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ORIGINAL PAPER

# Assessing the impact of an invasive plant in a Protected Natural Area: Island of Cozumel, Mexico

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**Abstract** The Island of Cozumel, located in the Mexican Caribbean, has been granted several protection denominations because of its high biodiversity. However, despite these efforts, several invasive species have been found on the island. Of these, published studies indicate that two plant species are invasive in beach and coastal dune vegetation, but information on their impact on native plant communities is lacking. This study aimed to analyze the impact that the invasive shrub, *Scaevola taccada*, has had on plant species composition, richness, diversity, and community structure of beach and coastal dune vegetation developing on the Island Cozumel. Our results suggest significant impacts on species composition: we observed 34% species turnover between invaded and non-invaded plots. Invaded plots also showed a decreased plant cover and changes in species dominance resulting in altered community structure. *S. taccada* has rarely been studied in Mexico, especially its invasiveness and impact on plant communities. Our results highlight the urgent need for programs to monitor and control the spread of this species throughout the coasts of the Island of Cozumel. Ultimately, the information reported here will be helpful to inform management actions regarding the need to control invasive species in this Biosphere Reserve.

**Resumen** La isla de Cozumel, localizada en el Caribe mexicano, ha recibido diferentes nominaciones de protección debido a su alta biodiversidad. Sin embargo, a pesar de estos esfuerzos, se han encontrado diversas especies invasoras en la isla. De éstas, en los estudios publicados se indica que existen dos plantas invasoras en la playa y dunas Costeras, pero la información sobre su impacto sobre las comunidades vegetales nativas no existe. Este estudio tiene como objetivo analizar el impacto que tiene el arbusto invasivo, *Scaevola taccada*, sobre la composición de especies, riqueza, diversidad y estructura de las comunidades vegetales que se desarrollan en la playa y dunas costeras de las costas de Cozumel. Nuestros resultados parecen indicar impactos significativos en composición de especies: observamos un recambio de especies (34%) entre los cuadros invadidos y no invadidos. Además, en los cuadros invadidos, la cobertura vegetal disminuyó, y la dominancia de especies se modificó, dando como resultado una estructura de la comunidad alterada. Aunque *S. taccada* ha sido poco estudiada en México, especialmente en cuanto a su capacidad invasora e impacto sobre las comunidades vegetales, nuestros resultados resaltan la necesidad ur-

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gente de contar con programas de monitoreo y control de la expansión de la planta invasora a lo largo de las costas de la isla. La información presentada en este trabajo será de utilidad para mejorar las acciones de manejo dirigido al control de la planta invasora en esta reserva de la biosfera.

**Keywords** Cozumel · *Scaevola taccada* · Mexico · Coastal dunes · Biosphere reserve · Invasive plant

## Introduction

With a total surface of 7419.8 km$^2$, the Mexican Insular Territory comprises 2128 islands, of which 294,855 people populate 82. Of these, Cozumel is the third-largest (477 km$^2$) and second most populated (88,626 inhabitants) (INEGI 2020) island in the country. Cozumel receives more than 4 million visitors per year (Datatur 2019), resulting in substantial economic revenues. Besides its socioeconomic relevance, the conservation and protection of Cozumel are considered a priority because of the wide variety of natural ecosystems that develop there. Such ecosystems include coral reefs, seagrass beds, coastal dunes, mangroves, coastal lagoons, and tropical forests (Comité Asesor Nacional sobre el Territorio Insular Mexicano 2012; DOF 2012). Furthermore, the high biodiversity of this island has granted it with several protection denominations, both at national (National Park for its Coral Reefs, Special Protection Area of its Flora and Fauna) international levels (Ramsar site, Biosphere Reserve, Alliance for Zero Extinction) (SEMARNAT 2016; CONANP 2021). In addition, the abundance of endemic and threatened animal species is relevant, primarily for vertebrates such as the emerald hummingbird (*Chlorostilbon forficatus*) and the pygmy raccoon (*Procyon pygmaeus*) (SEMARNAT 2016).

In spite of the conservation efforts mentioned above, several invasive species have been found on Cozumel, and these include the lion-fish (*Pterois volitans*) (Bogdanoff et al. 2018; SEMARNAT 2016), *Boa constrictor* (Martínez-Morales and Cuarón 1999; Vázquez-Domínguez et al. 2012), different frogs (*Eleutherodactylus planirostris*, *Trachycephalus typhonius*) (Palacios-Aguilar et al. 2016), and birds (*Amazona albifrons*) (Plasencia-Vázquez and Escalona-Segura 2012). In addition, several species from the plant species list of Cozumel (Téllez-Valdés and Cabrera-Cano 1987) can be potentially invasive. Invasive plants are defined as those ”*naturalized plants that produce reproductive offspring, often in vast numbers, at considerable distances from parent plants (approximate scales: > 100 m; < 50 years for taxa spreading by seeds and other propagules > 6 m/3 years for taxa spreading by roots, rhizomes, stolons, or creeping stems), and thus have the potential to spread over a considerable area*” (Richardson et al. 2000). Only four plant species have formally reported as invasives in Cozumel. The beach naupaka (sea-lettuce in Mexico) (*Scaevola taccada*) (Castillo-Campos et al. 2021) is the invasive plant most recently reported for the island. It grows on Cozumel's beaches and coastal dunes (Castillo-Campos et al. 2021). *Scaevola taccada* is a tropical shrub native to the Indo-Pacific and typically grows in coastal environments, including coastal dunes and mangroves (GISD 2020). Outside its native distribution range, the plant has been introduced and used in gardening and hedging; it is also frequently found in coconut plantations (GISD 2020).

Worldwide, *S. taccada* has escaped cultivation and is currently invading natural ecosystems, converting the diverse, native coastal dune vegetation into monospecific stands. This rapid expansion has led to the decline of many native species, including *Scaevola plumieri*, which is on the verge of local extinction in many locations, such as the Cayman Islands, Florida (USA) (Clubbe et al. 2010; GISD 2020), Cuba (Oviedo and González-Oliva 2015), Venezuela (Grande and Nozawa 2010) and the Bahamas (Sealey et al. 2014). The effective colonization of bare sand (IUCN 2009) and the high invasiveness of *S. taccada* are associated with the plant's tolerance to salt spray and efficient reproduction through year-round production of seeds and plant fragments that generate roots and become quickly established (GISD 2020). In addition, fruit dimorphism of *S. taccada* enables the species to be effectively dispersed via sea currents (C-morph, with cork and pulp, which facilitate flotation) and by birds and probably other vertebrates (NC-morph, having only pulp) (Emura et al. 2014). These attributes promote successful ecological invasions (Bryson and Carter 2004).

Even though *S. taccada* has been recently described as an invasive species on Cozumel (Castillo-Campos et al. 2021), there is still no evidence of its impact on the native vegetation of the island. The impact of invasives is highly relevant because of the high biodiversity of the island and its conservation nominations (SEMARNAT 2016; CONANP 2021). In particular, coastal dunes are considered very vulnerable to species invasions (Castillo and Moreno-Casasola 1996). However, studies in this regard are relatively scarce. For instance, on the coastal dunes of Southeastern Spain, Gallego-Fernández et al. (2019) found that as the plant cover of the American invasive *Oenothera drummondii* subs. *drummondii* increased, species richness and diversity decreased, and some native plants became locally extinct. Contrasting impacts of the invasive sand sedge *Carex kobomugi* were observed by Charbonneau et al. (2017) on Island Beach State Park, New Jersey, USA. The invasive species reduced the diversity and abundance of plant species and modified dune morphology (Wootton et al. 2005). Nevertheless, the invasive plant protected coastal dunes against erosion more effectively than the dunes covered with the native grass *Ammophila breviligulata*. To our knowledge, the impact of invasive plants on community structure and composition of coastal dunes vegetation has not been addressed in Mexico, although the susceptibility of this ecosystem to the invasion of exotic species has been acknowledged by Castillo and Moreno-Casasola (1996) and Parra-Tabla et al. (2018).

Based on the above, this study analyzes the impact of the invasive plant *S. taccada* on plant species richness, diversity, community structure, and composition of plant communities developing on the coastal dunes of the Island of Cozumel. We hypothesized that the presence of *Scaevola taccada* would have a negative impact on the vegetation by affecting the occurrence and abundance of native plant species. Ultimately, the information reported here will be helpful to inform management actions regarding the need to control invasive species of this Biosphere Reserve.

## Materials and methods

### The invasive plant: *Scaevola taccada*

*Scaevola taccada* is a shrub that grows from 1 to 3 m in height, forming a compact, dense cover of plants. Leaves are green, waxy, succulent, alternately arranged along the stem. Blades are 5–20 cm long and 5–7 cm wide with rounded at the tips. Flowers are 8–12 mm long, white, often with purple streaks, and a pleasant fragrance. In anthesis, when the flower opens, the five petals are left on one side, making it look like the flower is torn in half. Flowers are axillary, located in small clumps near the tip of the branches. Fruits are white fleshy berries about 1 cm long. Seeds are beige, corky, and ridged (Sutar et al. 2017) (Fig. 1).

The native distribution of *S. taccada* includes the tropical and subtropical coasts of SE Asia, the Indian Ocean, and the Pacific Islands. In addition, the species has been introduced to the Caribbean region (Bahamas, Bermuda, Florida, West Indies, including areas of the Caribbean coast and Central and South


**Fig. 1** *Scaevola taccada*. **A** Flowers, **B** fruits, **C** plant covering dune vegetation

America), while in some areas, it has become invasive (CABI.org; Castillo-Campos et al. 2021).

There is no specific information about how and when *S. taccada* was introduced to Mexico or Cozumel. However, it is likely associated with the expansion of tourism along the coasts of Mexico. Cozumel's first hotel was built in 1960, and tourism started to develop in the following decade (the 1970s). It is possible then that *S. taccada* was introduced in the 1970s and 1980s when it was promoted to control beach erosion and used for coastal landscaping in Florida and the Caribbean (CAB International 2021). Currently, the plant is found in the city of San Miguel Cozumel and throughout the island's coasts, and on the Caribbean coast of Mexico (Castillo-Campos et al. 2021).

Study site

The Island of Cozumel is located 17.5 km off the eastern coast of the Yucatan Peninsula in the state of Quintana Roo, Mexico (20° 31' N and 87° 30' W; Fig. 2). The island is located in the Mexican southeast and is surrounded by the waters of the Caribbean Sea. The climate is warm subhumid with an average annual temperature of 26 to 27 °C and a total annual rainfall varying between 800 and 1500 mm. The driest months are March and April, and September has the highest amount of rain (Orellana et al. 2007). The island's eastern shoreline is exposed to tropical storms, which occur every year during the summer months (Téllez-Valdés et al. 1989). The island is made of limestone material, making the soil very permeable, so the water drains quickly (Téllez-Valdés

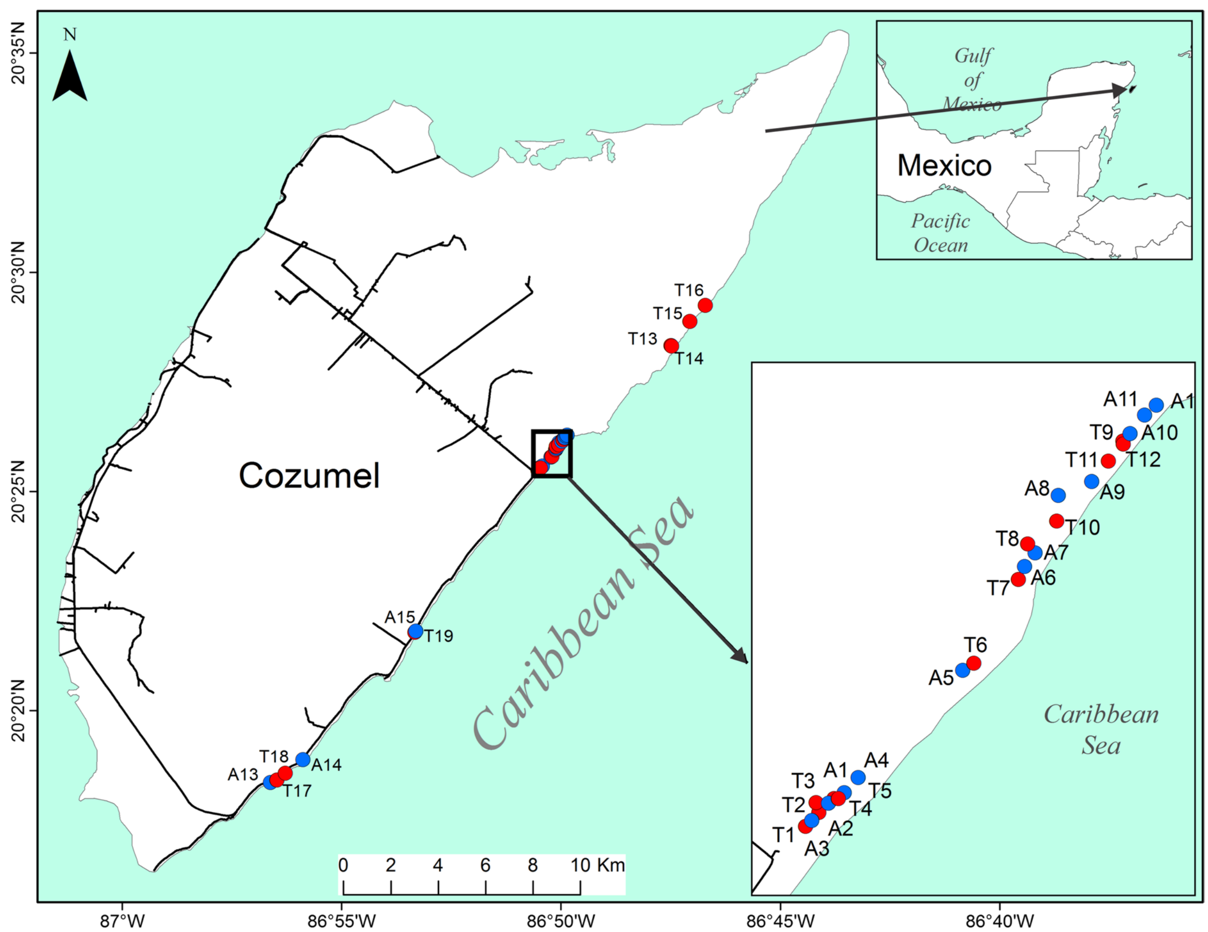


**Fig. 2** Study site and sampling points with the invasive plant, *Scaevola taccada* (red dots) and without the invasive plant (blue dots), on the Island of Cozumel, Mexico

et al. 1989). The vegetation types that characterize the island include medium to low height sub-deciduous forests, mangroves, wetlands, and coastal dune vegetation (Téllez-Valdés et al. 1989; Flores and Espejel 1994; Collantes-Chávez-Costa et al. 2019).

Because Cozumel was never attached to the continent, it is classified as an oceanic island of coral origin (SEMARNAT 2016). This isolation made it a favorable site for the evolution of endemism since, except for some taxonomic groups, populations cannot migrate from or into other territories. Nevertheless, knowledge about the endemic species is scarce. The Instituto de Biodiversidad y Áreas Naturales Protegidas de Quintana Roo (Institute of Biodiversity and Protected Natural Areas of the State of Quintana Roo) (IBANQROO 2016) reports 31 endemic species on the island, of which 19 are birds, 7 are mammals, 4 invertebrates and y 1 reptile. Furthermore, in the management program of the island, 34 species are listed as in need of special protection, 26 are threatened, six are at risk of extinction, and two are locally extinct (SEMARNAT 2016). From the 313 plant species that have been described for Cozumel, only six are designated as threatened (palm trees and mangroves), and four are considered as invasives: *Cocos nucifera*, *Casuarina equisetifolia*, and *Terminalia catapa* (CONANP 2020), and recently, *Scaevola taccada* (Castillo-Campos et al. 2021) was added to the list of invasive plants on the island.

## Vegetation sampling

The study took place on the island's eastern coast (Fig. 2), where coastal dune vegetation is included within the "Area for special protection of flora and fauna of Cozumel." Here, the impact of tourism is reduced because human activities are restricted (DOF 2012; SEMARNAT 2016). However, an abundant population of *S. taccada* was previously found by Castillo-Campos et al. (2021), even though it is a preserved site. Therefore, we randomly set 10 m × 10 m plots to determine the potential impact of *S. taccada* on the woody vegetation developing on the coastal dunes. Additionally, herbaceous vegetation was sampled in three 2 m × 2 m sub-plots randomly placed within each 10 m × 10 m plot. As much as possible, the larger 10 m × 10 m plots were placed in a pairwise manner so that we had one where *S. taccada* was present and its nearby counterpart where the invasive shrub was absent. However, the location of our plots does not represent a pairwise sampling design since we were not able to have the same number of plots with and without it. We chose the counterparts based on floristic associations: plots with and without the invasive plant, all placed on the beach and coastal dunes. Because of the high abundance of *S. taccada*, we had a total of 19 plots (1900 $m^2$) with the invasive and 15 (1500 $m^2$) without it. Therefore, we had 57 sub-plots (228 $m^2$) set to sample herbaceous vegetation in those plots with *S. taccada* and 45 (180 $m^2$) where the invasive was absent. We registered all the species present in each plot and the corresponding percent cover of each one, which was visually estimated. As the plants overlap, the total coverage in several plots was greater than 100 $m^2$.

Unfortunately, we were not able to collect botanical specimens because of the protection status of the island. Therefore, when species were unknown to us, we shot high-quality photographs with a Canon camera and a 20 × pocket magnifying lens. We used these photographs for species determination by comparing the images with the collected specimens stored in the national herbaria (MEXU, XAL, and ENCB) as well as available electronic databases (Tropicos.org) and floristic lists previously published for Cozumel (Téllez-Valdés and Cabrera-Cano 1987; Collantes-Chávez-Costa et al. 2019). Finally, we created a single species list in which growth forms (trees, shrubs, and herbs) were added.

## Data analyses

We first assessed the efficiency of our sampling effort by calculating the expected species richness with iNext online software (Chao et al. 2016). With this, we determined if the number of species found in our plots was representative of the coastal dunes plant communities. We thus compared observed species richness from our field data with extrapolated (expected) species richness, which considers undetected species.

After testing data for normality (with Shapiro–Wilk test $W = 0.9755$, $P = 0.6267$), we used a t-test to look for significant differences between total plant cover in plots with and without the invasive plant. This analysis was performed without considering the cover of *S. taccada* because we aimed to determine if plant cover was affected by the occurrence of this invasive. Later, the impact of an increasing cover of *S. taccada* on the cover of the most abundant species was tested through individual linear regressions.

Diversity was calculated by using the concept of "effective numbers of species" (Jost 2006), a method that is equivalent to Hill's number (Hill 1973). This method has mathematical properties that accurately capture the diversity concept and facilitates the comparison in diversity between contrasting conditions, (Cultid-Medina and Escobar 2016; Jost 2006). The method is based on the following equation:

$$^{q}D \equiv \left( \sum_{i=1}^{S} P_i^q \right)^{1/(1-q)}$$

where $^{q}D$ is the diversity of the community according to the chosen diversity index (Jost 2006). It depends on the proportional abundance per species ($P_i$) and the exponent $q$ (Cultid-Medina and Escobar 2016; Jost 2006). The exponent and superscript q is called the "order of diversity" and indicates the sensitivity to common and rare species (sensitivity to species abundance). The q values used were: 0 ($^{o}D$) is the species richness, 1 ($^{1}D$) emphasizes evenness among species abundances (Shannon diversity), and 2 ($^{2}D$) which weighs dominant species more heavily than rare species (Simpson diversity) (Jost 2006). Diversity-area curves were calculated for plots with and without *S. taccada* (iNEXT; iNterpolation and EXTrapolation). The 100 randomizations were automatically performed to soften the curves and create a continuous line in the extrapolation curve. In addition, the number of incidences (presence of species in each plot) was doubled to estimate how the curve would behave if the sampling effort doubled (Chao et al. 2012).

We used two-way cluster analysis to determine similarities in species composition between the two conditions, with data from the plots with and without *S. taccada*. We used the Bray–Curtis dissimilarity and the Group Average clustering methods with the mean calculated plant cover for each species for each plot. Statistical differences between the groups identified through the clustering method were tested with the multi-response permutation procedure (MRPP). Then, the most relevant species for each group were determined through an Indicator Species Analyses (ISA) at $P < 0.05$, which enabled us to identify the species most affected by the presence or absence of *Scaevola*. These statistical analyses were made using PCORD version 6 (McCune and Grace 2002).

Finally, we determined changes in community structure and species dominance for plots with and without *S. taccada* through ranked relative importance plots. For each condition, we calculated the Relative Importance Value for each species by adding relative frequency (the number of plots where each species was observed divided by the total frequency) and relative cover (the total cover per species divided by the total plant cover). The result was divided by two and multiplied by 100 to have percent values, facilitating comparisons between species and conditions (Brower and Zar 1977). Data analyses were performed using several statistical packages: Statistica (StatSoft 2004) and R studio 1.0.136 (R Core Team 2019; iNEXT; iNterpolation and EXTrapolation).

## Results

### Species composition, richness, and diversity

We found a total of 32 species belonging to 28 genera and 19 families (Table 1). Fifteen species were herbs, 12 shrubs, and five trees. A total of 27 species was found in plots with *S. taccada* and 26 in plots without it, and of these, 21 species occurred in both conditions. The dissimilarity between plots with and without the invasive was moderate since 11 species (34%) were not shared between the two types of plots. The above means that the similarity between plots with and without *S. taccada* was 66%. Four herbaceous species (27% of the total number of herbaceous species), five shrubs (42%), and two trees (40%) were not shared between conditions. Furthermore, the occurrence of *S. taccada* altered the natural species turnover between plots with and without the invasive. The mean similarity between plots without *S. taccada* was 23%, with a maximum value of 60%; very few pairs of plots (7%) showed similarities greater than 50%, whereas 17% had similarities lower than 10%. In contrast, the mean similarity between plots with *S. taccada* was 35%, with a maximum value of 83%.

**Table 1** List of species found on the beach and coastal dunes along the coast of the Island of Cozumel with and without the invasive shrub S. taccada

| Species (Family) | GF | Acron | With *S. taccada* | | | | Without *S. taccada* | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | Total cover ($m^2$) | Total Freq | Relative cover | Mean cover per plot ($m^2$) (std) | Total cover ($m^2$) | Total Freq | Relative cover | Mean cover per plot ($m^2$) (std) |
| *Ambrosia hispida* Pursh (Asteraceae) | H | Amb-his | 605 | 10 | 0.44 | 60.5 (31.8) | 685 | 10 | 0.19 | 68.5 (24) |
| *Borrichia arborescens* (L.) DC. (Asteraceae) | S | Bor-arb | 0 | 0 | 0 | 0 | 5 | 1 | 0.001 | 5 (0.0) |
| *Borrichia frutescens* (L.) DC. (Asteraceae) | S | Bor-fru | 16 | 2 | 0.01 | 8 (0.1) | 40 | 3 | 0.01 | 13.3 (10.4) |
| *Cakile lanceolata* (Willd.) O.E. Schulz (Brassicaceae) | H | Cak-lan | 5 | 1 | 0.004 | 5 (0.0) | 41 | 4 | 0.01 | 10.3 (10.5) |
| *Canavalia rosea* (Sw.) DC. (Fabaceae) | H | Can-ros | 81 | 2 | 0.06 | 40.5 (55.9) | 35 | 3 | 0.01 | 11.7 (7.6) |
| *Cenchrus pauciflorus* Benth. (Poaceae) | H | Cen-pau | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 (0.0) |
| *Coccoloba uvifera* (L.) L. (Polygonaceae) | T | Coc-uvi | 198 | 6 | 0.14 | 33 (29.8) | 430 | 11 | 0.12 | 39.1 (29.5) |
| *Cocos nucifera* L. (Arecaceae) | T | Coc-nuc | 20 | 1 | 0.01 | 20 (0.0) | 0 | 0 | 0 | 0 |
| *Conocarpus erectus* L. (Combretaceae) | T | Con-ere | 253 | 6 | 0.18 | 42.2 (29.8) | 90 | 3 | 0.02 | 30 (8.7) |
| *Crotalaria pumila* Ortega (Fabaceae) | H | Cro-pum | 18 | 2 | 0.01 | 9 (1.4) | 0 | 0 | 0 | 0 |
| *Ernodea littoralis* Sw. (Rubiaceae) | S | Ern-lit | 25 | 1 | 0.02 | 25 (0.0) | 6 | 2 | 0.002 | 3 (0.0) |
| *Euphorbia mesembryanthemifolia* Jacq. (Euphorbiaceae) | S | Eup-mes | 3 | 1 | 0.002 | 3 (0.0) | 7 | 3 | 0.002 | 2.3 (2.3) |
| *Euphorbia trichotoma* Millsp. (Euphorbiaceae) | H | Eup-tri | 100 | 9 | 0.07 | 11.1 (19.2) | 68 | 11 | 0.02 | 6.2 (5.9) |
| *Hymenocallis littoralis* (Jacq.) Salisb. (Amaryllidaceae) | H | Hym-lit | 26 | 3 | 0.63 | | 3 | 1 | 0.082 | 3 (0.0) |
| *Ipomoea pes-caprae* (L.) R. Br. (Convolvulaceae) | H | Ipo-pes | 338 | 7 | 0.25 | 48.3 (37.9) | 181 | 6 | 0.05 | 30.2 (29.6) |
| *Lantana involucrata* L. (Verbenaceae) | S | Lan-inv | 50 | 3 | 0.04 | 16.7 (7.6) | 31 | 5 | 0.01 | 6.2 (4.7) |
| *Lippia graveolens* Kunth (Verbenaceae) | S | Lip-gra | 20 | 1 | 0.01 | 20 (0.0) | 0 | 0 | 0 | 0 |

**Table 1** (continued)

| Species (Family) | GF | Acron | With *S. taccada* | | | | Without *S. taccada* | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | Total cover ($m^2$) | Total Freq | Relative cover | Mean cover per plot ($m^2$) (std) | Total cover ($m^2$) | Total Freq | Relative cover | Mean cover per plot ($m^2$) (std) |
| *Melanthera aspera* (Jacq.) Steud. ex Small (Asteraceae) | H | Mel-asp | 15 | 2 | 0.01 | 7.5 (3.5) | 40 | 1 | 0.01 | 40 (0.0) |
| *Metastelma schlechtendalii* Decne. (Apocynaceae) | H | Met-sch | 3 | 1 | 0 | 3 (0.0) | 0 | 0 | 0 | 0 (0.0) |
| *Panicum virgatum* L. (Poaceae) | H | Pan-vir | 400 | 6 | 0.29 | 66.7 (21.6) | 320 | 6 | 0.09 | 53.3 (32.5) |
| *Persea americana* Mill. (Lauraceae) | S | Per-ame | 0 | 0 | 0 | 3 (0.0) | 0 | 1 | 0.0005 | 2 (0.0) |
| *Pithecellobium keyense* Britton (Fabaceae) | T | Pit-key | 0 | 0 | 0 | 0 | 1 | 1 | 0.0003 | 1 (0.0) |
| *Portulaca oleracea* L. (Portulacaceae) | H | Por-ole | 1 | 1 | 0.001 | 1 (0.0) | 0 | 0 | 0 | 0 |
| *Rachicallis americana* (Jacq.) Hitchc. (Rubiaceae) | S | Rac-ame | 0 | 0 | 0 | 0 | 5 | 1 | 0.001 | 5 (0.0) |
| *Scaevola plumieri* (L.) Vahl (Goodeniaceae) | S | Sca-plu | 0 | 0 | 0 | 0 | 80 | 1 | 0.02 | 80 (0.0) |
| *Scaevola taccada* (Gaertn.) Roxb. (Goodeniaceae) | S | Sca-tac | 1037 | 19 | 0.76 | 54.6 (32.6) | 25 | 1 | 0.01 | 25 (0.0) |
| *Sesuvium portulacastrum* (L.) L. (Aizoaceae) | H | Ses-por | 93 | 8 | 0.07 | 11.6 12.6) | 416 | 8 | 0.11 | 52 (35.2) |
| *Sporobolus virginicus* (L.) Kunth (Poaceae) | H | Spo-vir | 191 | 12 | 0.14 | 15.9 (14) | 354 | 12 | 0.1 | 29.5 (23) |
| *Suriana maritima* L. (Surianaceae) | S | Sur-mar | 262 | 11 | 0.19 | 23.8 (11.6) | 265 | 6 | 0.07 | 44.2 (24.6) |
| *Tephrosia cinerea* (L.) Pers. (Fabaceae) | H | Tep-cin | 75 | 4 | 0.05 | 18.8 (17) | 98 | 4 | 0.03 | 24.5 (15.6) |
| *Thrinax radiata* Lodd. ex Schult. & Schult. f. (Arecaceae) | T | Thr-rad | 16 | 2 | 0.01 | 8 (9.9) | 14 | 3 | 0 | 4.7 (3.5) |
| *Tournefortia gnaphalodes* (L.) R. Br. ex Roem. & Schult. (Heliotropiaceae) | S | Tou-gna | 287 | 17 | 0.21 | 16.9 (12.4) | 433 | 13 | 0.12 | 33.3 (20.8) |

GF = Growth form; H = herb; S = shrub; T = tree; Acron = species acronym; std = standard deviation of the mean. Total cover values represent plant cover ($m^2$) per species after adding values in all plots. Total frequency (Total Freq) shows the total number of plots where each species was observed; Relative cover is relative to the added coverage from all plants in all plots with and without *S. taccada*; Mean cover per plot is the result of dividing the total cover by frequency of each species

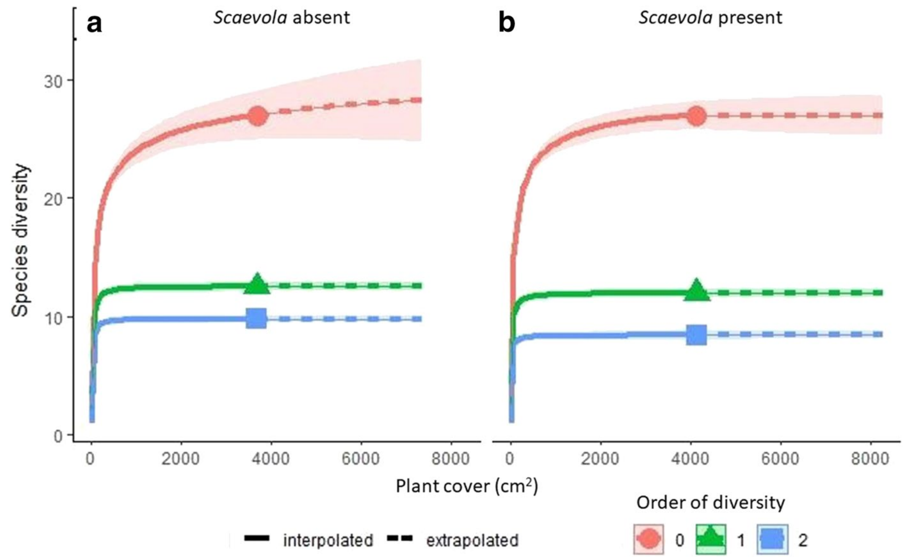


**Fig. 3** Species diversity based on Hill's numbers from cover values recorded in plots without (**a**) and with (**b**) *S. taccada* on the Island of Cozumel, Mexico. Orders of diversity: 0 corresponds to richness, 1 to Shannon's and 2 to Simpson's diversity. The extrapolation curves of species diversity in both conditions are shown by the discontinuous lines. Shadows show 95% confidence intervals

19% of the comparisons had a similarity > 50% in these plots, and only 2% showed similarity percentages < 10%. The above is indicative of a trend towards homogenization when *S. taccada* is present.

The analyses performed with the 95% CI did not reveal significant differences for any order of diversity ($^{o}D$, $^{1}D$, $^{2}D$) in any of the conditions (Fig. 3). The lack of significance means that differences in neither species richness nor the evenness or dominance of species varied significantly due to the occurrence of *S. taccada*. Furthermore, the extrapolation curve showed that the species diversity would not increase noticeably if the sampling effort doubled (Fig. 3).

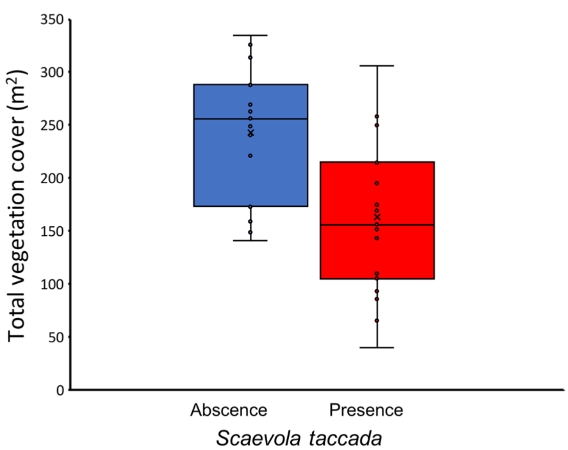


**Fig. 4** Total vegetation cover per plot in the absence and presence of *S. taccada* ($t = 3.484$, $P = 0.0015$). Total cover is greater than the sampled surface due to overlap between species

## Community structure and species dominance

Plant cover was affected by the occurrence of *S. taccada*. It was significantly higher when this species was absent compared to plots where *S. taccada* was found ($t = 3.484$, $P = 0.0015$; Fig. 4).

The impact of *S. taccada* on plant cover was not species-specific, except for *Tournefortia gnaphalodes*. In this case, regression analyses showed a significantly negative correlation between both species (Fig. 5). When plant cover of *S. taccada* was

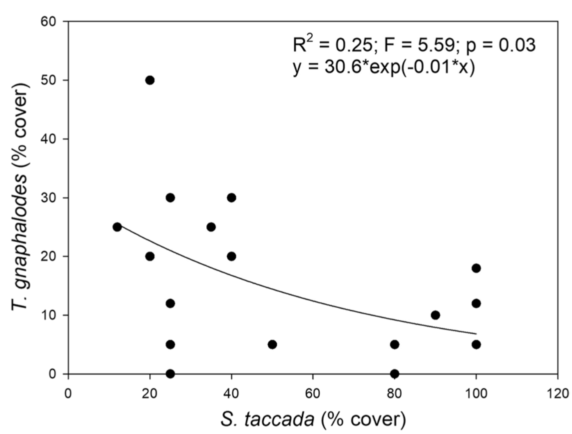


**Fig. 5** Negative correlation observed between plant cover of the invasive *S. taccada* and the native *T. gnaphalodes*

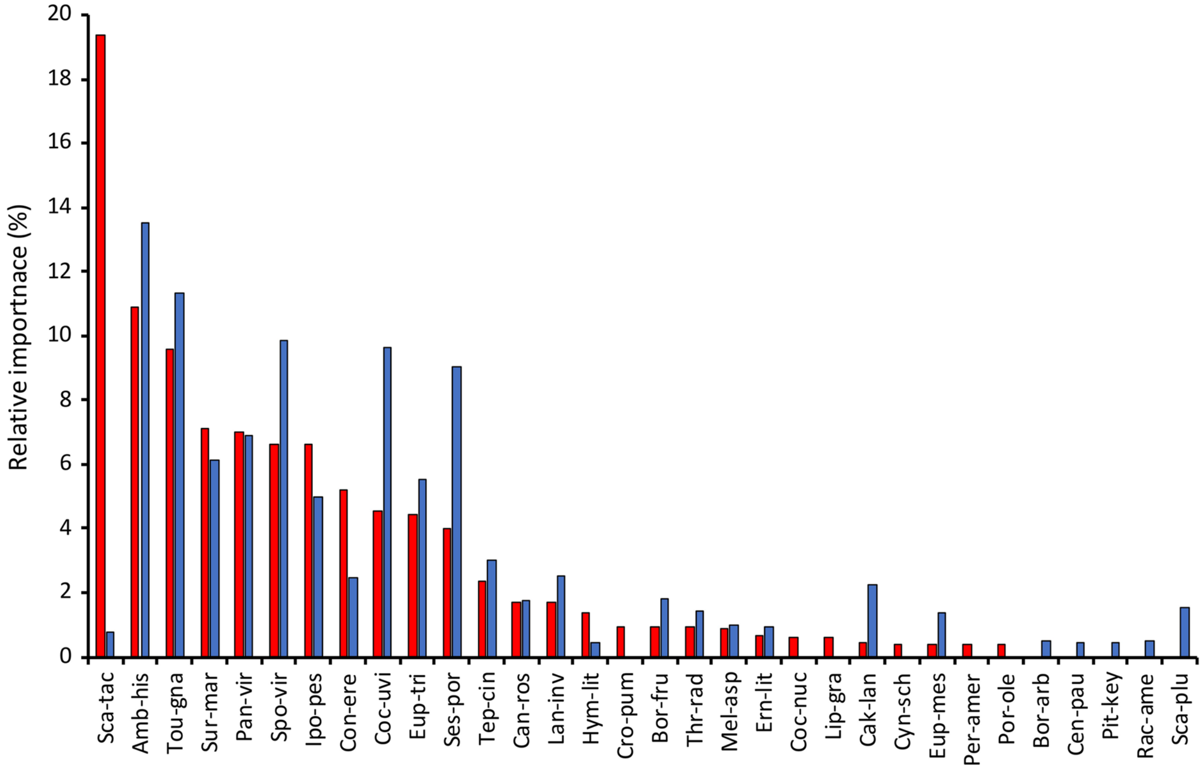


**Fig. 6** Relative importance values for species registered in the coastal vegetation of the Island of Cozumel. Red bars indicate presence of *S. taccada*; blue bars absence. Species acronyms are shown in Table 1

below 40%, there seemed to be no negative impact on the plant cover of *T. gnaphalodes*. Nevertheless, *T. gnaphalodes* decreased noticeably as *S. taccada* approached 100% plant cover.

The Relative Importance Value (RIV) of each species differed between the two conditions. Some species, such as *Ambrosia hispida, Cocoloba uvifera, Lantana involucrata, Sesuvium portulacastrum, Sporobolus virginicus, Tournefortia gnaphalodes*, and *Cakile lanceolata*, were more dominant in the absence of *S. taccada*. Their cover decreased when there was a coincidence with the invasive. In contrast, the relative importance values of *Ipomoea pes-caprae, Suriana maritima*, and *Conocarpus erectus* were higher in plots with *S. taccada* (Fig. 6).

The dendrogram shows how species abundance changed between conditions, with and without *S. taccada* (P and A respectively). Based on species composition and abundance, we found three groups (Fig. 7; Table 2), which were significantly different (MRPP, $A = 0.1211$, $P < 0.0001$). Five species were indicators of these groups. Group 1 (G1) concentrated most plots with only one indicator species, the dominant and invasive *S. taccada* (Table 2). However, other woody species such as *S. maritima, C. uvifera, and T. gnaphalodes* were observed coexisting with the invasive (Fig. 7). Several herbaceous species, such as *Ambrosia hispida, Panicum virgatum*, and *Hymenocallis littoralis*, were indicators of Group 2 (G2), where *S. taccada* also occurred but with a lower plant cover. Finally, Group 3 (G3) comprised all plots where *S. taccada* was absent, and the only indicator species was *C. uvifera*. Additional shrubby species (*S. maritima* and *T. gnaphalodes*), but with a lower plant cover, also were included in this group. Several herbaceous species were relatively abundant (*S. portulacastrum, S. virginicus, A. hispida*) when *S. taccada* was absent.

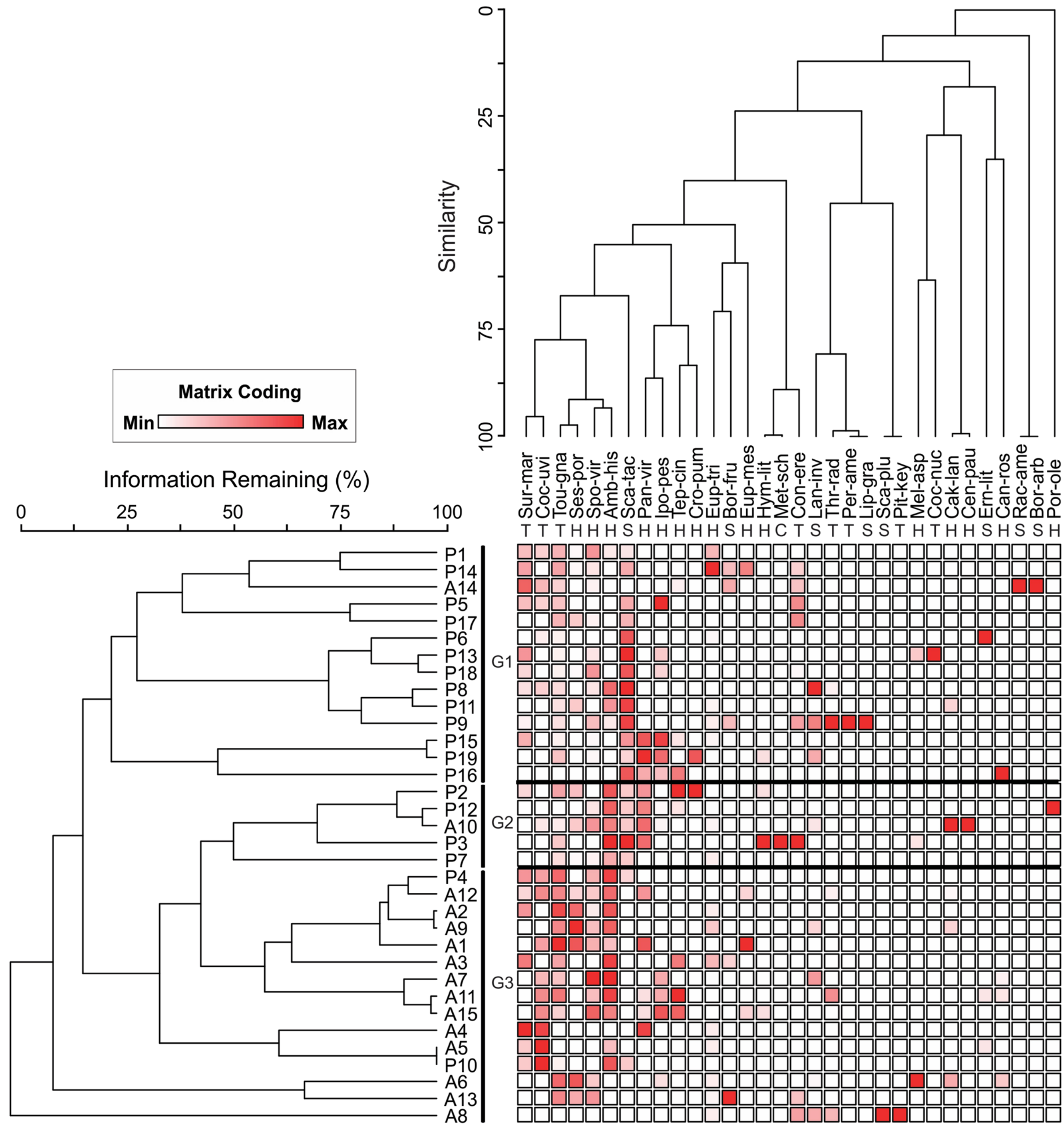


**Fig. 7** Two-way cluster analyses. Cluster analyses were performed to distinguish between plots with and without *S. taccada* (dendrogram to the left), and between plots according to the species found in them (dendrogram on the top). P: sites with *S. taccada* (Present) A: Sites without *S. taccada* (absent). Species acronyms are shown in Table 1. Red indicates species occurrence in the sampled plots; the intensity shows relative abundance; darker tones have higher abundances. T = trees; S = Shrubs; H = Herbs. The thick horizontal lines were drawn to distinguish the three groups (G1, G2 and G3) that were formed in the dendrogram of plots with and without *S. taccada*

**Table 2** Results of indicator species analysis (ISA), with the most relevant species for each group determined by the two-way cluster analysis

| Scientific name | Group | IV | Mean | SD | *P* |
|---|---|---|---|---|---|
| *Scaevola taccada* | 1 | 53.5 | 31.5 | 7.8 | 0.016 |
| *Ambrosia hispida* | 2 | 53.0 | 30.9 | 7.53 | 0.016 |
| *Panicum virgatum* | 2 | 48.6 | 23.8 | 8.64 | 0.022 |
| *Hymenocallis littoralis* | 2 | 36.7 | 14.8 | 7.93 | 0.040 |
| *Coccoloba uvifera* | 3 | 47.6 | 27.2 | 8.8 | 0.035 |

*Significances of indicator values (IV) are shown. SD = standard deviation*

## Discussion

Recently, the global analysis performed by Dawson et al. (2017) revealed that hotspots with a higher number of established alien species are predominantly located on islands and coastal mainland regions because aliens more readily invade them. Specifically, coastal dunes are considered highly invasible because of recurring disturbances, environmental heterogeneity, and reduced plant cover and species richness, facilitating the arrival and establishment of exotic aliens (Castillo and Moreno-Casasola 1996; Acosta et al. 2006; Giulio et al. 2020; Gallego-Fernández et al. 2019). Examples of species invasions on coastal dunes are manifold and occur on different coasts and countries, most of them with severe impacts on native species. Examples include the genus *Acacia* in Europe (Lorenzo et al. 2010); *Ammophila arenaria* in South Africa (Hertling and Lubke 2000); *Carpobrotus edulis* in Portugal (Souza-Alonso and González 2017); *Oenothera drummondii* in Spain (Gallego-Fernández et al. 2019) and even worldwide species invasions (Tordoni et al. 2019, 2020). In Mexico, however, only two studies analyze in detail the occurrence of invasive plants on coastal dunes (Castillo and Moreno-Casasola 1996; Parra-Tabla et al. 2018).

Additionally, the National Commission for the Conservation and Use of Biodiversity (CONABIO) reports seven invasive plant species occurring on natural protected areas (Comité Asesor Nacional sobre Especies Invasoras 2010). Three have been found growing on coastal dunes (*Arundo donax, Cynodon dactylon*, and *Casuarina equisetifolia*). In Cozumel, only three plant species have been officially considered exotic invasives: *Casuarina equisetifolia, Cocos nucifera,* and *Terminalia catapa* (CONANP 2020).

Based on the findings by Castillo-Campos et al. (2021) regarding the occurrence of *S. taccada* as an invasive species on the island of Cozumel, in this study, we quantitatively explored the impact of a recently reported invasive species on local plant communities. Our findings show that: a) species richness and diversity did not vary noticeably, although a difference in species turnover occurred; b) plant cover, community structure, and species dominance differed significantly when *S. taccada* was present.

### Species composition, richness, and diversity

The impact of invasive plants on plant communities developing on coastal dunes is diverse. Some studies show changes in species composition, richness, and diversity, while others reveal moderate or no alterations. In general, the impact of exotic plants on native plant communities has not been studied in detail on Mexican coastal dunes. However, the incipient evidence shows that invasive species may play a relevant role in coastal dune plant communities. For example, Parra-Tabla et al. (2018) noted that 26% of total plant species richness from the northern Yucatan Peninsula was invasive.

Nevertheless, these authors stated that apparently, these species did not seem to have a significant impact on diversity patterns. In turn, Castillo and Moreno-Casasola (1996) state that species from different vegetation types, which occasionally grow on coastal dunes, increase the richness of dune flora but pose potential problems for dune conservation since they may become invasive. Thus, in both studies, the authors warn against the potentially detrimental consequences of the increasing dominance of these invasives on native plant communities.

Unlike the study by Parra-Tabla et al. (2018), our results reveal a significant impact of *S. taccada* on species composition, showing 34% dissimilarity between invaded and non-invaded plots. The reduced species turnover observed between plots with the invasive and plots without could be indicative of a reduction in heterogeneity as the plant communities become homogenized with an increasing cover of the invasive shrub. An alternative explanation could be that *S. taccada* invades specific habitats resulting in more homogeneous *Scaevola* plots relative to non-scaevola plots, because the habitats originally invaded were similar in the first place. In this sense, because we did not collect data on temporal changes, we cannot demonstrate that homogenization (or lack of it) is caused by *Scaevola*.

However, differences in terms of species richness and diversity were not significant. Similar trends have been quantified on islands (Kueffer et al. 2010) and coastal dunes systems elsewhere (Doody 2012; Giulio et al. 2020). Specifically, islands have shown severe effects of invasive plant species. For example, in Hawaii, *Verbesina encelioides* reduced species richness (Feenstra and Clements 2008). In The Bahamas, invasive plant species were considered the most relevant factors negatively affecting community diversity (Sealey et al. 2014). Like our results, these authors found an increasing species turnover as invasive species expanded their distribution. Nevertheless, they observed a decrease in species richness which did not coincide with our findings.

### Community structure and species dominance

Although not frequently studied in detail, one of the most relevant impacts of invasive plants is the overwhelming change in community structure and species dominance. For instance, Doody (2012) showed how several introduced plants have become highly dominant (and invasive) on coastal dunes worldwide. Examples include *Ammophila arenaria* in North America, Australia, New Zealand, and South Africa; *Hippophae rhamnoides* in England and Ireland; *Rosa rugosa* and *Carpobrotus edulis* in Europe (Doody 2012).

Previous data on the impact of invasive plant species on Mexican coastal dunes do not show an extreme impact in terms of species dominance (Castillo and Moreno-Casasola 1996; Parra-Tabla et al. 2018). In contrast, our observations reveal changes in plant cover, which was higher in the absence of the *S. taccada* and altered species dominance. Specifically, the plant cover of the indicator species (i.e., *C. uvifera*, *S. maritima*, and *S. portulacastrum*) was not significantly affected by *S. taccada*. However, its impact on the plant cover of the native shrub, *Tournefortia gnaphalodes*, was significantly negative. Similar to our results, in Southern Spain, Gallego-Fernández et al. (2019) also observed a decrease in plant cover where the invasive herb (*Oenothera drumondii*) occurred.

Furthermore, Acosta et al. (2008) found that changes in community structure varied according to growth forms, with phanerophytes being the most dominant invasive plants. However, Acosta et al. (2006) observed that alien invasive plants had functional traits similar to native plants growing in different communities of the coastal dune zonation gradient from the beach inland. In this case, invasive alien species were associated with two major plant strategies: annual invasive aliens (quick-to-mature low grasses and herbs) and perennial invasive aliens (taller and often strongly clonal). Thus, the expansion of *S. taccada* along the coast of Cozumel is probably associated with its functional traits such as rapid growth rate, effective reproduction with fruits year-round, and efficient seed dispersal through the local fauna which eat the fruits, as well as ocean currents (Castillo-Campos et al. 2021; Gallego-Fernández et al. 2021; Emura et al. 2014).

### Invasiveness of *S. taccada*

*Scaevola taccada* is included in The Global Invasive Species Database (GISD 2020). Here, it is listed as an exotic invasive in 31 countries, although Mexico is not mentioned. Studies on the impact of *S. taccada* as an invasive plant on coastal dune habitats are still limited. However, Clubbe et al. (2010) acknowledged that *S. taccada* was introduced to the Cayman Islands as a landscaping plant, and it is widely used for hedging. Here, it escaped cultivation and has invaded native coastal dune vegetation, turning it into a monoculture of this fast-growing invasive. The expanding *S. taccada* has rendered many species in decline in the Cayman Islands, including the native *S. plumieri*, almost locally extinct. It has also been reported as an invasive plant in Cuba, with a coastal flora similar to Cozumel's (Oviedo and González-Oliva 2015). In Venezuela, this exotic shrub also was introduced for gardening and is now considered naturalized (Grande and Nozawa 2010). In these countries, the impact on native plant communities was not determined quantitatively.

Except for Castillo-Campos et al. (2021), *S. taccada* has remained invisible to the scientific literature and governmental publications by National

Protected Areas Commission and The National Advisory Committee on Invasive Species (Comité Asesor Nacional sobre Especies Invasoras 2010 and CONABIO 2020). This is relevant because of its potential high impact on plant communities developing on coastal dunes, as shown in this study. Furthermore, evidence from multiple studies confirms that it is an efficient invasive plant, decreasing plant cover of native species and altering community structure by modifying species dominance. Indeed, care is necessary to monitor and eradicate the expansion of *S. taccada*, especially in a Biosphere reserve such as Cozumel.

## Conclusions

Oceanic islands, like Cozumel, and coastal dunes, have long been considered particularly vulnerable to biotic invasions. Thus, in this study, we aimed to analyze the impact that the invasive plant *S. taccada* has had on plant species richness, diversity, community structure, and composition of the vegetation developing on coastal dunes on the Island of Cozumel in South-Eastern Mexico. Our results showed no relevant changes in terms of species richness and diversity. Nevertheless, we observed that the invasive plant seems to modify species composition, with a 34% species turnover, decreased plant cover, and changed species dominance resulting in altered community structure. Even though this species has rarely been studied in Mexico, especially in terms of its invasiveness and impact on plant communities, our results highlight the urgent need for programs to monitor and control the spread of this species throughout the coasts of the Island of Cozumel, which is a Biosphere Reserve. The information reported here serves as a stepping-stone to understanding the invasion processes and mechanisms from which improved management and control actions can be developed. Controlling invasive species is particularly relevant given Cozumel's high biodiversity and the vulnerability of oceanic islands to biological invasions.

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**Authors' contributions** Gonzalo Castillo-Campos and José G. García-Franco contributed to the study conception and design; Gonzalo Castillo-Campos, José G. García-Franco and Jesús Pale Pale collected field data; all authors contributed with data analyses; the first draft of the manuscript was written by M. Luisa Martínez and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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**Availability of data and material** The datasets generated during and/or analyzed during the current study are not publicly available because of confidentiality restrictions of the project but are available from the corresponding author on reasonable request.

**Code availability** Not applicable.

**Declarations**

**Conflict of interest** The authors declare no conflicts of interests.

**Ethics approval** Not applicable.

**Consent to participate** All authors read and approved the final manuscript.

**Consent for publication** All authors read and approved the final manuscript.

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