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Research Article

Structural and diversity changes in coastal dunes from the Mexican Caribbean: the case of the invasive Australian pine (*Casuarina equisetifolia*)

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Abstract

The coastal dune at the natural protected area of Cozumel Island has been impacted by the invasive Australian pine (*Casuarina equisetifolia*), which is highly competitive with the native species and only few native plant species can grow under its canopy. Our goal was to demonstrate that the Australian pine's presence reduces the cover and vegetation diversity of the coastal dune's native species. We used ten sampling plots (100 m^2 each), five of which included Australian pine (invaded), and five that did not (non-invaded). We recorded the number of different plant species and their cover, height, and diameter in each plot. We found 43 plant species belonging to 40 genera, from which 37 species were found in the non-invaded plots, while only 26 plant species were present in the invaded ones. The vegetation density (3547 ± 709 individuals ha^{-1}) and the cover (65%) in the plots that lacked Australian pine were higher compared to the density (2785 ± 802 individuals ha^{-1}) and cover (35%) of the plots that included it. According to our analyses, Australian pine presence negatively influenced the species composition and abundance of the native species. Moreover, we found significant differences in the native plant diversity between the invaded and non-invaded plots. Our results demonstrated that invasive species, such as the Australian pine, negatively affected the native plant community in the coastal dune because it constrained its community structure.

Key words: invasive species, species richness, native species displacement, restoration, Cozumel

Introduction

The coastal dunes are sandy ridges that provide stability to the coastal shoreline through the sediment reserves that arrive and accumulate from adjacent beaches (Lucas and Ranwell 1974; Cortés 1996). The structure of coastal dunes is linked to the dynamics of sediment transportation and the

structure and composition of the vegetation that grows there (Roig-Munar et al. 2012). The vegetation communities of the coastal dunes also facilitates sand accumulation and stabilization, produces organic matter, and retains nutrients, that create different topographic levels, and the existence of the environmental conditions necessary to the establishment of shrub species (Lithgow et al. 2013).

The coastal dunes' importance lies in their ecosystem services, especially protection against erosion by the winds and tides (Ricklefs and Miller 2000). Additionally, they provide habitats for various animal and plant species (Martínez et al. 2014). However, the coastal dunes are among the most threatened natural systems worldwide due to anthropogenic pressures (Mendoza-González et al. 2012). Furthermore, invasive species presence negatively affects the interactions between different native plant species (Huenneke 2002), and may replace them because of their reproductive efficiency (Díaz-Martínez et al. 2013). The Australian pine (*Casuarina equisetifolia* Linnaeus, 1759; Casuarinaceae) is among the invasive species that cause serious impacts to the dune native vegetation in places like the Caribbean and Gulf of Mexico (Moreno-Casasola et al. 2013; Rodríguez-Roiloa et al. 2015). It is well documented that the Australian pine invasions may negatively impact the coastal vegetation because its canopy reduces light accessibility for various native species. Additionally, the Australian pine is considered an allelopathic tree species capable of reducing or stopping the growth of other plant species by the production of secondary metabolites that escape to the environment as the Australian pine leaf litter breaks down in the soil. Consequently, intra and interspecific competition increases, and changes in plant community and soil microbiota structure are induced. Moreover, Australian pine presence diminishes water availability, causing the displacement of dunes and mangrove vegetation (Parrotta 1993), which in turn increases the probability of biodiversity loss.

The plant community in the Mexican coastal dunes are highly diverse and structured due to their physical, climatic, hydrologic, and edaphic heterogeneity (Seingier et al. 2009). However, nationwide, about 14% of the coastal dune vegetation cover is lost due to building of touristic infrastructure (Vallés et al. 2011), and because of the introduction of invasive species, especially in the Mexican Caribbean (Seingier et al. 2009). The Australian pine was recorded for the first time in Mexico in 1852, but since the 1970 decade it showed an exponential growth because of forestry plantations using this species in several coastal zones, but lacking studies of the possible ecological impacts (Arellano et al. 1996). At that time, the Australian pine plantations had the goal of coastal erosion control. However, their seed and clonal dispersion strategies had not been accounted for, and this invasive tree broadly dispersed, displacing, in some cases the native vegetation (Jadhav and Gaynar 1995; Hata et al. 2015; Hozayn et al. 2015; Carabias et al. 2017; de Vos et al. 2019).

In Mexico, Cozumel lies within a natural protected area that includes marine and terrestrial habitats. The interaction of coastal dune vegetation, mangrove, flooded forests, seagrasses, and even coral reefs provides habitat for at least 31 native plant species restricted to the Mexican Caribbean (Semarnat and Conafor 2016). This plant diversity helps support wildlife populations of different national and international conservation concerns because they are endemic or because they use Cozumel as breeding grounds. Because of its ecological value, Cozumel's vegetation community deserves protection against the adverse effects of invasive species. Such an effect may diminish the protection and soil retention capabilities of the coastal dunes and its resilience against the effects of climatic change. Thus, our goal was to demonstrate that the presence of Australian pine affects the structure of the plant community in the coastal dunes, and that it is reducing both the cover and the diversity of native plants. According to Pernas et al. (2013), the establishment of the Australian pine in different zones of the coastal dunes disrupts key geomorphological and biological processes creating beaches and modifying coastal plant communities. Although the Australian pine is an option for erosion control worldwide, several studies conducted on the east coast of the USA demonstrate that this tree species diminishes the onshore buildup of dunes by wave and wind action (National Invasive Species Council 2010; Pernas et al. 2013). Such an effect may diminish the protection and soil retention capabilities of the coastal dunes and its resilience against the effects of climatic change.

Materials and methods

Study area

In the Caribbean Sea, Cozumel Island is situated about 17.5 km from Playa del Carmen City on the shore of Quintana Roo, Mexico (Figure 1). It is the largest island among all the islands within the Mexican Caribbean and is one of the Mexican places with a scattered distribution of endemic plant and animal species (Semarnat and Conafor 2016). About 80% of Cozumel Island belongs to a large natural protected area that includes marine and terrestrial habitats of ecological concern for fisheries, plant communities and bird breeding grounds (Seto et al. 2009). The urban area occupies the remaining 20% (Collantes-Chávez et al. 2019).

The weather is humid and warm with heavy rainfall in summer. The yearly average temperature is about 25.5 °C (García 2004). The yearly average rainfall is approximately 1,570 mm, with the maximum from September to October (250 mm monthly), and the minimum from March to April (40 mm monthly) (Semarnat 1998).

Plant species richness

To assess the impacts caused by the invasive Australian pine, we used ten 100 m^2 plots, five of which included individuals of Australian pine (invaded),

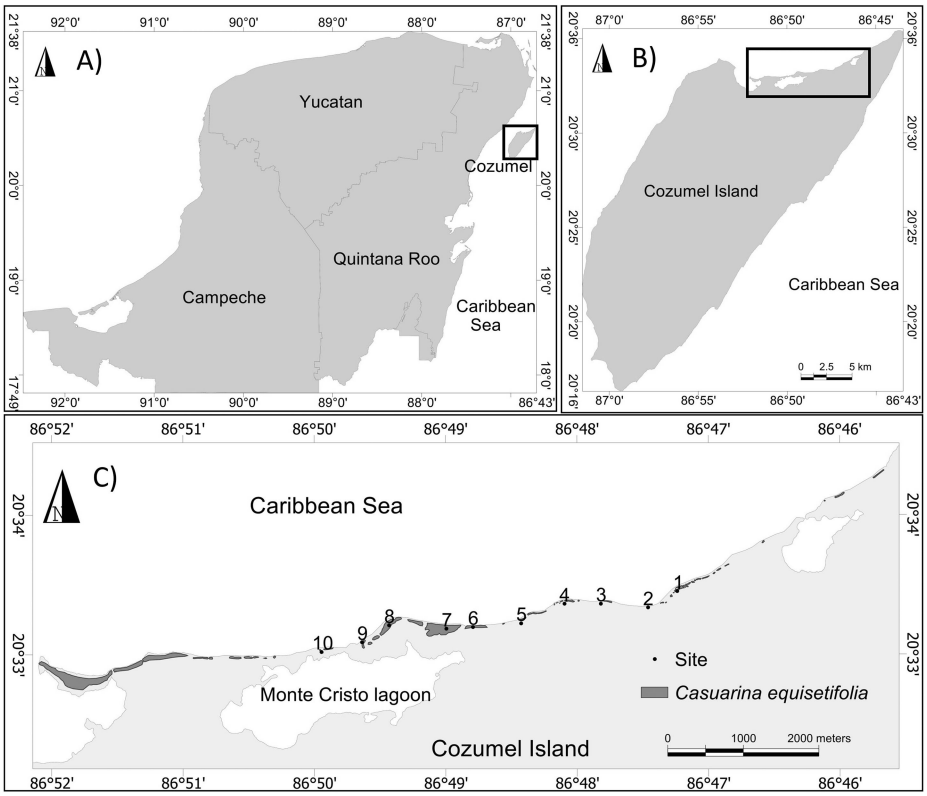

Figure 1. A) Location of Cozumel Island within the Yucatán Peninsula. B) Study area on the north side of Cozumel Island. C) The distribution of *Casuarina equisetifolia*, shown as dark gray polygons and the sampling plots (numbered circles). Plots 1, 6–9 are the invaded, while plots 2–5, 10 are non-invaded.

and five did not (non-invaded). The placement of the sampling plots began with the encounter of the first dune plant from the sea to the dune interior. Then we measured 10 × 10 m for each sampling plot, establishing a separation of at least 100 m^2 between replicates. Because of the narrowness of the coastal dune's study area, all the sampling plots were placed perpendicular instead of parallel to the shoreline (Moreno-Casasola et al. 2013). The area occupied by the coastal dunes is about 17 km long, from which we selected a section of eight km to place the sampling plots depending on terrain accessibility and public or private land property. Such a selection depended on the scattered presence/absence of the Australian pine patches within the coastal dune native vegetation matrix on the north side of Cozumel Island. Because of the Australian pine distribution in the selected area, most of the sampling plots, either non-invaded or invaded, were adjacent to each other (Figure 1). The taxonomic identification of the plant species in each plots was carried out *in situ* using taxonomic keys of Yucatan's flora (Tellez and Cabrera 1987; Tellez 1989). All the scientific names of families and genera were checked using the International Plant Names Index (Ipni 2020).

Community structure

We measured the dune's vegetation height (m), cover (%), density (individuals $hectare^{-1}$), and frequency (%) within each plot. The cover was

the vegetation layer covering the soil surface. We estimated it by first measuring the vertical projection of the outermost perimeter of the foliage spread. Then, a second measure of the vertical projection was taken using the narrowest perimeter of the foliage spread (Gold et al. 2004). The relative frequency was the number of times the individuals of a species were counted regarding the total number of individuals of all plant species present in the plot.

Data analyses

We classified the recorded species within each plot into broad life forms (herbaceous, shrubs, and trees) according to the biological information for each plant species available in the herbarium of the Yucatan Scientific Research Center (CICY) (Bautista et al. 2011). To assess the heterogeneity of the plant species composition, we estimated the importance value index (IVI), which is the sum of density, dominance, and relative frequency for each species within a vegetation matrix, and the Shannon-Wiener diversity index (H'), which is a measure of the diversity according to the abundance and evenness of each species in a sample (Bautista et al. 2011). To assess changes in the IVI value due to the presence of Australian pine, we divided the difference of IVI between invaded and non-invaded plots by the sum of these values ($Change\ of\ IVI = \frac{IVI\ inva - IVI\ no\_inva}{IVI\ inva + IVI\ no\_inva}$). Thus, the change of IVI ranged from −1 to 1, where negative values indicate decreased IVI of species, while positive values indicate increased IVI value.

To compare the vegetation structure in the invaded and non-invaded treatments, we used Kruskal-Wallis non-parametric test (Bernabeu and Batanero 2008) as implemented in STATGRAPHICS 16.1.11. We also compared the richness and abundance of plants between invaded and non-invaded plots through one-way permutational multivariate analysis of variance (PERMANOVA) test by the use the of the vegan function *adonis* (Oksanen et al. 2019), taking either species abundance or species composition as a dependent variable and the habitat condition (invaded/non-invaded) as an independent variable. With these tests, we ensure that differences in species composition between invaded and non-invaded plots are not due simply to the sampling units' location. To visualize PERMANOVA results, we plotted the PERMANOVA scores for each sampling plot through principal coordinates analysis (PCoA). The tests were performed using R 3.6.3 (R Core Team 2021).

To compare the estimated values of H' between both invaded and non-invaded sampling plots, we first linearized the H' values according to Jost (2006). The linearization is possible by first estimating the effective number of species in each sample (each sampling plot) as $D = \exp(H')$. Once D is obtained for each sample, the difference between any pair of samples (belonging to the same or different treatment, community) is calculated as

$M = D_{min}/D_{max.}$ Jost (2006) defined the M value as the difference in H' between any pair of samples. If M is close to 0, the difference in H' is strong, while M near to 1 means an irrelevant difference of H' between samples. To determine the significance of M between pairs of samples in each treatment, we used Hutchenson's *t-test*, which helps estimate p-values and confidence intervals using data from diversity measures (Hutcheson 1970):

$$t = \frac{H'_a - H'_b}{\sqrt{S^2_{H'_a} + S^2_{H'_b}}}$$

where a and b are the H' values of samples 1 and 2, and S^2 is the variance of each sample. All the tests were considered significant at $p < 0.05$, if not indicated otherwise.

Results

Species richness

We recorded 43 plant species, including a variety, distributed within 22 families and 40 genera (Table 1). The most representative families were Asteraceae and Poaceae (n = 5 each), and Combretaceae and Rubiaceae (n = 4 each). Most of the genera were represented by only one species, except for the genera Conocarpus, Euphorbia and Scaevola with two species. About 83% of the recorded families showed only one or two species within the study area. According to the life form, the herbaceous plants were dominant with 42% followed by tree species with 33% and shrubs with 25%.

Thirty-seven plant species were present within the non-invaded plots. Such a richness was composed of 21 families and 34 genera. In these plots, the families showing the highest number of species were Asteraceae (13.5%) and then Combretaceae (10.8%). Here, the herbaceous plants were dominant (40.5%), as compared with the number of trees (32.4%) and shrubs (27%) species.

Within the invaded plots, we recorded 15 families, 26 genera, and 26 species. Here, the family Cobretaceae showed the highest number of species (15.3%), and the herbaceous plants were also dominant by the proportion of recorded species (53.8%, compared to trees and shrubs with 23% each).

Community structure

Vegetation density and cover in the coastal dunes varied according to the presence/absence of Australian pine. The native plant species density was higher within the plots from non-invaded than invaded (Kruskal-Wallis $\chi^2 = 4.81$, $p = 0.02$, Table 2). Moreover, the plots from non-invaded showed about 20% more vegetation cover compared to invaded (Kruskal-Wallis $\chi^2 = 7.81$, $p = 0.009$). Most plants from the non-invaded plots showed a greater height, broader stems, and trunk diameter than plants and trees

Table 1. Floristic list of coastal dune vegetation of the Cozumel Island, Quintana Roo. Category: NR = Not rated LC = Least concer (IUCN 2021).

taxon / species	common name (English)	common name (Spanish)	growth form	category	distribution
Acanthaceae					
Avicennia germinans (L.) Linnaeus,1764	Black mangrove	Mangle negro	tree	LC	native
Aizoaceae					
Sesuvium portulacastrum Linnaeus, 1759	Shoreline seapurslane	Verdolaga de playa	grass	NR	native
Amaranthaceae					
Alternanthera flavescens Kunth, 1818	Yellow joyweed	Sak-mul	grass	NR	native
Hymenocallis littoralis (Jacq.) Salisbury,1812	Beach spiderlily	Lirio de mar	grass	NR	native
Anacardiaceae					
Metopium brownei Urbano, 1908	Unknown	Chechen prieto	tree	LC	native
Arecaceae					
Cocos nucifera Linnaeus, 1753	Coconut palm	Palma de coco	tree	NR	invasive
Thrinax radiata Lodd. ex Schult. & Schult, 1830	Guano palm	Palma chit	tree	LC	native
Asteraceae					
Ageratum maritimum Kunth, 1818	Unknown	Hauay-Ché	grass	NR	native
Ambrosia hispida Linnaeus, 1753	Sea altamisa	Altanisa de mar	grass	NR	native
Borrichia arborescens (L.) Candolle, 1836	Tree seaside tans	Margarita de mar	bush	LC	native
Melanthera nivea (L.) Small, 1903	Pineland squarestem	Levisa xiiw	grass	NR	native
Flaveria linearis Lagasca, 1816	Clustered yellowtops	Anis xiiw	grass	NR	native
Boraginaceae					
Cordia sebestena Willd ex Spreng. 1824	Beach siricote	Ciricote de playa	tree	LC	native
Tournefortia gnaphalodes (L.) R. Br. ex Roem. & Schult, 1819	Soldierbush	Tabaquillo	bush	NR	native
Casuarinaceae					
Casuarina equisetifolia Linnaeus, 1759	Sea pine	Casuarina, Pino de mar	tree	LC	exotic and invasive
Combretaceae					
Conocarpus erectus var. *sericeus* Fors ex DC. 1828	Gray mangrove	Mangle botoncillo plateado	tree	LC	native
Conocarpus erectus Linnaeus, 1759	Buttonwood mangrove	Mangle botoncillo	tree	LC	native
Laguncularia racemosa (L.) CF Gaertn, 1807	White mangrove	Mangle blanco	tree	LC	native
Terminalia catappa Linnaeus, 1759	Almond tree	Almendro	tree	LC	invasive
Cyperaceae					
Rhynchospora colorata (L.) H. Pfeiff, 1935	White star	Estrella blanca	bush	NR	native
Euphorbiaceae					
Euphorbia hirta Linnaeus, 1759	Pillpod sandmat	Golondrina	grass	NR	native
Euphorbia mesembrianthemifolia Jacquin, 1760	Unknown	Sak iits	grass	NR	native
Fabaceae					
Pithecellobium keyense Britton, 1928	Unknown	Ya'ax k'aax	tree	NR	native
Gentianaceae					
Eustoma exaltatum (L.) Salisbury, 1837	Seaside gentian	Lisianto	grass	NR	native
Goodeniaceae					
Scaevola plumieri (L.) Vahl, 1791	Gullfeed	Chunup	bush	LC	native
Scaevola taccada (Gaertn.) Roxburgh, 1814	Unknown	Lechuga de mar	bush	NR	invasive
Passifloraceae					
Passiflora foetida Linnaeus, 1953	Wild flower	Poch	grass	NR	native
Poaceae					
Cenchrus spinifex Cavanilles, 1799.	Spiny burrgrass	Rosetilla	grass	NR	native
Dactyloctenium aegyptium (L.) Willdenow, 1809	Beach wiregrass	Zacate egipcio	grass	NR	native
Distichlis spicata (L.) Kuntze, 1891	Saltgrass	Huizapol	grass	LC	native
Panicum amarum Elliott, 1816.	Bitter panicgrass	Zacate	grass	NR	native
Sporobolus virginicus (L.) Kunth, 1829.	Sea grass	Ch'ilibil su'uk	grass	NR	native
Polygonaceae					
Coccoloba uvifera Linnaeus, 1953.	Sea grape	Uva de mar	tree	LC	native
Rhizophoraceae					
Rhizophora mangle Linnaeus, 1953.	Red mangrove	Mangle rojo	tree	LC	native

Table 1. (continued).

Rubiaceae					
Erithalis fruticosa Linnaeus, 1959.	Black torch	Ocotillo	bush	LC	native
Ernodea littoralis Swartz, 1788.	Unknown	Bech	bush	LC	native
Rachicallis americana Kuntze, 1891.	Unknown		bush	LC	native
Randia aculeata Linnaeus,1753.	Lemongrass	Crucecita	bush	LC	native
Rutaceae					
Zanthoxylum fagara Sargent, 1890.	Unknown	Palo mulato	tree	LC	native
Sapotaceae					
Sideroxylon obtusifolium (Roem. & Schult.) Pennington, 1990.	Unknown	Zapotillo	tree	LC	native
Surianaceae					
Suriana maritima Linnaeus, 1753.	Bay cedar	Tabaquillo	bush	LC	native
Verbenaceae					
Lantana involucrata Linnaeus, 1756.	Dictum	Oregano xiiw	bush	NR	native
Phyla nodiflora (L.) Greene, 1899.	Frog fruit	Bella alfombra	grass	LC	native

Table 2. Forest structure parameters of the coastal dune vegetation according to the presence or absence of the invasive *Casuarina equisetifolia*. The values are mean ± standard deviation.

Treatment	Density (ind ha^{-1})	Cover (%)	Height (m)	Diameter at breast height (cm)
non-invaded	3547 ± 709	65%	1.24 ± 0.45	5.24 ± 3.45
invaded	2785 ± 802	35%	0.90 ± 0.09	5.66 ± 2.44
Statistic Kruskal-Wallis	$\chi^2 = 4.81$, $p = 0.02$	$\chi^2 = 7.81$, $p = 0.009$	$\chi^2 = 0.53$, $p > 0.05$	$\chi^2 = 0.002$, $p > 0.05$

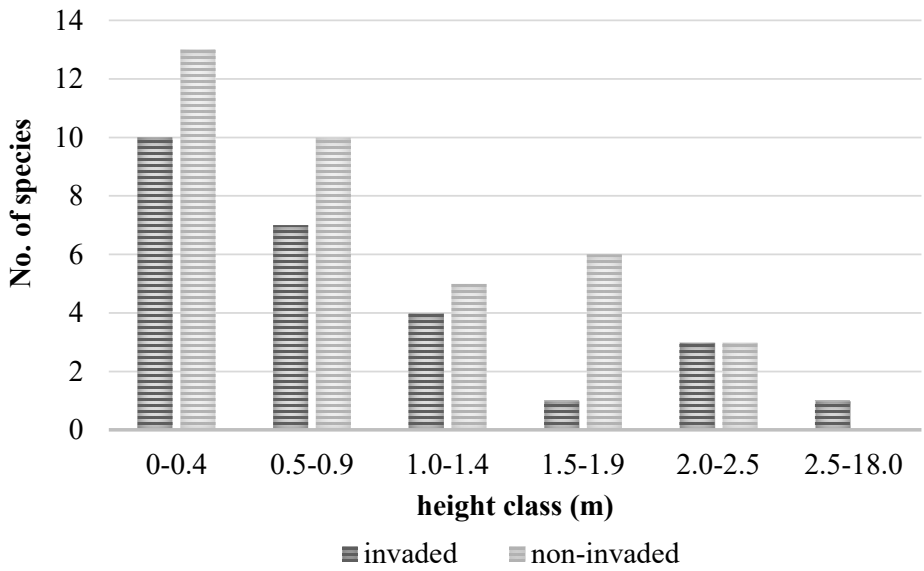

Figure 2. Height patterns of the coastal dune vegetation in the sampling plots.

from the plots with Australian pine individuals (Figure 2). However, such differences were non-significant (Figure 2). Although 15 species showed positive IVI changes, the presence of Australian pine decreased the IVI value of most native species (Table 3). Finally, *Coccoloba uvifera* (Linnaeus, 1953), *Dactyloctenium aegyptium* ((L.) Willdenow, 1809), *Lantana involuctrata* (Linnaeus, 19756), *Metopium brownie* (Urbano, 1908), *Phyla nodiflora* ((L.) Greene, 1899), and *Sporobolus virginicus* ((L.) Kunts, 1829) were found only in the plots invaded by the Australian pine. The *C. uvifera* and *M. brownie* trees showed an average canopy height of 1.47 m.

Table 3. Community structure according to the presence or absence of the invasive Australian pine. RF = Relative frequency, RD = Relative dominance, RDE = Relative density and IVI = Importance value index. Change of IVI, show changes in species importance due to the presence of Australian pine. Negative values indicate decreased IVI of species, while positive values indicate increased IVI value.

Treatment	invaded				non-invaded				Change of IVI
Specie / Percentage community structure	RF	RD	RDE	IVI	RF	RD	RDE	IVI	
Ageratum littorale	0.00	0.00	0.00	0.00	2.99	2.92	1.22	7.13	−1.00
Alternanthera flavescens	1.59	1.71	2.76	6.06	3.73	1.12	7.46	12.32	−0.34
Ambrosia hispida	6.35	2.97	10.77	20.09	3.73	3.02	11.73	18.48	0.04
Avicennia germinans	0.00	0.00	0.00	0.00	1.49	2.98	0.69	5.16	−1.00
Borrichia arborescens	4.76	2.19	0.97	7.92	2.99	3.87	1.45	8.31	−0.02
Casuarina equisetifolia	7.94	21.68	5.39	35.00	0.00	0.00	0.00	0.00	1.00
Cenchrus incertus	1.59	2.66	0.28	4.53	3.73	2.73	10.36	16.81	−0.58
Coccoloba uvifera	1.59	0.42	0.14	2.14	0.00	0.00	0.00	0.00	1.00
Cocos nucifera	0.00	0.00	0.00	0.00	2.24	1.33	0.46	4.03	−1.00
Conocarpus erectus	1.59	9.89	3.04	14.52	2.99	6.97	0.61	10.56	0.16
Conocarpus erectus var. sericeus	0.00	0.00	0.00	0.00	1.49	4.26	0.38	6.13	−1.00
Cordia sebestena	3.17	1.43	0.55	5.15	3.73	4.10	1.07	8.90	−0.27
Dactyloctenium aegyptium	1.59	0.38	0.14	2.11	0.00	0.00	0.00	0.00	1.00
Distichlis spicata	1.59	0.89	22.65	25.13	3.73	0.57	5.10	9.41	0.46
Erithalis fruticosa	4.76	2.99	2.49	10.24	3.73	1.86	3.20	8.79	0.08
Ernodea littoralis	3.17	3.42	2.76	9.36	3.73	4.72	1.45	9.90	−0.03
Euphorbia hirta	0.00	0.00	0.00	0.00	1.49	2.49	0.46	4.44	−1.00
Euphorbia mesembrianthemifolia	6.35	0.94	2.62	9.91	3.73	1.11	5.41	10.25	−0.02
Eustoma exaltatum	0.00	0.00	0.00	0.00	2.24	2.49	0.76	5.49	−1.00
Flaveria linearis	3.17	4.75	1.80	9.72	2.99	2.14	1.45	6.58	0.19
Hymenocallis littoralis	1.59	2.42	0.14	4.15	2.99	1.19	0.61	4.79	−0.07
Laguncularia racemosa	0.00	0.00	0.00	0.00	1.49	1.80	0.23	3.52	−1.00
Lantana involucrata	3.17	3.68	0.28	7.13	0.00	0.00	0.00	0.00	1.00
Melanthera aspera	3.17	2.85	1.93	7.96	3.73	1.14	4.80	9.66	−0.10
Metopium brownei	1.59	4.18	0.28	6.05	0.00	0.00	0.00	0.00	1.00
Morinda citrifolia	0.00	0.00	0.00	0.00	1.49	1.28	0.30	3.07	−1.00
Panicum amarum	6.35	3.61	7.04	17.01	3.73	1.85	11.20	16.78	0.01
Passiflora foetida	0.00	0.00	0.00	0.00	1.49	1.26	0.38	3.14	−1.00
Phyla nodiflora	1.59	0.48	1.24	3.31	0.00	0.00	0.00	0.00	1.00
Pithecellobium keyense	1.59	4.64	0.28	6.50	2.24	5.10	0.76	8.10	−0.11
Rachicallis americana	0.00	0.00	0.00	0.00	1.49	2.39	0.46	4.34	−1.00
Randia aculeata	0.00	0.00	0.00	0.00	0.75	1.12	0.23	2.10	−1.00
Rhizophora mangle	0.00	0.00	0.00	0.00	1.49	5.84	3.50	10.84	−1.00
Rhynchospora colorata	0.00	0.00	0.00	0.00	2.99	1.52	6.63	11.14	−1.00
Scaevola taccada	0.00	0.00	0.00	0.00	3.73	2.46	1.07	7.25	−1.00
Scaevola plumieri	0.00	0.00	0.00	0.00	2.99	1.64	1.45	6.07	−1.00
Sesuvium portulacastrum	7.94	3.61	11.88	23.43	3.73	3.01	7.24	13.98	0.25
Sideroxylon obtusifolium	0.00	0.00	0.00	0.00	1.49	1.69	0.23	3.41	−1.00
Sporobolus virginicus	7.94	0.42	16.71	25.07	0.00	0.00	0.00	0.00	1.00
Suriana maritima	6.35	9.60	2.07	18.03	2.99	4.83	1.22	9.03	0.33
Terminalia catappa	0.00	0.00	0.00	0.00	2.24	1.16	0.84	4.24	−1.00
Thrinax radiata	4.76	2.14	1.38	8.29	2.99	2.42	4.11	9.51	−0.07
Tournefortia gnaphalodes	4.76	6.02	0.41	11.20	2.99	6.84	1.14	10.96	0.01
Zanthoxylum fagara	0.00	0.00	0.00	0.00	2.24	2.76	0.38	5.38	−1.00

In the invaded plots, the species with the higher IVI value was the Australian pine (35.00), followed by the natives *D. spicata* and *S. virgicus* (25.13 and 25.07, respectively). The Australian pine density ranged from 19 to 69 ind 0.01 ha^{-1}, and its canopy height ranged from 8.7 to 23.8 m. The most common plant species in the invaded plots were *Sesuvium portulacastrum* (Linnaeus, 1753), *Ambrosia hispida* (Linnaeus, 1753), *Panicum amarum*

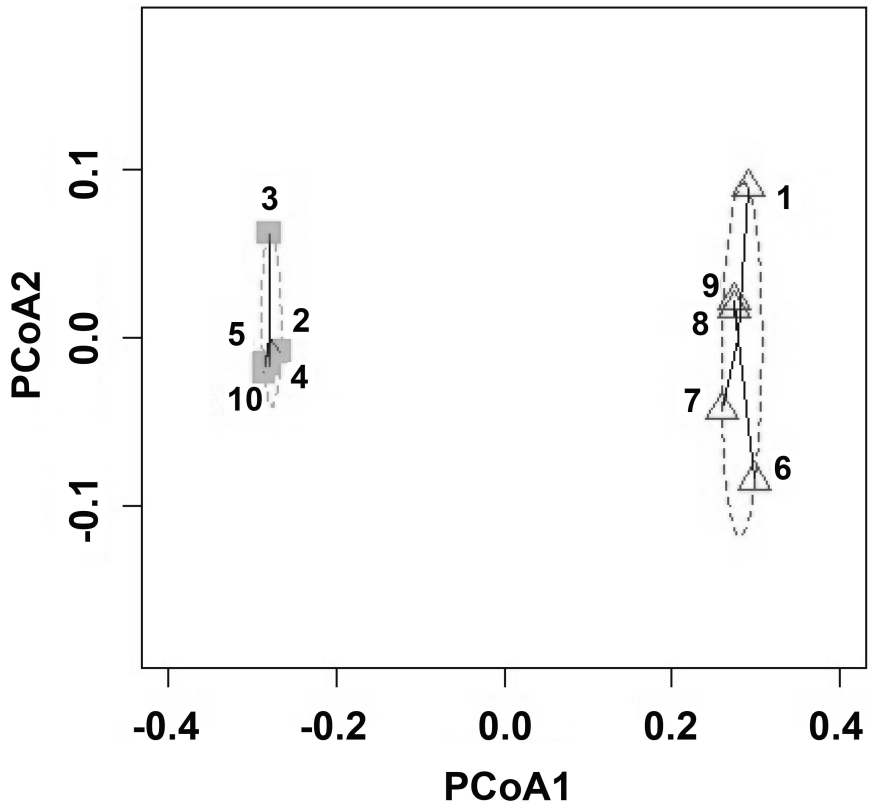

Figure 3. Grouping of invaded (triangles) and non-invaded (squares) sampling plots according to their species composition similarity (PERMANOVA). The numbers close to the symbols are the assigned sampling plot number. The dotted lines represent the scores' standard deviation of each group. The solid black lines represent the distance (similarity) between sampling plots.

(Elliott, 1816), *C. equisetigolia, S. virginicus,* and *Euphorbia mesembrianthemifolia* (Jacquin, 1760) (Table 3).

In the non-invaded plots the most common plant species were *A. hispida*, *Alternanthera flavescens* (Kunth, 1818), *C. spinifex*, *Distichlis spicata* ((L.) Greene, 1887) and *Tournefortia gnaphalodes* ((L.) R. Br. ex Roem. & Schult, 1819). The species with the highest IVI was *A. hispida* (18.48), followed by *C. spinifex* (16.81) and *P. amarum* (16.78) (Table 3). In the non-ivaded plots we also recorded tree species like *Conocarpus erectus* (Linnaeus, 1753) and *Rhizophora mangle* (Linnaeus, 1753). In the plots lacking Australian pine, *A. hispida* and *Cenchrus spinifex* (Cavanilles, 1799) showed the highest relative density values.

The results indicated that species richness and native plant abundance in Cozumel Island varied between plots with and without the invasive Australian pine. However, some native species, such as *S. virginicus, D. spicata, C. erectus,* and *P. nodiflora*, showed tolerance to the invasive tree presence, and were strongly associated with the plots that included Australian pines. On the other hand, the PERMANOVA test demonstrated that the presence of Australian pine significantly changes (source: invaded/non-invaded, $SS = 0.78$, $R^2 = 0.953$, $p = 0.005$) the species composition of the native coastal dune vegetation (Figure 3). PERMANOVA results based on species abundance were similar.

Index and diversity differences

The estimated diversity of native plants was higher within the non-invaded plots (2.5 ± 2.9) than in the invaded (1.7 ± 2.1). Moreover, we found significant differences in the diversity between the non-invaded and the invaded plots (Supplementary material Table S1). However, there was no significant difference in species evenness between invaded and non-invaded plots (Kruskal-Wallis: $\chi^2 = 0.27$, $p > 0.050$). According to Pileou's evenness, species showed similar proportions in the invaded and non-invaded plots (0.69 ± 0.81 and 0.79 ± 0.85 respectively).

Discussion

The Australian pine presence in the coastal dune of Cozumel Island reduced the density, species richness, and cover of the native vegetation. The distribution of the Australian pine patches within the study area showed different density levels that may affect the structure of the native plant community. For example, in coastal zones of Florida State, US, where high Australian pine densities occur, some structural features of the coastal dune vegetation are constrained (Wheeler et al. 2013). On the other hand, the Australian pine leaf litter breakdown is likely inducing changes in soil chemistry and microclimate while modifying the biotic and abiotic characteristics of the dune (Sakai et al. 2001; Shimizu 2005; de Vos et al. 2019).

The main factor related to such results is the increased competition for light and nutrients, and the allelopathy produced by the Australian pine, which may occur simultaneously or sequentially along with the availability of biotic and abiotic resources (Batish and Singh 1998). Besides the native plant species displacement, Australian pine allelopathy is related to diversity loss in various habitat types (Batish and Jain 2001; Shimizu 2005). We accounted for adverse effects due to high density, displacement, and resource competition between the native and the invasive species. However, studying the effects of soil chemical changes produced by the Australian pine secondary metabolites released to the environment in Cozumel Island is still necessary. The leaf litter produced by the Australian pine stays for long periods under the trees canopy (Parrotta 1999), and its breakdown occurs very slowly (Hata et al. 2015). Additionally, while decaying, the Australian pine leaf litter produces potent allelopathic substances with high levels of nitrogen that modify the soil characteristics, hampering the growth and establishment of other plant species (Mailly and Margolis 1992; Ndiaye et al. 1993).

According to the botanical records of the management plan for Cozumel Island (Programa de Manejo del Área de Protección de Flora y Fauna de Isla de Cozumel (Semarnat and Conafor 2016)), about 80% of all recorded plant species in the island were recorded within our study area (Tellez 1989). It is well known that biodiversity loss is related to invasive species

presence (Capdevila-Argüelles et al. 2013), and the lack of control could have severe consequences on Cozumel Island. Several authors pointed out that the presence of the invasive Australian pine caused the loss of approximately 40% of the native plant species in different habitat types (Díaz-Martínez et al. 2013; Parrotta 1995; Shimizu 2005; Suresh et al. 1988). Our results demonstrated that the diversity and cover of vegetation is lower under the canopies of the Australian pines inhabiting the coastal dunes of Cozumel.

The absence of tree species other than the Australian pine within the invaded plots could be related to the hydrological shortfall caused by this species (Moreno-Casasola et al. 2013), which sharply limits the establishment of plant species of heights above 2 m. This effect explains why the xerophytic vegetation (plants with small and succulent leaves) like *S. portulacastrum*, *Borrichia arborescens* ((L.) Candolle, 1836), *Ernodea littoralis* (Swartz, 1788), and *Flaveria linearis* (Lagasca, 1816) were present in the invaded plots (Espejel et al. 2017).

The distribution of a variety of coastal dune plants is typical in some places in the Caribbean islands due to the availability of freshwater and the chemical gradient of the soil components, which are critical for the presence/absence of the species (Munguía-Rosas et al. 2019). Because of the presence of the Australian pine, the vegetation structure changed in the invaded plots, and the growth of some species was negatively affected, while the native species capable of growing under the Australian pine canopy (*S. portulacastrum, A. hispida, P. amarum,* and *S. virginicus*), did so with limited access to light intensity, sand movement, and the possible stress caused by the leaf litter allelopathy, besides the water resources deficit.

Over time, the Australian pine can change the coastal dune vegetation from a heterogeneous scrub-like type into a monospecific forest, which could be the more harmful consequence for the vegetation dunes of Cozumel (de Vos et al. 2019). For example, in the invaded plots, the relict vegetation was represented by shrubs such as *C. uvifera* and *M. brownie*. Additionally, there were similar patterns of species dominance as those reported for invasive species-perturbed coastal dunes from Spain (Gallego-Fernández et al. 2019). Also, similar to our results, the number of native taxa recorded in invasive species-perturbed coastal dunes from Scotland was lower than in non-perturbed areas, showing a higher cover in the herbaceous stratum (Pakeman et al. 2015). Among the dominant herbaceous species in the invaded plots were *A. hispida, P. amarum, S. virginicus,* and *S. portulacastrum.* According to Pakeman et al. (2015), species such as *S. portulacastrum, P. amarum,* and *S. virginicus* are typically present in perturbed environments. Although most of these species can be found in primary dunes, this group of native species is considered the most resistant against invasions (Roig-Munar et al. 2012) because of their rhizome-like growth that allows them to obtain nutrients and water outside the invaded

areas (Mendoza-González et al. 2014). Thus, they can share habitat with the Australian pine.

The spatial distribution of the coastal dune vegetation is critical for maintaining the ecosystem structure (Silva et al. 2016). As the Australian pine canopy reduced the amount of light reaching the ground, the seedling growth was hampered, resulting in the reduction of the number of species and the alteration of the distribution patterns in Cozumel's coastal dunes. In contrast, in the non-invaded plots, species such as *Eustoma exaltatum* ((L.) Salisbury, 1837), *Passiflora foetida* (Linnaeus, 1753), *Ageratum maritimum* (Kunth, 1818), and *Rachicallis americana* (Kuntze, 1891), which are highly tolerant to sunlight and extreme environmental conditions, helped create microclimate areas where less tolerant plant species were able to find a shadow and grow (Awale and Phillott 2014).

Our results suggest that Australian pine in the study area altered some biotic interactions, such as competition and specialization, which are key factors for community structure (Castiñeira et al. 2013). Assessment of phylogenetic diversity patterns and functional diversity are needed to better understand the mechanisms determining the changes induced in the coastal dune vegetation community because of invasive species.

As the presence of the invasive Australian pine in the natural protected area of Cozumel Island represents a serious threat to its biodiversity, it is necessary to implement management strategies to stop the propagation of this species, for example removing adult and young trees and the leaf litter produced by the Australian pine. Then, design ecological restoration actions in the most degraded zones by the Australian pine invasion to allow the growth and establishment of different native plant species, especially those showing low tolerance to environmental changes.

Conclusions

The species richness in the invaded plots was 26, while in the non-invaded we recorded 37 plant species. The community structure (richness, height, density, and cover) in the plots lacking Australian pine was more complex, and it was not constrained compared to the plots where this species was present. Given the observed diversity differences in Cozumel coastal dunes invaded with Australian pine, we emphasize the need for restoration programs to conserve the native plant community and its habitat in this ecologically important area.

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Authors' contribution

BZC analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft. RPC conceived and designed the experiments, analyzed the data, contributed reagents/materials/analysis tools, prepared figures and/or tables. AZJ conceived and designed the experiments, analyzed the data, contributed reagents/materials/analysis tools. JCD analyzed the data, contributed reagents/materials/analysis tools, prepared figures. EEH performed the experiments. ABF authored or reviewed drafts of the paper. JTG authored or reviewed drafts of the paper, approved the final draft.

References

Arellano A, García G, Manzanero LA (1996) Programa de erradicación de la casuarina (*Casuarina* sp.) en la Reserva de la Biósfera de Sian Ka'an. Mexico, D.F., 47 pp

Awale D, Phillott A (2014) A review of the adverse effects of *Casuarina* spp. on coastal ecosystems and sea turtle nesting beaches. *Indian Turtle Newsletter* 19:14–19

Batish D, Jain S (2001) Vegetation exclusion under *Casuarina equisetifolia* L.: Does allelopathy play a role? *Community Ecology* 2: 93–100, https://doi.org/10.1556/ComEc.2.2001.1.10

Batish D, Singh H (1998) Role of Allelopathy in Regulating the Understorey Vegetation of *Casuarina equisetifolia*. In: Sassa K (ed), Environmental Forest Science. Springer, Dordrecht, pp 317–323, https://doi.org/10.1007/978-94-011-5324-9_34

Bernabeu C, Batanero C (2008) Análisis de datos con Statgraphics. Facultad de ciencias de la Educacion, Universidad de Granada, Granada, España, 316 pp

Capdevila-Argüelles L, Zilletti B, Suárez-Álvarez V (2013) Causas de la pérdida de biodiversidad: Especies Exóticas Invasoras. *Memorias Real Sociedad Española de Historia Natural* 10: 55–75

Carabias J, Arriaga V, Cervantes-Gutiérrez V (2017) Las políticas públicas de la restauración ambiental en México: limitantes, avances, rezagos y retos. *Botanical Sciences* 85: 85–100, https://doi.org/10.17129/botsci.1759

Castiñeira E, Fagúndez C, da Costa E, Canavero A (2013) Composition and vegetation structure in a system of coastal dunes of the "de la Plata" river, Uruguay: A comparison with Legrand's descriptions (1959). *Brazilian Journal of Botany* 36: 9–23, https://doi.org/10.1007/s40415-013-0009-2

Cortés R (1996) La formación de suelos sobre las dunas costeras. *Revista Xeoloxico Galega* 21: 597–603

Collantes-Chávez A, Alanís E, Yam O, López-Contreras C, Sarmiento-Muñoz T, Tapia-Muñoz JL (2019) Composition, structure and diversity of coastal vegetation in the northeastern of Cozumel, Mexico. *Botanical Sciences* 97: 135–147, https://doi.org/10.17129/botsci.2044

de Vos D, Nel R, Schoeman D, Harris LR, du Preez D (2019) Effect of introduced *Casuarina* trees on the vulnerability of sea turtle nesting beaches to erosion. *Estuarine, Coastal and Shelf Science* 223: 147–158, https://doi.org/10.1016/j.ecss.2019.03.015

Díaz-Martínez M, Alarcón A, Ferrera-Cerrato R, Almaraz-Suarez J, Garcia-Barradas O (2013) *Casuarina equisetifolia* (Casuarinaceae) growth in soil with diesel and application of biostimulation and bioaugmentation. *Revista de Biolologia Tropical* 61: 1039–1052, https://doi.org/10.15517/rbt.v61i3.11779

Espejel I, Jiménez-Orocio O, Castillo-Campos G, Garcillán P, Álvarez L, Castillo-Argüero S, Durán R, Ferrer M, Infante-Mata D, Iriarte S, León de la Luz JL, López-Rosas H, Medel A, Monroy R, Moreno-Casasola P, Rebman JP, Rodríguez-Revelo N, Sánchez-Escalante J, Vanderplank S (2017) Flora en playas y dunas costeras de México. *Acta Botánica Mexicana* 129: 39–81, https://doi.org/10.21829/abm121.2017.1290

Bautista F, Palacio Prieto J, Delfín H, Paéz R (2011) Técnicas de muestreo para manejadores de recursos naturales. 1st ed. México, D.F: Universidad Nacional Autónoma de México, 790 pp

Gallego-Fernández JB, Martínez ML, García-Franco JG, Zunzunegui M (2019) The impact on plant communities of an invasive alien herb, *Oenothera drummondii*, varies along the beach-coastal dune gradient. *Flora* 260: 151466, https://doi.org/10.1016/j.flora.2019.151466

García E (2004) Modificaciones al sistema de clasificacion climatica de Koppen. Instituto de Geografía-UNAM, Mexico, D.F., 96 pp

Gold K, León-Lobos P, Way M (2004) Manual de recolección de semillas de plantas silvestres para conservación a largo plazo y restauración ecológica. *Boletín INIA* 110, 62 pp

Hata K, Kawakami K, Kachi N (2015) Higher Soil Water Availability after Removal of a Dominant, Nonnative Tree (*Casuarina equisetifolia* Forst.) from a Subtropical Forest. *Pacific Science* 69: 445–460, https://doi.org/10.2984/69.4.2

Hozayn M, El Shahawy TA, Abd E, El Saady, Darwish M (2015) Allelopathic effect of *Casuarina equisetifolia* L. on wheat, associated weeds and nutrient content in the soil. *African Journal of Agricultural Research* 10: 1675–1683, https://doi.org/10.5897/AJAR2015.9482

Huenneke L (2002) Invasive Species in a Changing World. *Restoration Ecology* 10: 603–603, https://doi.org/10.1046/j.1526-100X.2002.t01-1-02037_1.x

Hutcheson K (1970) A test for comparing diversities based on the shannon formula. *Journal of Theoretical Biology* 29: 151–154, https://doi.org/10.1016/0022-5193(70)90124-4

Ipni (2020) Índice internacional de nombres de plantas. The Royal Botanic Gardens, Kew, Harvard University Herbaria & Libraries and Australian National Botanic Gardens. http://www.ipni.org

IUCN (2021) The IUCN Red List of Threatened Species. Version 2021-1. https://www.iucnredlist.org (accessed 25 July 2021)

Jadhav B, Gaynar D (1995) Effect of *Casuarina equisetifolia* JR leaf litter leachates on germination and seedling growth of rice and cowpea. *Allelopathy Journal* 2(1): 105–118

Jost L (2006) Entropy and diversity. *Oikos* 113: 363–375, https://doi.org/10.1111/j.2006.0030-1299.14714.x

Lithgow D, Martínez ML, Gallego-Fernández JB, Hesp P, Flores P, Gachuz S, Rodríguez-Revelo N, Jiménez-Orocio O, Mendoza-González G, Álvarez-Molina L (2013) Linking restoration ecology with coastal dune restoration. *Geomorphology* 199: 214–224, https://doi.org/10.1016/j.geomorph.2013.05.007

Lucas GL, Ranwell DS (1974) Ecology of salt marshes and sand dunes. Chapman and Hall, London, 258 pp, https://doi.org/10.2307/4108017

Mailly D, Margolis H (1992) Forest floor and mineral soil development in *Casuarina equisetifolia* plantations on the coastal sand dunes of Senegal. *Forest Ecology and Management* 55: 259–278, https://doi.org/10.1016/0378-1127(92)90105-I

Martínez ML, Moreno-Casasola P, Espejel I (2014) Diagnóstico de las dunas costeras de México. CONAFOR, 8 pp

Mendoza-González G, Martínez ML, Lithgow D, Pérez-Maqueo O, Simonin P (2012) Land use change and its effects on the value of ecosystem services along the coast of the Gulf of Mexico. *Ecological Economics* 82: 23–32, https://doi.org/10.1016/j.ecolecon.2012.07.018

Mendoza-González G, Martínez ML, Lithgow D (2014) Biological Flora of Coastal Dunes and Wetlands: *Canavalia rosea* (Sw.) DC. *Journal of Coastal Research* 30: 697–713, https://doi.org/10.2112/JCOASTRES-D-13-00106.1

Moreno-Casasola P, Martínez ML, Castillo-Campos G, Campos A (2013) The Impacts on Natural Vegetation Following the Establishment of Exotic *Casuarina* Plantations. In: Martínez ML, Hesp A, Gallego-Fernandez JB (eds), Coastal Dune Restoration. Springer Berlin Heidelberg, Luxemburg, pp 217–233, https://doi.org/10.1007/978-3-642-33445-0_14

Munguía-Rosas MA, Angulo DF, Arceo-Gómez G, Parra-Tabla V (2019) Variation in leaf traits across a precipitation gradient in coastal sand dunes in Yucatan Peninsula. *Journal of Arid Environments* 162: 10–17, https://doi.org/10.1016/j.jaridenv.2018.12.001

Ndiaye P, Mailly D, Pineau M, Margolis H (1993) Growth and yield of *Casuarina equisetifolia* plantations on the coastal sand dunes of Senegal as a function of microtopography. *Forest Ecology and Management* 56: 13–28, https://doi.org/10.1016/0378-1127(93)90100-2

National Invasive Species Council (2010) National Invasive Species Council, U.S Department of the Interior, https://www.doi.gov/invasivespecies/isac-resources (accessed 28 August 2021)

Oksanen J, Guillaume-Blanchet F, Friendly M, Kind M, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Henry M, Stevens H, Szoecs E, Wagner H (2019) Vegan: Community Ecology Package. R package version 2.5-6. https://cran.r-project.org/package=vegan%0A%0A

Pakeman R, Alexander J, Brooker R, Cummins R, Eastwood A, Fielding D, Fisher J, Gore S, Hewison R,Hooper R, Lennon J, Mitchell R, Moore E, Nolan A, Orford K, Pemberton C, Riach D, Sim D, Stockan J, Trinder C, Lewis R (2015) Species composition of coastal dune vegetation in Scotland has proved resistant to climate change over a third of a century. *Global Change Biology* 21: 3738–3747, https://doi.org/10.1111/gcb.12999

Parrotta J (1993) *Casuarina equisetifolia* L. ex J.R. & G. Forst. Forst. Forest Service, United Stated Departament of Agriculture, Washington D.C., USA, 9 pp

Parrotta J (1995) Influence of overstory composition on understory colonization by native species in plantations on a degraded tropical site. *Journal of Vegetation Science* 6: 627–636, https://doi.org/10.2307/3236433

Parrotta J (1999) Productivity, nutrient cycling, and succession in single- and mixed-species plantations of *Casuarina equisetifolia*, *Eucalyptus robusta*, and *Leucaena leucocephala* in Puerto Rico. *Forest Ecology and Management* 124: 45–77, https://doi.org/10.1016/S0378-1127(99)00049-3

Pernas A, Wheeler G, Langeland K, Golden E, Purcell M, Taylor J, Brown K, Taylor D, Allen E (2013) Australian Pine Management Plan for Florida. Recommendations from the Australian Pine Task Force of the Florida Exotic Pest Plant Council, 44 pp

R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Ricklefs RE, Miller GL (2000) Ecology, 4th edn. W.H.Freeman & Co., New York, USA., 822 pp

Rodríguez-Roiloa S, González J, Retuerto-Franco J (2015) Importancia de la integración clonal en las invasiones biológicas. *Ecosistemas* 24: 76–83, https://doi.org/10.7818/ECOS.2015.24-1.12

Roig-Munar FX, Martín-Prieto J, Rodríguez-Perea A, Pons GX, Gelabert B, Mir-Gual M (2012) Risk Assessment of Beach-Dune System Erosion: Beach Management Impacts on the Balearic Islands. *Journal of Coastal Research* 285: 1488–1499, https://doi.org/10.2112/JCOASTRES-D-11-00187.1

Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN, Weller SG (2001) The Population Biology of Invasive Species. *Annual Review of Ecology and Systematics* 32: 305–332, https://doi.org/10.1146/annurev.ecolsys.32.081501.114037

Seingier G, Espejel I, Almad J, Fermán-Almada JL (2009) Cobertura vegetal y marginación en a costa mexicana. *Investigación ambiental Ciencia y política pública* 1: 54–69

Semarnat [Secretaria de Medio Ambiente y Recursos Naturales], Conafor [Comision Nacional Forestal] (2016) Programa de Manejo Área de Protección de Flora y Fauna la porción norte y la franja costera oriental, terrestres y marinas de la Isla de Cozumel, Primera. Mexico, 243 pp

Semarnat [Secretaria de Medio Ambiente y Recursos Naturales] (1998) Programa de Manejo Parque Marino Nacional Arrecifes de Cozumel, Quintana Roo. Mexico, D.F., 164 pp

Seto SW, Lam HY, Lau WS, Au A, Lam T, Chim S, Ngai SM, Chan S, Leung T, Yeung J, Kong S, Leung G, Lee S, Kwan Y (2009) Role of monoamine oxidases in the exaggerated 5-hydroxytryptamine-induced tension development of human isolated preeclamptic umbilical artery. *European Journal of Pharmacology* 605: 129–137, https://doi.org/10.1016/j.ejphar.2008.12.054

Shimizu Y (2005) A vegetation change during a 20-year period following two continuous disturbances (mass-dieback of pine trees and typhoon damage) in the Pinus-Schima secondary forest on Chichijima in the Ogasawara (Bonin) Islands: which won, advanced saplings or new seed. *Ecological Research* 20: 708–725, https://doi.org/10.1007/s11284-005-0087-0

Silva R, Martínez ML, Odériz I, Mendoza E, Feagin RA (2016) Response of vegetated dune-beach systems to storm conditions. *Coastal Engineering* 109: 53–62, https://doi.org/10.1016/j.coastaleng.2015.12.007

Suresh K, Rai R, Vianaya S (1988) Allelopathic exclusion of understorey by a few multi-purpose trees. *International Tree Crops Journal* 5: 143–151, https://doi.org/10.1080/01435698.1988.9752849

Tellez O (1989) Las Plantas de Cozumel: (guía botánico-turística de la Isla de Cozumel, Quintana Roo). Universidad Nacional Autónoma de México, Mexico, D.F., 75 pp

Tellez O, Cabrera EF (1987) Listados florísticos de México: VI. Florura de la Isla de Cozumel, Q.R. Universidad Nacional Autónoma de México, 67 pp

Vallés SM, Gallego Fernández JB, Dellafiore CM (2011) Dune Vulnerability in Relation to Tourism Pressure in Central Gulf of Cádiz (SW Spain), a Case study. *Journal of Coastal Research* 27: 243–251, https://doi.org/10.2112/JCOASTRES-D-09-00125.1

Wheeler G, Taylor G, Gaskin J, Purcell M (2013) Australian Pine (*Casuarina equisetifolia* L.) Management Plan for Florida, USA. *Journal of Coastal Research* 27: 485–492

Supplementary material

The following supplementary material is available for this article:

Table S1. Estimated differences ($M = D_{min}/D_{max}$) in the diversity of coastal dune vegetation.

This material is available as part of online article from:
http://www.reabic.net/journals/mbi/2022/Supplements/MBI_2022_Zaldivar-Cruz_etal_SupplementaryTable.xlsx