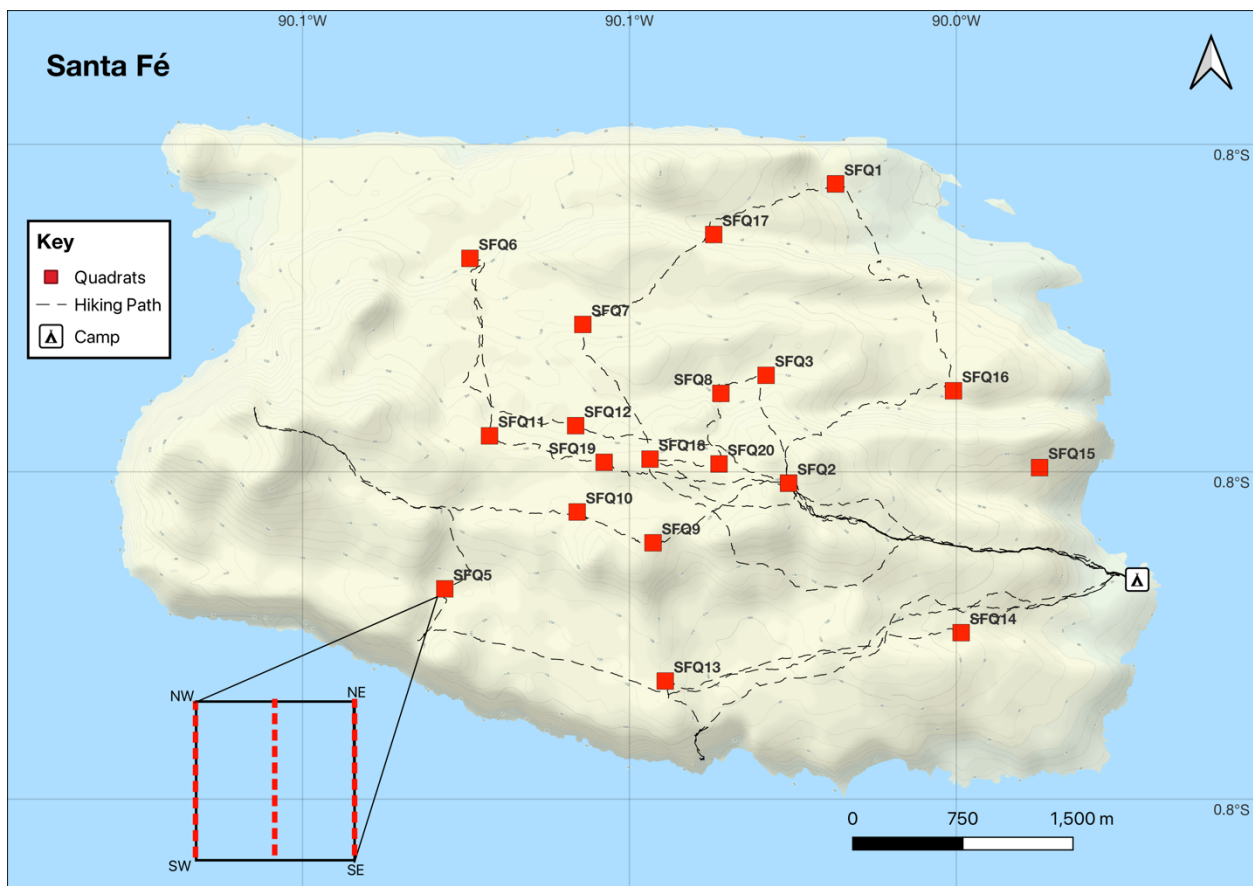
However, the long-term impacts of ecological replacements in their new environments are poorly understood, making it a controversial conservation strategy (Ricciardi & Simberloff 2009; Parker et al., 2008; Griffiths et al., 2012). Furthermore, ecological replacements as a restoration strategy have focused primarily on restoring ecological function rather than species diversity (Moorhouse-Gann et al. 2022). While the reintroduction of giant tortoises to SFI may offer valuable insight into the island's ecology pre-human contact, additional research is needed to understand their potential impact on the native plant diversity on SFI. Despite observations indicating *C. hoodensis* populations on SFI are becoming stable and self-sufficient (Tapia et al., 2022), the implications of their present and future distribution on the island's vegetation are still unknown.

The objective of this study is to investigate how the introduction of giant tortoises may be influencing plant diversity on Santa Fé Island since their introduction in 2015. We aim to determine how active tortoises are in different parts of the island and assess plant diversity within those areas. Because large herbivores contribute to species richness via herbivory, trampling, and nutrient cycling (Hunter et al., 2013; Richardson & Stiling 2019; Moorhouse et al., 2022), I hypothesize that areas with higher activity of *C. hoodensis* will have greater plant diversity due to the return of native plant-herbivore interactions. In contrast, areas with low or zero tortoise activity will have less diversity due to a lack of disturbance via herbivory, trampling, and nutrient cycling by the introduced tortoises.

Methods

Fieldwork

Along with six historical 10 m × 10 m permanent quadrats (PQ) on SFI (Hamann 2004), fourteen additional PQs were established and assessed along a gradient of high, low, and zero tortoise activity across SFI (Figure 1) for two 1-week long field trips in June and July. Following the methods of Moorhouse-Gann et al. (2022) and Jäger et al. (2009), each PQ contained three parallel 10-m transects that were always measured north to south: one from the northeast to southeast corners, northwest to southwest corners, and one in the middle of the PQ. In each of the 19 PQs, monitoring of plant species or substrates “rock” and “bare ground” was carried out along the three parallel 10-m transects using the line-intercept method (Jäger et al., 2009, 2024) and always by the same investigator. After monitoring each transect, additional species not accounted for on any of the transects but were still present in each PQ were recorded. Observations on soil characteristics were also made for each PQ. To estimate tortoise activity, a 50 m transect running west from the northwest corner of each PQ was established. Numbers of



tortoise individuals or scat was conducted using a belt-transect of 1 m on both sides of the 50 m transect.

Statistical Analyses

All statistical analyses were performed using R statistical software version 2024.04.2+764 (R Core Team 2024). Species percent cover values were calculated for all species present in each PQ. Percent cover values were then used to create a data matrix with species as columns and PQs as rows. Shannon's diversity indices were computed in the vegan package (Oksanen et al., 2024) for each plot. Plant diversity for each plot was compared using non-metric multidimensional scaling (NMDS) using Brays-Curtis dissimilarity in the vegan package (Oksanen et al., 2024).

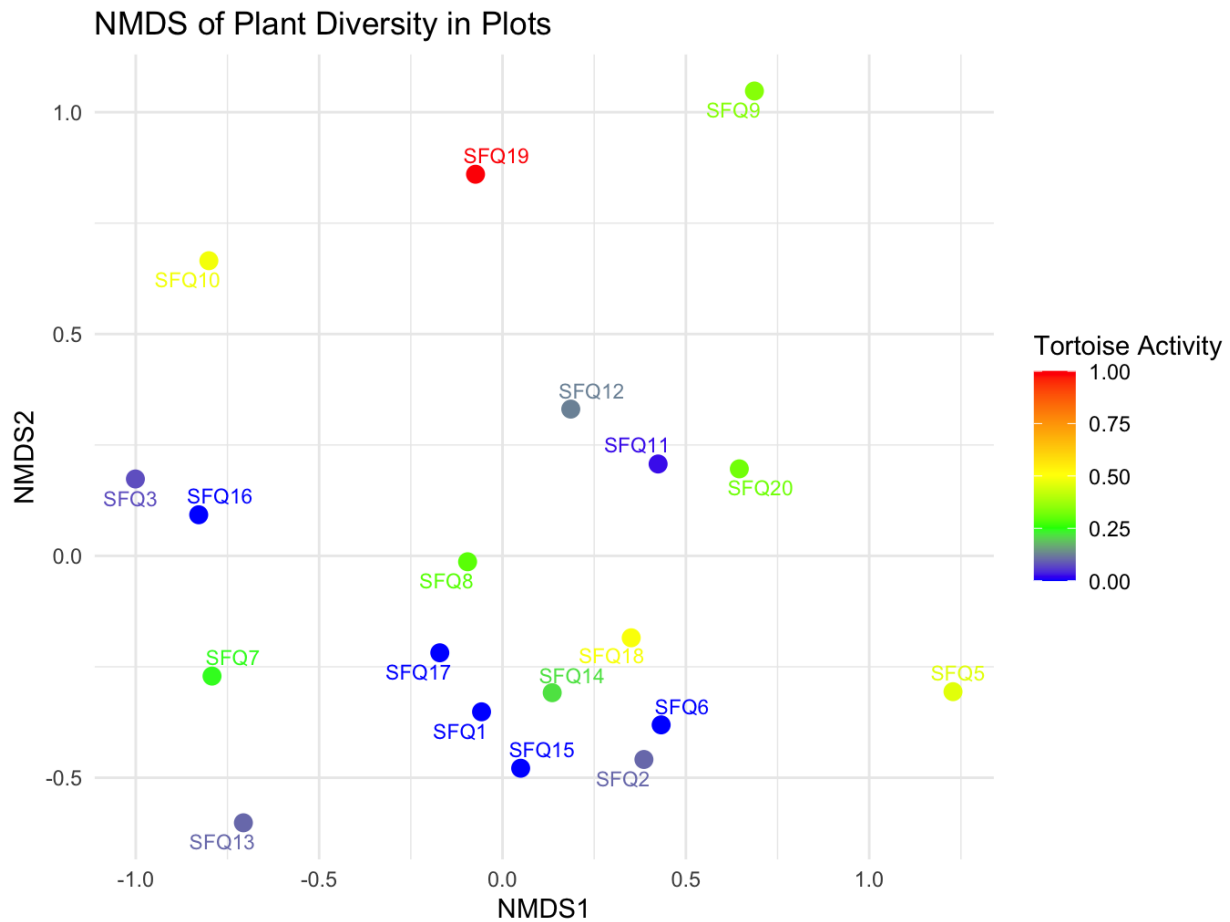


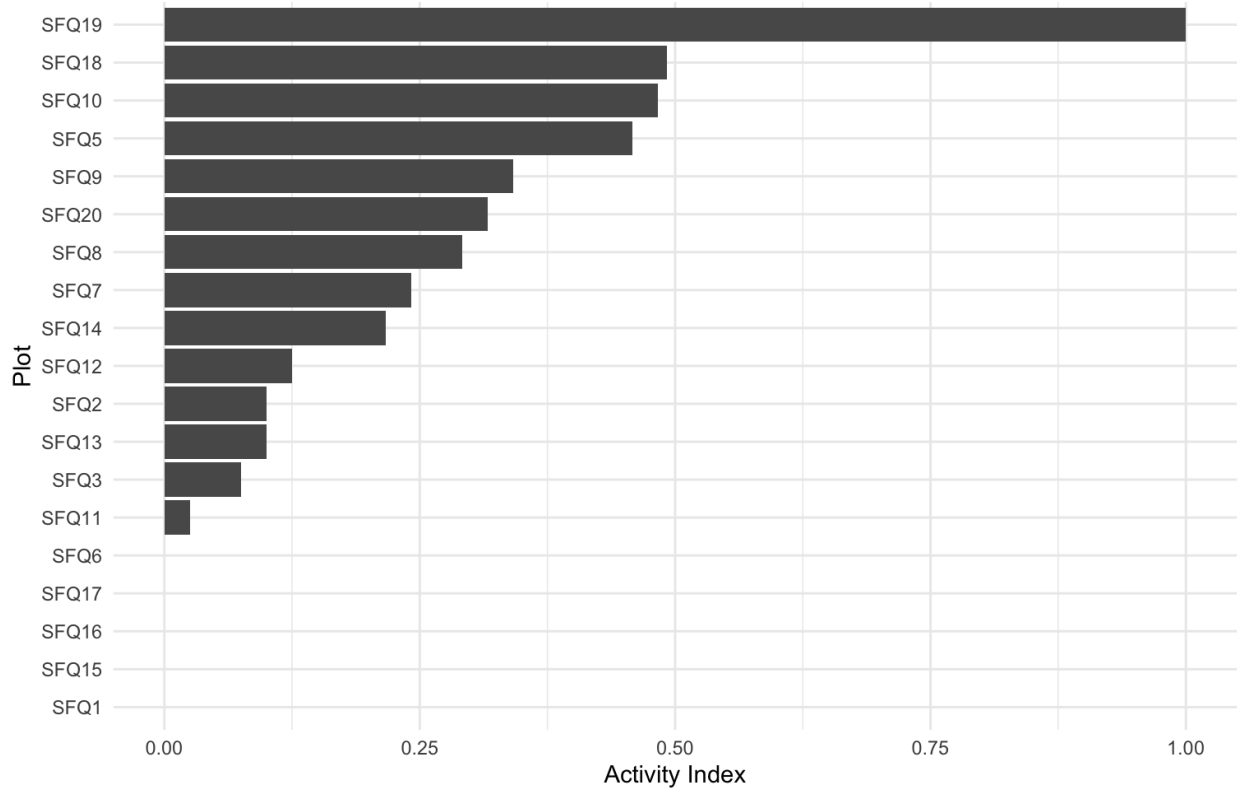
Figure 2: NMDS showing plant diversity across plots with different levels of tortoise activity.

To estimate the level of tortoise activity for each plot, the number of tortoises and tortoise scat for each plot was used to create an activity index. The count of tortoises and tortoise scat was normalized using min-max normalization. The normalized values were then combined to create the activity index, where tortoise presence was weighed more than scat. PQs with activity index values close to or at zero represented low tortoise activity, and values close to or at 1 represented PQs with high activity. Finally, the Shannon's diversity indices for each plot were compared with the tortoise activity index using a general linear model (GLM).

Results

There was evidence of tortoise activity in 14 of the 19 PQs (Figure 3). Additionally, 53 plant taxa were observed across all plots, of which 40 were identified morphologically to species and 3 to genus (Fig. 4). The mean percent cover for all species across all plots showed that *Cordia lutea* (Boraginaceae), *Aristida subspicata* (Poaceae), and *Panicum alatum* (Poaceae) were the dominant taxa (Figure 5). Pearson's correlation test of the GLM of Shannon's diversity indices for each plot with tortoise activity levels resulted in a coefficient value of $r = 0.0406$ and

Gradient of Tortoise Activity by Plot

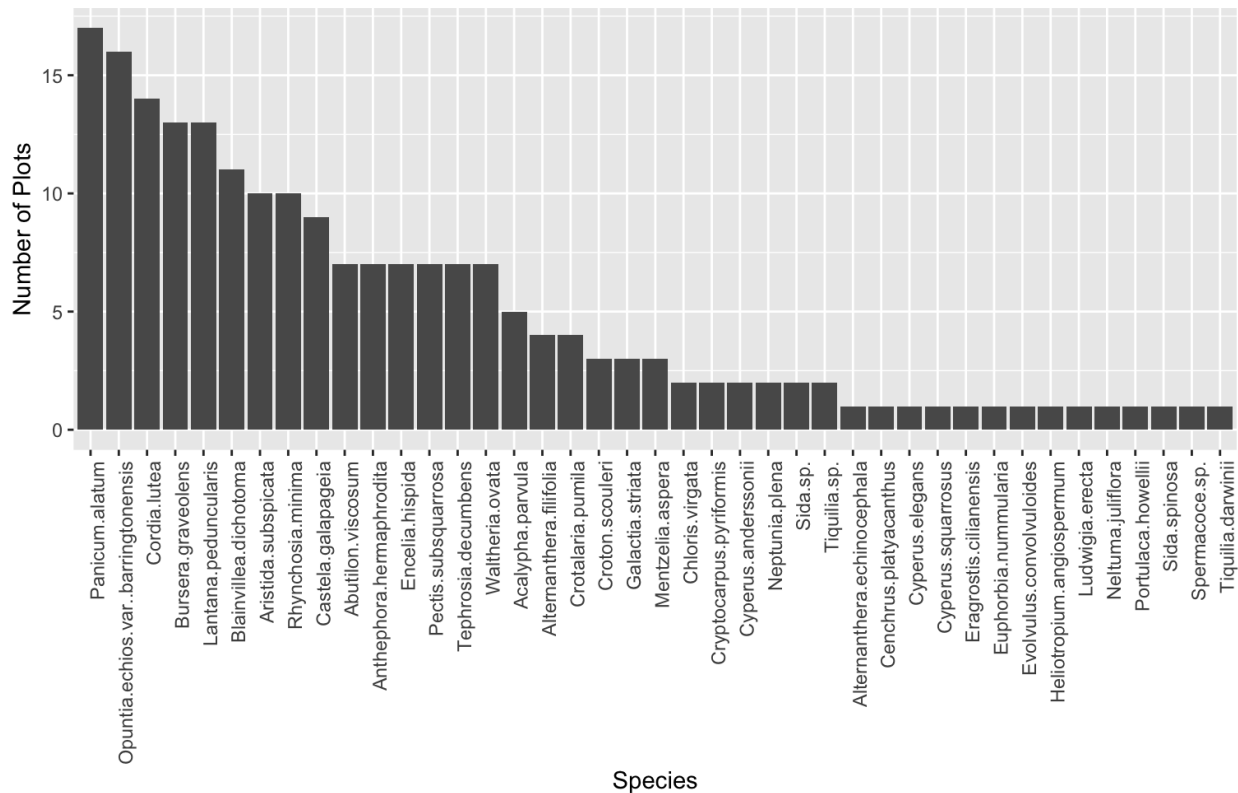


a p-value of 0.9.

Discussion

Giant tortoises had no impact on plant diversity across Santa Fé

Our findings indicate that there is no significant correlation between tortoise activity and plant diversity as measured by Shannon’s diversity index (Figure 6). Our Pearson’s correlation



coefficient value of $r = 0.0406$ indicates a very weak linear relationship between tortoise activity and plant diversity. This is further supported by having a p-value of 0.9, which tells us that our results are not statistically significant. This lack of correlation suggests that the presence and activity level of giant tortoises are currently not influencing plant diversity across the studied plots.

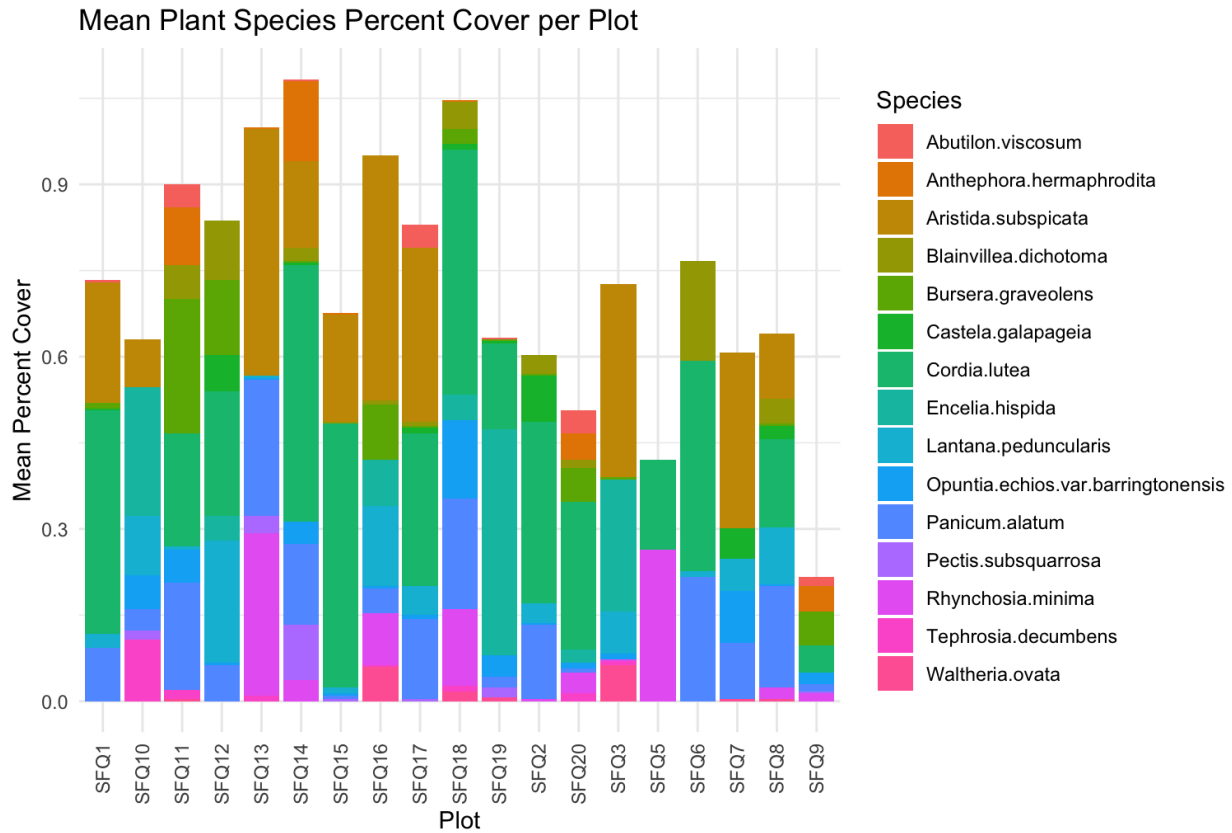
Potential reasons for the lack of significant findings

Giant tortoises are known to provide key ecological roles in their native habitats via herbivory, seed dispersal, and nutrient cycling (Hansen et al., 2010; Blake et al., 2012.) The reintroduction of *C. hoodensis* to SFI aimed to restore these ecological functions, which were presumably lost with the extinction of the undescribed, extinct, and possibly endemic Santa Fé *Chelonoidis* species. However, this study did not find evidence that the introduced tortoises altered plant diversity across SFI.

The introduction of *C. hoodensis* to SFI in 2015 might be too short of a timescale to observe any impacts on the ecosystem. With most tortoises observed to be juveniles on SFI, the impacts of these ecological replacements may become more pronounced over a longer period. And because the vegetation on SFI had already undergone significant recovery after goat

eradication in 1971 (Hamann 2004), plant communities may have already been stable before the introduction of tortoises in 2015.

Additionally, while we recorded tortoise activity across plots, the intensity and frequency

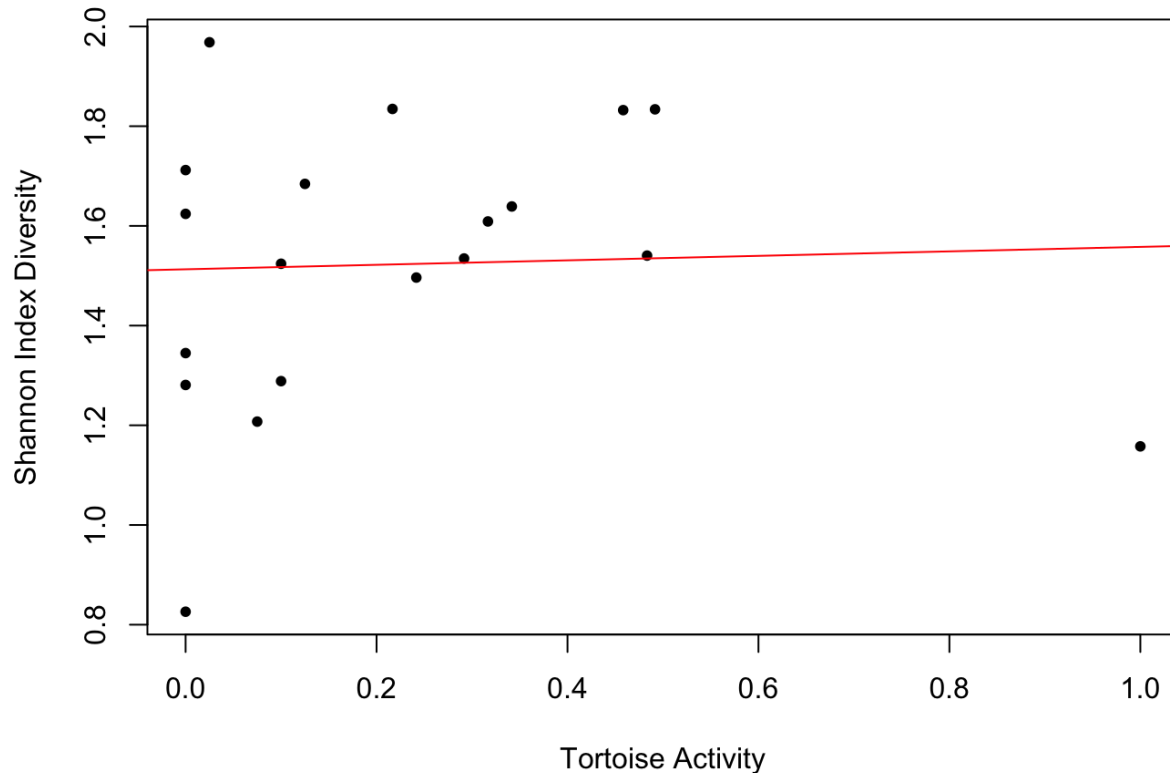


of their interactions with specific species might vary, which may reduce their overall impact on plant diversity. Some species might benefit from tortoise presence, while others might be negatively affected or experience no effect at all. For example, Moorhouse-Gann et al. (2022) found that Aldabra giant tortoises (*Aldabrachelys gigantea*), an ecological replacement species to Round Island, Mauritius, had reduced populations of *Boerhavia spp.* and *Ipomoea pes-caprae* due to herbivory, which was analyzed using dietary metabarcoding.

Management implications

While our findings did not show a significant impact of tortoise activity on plant diversity, continuous and long-term monitoring is necessary to understand the dynamics at play for an ecological replacement species. The introduction of *C. hoodensis* to Santa Fé should be viewed in a broader ecological restoration framework that considers multiple factors, such as ongoing environmental changes, pressures from climate change, and other species interactions. Comparative studies should also be conducted where similar reintroduction efforts have occurred. For example, giant tortoises were reintroduced on Pinta Island to act as ecological replacements for the now-extinct Pinta Island giant tortoise *Chelonoidis abingdonii* (Hunter et al., 2013), to which the methodologies of this study could also be applicable.

In conclusion, while the impact of *C. hoodensis* on plant diversity was observed to not be significant, the ecological benefits or drawbacks of their introduction may become more apparent



over a much longer period, highlighting the importance of long-term monitoring on Santa Fé, and consideration of other abiotic and biotic factors that may be influencing plant diversity across the island. This study contributes to our understanding of the complexities involved with ecological replacements and highlights the need for adaptive management in conservation and restoration efforts globally.

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