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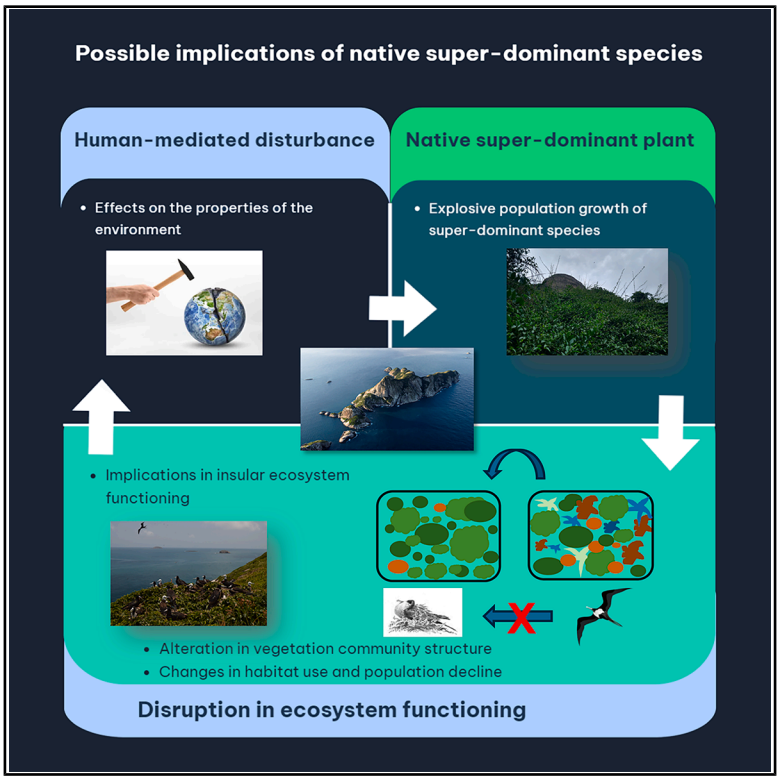
When natives become villains: Plant super-dominance and its implications on island ecosystems

Graphical abstract



Highlights

- Human activities may cause overabundance of native plants, altering plant communities
- Super-dominant native plants can negatively impact other species groups
- Unmanned aerial vehicles improve ecological studies in highly challenging environments
- Managing super-dominant species is key for restoring ecosystem function on islands

Authors

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In brief

Native plant super-dominance, often overlooked in conservation, can disrupt island ecosystems by altering habitat structure, species diversity, and nutrient cycling. Using field data and drone imagery, we show how the liana *Seguieria americana* reduces nesting habitat for the largest South Atlantic magnificent frigatebird colony, triggering cascading ecological impacts. Our findings underscore the importance of managing even native species when they become ecologically dominant, especially in fragile island systems increasingly vulnerable to anthropogenic disturbances and climate change.

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When natives become villains: Plant super-dominance and its implications on island ecosystems

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SCIENCE FOR SOCIETY Human activities significantly disrupt natural ecosystems, leading to the loss of critical ecological functions, especially in sensitive island environments. Our study, employing cutting-edge drone technology, delves into these disturbances and their cascading effects. We demonstrate how unmanned aerial vehicles can significantly advance the study of changes in ecological dynamics related to anthropogenic disturbances in extreme environments. Our findings reveal that the super-dominance of a native plant species drastically alters vegetation structure, reshaping habitats and influencing animal behavior. For instance, the magnificent frigatebird avoids areas affected by this dominance, highlighting the broader ecological implications of such ecosystem changes. These birds are crucial nutrient vectors between marine and terrestrial ecosystems, emphasizing the intricate balance within island ecologies. This research highlights the urgent need to understand and manage native dominant species, particularly as climate change exacerbates ecological instability. Our findings provide essential insights for environmental policymakers and conservationists, offering support to mitigate the adverse effects on fragile island habitats worldwide. Interdisciplinary collaboration is vital to developing informed strategies that protect these unique ecosystems and enhance their resilience against future disturbances.

SUMMARY

Human disturbances can disrupt ecosystem functioning by promoting the overabundance of dominant species, negatively impacting other species. In insular systems, native plant super-dominance employs complex, context-dependent effects on species diversity and community structure. Combining fieldwork with aerial imagery captured by unmanned aerial vehicles (UAVs), we outline how the super-dominance of a native plant (*Seguieria americana*) affects island ecosystem functioning. We show that breeding habitat used by the largest magnificent frigatebird (MFB) colony in the South Atlantic depends on the vegetation structure. Increased *S. americana* occupancy is associated with reduced MFB nesting and altered species diversity and composition, which also varied with elevation and soil conditions. Declines in nesting habitat likely reduce guano deposition and nutrient input, triggering cascading negative impacts. Thus, we advocate further research on these mechanisms and UAV technology to guide conservation management, mitigate adverse effects, and conserve biodiversity amid climate change, particularly in vulnerable island systems.

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INTRODUCTION

Ecosystems are subject to disturbances, both natural[1] and human mediated,[2,3] which can lead to significant changes in their structure and functioning. Natural disturbances such as fires, floods, and storms are part of natural ecological processes, influencing species diversity and distribution, and can lead to succession and changes in ecosystem structure. In contrast, human-mediated disturbances, including habitat destruction and the introduction of invasive species, typically cause more immediate and severe alterations. These changes can lead to the loss of biodiversity, disruptions in nutrient cycles, and compromised ecosystem services.[4]

Human activities can also promote the overabundance of certain species, both native and alien, favoring generalist and invasive species adapted to disturbed environments.[5] This can lead to homogenization of ecosystems and further loss of native biodiversity.[6] In addition, the disruption of ecological networks and interactions such as predation and competition may occur as well, which can further amplify the effects of disturbances on ecosystem functioning.[7] The promotion of super-dominance due to human-mediated disturbances can have cascading effects on ecosystem resilience and functions. However, understanding the impact of human activities on plant communities and their influence on the spread and establishment of native species within island ecosystems remains an area of active research.

Biological invasions by exotic species have drawn the attention of science since the 19th century,[8,9] being recognized as a significant threat to biodiversity.[10–13] Research on the ecology of invasions has been analyzing the factors that make some environments more susceptible to invasions than others and which intrinsic attributes increase invasive behavior on species.[11,14–16] Exotic invasive plants can expand their ranges and accelerate their spread in a climate-change scenario,[17–19] potentially amplifying the homogenization of floras, which impacts overall diversity.[20] This can lead to negative changes in community structure and composition[21] and may even contribute to extinctions.[22] Similarly, native species populations can become overabundant and cause significant ecological harm. These are referred to as *super-dominant* species—native species that, when released from controlling mechanisms, proliferate intensely, disrupt ecosystems, and create severe demographic imbalances without implying an external origin.[23] This proliferation can lead to a simplified community structure and composition.[24,25] Such homogenization may trigger cascading effects on ecosystem functioning and on other organisms, such as pollinators and herbivores, which depend on a diverse array of plant species for food and habitat.[26,27]

Understanding the effects of native species that behave as super-dominant on the ecosystem functioning and identifying the ecological mechanisms that render systems more susceptible to uncontrolled population growth are still unresolved questions in the field of ecology.[28] Specifically, studies have reported that the uncontrolled population growth of native species is primarily triggered by anthropogenic changes in the environment, leading to economic and ecological impacts comparable to those caused by exotic species.[23,29] Although the awareness of adverse impacts resulting from super-dominance by native plant species has started to grow,[23,30] there is still a lack of studies focusing on island systems, which are often more vulnerable to disturbances caused by human activities.[31]

Insular ecosystems often host unique biota characterized by high endemism, acting as a natural laboratory and offering opportunities for understanding biogeographic patterns.[32,33] Despite covering only 5% of the Earth's surface, islands harbor approximately 25% of described vascular plant species.[34] Islands also may function as a refuge and ecological nursery for various organisms.[35] Some seabirds that depend closely on islands for nesting[36] can act as a bridge of essential nutrients, allowing a strong connection between the oceanic and terrestrial ecosystem.[37–39]

However, the spatial limitations inherent in insular environments can promote a higher intensity of biotic interactions (e.g., competition), often resulting in greater vulnerability to biological invasions.[40,41] Specifically, younger islands tend to accommodate larger populations, intensifying competition.[42] Thus, island systems may be more susceptible to alterations in their ecosystem properties induced by disturbances, which intensify the competitive advantages of certain species.[43] Similarly, islands should also be sensitive to changes that lead to uncontrolled growth of native plant species, potentially negatively affecting unique populations. Despite this, there is a dearth of studies reporting the ramifications of the overwhelming dominance of native plant species in other organism groups in an insular environment.

In this paper, we present the first documented case of super-dominance by a native plant species in an island ecosystem historically affected by human-mediated disturbances. Specifically, we combined field surveys (plots and transects) with unmanned aerial vehicle (UAV)-captured georeferenced orthomosaics to assess the breeding habitat use of the South Atlantic's largest magnificent frigatebird (*Fregata magnificens*, MFB) colony. Our main questions were as follows: (1) what is the impact of a native super-dominant plant species in both vegetation structure and *F. magnificens* colony? (2) How does tree/shrub diversity and composition vary with elevation and local soil conditions? By integrating these ecological dimensions, we develop a conceptual framework that elucidates the potential cascading effects of human disturbances on island ecosystem functioning.

RESULTS

Habitat selection for nesting by MFBs

For the georeferenced orthomosaic analysis, we selected 10,982 polygons for the training phase and an additional 7,123 for validation. Classification accuracy was evaluated through this matrix, presenting a high overall accuracy of 88% and a Kappa index of 0.81 (Table S1). The values of these indices demonstrated consistent results, indicating an excellent degree of discrimination between classes. However, the object-based image analysis (OBIA) classification revealed confusion between the "vegetation without *Seguieria americana* super-dominance (VwoSD)" and "vegetation with *S. americana* super-dominance (VwSD)" classes, possibly due to its canopy structure and color. Out of the 5,291 m^2 recorded in the orthomosaic (Figure 1A), the

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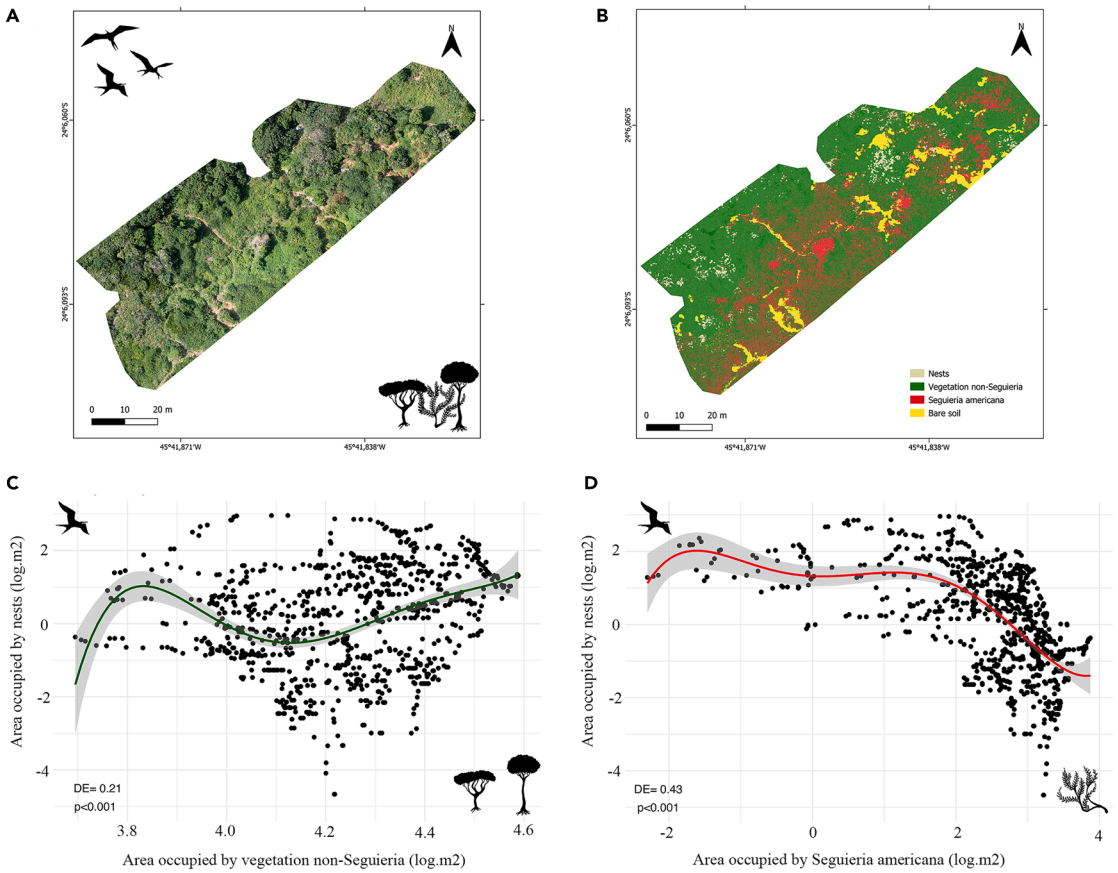

Figure 1. Habitat selection for nesting by MFBs

Orthomosaic image (A) and land cover classification map (B) of the MFB nesting site. Relationships (generalized additive models [GAMs]) are depicted between the area occupied by nests and the area occupied by VwoSD (C), as well as the area occupied by VwSD (D) on Alcatrazes Island, State of São Paulo, southeastern Brazil. The shaded area represents the 95% confidence interval of the model. Refer to the methods for additional details. DE, deviation explained.

VwoSD class represents 75.5% of the total area, followed by the VwSD class (15.7%), bare soil (5.9%), and "nests" (2.7%) (Table S1), represented in the final map of land cover classification (Figure 1B). Interestingly, we identified a slight increase (deviation explained [DE] < 0.3) in the area occupied by nests compared with VwoSD (Figure 1C). Conversely, there was a notable negative correlation (DE > 0.3) between the area occupied by *S. americana* and nest occupancy (Figure 1D).

Across five 25-m transects in the nesting area, we identified the tree and shrub species preferred by the MFB (*Fregata magnificens*) for nesting on Alcatrazes Island. *Cynophalla flexuosa* (Capparaceae) hosted the highest number of nests, with 75 recorded across three of the 5 transects, followed by *Guapira opposita* (Nyctaginaceae), with 31 nests across 4 transects. *Ficus luschnathiana* (Moraceae) had 14 nests, all within a single transect, whereas only 1 nest was recorded on *Seguieria americana*. Regarding the potential success of species management, after 25 weeks of the complete removal of *S. americana* from the *F. luschnathiana* individual, we recorded nine nests of MFB, indicating that the canopy became more suitable for landing, takeoff, and nesting after the management (see Video S1).

Consequences of plant super-dominance for island diversity and soil properties

The plots sampled in areas of MFB nesting sites showed lower tree diversity compared with those sampled in two other types of forests (Figure 2A), comprising lowland forest (LF, 80–150 m. a.s.l.) and submontane forest (SF, 230–275 m.a.s.l.). In the plots located in LF, 34 tree species were found, whereas in SF, we encountered 23 tree species. Only four species were recorded within the MFB nesting area: *C. flexuosa*, *G. opposita*, *F. luschnathiana*, and *Randia armata* (Rubiaceae). The rarefaction curve confirmed sufficient sampling across all sites (Figure 2B). The density of *S. americana* was significantly higher in the MFB nesting area (Figure 2C), with an average density of 11.8 individuals per 100 m^2 (compared with 0.009 ind/100 m^2 in LF; no *S. americana* individuals were found in SF plots). The highest density of *S. americana* recorded was 17.8 ind/100 m^2, located within the MFB nesting site. Although LF and SF showed no significant difference in species count, LF exhibited higher estimated richness. This was attributed to a more distinct species composition in the sampled plots within this area, as indicated by non-metric multidimensional scaling (NMDS) ellipses (Figure 2D).

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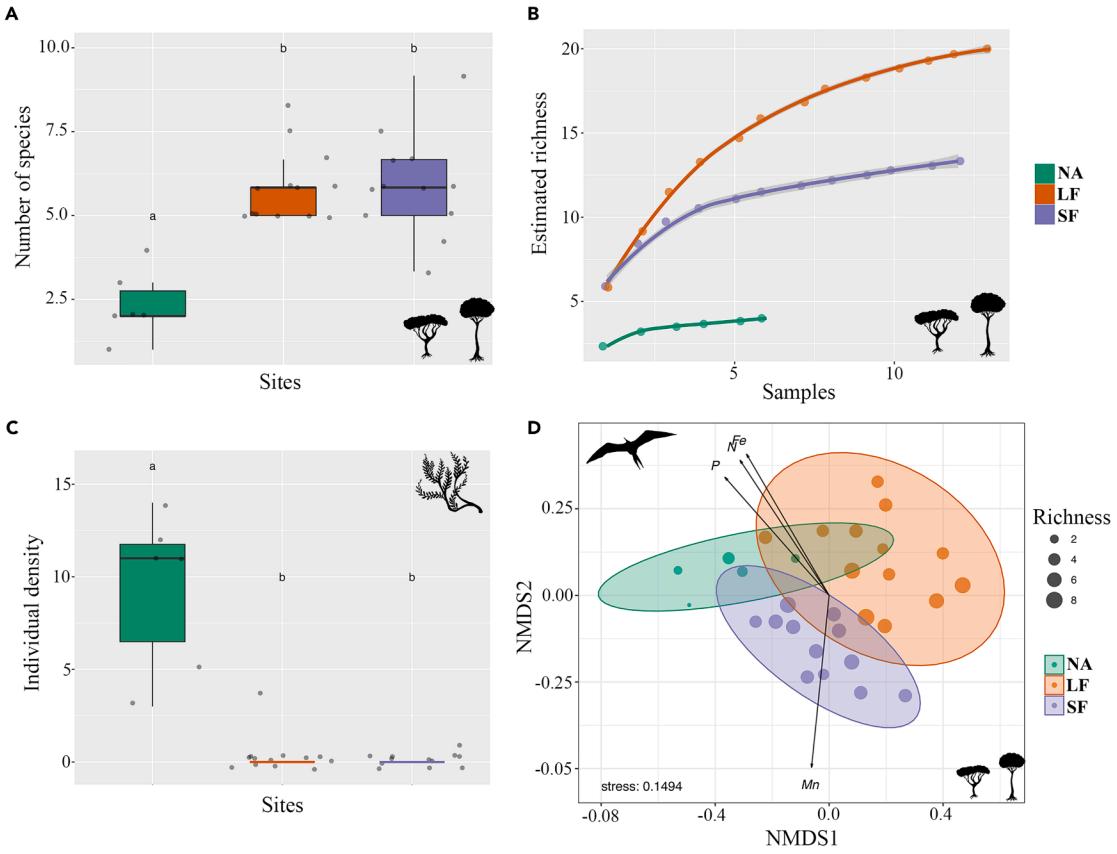

Figure 2. Consequences of plant super-dominance for island diversity and soil properties

Differences in tree richness (A), the estimated number of tree species (B), and the abundance of *Seguieria americana* individuals (C), along with the relationships between species composition and soil variables (D), were assessed within sites dominated by *S. americana* (nesting area [NA]) and sites not dominated by *S. americana* (LF, lowland forest; SF, submontane forest) on Alcatrazes Island, State of São Paulo, southeastern Brazil. The spatial distribution of sites in an ordination space was evaluated using NMDS. Different letters indicate significant differences ($p < 0.01$), and the ellipses represent a 95% confidence level for a multivariate t-distribution. For further details, please refer to the methods section. P, phosphorus; N, nitrogen; Fe, iron; Mn, manganese.

Generally, the mean soil nutrient concentrations beneath MFB nests exceeded those in SF and LF samples, as illustrated in Figure S1. We observed significant differences for 13 of the 15 analyzed variables ($p < 0.01$). The NMDS ordination revealed distinct floristic patterns across surveyed sites, with the first axis clearly segregating nesting area plots. The second axis of NMDS demonstrated significant variation, particularly between lowland and nesting submontane plots compared with other forest areas (Figure 2D). The stress value and the high coefficients of determination of the four selected variables in the multiple regression affirmed the robustness of both the data and the model (Table S2). Typically, nesting plots exhibited elevated levels of phosphorus, nitrogen, and iron, whereas notable differences in manganese were associated with the characteristics of LF and SF forests.

DISCUSSION

Human impact and effects of plant super-dominance on island ecosystems

Species super-dominance may disrupt abiotic and biotic interactions,[23,29] and such effects may be more severe on vulnerable ecosystems such as islands.[40,41] Through different approaches, we have shown how the super-dominance of a native plant can lead to consistent impacts on the local tree community as well as on the largest breeding concentration of the MFB from the southern Atlantic on the Alcatrazes Island, Brazil. We have also found that the presence of MFB may influence the soil heterogeneity on the island through the cumulative deposition of guano. Main findings suggested that areas with higher densities of *S. americana* have much lower tree diversity compared with those of lower density or absence of this species. Interestingly, through the analysis of the georeferenced orthomosaic obtained by UAV, we found the clear preference of MFB for nesting in areas not occupied by *S. americana*, corroborating our initial observation. These findings show, for the first time, the implications of plant super-dominance in a bird population, contributing to the advancement of knowledge about how anthropogenic disturbances can affect complex and unique systems (Figure 3).

Disturbances change the inherent characteristics of space and the availability of local resources, potentially providing an advantage to populations with competitive traits.[15,29] We believe that the high density of *S. americana* is closely related to the

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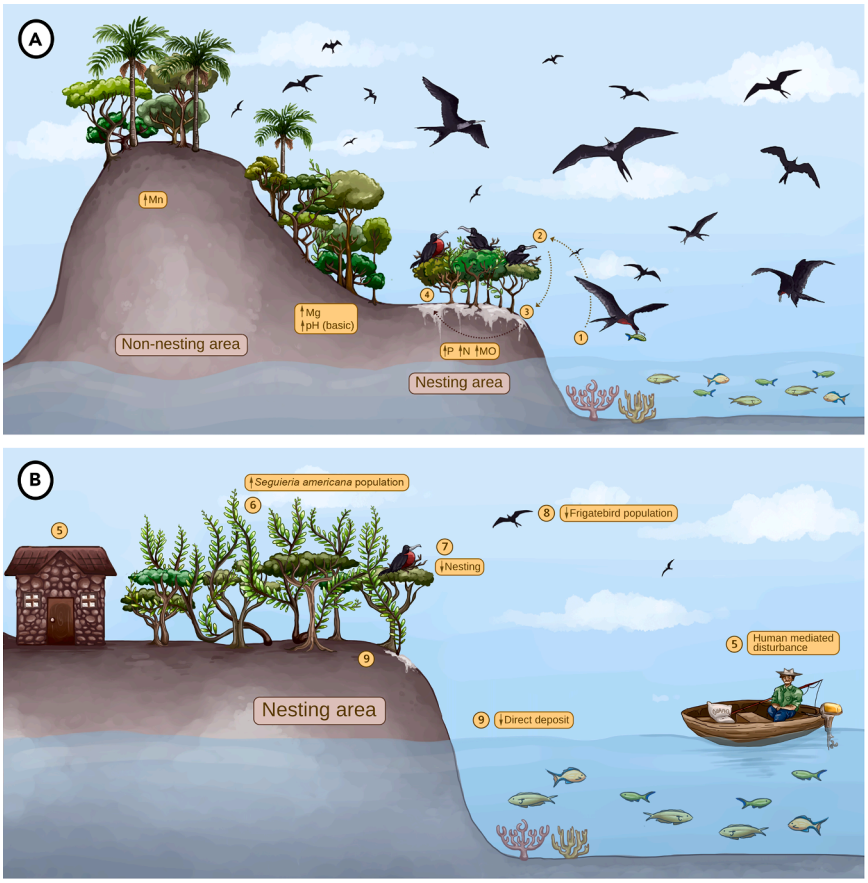

Figure 3. The implications of native plant super-dominance on island ecosystems in two different disturbance scenarios

(A) Whole island without human disturbance and (B) MFB nesting area with human disturbance; arrows indicate the directions, and numbers indicate the sequence of events; (A) (1) fish are eaten by MFB that (2) nest on the top of the canopies and (3) deposit guano on island, which enters the island soil that is then (4) utilized by plants; (B) (5) human-mediated disturbances that (6) change the structure of native vegetation, increasing the population of the super-dominant *Seguieria americana* that cause (7) disruptions in the canopies' architecture, reducing the MFB nesting sites and therefore (8) affecting its local population and, consequently, (9) the nutrient influx via guano from the ocean to the island. Figure by Giovana Narezi Trotta.

anthropogenic disturbances experienced in the area in the past.[44] Such anthropogenic disturbances may have freed up space and increased the availability of resources, favoring the establishment of the species population, clearly with competitive advantages over other plant species. The accumulation and intensity of habitat alterations also trigger the expression of traits associated with a sudden population expansion.[45] Areas of Alcatrazes Island without recent anthropogenic disturbances showed sparse individuals of *S. americana*, which reinforces that the super-dominance of this species is related to the anthropogenic disturbances experienced in the past.

Plant super-dominance: Consequences for tree diversity and habitat use by birds

Our study, utilizing a UAV for orthomosaic analysis, elucidated the clear preference of MFB for nesting in areas devoid of *S. americana*, supporting our initial field observations. This underscores the importance of employing new technologies to enhance ecological studies in vulnerable and inaccessible systems like island communities, advocating for their widespread adoption in conservation efforts.[46,47] In contemporary conservation ecology, the integration of cutting-edge technologies has revolutionized our understanding of complex ecosystems, particularly in challenging environments. Drones provide unmatched access to remote landscapes, allowing researchers to efficiently gather high-resolution ecological data. They aid in mapping habitats, monitoring wildlife populations, and assessing habitat quality, yielding insights previously unattainable in a shorter amount of time.[48–50] Moreover, their low-cost nature makes UAVs an attractive option for ecological research, allowing for extensive data collection without the need for expensive equipment or infrastructure.[49–51]

Despite the limited knowledge and discussion about the overabundant plant species, Pivello et al.[23] provide a compilation listing Brazilian native plant species from different life forms that cause impacts due to their explosive population growth. Here, we recorded for the first time *S. americana* as a super-dominant liana species. None of the scientific expeditions conducted between 1920 and 2017 on Alcatrazes Island by Luederwaldt and Fonseca,[52] Lucia Rossi,[44] Muscat et al.,[53] and Pompéia et al.[54] reported the high abundance of the species, suggesting that its population explosion occurred recently. The overpopulation of climbing plants has a positive correlation with human-mediated disturbances,[55–57] and explosive populations of this lifeform can negatively impact local biodiversity.[55,58,59] This suggests that large populations of climbing plants may influence a forest's functioning, structure, and composition. We observed significantly lower tree diversity in areas with a high density of *S. americana* than in areas with scattered individuals. Although differences in species composition are evident, and current conditions would make it highly challenging for new tree species to establish and thrive in the area, it is unlikely that the dense and aggressive canopy cover of *S. americana* itself is the sole environmental factor inhibiting the tree species present in the area. According to the Hórus Institute,[60] no other species belonging to the Phytolaccaceae family is classified as super-dominant in Brazil. However, some species of the genus *Phytolacca* and *Rivina humilis* are reported as invasive in other countries,[61–64] some of them exhibiting allelopathic compounds.[65] Future studies should investigate whether *S. americana*, besides the effect of shading

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from tree canopies, also possesses potentially allelopathic substances. This trait would enhance competitive advantages over other species.

The significant presence of the *S. americana* population within the MFB nesting site on Alcatrazes Island has led to alterations and disturbances in the architecture of tree and shrub canopies, thereby influencing the habitat selection of MFB. The avoidance behavior exhibited by MFB in the presence of *S. americana*-covered canopies highlights the potential impact of this plant species on the island's avian community. The scenario presented here of a population explosion exhibited by native plant species negatively impacting bird populations is unprecedented in scientific literature. Burger[66] reports the case of *Pisonia grandis* (Nyctaginaceae), which negatively affects populations of seabirds inhabiting Cousin Island in the Indian Ocean. *P. grandis* is almost exclusively found on small islands used as seabird colonies in the tropical Indo-Pacific, often being the dominant tree in the forests of these islands. The fruits of this species are enclosed in a calyx that exudes an extremely sticky resin, which strongly adheres to feathers, often entangling birds and causing fatal consequences. However, it remains unclear whether local populations of *P. grandis* have benefited from anthropogenic impacts or whether they are naturally abundant on the islands where they occur. This example reinforces that native plant species can also impact other groups of organisms, such as seabirds, which play an essential role in the functioning of insular ecosystems.

The canopy architecture profoundly influences MFB nesting, as their large size and inability to walk mean that they require flat surfaces for takeoff and landing.[67] Nest sites typically occur on flat tops of small trees or shrubs, predominantly *Avicennia* sp. mangroves,[68] although sea-grape (*Coccoloba uvifera*), cactus, and gumbo limbo (*Bursera simaruba*) have also been documented.[69] Kepler[70] identified *Cynophalla flexuosa* as the most utilized shrub for MFB nesting on Monito Island, Puerto Rico. Our study recorded only four tree species in the MFB nesting area, but with differences in nest numbers among these species, suggesting preferences for nesting architecture.

The return of nesting following the experimental management of an individual of *Ficus luschnathiana* suggests that the habitat became suitable for MFB after the complete removal of *S. americana* from its canopy. This positive effect observed should be implemented alongside periodic monitoring of open areas, as invasive exotic species such as *Melinis minutiflora*, *Megathyrsus maximus*, and *Ricinus communis* are present on Alcatrazes Island[44,71,72] and may disrupt the structure and composition of the local plant community or facilitate wildfires due to the accumulation of dry plant material as fuel.[73–76] The low species richness found in the nesting area may indicate environmental filtering, possibly driven by guano deposition altering soil properties. *C. flexuosa* exhibits wide distribution in the Neotropics and thrives in various soil types, from sandy Restinga[77,78] to acidic soils enriched with seabird guano, as reported by Kepler et al.[70] and in the present study, making it a generalist species compatible with peripheral environments such as islands. Similarly, *Guapira opposita* (Nyctaginaceae) is a common species with widespread distribution in various Atlantic Forest vegetation types.[79]

Island ecosystem: Functioning and conservation challenges

Seabirds play a crucial role in transferring nutrients from vast marine areas to island nesting sites through guano deposition.[37–39,79] Beneath MFB nests, soil nutrient concentrations significantly increase in nitrogen and phosphorus compared with controls, as expected due to the extensive MFB colony and year-round breeding on Alcatrazes Island[53,80] enabling direct guano deposition into the terrestrial ecosystem. Nitrogen, essential for plant physiological functions,[81,82] is abundant in seabird guano, with its isotopes found across various trophic levels in island environments.[37,38] Elevated soil phosphate levels can stimulate highly competitive species, hindering ancient-forest plant growth,[83] potentially limiting and favoring specific plant species in our study's nesting area, such as *S. americana*, which likely withstands high phosphorus levels, possibly due to guano accumulation post-1950s extraction cessation, explaining its recent population expansion. Similar phosphorus concentrations on Cagarra Grande Island, Rio de Janeiro, were reported by Rodrigues et al.,[84] with the high phosphorus concentration attributed to limited plant species occurrence in the significant MFB nesting site on the island.

Tropical forests typically have higher nitrogen levels relative to other nutrients like phosphorus,[85] owing to efficient nitrogen cycling mechanisms.[86–88] However, tropical islands with large seabird colonies serve as notable exceptions, acting as significant phosphorus reservoirs amid typically nitrogen-rich environments. Macfadden et al.[39] found a substantial nutrient influx of essential nutrients by waterbirds from the sea to the soils and vegetation of the mangrove rookery within an island system. However, nutrients brought by birds may not be solely to the terrestrial ecosystems; they could also provide nitrogen to the corals near the island,[38] which, in turn, serve as shelter and food for numerous other marine organisms. Therefore, a loss of suitable nesting areas triggered by *S. americana* could lead to a population reduction of MFB and the subsequent decrease in the nutrients input, which may have cascading consequences on the terrestrial and aquatic ecosystems of the Alcatrazes Island, a nursery for many fish species[89] and home to many endemic animal and plant species.[2,71,72,90–92]

In a nutshell, our study underscores the urgent necessity for expanded research endeavors in island environments within the realm of conservation ecology. Islands, characterized by their unique susceptibility and complexity, present formidable challenges for management and conservation initiatives. Prevention is paramount in these settings, particularly where management encounters significant technical hurdles.[10,12] Our findings emphasize the importance of identifying potentially dominant native species and comprehending their potential impacts on biodiversity loss and ecological services. Additionally, we stress the significance of enhancing understanding regarding the effects of anthropogenic disturbances in vulnerable and underexplored systems such as island ecosystems. Furthermore, we affirm the critical importance of utilizing new technologies, like UAVs, to enhance the study of various ecological aspects in challenging environments, offering valuable insights for effective conservation and management strategies.

Conclusions

Taken together, our results demonstrate the significant impact of a native liana species, *Seguieria americana*, on the Alcatrazes Island ecosystem. As the first study to examine the potential negative consequences of plant super-dominance on avian populations, our findings contribute to further elucidating the role of biotic and abiotic interactions in communities where super-dominant species occur. Although we found evidence of negative interactions between *S. americana* and the MFB population at Alcatrazes Island, the overall picture is more complex. Anthropogenic disturbance probably triggered the super-dominance of *S. americana*, and the presence of a large MFB colony has led to increased soil nutrient concentrations through guano deposition. This nutrient enrichment may favor the growth of *S. americana* at the expense of other plant species. Consequently, a decline in the MFB population due to habitat loss could disrupt nutrient cycling on the island, potentially impacting both terrestrial and aquatic ecosystems. Our study not only informs us about the negative consequences of anthropogenic disturbances but also contains important information to discuss how super-dominant species may be overlooked in current environmental legislation. Traditionally, most studies and management procedures are focused on exotic super-dominant species.[10,12,93] Thus, both the scientific community and public environmental institutions should be aware of how some native species may increase the instability of ecosystems, especially considering the scenario of climate change and highly fragile environments such as islands. These environments often present unique conservation challenges due to their remote location and restricted space. In such circumstances, several logistic challenges may restrict management measures, which are also prone to stochastic events commonly observed in islands.[94,95] Due to their inherent susceptibility to instability, small ecosystems may experience magnified fluctuations in natural population dynamics, potentially escalating these fluctuations into cycles that threaten the persistence of populations.[96] Thus, further research is needed to fully understand the reasons behind this behavioral change of super-dominant species and its potential implications for the island's ecosystem. Future studies should take advantage of genomic data to understand the demographic trends governing the populations of super-dominant species and the changes occurring in the soil microbiome associated with the high abundance of such species. Tracking the community changes after removing super-dominant species will also give an idea about the intensity of the negative and positive interactions. Considering all these contributing factors jointly will provide us with a more complete picture of the ecological origins and consequences of native super-dominant species.

METHODS

Study site and island ecosystem characteristics

We conducted the study on Alcatrazes Island (166 ha; 24° 6′S, 45°41′W), the main island of an archipelago with the same name in southeastern Brazil. The island is an inselberg-like environment, composed mainly of granitic outcrops, situated in the Atlantic Ocean, 35 km away from the mainland (Figures 4A and 4B). It is well known for its stunning biota, and the landscape is mainly composed of rocky outcrops of vegetation, with patches of Atlantic Forest where soil accumulates. The archipelago is considered a nursery for several species of fish[89] and is home to endemic species of plants and animals.[2,71,72,90–92] The archipelago is also an important nesting site for marine birds, hosting the largest breeding concentration of the MFB (*Fregata magnificens*) in the Southern Atlantic, with approximately 6,000 individuals.[53,80] Due to its ecological importance, Alcatrazes Island has been designated as a part of Alcatrazes Wildlife Refuge, a federal non-take protected area since 2016.[44]

Despite its significant ecological relevance, the island has a history of anthropogenic disturbance dating back to the 1910s when three houses were built for lighthouse keepers who resided here for a few years.[44] Part of the native vegetation was cleared for subsistence crops (e.g., sugarcane, banana, and cassava), which persist on the island today. The island also served as a temporary stopover for fishermen[52] and for guano extraction from seabirds, which was used as fertilizer, an activity that extended until the 1990s.[97] Most of the MFB nesting area is located in the western portion of the island, where lighthouse keepers' houses and cultivated fields were established. In the 1970s, the Brazilian Navy began restricting access and conducting shooting exercises for target practice, with targets spread across the island.[44] In 2004, the Northeast portion of the island suffered a large-scale fire caused by a Brazilian Navy training course, destroying 20 hectares of native vegetation, and favoring the proliferation of exotic plants such as *Melinis minutiflora*.[44] Under pressure from environmentalists, such activities were transferred to Sapata Island, a small islet located approximately 4 km northeast of Alcatrazes Island, in 2013.[44] Furthermore, a recent invasion of sun corals (*Tubastrea* spp.), considered one of the main threats to Brazilian coastal marine ecosystems,[98] has been reported in the archipelago.[99]

Description of the studied organisms

Through a floristic survey of the Alcatrazes Island carried out by the first author during 2022 and 2024, we found a significant population of *Seguieria americana* (Phytolaccaceae) in the West portion of the island (Figure 4C). *S. americana* is a thorny liana or small tree species with a wide distribution across South America. In Brazil, it is native and occurs in all regions, with a notable presence in the Southeast and Northeast, particularly within the Atlantic Forest and Caatinga biomes.[100–102] On Alcatrazes Island, the species grows exclusively as a liana. In sites where it has been behaving as a super-dominant species, it densely covers the canopies of trees and shrubs and, in some cases, blankets the ground. The younger branches are very long (some exceed 2.5 m in height) and often grow vertically (Figure S2). When the branches become heavy, they bend, eventually making contact with the soil, where new roots may develop, making the species very difficult to manage.

MFB (Fregatidae) is an imposing seabird found predominantly in tropical and subtropical America, inhabiting coastal regions and islands.[67] With their impressive wingspans ranging from 2.14 to 2.44 m,[103] MFBs are equipped with long, pointed wings and a deeply forked tail, allowing them to gracefully soar for extended periods without requiring continuous flapping, using thermals and wind currents to stay aloft.[67] MFB legs are

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Figure 4. Location and photos of the study area

(A) Geographical location of Alcatrazes Island, state of São Paulo, Southeastern Brazil; (B) an overview of Alcatrazes Island, photo by Luciano Candisani; (C) *Seguieria americana* in the early stages of fruiting, photo by Gabriel Pavan Sabino; (D) nesting site of MFB, photo by Gabriel Pavan Sabino.

extremely short, and they are incapable of typical bipedal walking. Nevertheless, they have strong toes for perching, which this species does on almost any surface from which takeoff is facilitated and visibility is good[104] (Figure 4D). MFBs also play a crucial ecological role in their marine habitats. They are skilled predators that feed on fish or squid near the ocean surface, often engaging in aerial piracy (kleptoparasitism), stealing food from other seabirds.[67] Additionally, their guano (feces) contributes nutrients to island ecosystems, supporting terrestrial food webs.[37–39] MFB nesting sites are exclusively located on islands, typically on flat tops of low bushes or trees. Suitable habitat characteristics are critical for the colonies to thrive.[67,105] In the context of this change of vegetation architecture triggered by anthropogenic disturbances, the staff from the Alcatrazes Wildlife Refuge made an intriguing discovery: a distinct behavioral change among the MFB that nest in the heavily affected West region of the island. These birds started to actively avoid areas where the *S. americana* behaves like a super-dominant species.

Nesting vegetation selection in MFBs

To assess MFB breeding habitat use and classify land cover types within the nesting area, a georeferenced orthomosaic was captured using a DJI AIR2S UAV equipped with an RGB (red, green, and blue) camera and a 1-inch CMOS (complementary metal-oxide-semiconductor) sensor with a resolution of 20 megapixels (5,472 × 3,648). The flight was conducted at a constant altitude of 70 m above sea level and the acquired images were processed using Maps Made Easy (https://www.mapsmadeeasy.com). To classify the 0.52-ha resulting orthomosaic from the images, we used OBIA. This processing was carried out using the Orfeo ToolBox (OTB) package (OTB www.orfeo-toolbox.org) configured in the QGIS (quantum geographic information system) environment, version 3.22 (QGIS.org, 2021). The image segmentation was carried out using the large-scale mean-shift (LSMS) algorithm according to De Luca et al.[106] and Hinojosa-Espinoza et al.[107]

Supervised classification using the support vector machines (SVMs) algorithm was conducted for four categories of land cover: nest, VwoSD, VwSD, and bare soil. Training and validation polygons were manually selected for each land cover class, ensuring a well-balanced distribution among the land cover classes and encompassing different chromatic tones that characterized the study area. Well-distributed geo-coordinates recorded in the field were used for the validation, but prior knowledge of the area was also helpful for the interpretation of the image. We used the default values for the classification algorithms integrated into the OTB.[106,108,109] Classification accuracy evaluation was obtained from the generated confusion matrix, calculating overall accuracy, producer's accuracy, user's accuracy, and the Kappa coefficient.[110] To enhance the classification accuracy, we conducted a manual refinement where the image was overlaid

onto the orthomosaic, allowing for a careful correction of errors. The training polygons played a crucial role in the algorithm's model learning process, while the validation polygons were used to construct the confusion matrix (Table S1).

To evaluate the suitability of vegetation for nesting by MFB, we explored relationships between the areas occupied by nests, the areas inhabited by *S. americana* individuals, and areas with vegetation devoid of *S. americana*. To this end, we first constructed a dataset of these areas by employing a bootstrap resampling procedure with 1,000 permutations on the polygons' dataset, which were classified using the SVM algorithm (as detailed earlier). In each permutation, we randomly selected 10,000 subsequent polygons, constituting 1% of the total classified polygons. The areas were computed as the sums of pixels, in cm^2, from each class in the subset of 10,000 polygons. Here, we excluded areas with bare soil from our analysis, as they do not provide a suitable habitat for MFB. We then employed GAMs from the R package "mgcv[111]" to analyze and visualize the relationship between nest occupancy areas and areas with *S. americana* vegetation, as well as areas with vegetation lacking *S. americana*. Analyses were conducted using R software.[112]

GAMs utilize nonparametric smoothers to flexibly estimate both linear and nonlinear relationships between response and explanatory variables.[113] We set the smooth function to k = 5 to prevent overparameterization and used the Gaussian data family. Finally, we ensured normality, heterogeneity, and homogeneity of model residuals by using the "gam_check" function from the R package mgcv[108]. To better visualize the results in plots, we used the log of areas that were measured in m^2.

To evaluate the tree/shrub species that MFBs prefer for nesting, we also conducted a survey *in situ* by counting MFB nests along five 25-m transects. We tallied the number of nests within each transect for each observed tree/shrub species. Finally, to demonstrate the negative effects of canopy disruption by *S. americana* on MFB nesting, as well as the potential success of species management, we selected a specific tree individual of *Ficus luschnathiana* that was covered by *S. americana* but had no MFB nests. We then managed the canopy, removing the *S. americana* to restore its original architectural aspects, and computed the nests in the following weeks.

Super-dominance and ecosystem properties

To assess the density of *S. americana* in areas with recent historical human-mediated disturbances compared with undisturbed areas, we implemented plots (each measuring 100 m^2) within each designated area based on its extent of occupancy on the island and corresponding landscape characteristics (landscape shape and topography). Thus, we analyzed 6 plots within the disturbed MFB nesting area and examined 13 and 12 plots in 2 forests located in different elevational belts of the island, LF (80–150 m.a.s.l.) and SF (230–275 m.a.s.l.), respectively, both situated outside the nesting area and devoid of historical human-mediated disturbances. Within each plot, we recorded the number of all *S. americana* individuals, including saplings, and tree species with a diameter at breast height (DBH) greater than 5 cm. Given the potential positive geotropism exhibited by *S. americana* at the study site, each ramet was considered an individual. Every stem that was independently rooted and did not appear to be connected to another climbing stem included in the census was treated as a separate individual.[113] To assess differences in tree richness and density of *S. americana* among the sites studied, we utilized the Kruskal-Wallis test. Upon detecting significance, post hoc Dunn tests were employed for pairwise comparisons between individual sites. To compare species accumulation across island categories of land cover, we constructed sample-based rarefaction curves using point count data with the iNEXT (interpolation and extrapolation) package.[114] The rarefaction analyses followed the Hill number framework to estimate three measures of effective species numbers. We extrapolated tree detections to a standardized upper sample size of 100 individuals for direct comparisons and generated 95% confidence intervals for the curves. Differences between curves were considered statistically significant when their confidence intervals did not overlap, which corresponds to a p value of 0.05.[115] Statistical analyses were conducted using R software,[112] with significance set at $\alpha < 0.05$.

To investigate the impact of MFB habitat use on soil properties, we conducted a quantitative analysis of soil nutrients within the study area. Soil samples were gathered from the specified plots (13 within LF, 12 within SF, and 6 at the MFB nesting area). The samples were randomly collected within each plot at a depth of 0–20 cm. Control samples were obtained outside the MFB nesting region (SF and LF plots) to ensure that any observed nutrient effects were specifically attributed to the frigatebirds' nesting activities. For each sample, we quantified macro and micronutrients (Kjeldahl nitrogen, phosphorus, potassium, calcium, magnesium, boron, copper, iron, manganese, zinc, organic matter [OM], cation exchange capacity [CEC], sum of bases [SOB], base saturation [BS], pH, and potential acidity by H+Al−). The soil analysis methodology followed van Raij et al.[116]

Finally, we compared soil variable variations across the study sites using the Kruskal-Wallis test, as described above. Then, to analyze the relationships between tree species compositions and soil variables, we initially assessed floristic variation using NMDS[117] with the Simpson dissimilarity. Ordination analysis was conducted after excluding singletons (species found at a single site),[118] using a Hellinger transformation of binary presence/absence data.[119] Additionally, we computed a 95% confidence level for a multivariate t-distribution.[120] Subsequently, multiple linear regression analysis using ordinary least squares (OLS)[121] was employed to explore the connections between tree composition and soil variables, with the removal of any collinearities (variance inflation factor > 10).[122] Finally, the axes of the NMDS were integrated into the OLS models, and soil variables that were not significant ($p > 0.05$) were eliminated from the models. The analyses were conducted with the R software[112] and using the R package "vegan.[123]"

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to, and will be fulfilled by, the lead contact, Fábio Pinheiro (biopin@unicamp.br).

Materials availability

This study did not generate new, unique materials.

Data and code availability

This paper does not report any original code.

Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

G.P.S., V.d.A.K., and F.P. contributed to the conceptualization of the study, data collection, writing, and analyses. M.L.d.A. and I.K. contributed to the analyses and writing. M.M.T., C.L.B.F., G.N.T., I.M.C., J.S., K.L.L., R.A.P., and P.I.P. assisted with data collection and writing.

DECLARATION OF INTERESTS

The authors declare no competing interests.

SUPPLEMENTAL INFORMATION

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