Journal of Coastal Conservation 2: 13-22, 1996

Coastal sand dune vegetation: an extreme case of species invasion

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Abstract. The coastal sand-dune flora of the Gulf and Caribbean region of Mexico was analyzed to understand differences in floristic composition and richness found along the coast. Each of the 655 species reported was classified according to its ecology and distribution range by checking herbaria specimens, literature and specialists. Three groups were formed: (a) species with predominantly coastal distribution; (b) ruderal or secondary species frequently found inland, common of disturbed areas such as roadsides, abandoned fields or forming part of secondary growths; (c) inland species frequently found in other vegetation types such as tropical dry or seasonal forest and grassland. A total of 71 coastal species, 237 ruderal/secondary and 336 species from other community types were found. The distribution of these groups was analyzed along 44 sites of the Gulf and Caribbean, in the different dune habitats and for the dominant growth forms. Coastal species are more widely distributed; they predominate in habitats with sand movement and the herbaceous component prevails. Ruderal/secondary species and especially those belonging to other vegetation types frequently appear in only one or two sites occupying more protected or stabilized habitats. The two latter groups considerably increase species richness of sand dune flora, but also pose interesting problems for dune conservation.

Keywords: Coastal dune; Species distribution; Richness.

Introduction

The floristic composition of a plant community is the result of its disturbance history, its present dynamics, the life history (attributes) of the species colonizing and reproducing successfully in that particular environment and species availability (Guevara 1982). Sand dune vegetation is a clear example of this and we believe that invasion of species with different traits are important contributors to floristic richness and biodiversity. Once their propagules have dispersed into the dune systems, species attributes (such as germination, establishment and growth requirements) will be important in defining in which part of the dune mosaic invading species will survive and reproduce.

Coastal sand dunes in the Gulf of Mexico are characterized by a sandy, nutrient-poor substrate of siliceous particles with variable amounts of calcareous sand. There are systems with narrow beaches and one or more parallel dune ridges 3-8 m high. There are also topographically complex systems with 25-m high dunes with different degrees of stabilization. Caribbean dunes in Mexico are formed by ridges of calcareous sand, derived from coral reefs and shells as well as from the limestone Peninsula of Yucatan. Both regions have many floristic and physiognomic differences (Sauer 1967; García 1987; Moreno-Casasola 1991).

In patch dynamics, natural systems are seen as mosaics of local, suitable patches colonized by various species at different times. Species ranges show that a species' internal geographical abundance is usually dynamic, even when the range limits are stable. Thus, invasions can be conceived as temporary disturbances leading to spatial dynamism and viewed more broadly, species ranges can be regarded as being in a constant state of flux, both internally and externally (Hengeveld 1989). Plant community boundaries are not static; ecotones show a constant exchange of species. Seed dispersion can take place between communities that are not necessarily close.

Invading species have been identified as those being indigenous to some region other than the area being invaded. In many cases, this is not always clear-cut: it is difficult to define community boundaries, modification of scale in the analysis makes results differ, and population density as well as species presence should be taken into account to define the native range of a species. For the purpose of this paper a difference is made between exotics and invaders. Exotics can be defined as alien species introduced intentionally or non intentionally to the region. Often, ecosystem invasion by exotic plants can have detrimental effects. Exotics displace native species by competing for resources, interfere with successional processes, alter disturbance regimes and disrupt food chains (Van Wilgen & Richardson 1985; MacDonald & Frame 1988; Elliott & White 1989). We define invaders as species with an occasional presence for that type of community (arbitrary frequency values of 10-20% for the sites) which can have low or high population numbers on a site and are frequently characteristic of other community types. Huston (1994) considers that invasions potentially lead to an increase in species richness, as the invading species are added to the existing species pool, although numerous examples demonstrate that they can also lead to extinctions.

In biological invasions there are two components, modulated by timing and chance: the invasive species and the invaded community. Consequently, community invasibility varies according to the characteristics of the community and the life history traits of the potential invaders (Ewel 1986). Disturbed communities are more often subject to invasions than intact communities and disturbance regime (type, frequency, duration and magnitude of disturbance) is recognized as the most important overall factor allowing invasion of exotic species (Elton 1958; Myers 1984; Ewel 1986; Fox & Fox 1986; Crawley 1987; Rejmánek 1989; DeFerrari & Naiman 1994; Huston 1994). However, there are

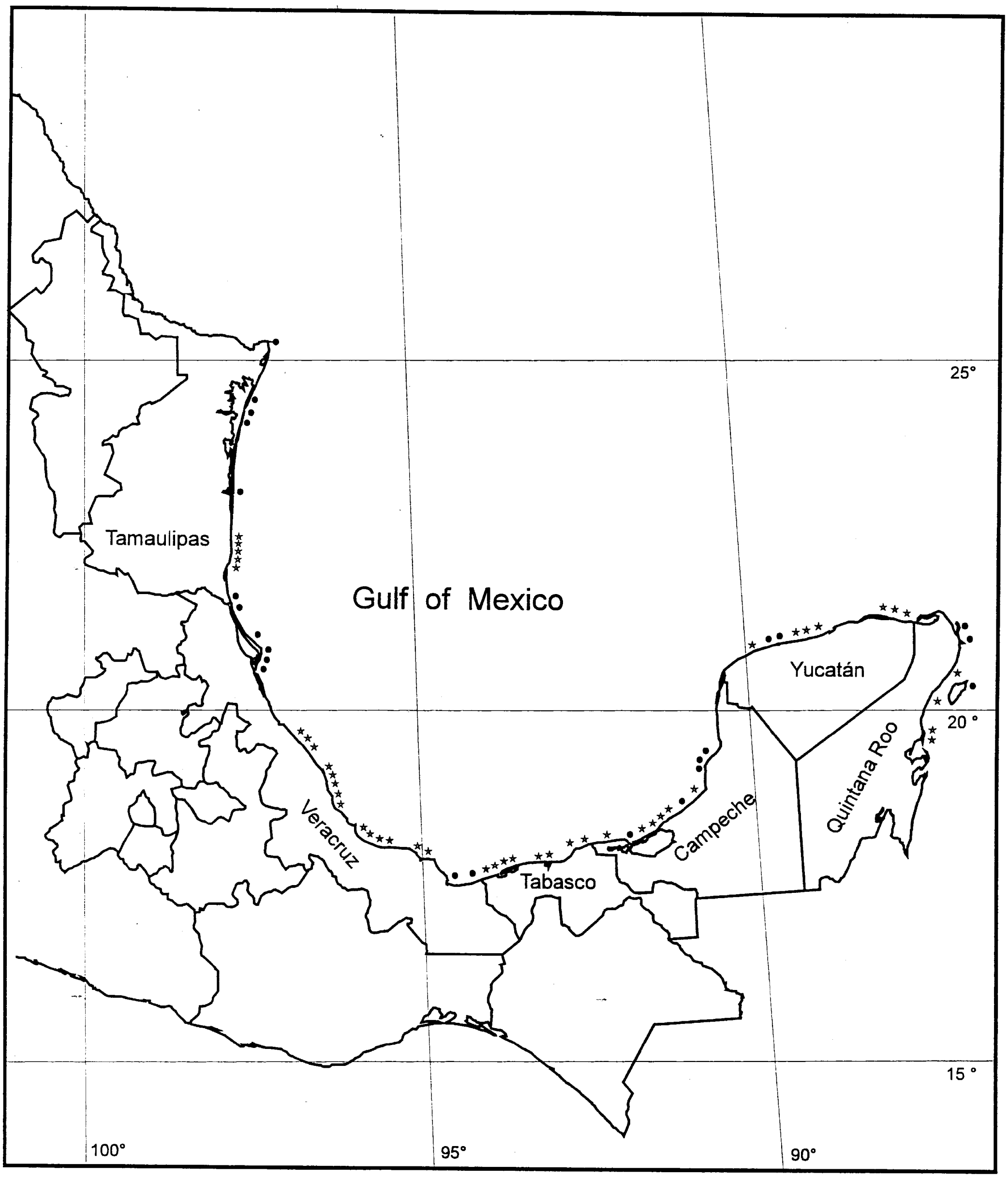

Fig. 1. Location of the 44 beach and dune study sites sampled (*). Sites include the Gulf (Northern Gulf- sites 1 to 6 and Central Gulf- sites 7 to 29) and the Caribbean (sites 30 to 44). Other beaches and dunes studies (reported in the literature) are indicated with a dot. See text for references.

several examples in which invasion occurs in the absence of disturbance (Mack 1985; Burdon & Chilvers 1977; Kruger 1977). Huston (1994) considers that there has been little progress in generalizations about which ecosystems are most likely to be invaded.

Coastal dunes are very dynamic systems comprising a wide variety of habitats with different physical and biotic conditions, allowing the existence of species with very diverse life history traits. They can be visualized as a permanently changing environment with distinct degrees of stabilization closely correlated with the topography and the disturbance produced by sand movement (Barbour et al. 1985; Moreno-Casasola 1986; Maun & Lapierre 1984) and slack inundation (van der Laan 1979; Sykes & Wilson 1987; Grootjans et al. 1991). It results in a vegetation mosaic which has been described by several authors (see Methods).

The aim of this work is to understand the floristic composition, richness and variability of the regional sand-dune systems along the Gulf and Caribbean through a detailed analysis of species composition, trends in species distribution patterns, species richness under different habitats and disturbance regimes and growth forms that compose the present dune flora. Strategies for conservation and management of the dune flora will be influenced by the resulting species analysis.

Methods

We accumulated a list of 655 species for the coastal beach and dune vegetation along the Gulf and Caribbean Sea of Mexico. A data base was elaborated to allow for consultations. Data from the vegetation analysis of 44 beach and dune sites (Fig. 1) totalling 492 species was used (Moreno-Casasola et al. 1982; Espejel 1984; Moreno-Casasola & Espejel 1986; García 1987; Castillo et al. 1991). This list was augmented with information from publications (Flores 1984; Gonzalez-Medrano 1972; Poggie 1962; Puig 1976; Sauer 1967) and herbaria specimens in the National Herbarium at the National Autonomous University of Mexico (MEXU) and in the Herbarium of the Institute of Ecology in Xalapa (XAL). Finally, a partial list of some of the species belonging to each species type is given in Table 4. The complete list is available from the authors.

Each of the 655 species was assigned to one of three categories of distribution patterns. This was done by examining all specimens for each of the listed species in the collections of both herbaria. A category was assigned when 60% or more of the specimens indicated a certain type of distribution. This was further checked against the literature and by specialists (see Acknowledgements). We were not able to classify several species mainly because of absence of herbaria collections and these were left out of the calculations (*Amaranthus arenicola, Eragrostis excelsa, E. yucatana, Eriochloa boxiana, Mandevilla subsagittata, Matelea yucatanensis, Panicum rigidulum, Paspalum clavuliferum, Pithecellobium grisebachi, Solanum yucatanum, Strumpfia maritima*).

Species distribution patterns were divided into three categories:

(1) species with a predominantly coastal distribution (sand dunes, coastal marshes or mangroves) henceforth referred to as coastal (C);

(2) inland ruderal or secondary species frequently found inland and common inhabitants of disturbed areas such as roadsides, abandoned fields or secondary growths; henceforth ruderals /secondary (R/S);

(3) inland species, frequently found in other vegetation types (OT) which can be considered mature, such as tropical seasonal forest, oak woodland or grassland.

For most of the analyses the complete floristic list was used (655 species). Where geographical or local habitat distributions were analyzed only data for the 44 sites sampled with the same methodology and intensity were utilized (492 species), so as to avoid errors caused by intensity of sampling during floristic collections.

Results

Species numbers varied considerably among sites and distribution patterns. A total of 71 (10.83%) coastal species (C) were found. The sand dune flora also comprised 237 ruderal/ secondary species (R/S- 36.2 %), as well as 336 species characteristic of other communities (OT- 51.3 %). Species richness per site (Fig. 2) is very variable (18 - 157 species). The number of species in the three categories (out of a total of 492) in each of the 44 sites also varies considerably. The mean number of C-species found was 15.5 (± 4.6), of R/S-species was 18.5 (± 9.7) and OT-species was 21.4 (± 14.7).

Although the coastal flora between the Gulf and the Caribbean is quite distinct in species numbers and composition (Sauer 1967; Moreno-Casasola & Espejel 1986; Espejel 1984; Moreno-Casasola 1988) the same trends in species number per pattern of distribution is maintained (Table 1). To further understand this distribution, a more detailed analysis of the flora of the Gulf coast was made by subdividing this region’s flora into two distinct floristic groups based on distribution of predominant growth forms, presence of endemics, biogeographical relations and general floristic composition (Moreno-Casasola 1988, 1991). The Northern Gulf group (State of Tamaulipas and northern part of Veracruz – sites 1 to 6 in Fig. 2 – has many similarities with the

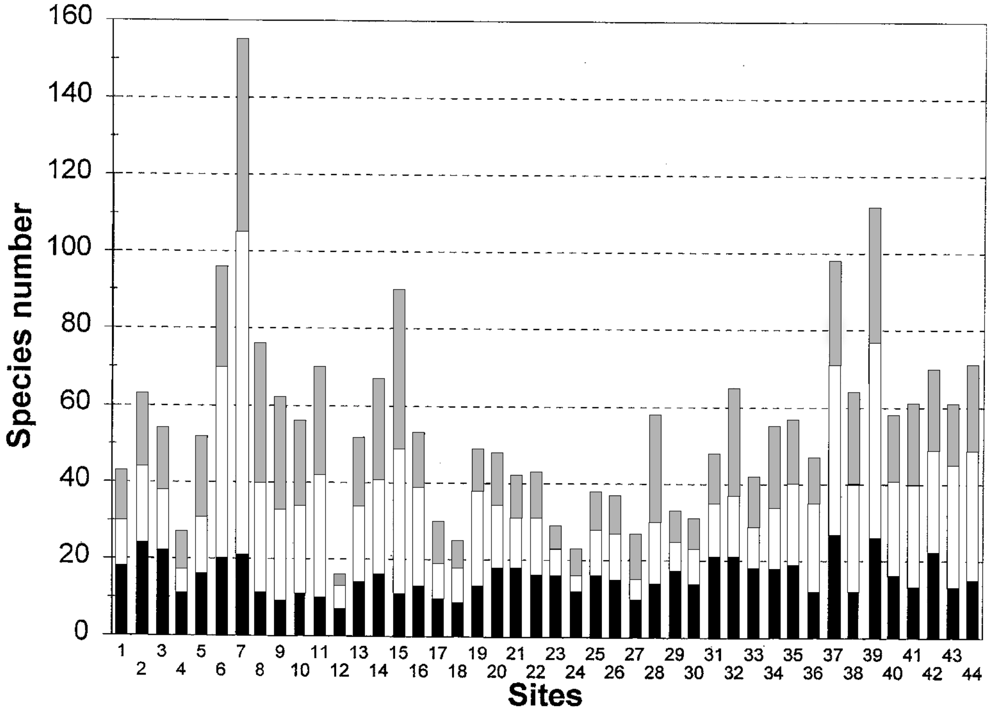

Fig. 2. Species richness along the 44 Gulf and Caribbean sites. Black low parts of columns represent coastal species (C), open middle parts species from other vegetation types (OT), and shaded parts ruderal/ secondary species (R/S).

Texas coastal flora; the Central Gulf group (States of Veracruz and Tabasco – sites 7-29) has many different elements. Comparisons between both Gulf groups show that the Central group has the lowest proportion of C-species, sharing 32 species with the Northern group. Species numbers vary between floristic groups but proportions of the three categories are roughly maintained, especially when comparing both Gulf groups with the Caribbean.

Species presence along sites varied greatly. A high number of species were very infrequent, appearing only in one or two sites. Species frequency distribution was analyzed for the three categories. Fig. 3a, b shows that C-species, both along the Gulf and the Caribbean, have higher frequency values. This means that more species are found along a high number of beach and dune sites. The species most frequently occurring on the beach and embryo dunes along the Gulf coast are: *Ipomoea stolonifera, Oenothera drummondii, Chamaecrista chamaecristoides*, *Schizachyrium scoparium* var. *littoralis, Palafoxia lindenii, Amaranthus greggii* and *Fimbristylis spadicea.* They are present in more than half of the sampled sites. Several of them are important sand stabilizers in active dunes, which are found along this coast. *Hibiscus pernambucensis* is less frequent but also a characteristic tree species along these coasts. Another group of beach species is mainly found along the Caribbean (*Scaevola plumierii, Coccoloba uvifera,*

Table 1. Number of species (out of a total of 655) and percentage of coastal (C), ruderal/secondary (R/S) and species from other vegetation types (OT) found in the Gulf and Caribbean regions. The Northern Gulf floristic group is found in Tamaulipas and North Veracruz, the Central Gulf group inhabits central and southern Veracruz and Tabasco and the Caribbean group includes Campeche and the Yucatan Peninsula (Moreno-Casasola 1991).

	Northern Gulf		Central Gulf		Total Gulf		Caribbean	
	No. spp.	%	No. spp.	%	No. spp.	%	No. spp.	%
Coastal	49	19.2	41	10.7	58	14.3	51	16.4
Ruderal/secondary	70	29.0	149	39.0	168	41.4	129	39.3
Others	126	51.8	192	50.3	179	44.3	137	44.3

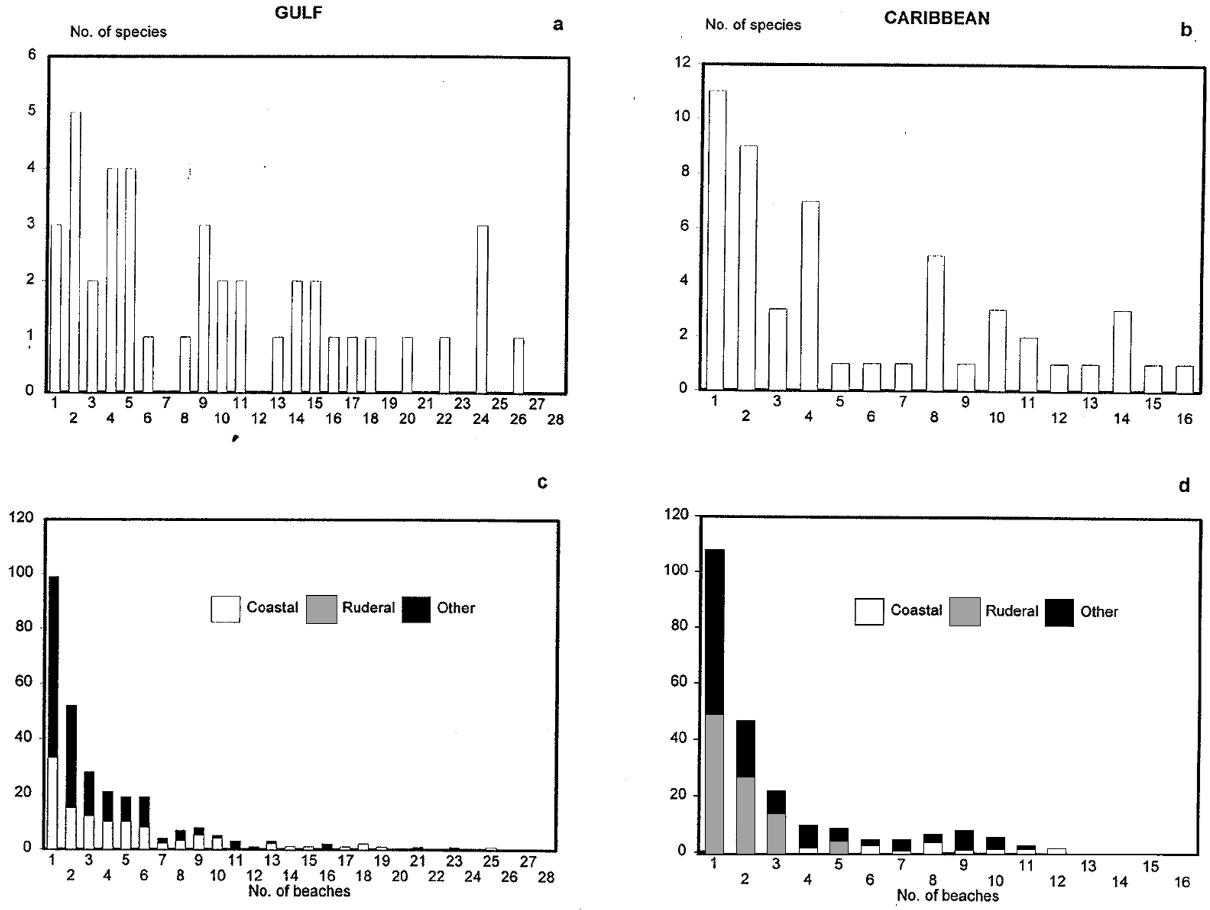

Fig. 3. Frequency distribution of coastal species (C) along 44 sites on the Gulf (a) and Caribbean (b). Frequency distribution of ruderal/secondary species (R/S) -shaded bars- and for species characteristic of other vegetation types (OT) -darkened columns- along the Gulf (c) and Caribbean (d). See text for explanation.

Ambrosia hispida, Tournefortia gnaphalodes, Ernodea littoralis, Suriana maritima, Tribulus cistoides) and still other species (*Ipomoea pes-caprae, Sesuvium portulacastrum, Sporobolus virginicus, Canavalia rosea, Okenia hypogea, Croton punctatus*) are widely distributed in both areas. Coastal species in stabilized dunes also vary between the Gulf and Caribbean. *Schizachyrium scoparium* var. *littoralis, Schrankia quadrivalvis* and *Cenchrus tribuloides* are frequent along the Gulf. In the Caribbean the following species are common: *Tribulus cistoides, Ernodea littoralis, Scaevola plumierii, Coccoloba uvifera* and *Pithecellobium keyense*. The latter form dense thickets.

The frequency distribution of R/S and OT-species follows a much more pronounced J-curve (Fig. 3c, d). Many of them occur in only one or two sites, and very few appear in more than one third of the sites. Data for Gulf and Caribbean species together, showed that 55 % of R/S and 62 % of OT-species were recorded in one or two sites (in contrast with 52 % of C-species in seven sites). Values on the Y-axis are much higher in Fig. 3b than in Fig. 3a. Along the Gulf, 43.2 % of R/S-species appeared in only 1-2 sites and only seven species (*Bidens pilosa, Panicum maximum, Commelina erecta, Iresine diffusa, Lippia nodiflora, Porophyllum punctatum* and *Crotalaria incana*) occur in more than a third of the sampled sites (which is equivalent to ten sites). For the Caribbean 68.5 % of the species appeared in 1-2 sites and seven species (*Lantana involucrata, Jacquinia aurantiaca, Gossypium hirsutum, Gymnopodium floribundum, Cenchrus echinatus, C. incertus* and *Portulaca pilosa*) are also found in more than one third of the sites (seven sites). *Passiflora foetida, Portulaca oleracea, Commelina erecta, Macroptilium atropurpureum, Malvaviscus arboreus* and *Rivina laevis* are widely distributed in the Gulf and Caribbean.

Table 2. Number and percentage of coastal species (C), ruderal/secondary (R/S) and species from other vegetation types (OT) in habitats of the dune system. Percentages in bold letters indicate values along horizontal lines. Three main habitats based on the subdivisions elaborated by Doing (1981) and Moreno-Casasola & Espejel (1986) are used. Dune habitats are characterized mainly by sand movement (and low salinity). Water-dependent habitats are the slacks where the elevation of the water table produces inundation during the rainy season and a higher concentration of nutrients. Stabilized areas — such as grasslands, thickets or tropical forest — have a dense plant cover, no sand movement, roots are out of reach of the phreatic table and physical factors lose importance as agents of disturbance.

	Dry dune habitats			Wet slacks			Stabilized habitats		
	No. spp.	%	%	No. spp.	%	%	No. spp.	%	%
Coastal	39	*40.6*	**41**	20	*12.3*	**21**	36	*7.4*	**37.8**
Ruderal/Secondary	30	*31.2*	**11**	56	*34.5*	**20.5**	186	*38.5*	**68.3**
Others	27	*28.1*	**7.2**	86	*53*	**22.9**	261	*54*	**69.7**
Total	96	*99.9*		162	*99.8*		483	*99.9*	

OT-species show the same trend as R/S-species (Fig. 3c, d). Many of the Gulf species (60.9%) appear exclusively in one or two sites and only a few appear in more than a third of them (*Chamaesyce dioica, Cyperus articulatus, Hydrocotyle bonariensis, Erigeron myrionactis, Chamaesyce ammanioides, Citharexyllum ellipticum, Cissus sicyoides* and *Psychotria erythrocarpa*). Shared by the Gulf and Caribbean beaches and dunes are *Chiococca alba, Metastelma pringlei, Randia laetevirens, Waltheria indica* and *Bursera simaruba*. In the Caribbean 64.2% species occur in 1-2 sites and 11species appear in more than one third (*Agave angustifolia, Cocccothrinax readii, Cordia sebestena, Capparis flexuosa, C. incana, Commicarpus scandens, Metopium brownei, Thrinax readii, Bumelia retusa, Caesalpinia vesicaria* and *Hymenocallis littoralis*).

Coastal dune vegetation is characterized by a mosaic of habitats in which environmental factors change. C, R/S and OT-species differ in their presence among habitats (Table 2). Dune habitats are formed by the sandy beach, embryo dunes and foredunes in which sand movement is the dominating environmental factor. C-species predominate in the dune habitat (40.6%), R/S and OT-species represent 31.21% and 28.1% respectively. Humid and wet slacks are those habitats which become inundated during the rainy season when the water table rises. OT-species also represent more than half of the species present (53%), R/S represent more than a third (34.5%) and C-species 12.3%. In stabilized habitats where there is no sand movement and conditions are less stressful such as grassland, thickets and tropical forest — including the protected area behind the foredune —, OT-species represent more than half (54%), R/S-species 38.5% and C-species only 7.4%. If we analyse distribution of C-species among habitats (Table 2, percentages in bold letters), we find that 41% of them occur in dune habitats, 37.8% in stabilized communities and 21% in slacks or water-dependent habitats. R/S and OT-species have low values in dune habitats (11 and 7.2% respectively), intermediate values in slacks (20.5 and 22.9% respectively) and high percentages in stabilized habitats (68.3% and 69.7%).

Growth forms also vary among the species groups (Table 3). Herbaceous species can be divided into (1) grasses and sedges — in which OT-species account for 48.3% and R/S-species for 33.3% — and (2) forbs (where R/S-species account for 45.1%). OT-species are the dominant group among shrubs (51.2%), and especially trees, where they represent 77.6%. In both shrubs and trees coastal species have few representatives. If we analyse the growth forms of C-species (Table 3, percentages in bold letters), we find that 71% of them are

Table 3. Number and percentage of coastal (C), ruderal/secondary (R/S) and species from other vegetation types (OT) for the various growth forms. Other growth forms include cacti, agaves and epiphytes. Percentages in bold letters indicate values along horizontal lines.

	Grasses and sedges		Forbs		Total		Shrubs		Trees		Total		Cacti, Agaves, Epiphytes		
	No. spp.	%	No. spp.	%	No. spp.	%	No. spp.	%	No. spp.	%	No. spp.	%	No. spp.	%	%
C	11	*18.3*	38	*17.6*	49	**71**	14	*11.7*	5	*5.8*	19	**27.5**	1	*7.6*	**0.69**
R/S	20	*33.3*	97	*45.1*	117	**66**	44	*36.9*	14	*16.4*	58	**33.1**	---	---	---
OT	29	*48.3*	80	*37.2*	109	**43.9**	61	*51.2*	66	*77.6*	127	**51.2**	12	*92.3*	**4.8**

Table 4. Partial list of coastal (C), ruderal/secondary (R/S) and species from other vegetation types (OT).

Coastal	**Ruderal / secondary**	**Other vegetation types**
Amaranthus greggii	*Acacia farnesiana*	*Abrus precatorius*
Ambrosia hispida	*Ambrosia artemisiifolia*	*Acacia macracantha*
Avicennia germinans	*Andropogon glomeratus*	*Acanthorecereus pentagonus*
Batis maritima	*Aristida adscensionis*	*Aechmea bracteata*
Caesalpinia bonduc	*Asclepias curassavica*	*Agave angustifolia*
Cakile edentula	*Axonopus compressus*	*Amphilopium paniculatum*
Cakile lanceolata	*Bidens pilosa*	*Borreria densiflora*
Canavalia rosea	*Borrichia frutescens*	*Bumelia retusa*
Chamaecrista chamaecristoides	*Cardiospermum halicacabum*	*Bursera simaruba*
Chrysobalanus icaco	*Cenchrus echinatus*	*Casearia nitida*
Coccoloba uvifera	*Cnidoscolus urens*	*Chamaesyce dioica*
Conocarpus erecta	*Commelina erecta*	*Chiococca alba*
Croton punctatus	*Crotalaria incana*	*Coccoloba barbadensis*
Erithalis fruticosa	*Cyperus esculentus*	*Coccothrinax readii*
Ernodea littoralis	*Desmodium incanum*	*Cordia sebestena*
Fimbristylis spadicea	*Fimbristylis spathacea*	*Cyperus articulatus*
Hisbiscus pernambucensis	*Florestina tripteris*	*Diphysa robinoides*
Ipomoea pes-caprae	*Gossypium hirsutum*	*Eleocharis caribaea*
Ipomoea stolonifera	*Guazuma ulmifolia*	*Eugenia capuli*
Iva asperifolia	*Gymnopodium floribundum*	*Hydrocotyle bonariensis*
Laguncularia racemosa	*Indigofera suffruticosa*	*Jacquinia pungens*
Oenothera drummondii	*Iresine diffusa*	*Krugiodendrum ferreum*
Okenia hypogaea	*Jacquinia aurantiaca*	*Lycium carolinianum*
Opuntia stricta var. dillenii	*Lantana camara*	*Metastelma pringlei*
Palafoxia lindenii	*Lantana involucrata*	*Nectandra coriacea*
Panicum amarum	*Macroptilium atropurpureum*	*Nymphaea ampla*
Panicum repens	*Malvaviscus arboreus*	*Pectis satureioides*
Pithecellobium keyense	*Panicum maximum*	*Pithecellobium dulce*
Philoxerus vermicularis	*Passiflora foetida*	*Prosopis juliflora*
Rhizophora mangle	*Phyla nodiflora*	*Psychotria erythrocarpa*
Salicornia begelovii	*Porophyllum punctatum*	*Randia laetevirens*
Scaevola plumierii	*Portulaca oleracea*	*Scheelea liebmanii*
Schizachyrium scoparium	*Rhynchelytrum repens*	*Sporobolus jacquemonti*
Sesuvium portulacastrum	*Rivina laevis*	*Stemmadenia decipiens*
Sophora tomentosa	*Solanum americanum*	*Stenocereus laevigatus*
Sporolobus virginicus	*Sporobolus pyramidatus*	*Thrinax radiata*
Suriana maritima	*Tecoma stans*	*Turnera diffusa*
Tournetortia gnaphalodes	*Tephrosia cinerea*	*Typha latifolia*
Trachypogon gouini	*Verbesina persicifolia*	*Vigna vexillata*
Uniola paniculata	*Vigna luteola*	*Zamia furfuracea*

herbaceous (grasses and sedges: *Schizachyrium scoparium, Panicum amarum, Sporobolus virginicus, Trachypogon gouini, Uniola paniculata, Fimbristylis spadicea,* and forbs: *Ipomoea pes-caprae, Canavalia rosea*. See Table 4). 27.5% of the C-species are woody (shrubs or trees: *Chrysobalanus icaco, Ernodea littoralis, Coccoloba uvifera, Chamaecrista chamaecristoides, Hibiscus pernambucensis, Suriana maritima*) and 0.7% have particular growth forms such as cacti (*Opuntia stricta*).

R/S-species are also mainly herbaceous (66.8% - *Asclepias curassavica, Cenchrus echinatus, Commelina erecta, Desmodium* spp., *Macroptilium atropurpureum, Rhynchelitrum repens, Sida rhombifolia, Solanum nigrum*) and the woody species represent 33.1% (*Acacia farnesiana, Celtis pallida, Caesalpinia cacalaco, Guazuma ulmifolia, Senna occidentalis, Thevetia gaumeri, Verbesina persicifolia)*. OT-species show a different trend. Herbaceous elements represent 43.9% (*Eleocharis* spp., *Fimbristylis castanea, Nymphaea ampla, Typha domingensis, Rhynchosia americana*) and woody species account for more than half (51.2% — *Acacia cornigera, Bursera simaruba, Bumelia* spp., *Cedrela odorata, Enterolobium cyclocarpum*). Palms were considered under shrubs and trees, because of their physiognomy (*Acrocomia mexicana, Thrinax radiata, Coccothrinax readii, Scheelea liebmanii*). No other data are available on various ecological or physiological traits.

Discussion

Frequently, exotics are considered synonymous to invaders. There are few data on dune colonization by exotics from abroad (*Rhynchelytrum repens, Cocos nucifera, Casuarina equisetifolia)*. Exotics are known to compete with native species, even to the point of replacing them. It is difficult to imagine the implications that such invasions have had on dune systems, as studies on dune communities are recent, and human activities both on the coastal plain and on dunes are quite old. Johnson & Barbour (1990) mentioned three exotics that tend to take over habitats they invade in the coasts of Florida: *Agave sisalana, Schinus terebinthifolius* and *Casuarina equisetifolia*. In this study invaders (OT and R/S) are those species which have not evolved in coastal environments, but their life history traits allow them to colonize and reproduce successfully. Their presence is highly variable and they are not so frequent as to be considered characteristic elements of the communities. 59% of invaders are found in just one or two sites. The analysis performed on the 655 species that constitute the coastal dune flora of the Gulf and Caribbean of Mexico helps to understand why dune communities behind the foredune are so different both floristically and structurally from one place to another. The dune system seems to tolerate and enrich its flora with invaders.

The results of this study show that species richness for any one site depends on the presence of several groups of species, each of which predominates in particular habitats within the dune system and in different periods of the stabilization process. There is essentially no biological difference between the process of invasion and the process of colonization or recolonization by native plants. Colonization after a disturbance is a fundamental process of plant succession (Huston 1994). C-species, which include those solely adapted to sand dune environments, mangroves and coastal marshes, have a more uniform distribution throughout the littoral areas (Fig. 2 and Table 1) although, numerically, they often constitute a minor component on each site (Fig. 2).

Populations may disappear from any one area, but they will soon recolonize and reestablish. They occupy environments with stressful physical conditions (sand movement, airborne salinity, sea-water inundation) in which other species are not successful such as beaches, embryo dunes and active dunes. In these habitats disturbance by sand movement is determinant and is constantly opening new spaces for colonization. C-species are the most abundant here and they have probably evolved under these drastic conditions (Table 2). This explains their higher frequency distribution along the sites (Fig. 2). Barbour et al. (1987) analyzed growth forms of beach vegetation along the northern Gulf of Mexico. 46% of the taxa were perennial, non-succulent forbs, 29% were perennial grasses and allies and 26 % woody perennials, mostly sclerophyllous. Percentages of herbaceous and woody C-species in dune habitats are very similar to those found by Barbour et al. (1987).

Most R/S and OT-species were found in only one or two sites. They invade the dunes and some propagules are able to germinate and establish. Stabilized habitats and slacks have adequate conditions for their successful establishment and reproduction. Their presence probably depends on nearby sources, time, chance, species attributes and adequate microhabitats in the dune system. These are found further away from the beach: humid slacks and stabilized areas. OT-species are able to invade as well as S/R-species but with lower numbers. Slacks are also subjected to disturbances produced by inundation. Wetland flora is adapted to these conditions and easily invades new sites in which humid conditions predominate. This would explain the high number of OT-species found in water dependent habitats. R/S-species are able to colonize newly opened spaces in which vegetation has died after a prolonged inundation period.

Species adapted to stable mature communities (OT) are constantly invading and colonizing. Succession tends towards grasslands and tropical forests — dry and semideciduous forests — (Novelo 1978; Moreno-Casasola & Espejel 1986) where OT-species will dominate. They show the highest percentage of invaders (Table 2), having more OT-species than S/R species. The standard deviation for OT-species number along the 44 sites is the highest (21 $\pm$14.7), the minimum being 6 and the maximum 184. In these habitats there is usually an almost closed vegetation cover and probably more competition among plants both for nutrients and water. Disturbances are more sporadic and less intense. Thickets and tropical forests on coastal dunes are mainly formed by invaders (mostly OT-species) and with time will resemble these types of communities established inland, although always with some coastal elements (C-species).

The results obtained for the three habitat types do not show any direct relationship between disturbance and invasibility. R/S-species account for approximately one third of the richness in the three of them, regardless of their disturbance regime. OT-species account for 54% of the flora of stabilized sites, where sand movement and inundation are not important.

During the last decades, many tropical sand dune areas have increasingly been bordered by agricultural land. The coastal plain has rich soils with crops and managed grasslands for cattle. They are connected by dirt roads and other types of corridors that favour the spread and persistence of weeds, thus facilitating movement of plants through the landscape (DeFerrari & Naiman 1994; Romano 1990). Human activities favour the presence of weeds and ruderal species, many of which produce small, easily dispersed seeds. It is probable that the disappearance of forests and the increase in croplands, pastures and secondary vegetation will increase the R/S component and modify the composition of the vegetation covering stabilized dunes. This will increase the presence of herbaceous growth forms (Table 3).

Many other physiological parameters will also be modified. As Barbour et al. (1985) have shown, beach species show trends in life forms, leaf traits and physiological behaviour (for example germination, growth and photosynthesis have broad temperature optima). We do not have information on these differences for C, R/S and OT-species.

Currently, the result is a highly variable flora between different dune systems in a geographic region, the coastal element (C) being the common link because of its higher frequency distribution. At the regional level other vegetation types, i.e. mediterranean-type shrublands, also show a high level of floristic variation although structure remains fairly uniform (Griffin et al. 1983).

Biodiversity and its conservation is now becoming one of the main concerns of humankind. Coastal dune systems occupy a very low percentage of the land environments. In subtropical and tropical regions it is rapidly diminishing with the impressive growth of touristic developments. Species richness in dune systems cannot be approached in a simple way. It varies geographically (Gulf and Caribbean) as well as locally (Figs. 1 and 2), depending on the degree of stabilization, mosaic of environmental conditions, floristic composition (percentage of C, OT and R/S-species) and potential sources of propagules of invading species. The dune flora must be considered as a floristically variable and rich entity formed by species with very different evolutionary histories. The sand dune patchwork of environmental conditions and communities changes in space and also in time. It is a highly dynamic system in which processes of succession and disturbance constantly produce heterogeneity and allow the presence of numerous invading species.

Dunes are complex mosaics of habitats, each with dynamics that are closely linked with particular disturbance regimes (mainly sand movement and inundation). Conservation and management of dune communities should take into account the preservation of this heterogeneity, as each element-type of this patchwork responds differently to human alterations. Of primary concern are habitats needed by C-species. These habitats are characterized by the intensity of disturbances and are associated with the first stages of dune stabilization. Dune conservation should reproduce spatially the temporal sequence of dune stabilization. By favouring this mosaic of habitats, species whose existence depend on the physical factors determining each habitat are guaranteed a place where they can reproduce successfully. Later stages favour the presence of invaders (OT and R/S) which drastically increase local biodiversity. Their presence probably depends on nearby sources, mainly of OT-species.

The data presented in this paper seem to imply a contradiction between favouring habitats for C-species and facilitating stabilized conditions more adequate for OT-species (and quite a number of R/S-species) and thus richer communities. We believe dune conservation strategies should take into account the simultaneous maintenance of several degrees of stabilization in nearby systems as well as preserved patches of communities inland (forests, thickets, grasslands) which can act as seed sources. Efforts should be encouraged to preserve the dynamics and ecosystem functioning of dunes, which include both the habitats in which coastal species survive successfully and those in which thickets and trees predominate.

Acknowledgements. We are grateful to Jerzy Rzedowski, Gonzalo Castillo, Patricia Dávila, Fernando Chiang and Javier Valdés for checking the assigned species categories, and to Sergio Guevara, Carlos Vazquez-Yanes and Guadalupe Williams-Linera for their helpful comments on an earlier version of the manuscript.

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Received 10 April 1995;
Revision received 27 February 1996;
Accepted 10 April 1996.