

Vascular Plant Species Diversity on Two Barrier Islands in Southwest Florida

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ABSTRACT



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The equilibrium theory of island biogeography was examined in relation to the indigenous vascular floras of two barrier islands of different size and distance from the southwest Florida mainland. On Cayo-Costa Island, which has a land area of 5.6 km² and is located 12.8 km from the mainland, 261 species were identified. On Sanibel Island, which has a land area of 43.6 km² and is located 3.2 km from the mainland, an inventory in the mid-1950's identified 266 species. The similar number of species, despite the differences in island area and distance from the mainland, was attributed to the incompleteness of the inventory of Sanibel in the 1950's. An inventory of Sanibel from 1965 to 1985 identified 432 native species. This almost two-fold difference in the number of species on Sanibel as compared with Cayo-Costa is more consistent with equilibrium theory which predicts a significantly greater number of species on a larger island located closer to the mainland. However, comparison of the species-area relations of Cayo-Costa and Sanibel with other studies of island floras suggests that Sanibel should have had even more species. Urban development and the spread of alien plant species following the construction of a causeway linking Sanibel to the mainland in 1963 may have reduced the number of native plant species on Sanibel.

ADDITIONAL INDEX WORDS: *Barrier islands, coastal plants, Cayo-Costa Island, equilibrium theory, Florida, native species, Sanibel Island, species composition.*

INTRODUCTION

The equilibrium theory of island biogeography has stimulated much research since it was first formulated by MACARTHUR and WILSON (1963). According to the equilibrium theory, species composition on islands is not fixed, but rather changes over time due to on-going immigration and extinction. The balance between these two processes is believed to result in a nearly constant equilibrium number of species. The theory also predicts that a large island located close to a mainland source area should have a higher equilibrium number of species than a smaller island located further from the mainland.

The equilibrium theory has been tested for microorganisms (CAIRNS *et al.*, 1969; HAVE, 1987), fungi (ANDREWS *et al.*, 1987), arthropods (SIMBERLOFF and WILSON, 1970; STRONG and REY, 1982), ants (GOLDSTEIN, 1975; BOOMSMA *et al.*, 1987), land snails

(SOLEM, 1973), fish (SMITH, 1979), birds (DIAMOND, 1969; JOHNSON, 1975; ABBOTT and GRANT, 1976), lizards (WILCOX, 1978) and mammals (LAWLOR, 1983). The theory also has been considered in relation to the vascular floras of high altitude paramo vegetation in South America (SIMPSON, 1974), lake islands in Sweden (NILSSON and NILSSON, 1978; RYDIN and BORGEGARD, 1988), very small islands and offshore cays in Australia, Venezuela, and Puerto Rico (ABBOTT, 1977; BUCKLEY, 1982; HEATWOLE and LEVINS, 1983; BURANDT and CAMPINS, 1986; FLOOD and HEATWOLE, 1986), the Galapagos Islands (VAN DER WERFF, 1983), and the Gulf of California Islands (CODY *et al.*, 1983). The studies by VAN DER MAAREL (1982) and MENNEMA and WEEDA (1983) on the Frisian Islands along the coasts of the Netherlands and Germany are among the few that have documented plant species numbers on barrier islands of different size and distance from the mainland.

Barrier islands differ geologically from oceanic islands (such as the Galapagos) and

continental islands (such as those in the Gulf of California) which originate by volcanic and tectonic processes. Barrier islands, which comprise roughly 10 to 13% of the world's continental coastline (SCHWARTZ, 1973), are $<10^4$ yr old and are composed of unconsolidated sediments lying offshore on gently sloping continental shelves. They are generally separated from the mainland by a shallow lagoon or bay, and they rarely have elevations exceeding 10 m above sea level. Due to their depositional nature and their limited topographic relief, barrier islands are actively reworked by shoreline processes and are vulnerable to storm overwash. The objective of our study was to consider the equilibrium theory of island biogeography in relation to the indigenous floras of two barrier islands in southwest Florida.

STUDY AREA

The two barrier islands examined in this study are Cayo-Costa and Sanibel Islands. These islands are part of the Charlotte Harbor barrier island system located west of Fort Myers (latitude $26^{\circ}45'N$, longitude $82^{\circ}10'W$) (Figure 1). The north end of Cayo-Costa is adjacent to Boca Grande Pass which is the major tidal inlet serving Charlotte Harbor and the discharge site of the Myakka and Peace Rivers. The south end of Sanibel Island is adjacent to San Carlos Bay, the discharge site of the Caloosahatchee River.

Sanibel Island is the largest of the five islands that comprise the chain. It has a land area of 4,362 hectares and recurves landward at its southern end to a distance of 3.2 km from the mainland. Cayo-Costa Island is located 14.9 km to the north. It has a land area that is 13% of the land area of Sanibel, and it is 4 times further from the mainland.

Both islands are composed mainly of calcareous biogenic marine sediments and some quartz sands derived from river discharge (HUANG and GOODELL, 1967). The Gulf coast of Florida is periodically subject to hurricane disturbances and storm overwash events. Accretionary beach ridges with the characteristic ridge and swale topography comprise the Gulf side of both islands. The more protected bay side consists of tidal swamp deposits.

Southwest Florida has a moist subtropical climate with a mean annual temperature of $23^{\circ}C$

and a mean annual precipitation of 1360 mm (NATIONAL CLIMATIC CENTER, 1982). Floristically, the islands are a mixture of southern temperate and tropical Caribbean species.

METHODS

An inventory of vascular plant species on Cayo-Costa Island was made over the two-year period from 1975 to 1977. The results from Cayo-Costa were compared with two inventories made on Sanibel Island: (1) an inventory carried out in 1953 and 1954 (COOLEY, 1955), and (2) a more recent inventory carried out from 1965 to 1985 (WUNDERLIN and HANSEN, 1985). We assumed that the number of plant species on Cayo-Costa did not change significantly over the period 1977 to 1985.

Our study consisted of comparing only the native vascular plant species from the three inventories. Obsolete nomenclature was updated. Ruderal species, naturalized exotics, and ornamentals that had escaped from cultivation were excluded from the comparison.

To evaluate the predictions of the equilibrium theory, the number of species on each island was considered in relation to the land area of the island and its distance from the mainland. The species-area relationship was expressed in the standard form $S = CA^z$, where S is the species number, A is the island area, C is a coefficient that relates to biogeographic region and is generally less in regions where there are fewer potential colonizing species in a given taxon, and z is an exponent that tends to increase as a function of increasing island isolation (MACARTHUR and WILSON, 1967). The best-fit equation was determined for Cayo-Costa and Sanibel Islands by plotting the two data points on log-log graph paper and then fitting a line through these points. Comparisons were made between the equation from our study and those equations derived from other studies of plant species number and island area.

RESULTS

The extent of land development on Sanibel at the time of COOLEY's inventory was comparable to Cayo-Costa in the 1970's. Both islands were sparsely inhabited, and had essentially the same habitat diversity consisting of beach strands, savannas, cabbage palm forests, slash

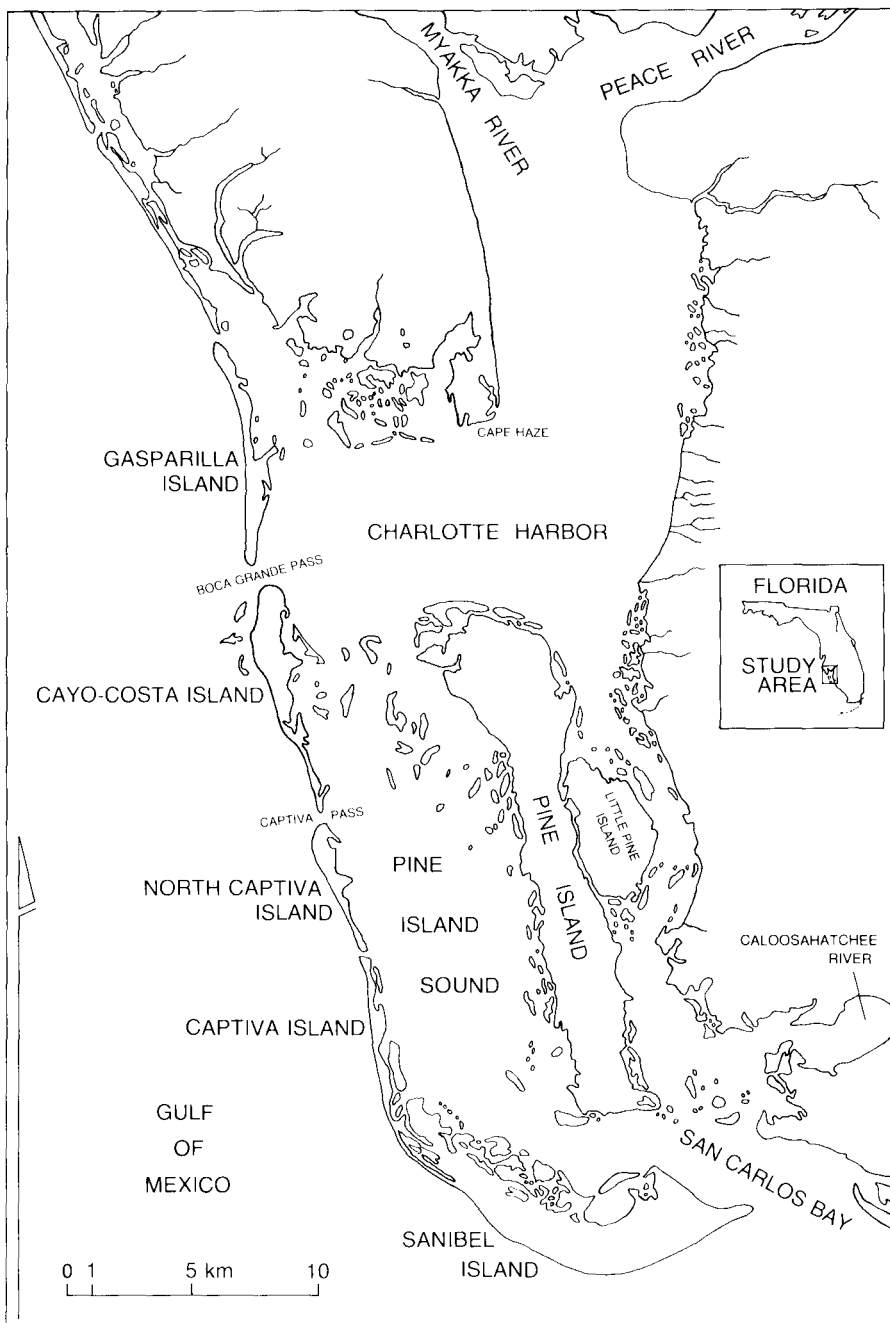


Figure 1. Location of Cayo-Costa and Sanibel Islands in the Charlotte Harbor barrier island system of southwest Florida.

pine flatwoods, freshwater marshes, mangrove swamps, salt marsh tidal flats, and tropical hardwood hammocks (COOLEY, 1955; HER-

WITZ, 1977). In 1963, the construction of a causeway linking Sanibel to the mainland led to urban development on parts of Sanibel dur-

ing the period of WUNDERLIN and HANSEN's inventory. Sanibel continues to have the same habitat diversity as Cayo-Costa, but the areal extent of these habitats on Sanibel has been reduced.

Table 1 shows the number of native vascular plant species and genera on the two islands. The inventories of Sanibel reported by COOLEY (1955) and by WUNDERLIN and HANSEN (1985) are shown separately in Table 1.

On Cayo-Costa, 261 species were found representing 203 genera. Thirty-nine genera were represented by two or more species. COOLEY (1955) reported 266 native vascular plant species representing 196 genera. Forty-five genera were represented by two or more species. Non-co-occurring species on islands having similar habitat diversity may be considered suggestive of species turnover (CODY *et al.*, 1983). On the basis of the COOLEY (1955) inventory, Sanibel had 34% of its species and 25% of its genera not co-occurring on Cayo-Costa, while Cayo-Costa had 33% of its species and 27% of its genera not co-occurring on Sanibel (Table 1).

WUNDERLIN and HANSEN (1985) identified >1.6 times more species on Sanibel than COOLEY (1955). They found 432 species representing 282 genera. Seventy-nine genera were represented by two or more species. On the basis of the WUNDERLIN and HANSEN (1985) inventory, Sanibel had 51% of its species and 34% of its genera not co-occurring on Cayo-Costa, while Cayo-Costa had only 15% of its species and 8% of its genera not co-occurring on Sanibel (Table 1). Many of the non-co-occurring species were represented by co-occurring genera. On Sanibel, 54% of the non-co-occurring species were represented by co-occurring genera on Cayo-Costa. On Cayo-Costa, 62% of the non-co-occurring species were represented by genera co-occurring on Sanibel.

DISCUSSION

On the basis of the land areas and distances from the mainland of Cayo-Costa and Sanibel Islands, equilibrium theory predicts that Sanibel should have significantly more species than Cayo-Costa. Different-sized islands are expected to have different species numbers due to the relationship between population size and island area. The land area of Sanibel is more than 7 times greater than Cayo-Costa.

Comparison Based on COOLEY Inventory

The number of species identified on Sanibel between 1953 and 1954 by COOLEY (1955) was essentially the same number of species identified on Cayo-Costa. Some variance in species numbers would be expected due to turnover noise (DIAMOND, 1969), but this variance cannot explain why the species numbers should be so similar. Four possible explanations may be presented.

(1) Sanibel may have been in a nonequilibrium condition at the time of Cooley's inventory. The physiography of the Charlotte Harbor barrier island chain and radiometric dates from Sanibel suggest that Sanibel may be the youngest island in the chain, and may have had less time to establish the equilibrium species number. Barrier islands in many different geographic localities date from about 7000 yr BP (PETHICK, 1984); however, barrier islands that originate from elongating breached spits (FISHER, 1968) would be expected to differ in age. The oldest beach ridges on Sanibel are only 4300 ± 50 yr old and the landward-recurving progradational lobe, which constitutes the bulk of Sanibel's land area (Figure 1), has been dated at less than 2000 years (MISSIMER, 1973). The Charlotte Harbor barrier island chain may

Table 1. Comparison of numbers of native vascular plant species and genera.

	Cayo-Costa 1975-77	Sanibel† 1953-54	Cayo-Costa 1975-77	Sanibel* 1965-85
Number of species	261	266	261	432
Co-occurring (%)	67.0	65.8	84.7	51.2
Not co-occurring (%)	33.0	34.2	15.3	48.8
Number of genera	203	196	203	282
Co-occurring (%)	72.9	75.5	91.6	66.0
Not co-occurring (%)	27.1	24.5	8.4	34.0

† Based on Cooley (1955).

* Based on Wunderlin and Hansen (1985).

have developed in a southerly direction with Cayo-Costa being >1000 years older and therefore closer to the equilibrium condition. The weakness of this explanation is that 1000 years should be adequate time for a nearshore island to achieve equilibrium (RYDIN and BORGEGARD, 1988).

(2) Prior to Cooley's inventory, Sanibel may have undergone an environmental perturbation. For example, storm overwash, which can be extremely disruptive to the vegetation of barrier islands (GODFREY and GODFREY, 1976), may have resulted in a significant reduction in species numbers on Sanibel. Sanibel would be vulnerable to storm overwash from the south and southwest because of the orientation of its coastline. Cayo-Costa would be most vulnerable to storm overwash from the west because of the north-south orientation of its coastline. Meteorological records for southwest Florida over the last 60 years indicate a relatively high frequency of storms from the south and southwest (GENTRY, 1974) with at least four hurricanes known to have been destructive to vegetation on Sanibel between 1922 and 1953. The weakness of this explanation is that, despite the different orientation of Cayo-Costa's shoreline, it would be difficult to envisage Cayo-Costa being unaffected by these storm events.

(3) Islands that have undergone a reduction in land area, for example, as a result of shoreline erosion, may initially support more species than the equilibrium number (WILCOX, 1978). The southern half of Cayo-Costa (Figure 1) has undergone significant shoreline erosion as evidenced by the exposure of mangroves on the Gulf side of the island. The number of plant species on Cayo-Costa, therefore, could represent a number that exceeds the equilibrium condition. This explanation is weakened by the fact that there has been a corresponding accretion of beach ridges on the northern half of Cayo-Costa, and no significant net reduction in land area (HARVEY, 1979).

(4) The floristic inventory of Sanibel by COOLEY (1955) may have been incomplete. If we consider it complete, a total of 166 additional species of native vascular plants would have had to colonize the island in the 30-year period from 1955 to 1985. While the construction of the causeway could have increased the opportunities for both deliberate and inadvert-

ent introduction of mainland species, a 62% increase in the number of native species seems unlikely. The unusually high proportions of non-co-occurring species (>30%) on the two islands, therefore, probably reflects the incompleteness of COOLEY's inventory.

Comparison Based on Wunderlin and Hansen Inventory

According to the WUNDERLIN and HANSEN (1985) inventory, Sanibel had 171 more native vascular plant species than Cayo-Costa. This result is more consistent with equilibrium theory. Species-area curves of MACARTHUR and WILSON (1967) predict a doubling in species number with roughly a ten-fold increase in island area.

The species-area relationship for Cayo-Costa and Sanibel Islands is best expressed by the equation $S = 171A^{0.25}$. Figure 2 shows this relationship on log-log axes together with the best-fit lines found for vascular plant species numbers on the Galapagos Islands (VAN DER WERFF, 1988), the Gulf of California Islands (CODY *et al.*, 1983), and the Frisian Islands (MENNEMA and WEEDA, 1983). These studies all found an exponential increase in species number with increasing island area; however, there were some marked differences in the C and z values (Table 2).

As would be expected for oceanic islands located >700 km from the mainland, the species numbers on the Galapagos were lower than the numbers on comparable-sized continental islands (Figure 2). Both the Galapagos and the Gulf of California Islands had low C values presumably because they are located in relatively dry biogeographic regions with a smaller pool of potential colonizing species. Higher C values would be expected in the more favorable, mesic biogeographic regions of Florida and Europe.

The range of z values is generally between 0.20 and 0.35. According to MACARTHUR and WILSON (1967), the values at the lower end of this range correspond to islands located close to the mainland where there tends to be a higher colonization rate of transient species. The z values of 0.20 for the Gulf of California Islands and 0.25 for Cayo-Costa and Sanibel are consistent with the prediction that the logarithm of species number increases less rapidly on nearshore islands. The z value of 0.31 for the Galapagos

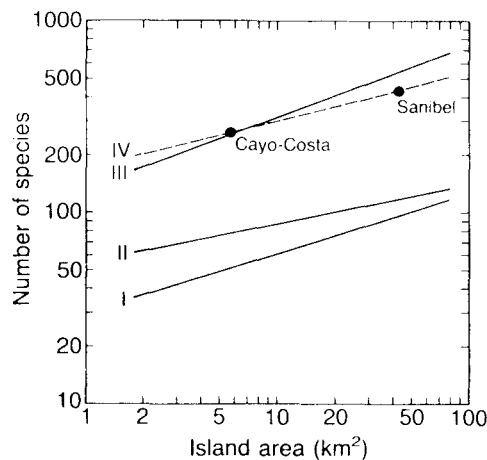


Figure 2. Relationship between number of vascular plant species and island area shown for: (I) the Galapagos Islands (VAN DER WERFF, 1983), (II) the Gulf of California Islands (CODY *et al.*, 1983), (III) the Frisian Islands (MENNEMA and WEEDA, 1983), and (IV) Cayo-Costa and Sanibel Islands.

Table 2. Species-area slopes and coefficients for different island systems.

Islands	C	z	n	r	P
Galapagos	30	0.31	18	0.89	< 0.001
Gulf of California	55	0.20	30	0.87	< 0.001
Frisian	133	0.37	17	0.90	< 0.001
Cayo-Costa & Sanibel	171	0.25	2	NA	NA

Species-area equation $S = CA^z$.

n = number of islands.

r = correlation coefficient.

P = significance probability.

NA = not applicable.

Islands is at the higher end of the expected range as predicted for oceanic islands located far from a mainland source area.

The z value of 0.37 for the Frisian Islands is greater than that found for the other island systems including the Galapagos (Table 2). This finding is contrary to the MACARTHUR-WILSON prediction that the logarithm of species number increases less rapidly on nearshore islands. SCHOENER (1976), CONNOR and McCOY (1979), and WILLIAMSON (1988) have rejected the MACARTHUR-WILSON prediction, and they have argued that the z values tend to be lower for more distant and isolated archipelagoes. In the case of nearshore barrier islands such as Cayo-Costa, Sanibel, and the Frisian Islands, high z values perhaps could be expected. The characteristic narrowness of bar-

rier islands and their susceptibility to the influences of storm overwash, subsurface saltwater intrusion, and salt spray may limit the colonization rate of transient mainland species, thus increasing the z value.

The Frisian Islands are comparable to Cayo-Costa and Sanibel both in terms of their geomorphogenesis, and their land area and distance to the mainland. The Frisian Islands best-fit equation $S = 133A^{0.37}$ is based on species inventories of 17 islands and is highly significant ($r = 0.90$; $P < 0.001$). If the high z value for the Frisian Islands is representative of barrier islands in general, the z value of 0.25 obtained for Cayo-Costa and Sanibel may be considered low.

Figure 2 shows how the number of species on Cayo-Costa is almost directly on the Frisian species-area best-fit line, while the number of species on Sanibel is well below the line. Adding those species on Cayo-Costa not co-occurring on Sanibel to the Sanibel species list yields a sum of 472 species. This sum is still less than the number predicted using the Frisian Islands species-area equation.

A lower-than-predicted number of plant species on Sanibel would suggest that Sanibel may have been in a nonequilibrium condition at the time of the Wunderlin and Hansen inventory. This finding would be consistent with the fact that urban development on Sanibel has mark-

edly increased following the construction of the causeway linking Sanibel to the mainland in 1963. The reduction in the area of native habitats as a result of human disturbance would be expected to decrease species numbers. In addition, HEATWOLE and WALKER (1989) recently noted that the spread of alien plant species on islands may reduce the number of native plant species.

Barrier islands often are desirable shoreline localities vulnerable to human activity. Establishment and maintenance of an equilibrium condition may be less commonly achieved on readily accessible barrier islands such as Sanibel Island. We conclude that human disturbance of native habitats and the spread of alien plant species into undisturbed native habitats may have caused a significant reduction in the number of native plant species on Sanibel.

Appendix I. Native Vascular Plant Species on Cayo-Costa and Sanibel Islands

- Acrostichum danaeifolium* Langsd. & Fisch.
Agalinis maritima (Raf.) Raf.
Agave decipiens Baker
Alternanthera flavescens Kunth
Amaranthus australis (A. Gray) Sauer
Amaranthus floridanus (S. Wats.) Sauer
Ambrosia artemisiifolia L.
Ambrosia hispida Pursh
Ammannia latifolia L.
Andropogon glomeratus (Walt.) BSP.
Andropogon virginicus L.
Ardisia escallonioides Schlecht. & Cham.
Aristida patula Chapm. ex Nash
Aristida purpurascens Poir.
Aster subulatus Michx.
Atriplex pentandra (Jacq.) Standl.
Avicennia germinans (L.) L.
Baccharis angustifolia Michx.
Baccharis halimifolia L.
Bacopa monnieri (L.) Pennell
Batis maritima L.
Bidens alba (L.) DC.
Blechnum serrulatum L. Rich.
Blutaparon vermiculare (L.) Mears
Boerhavia diffusa L.
Borrchia frutescens (L.) DC
Bouteloua hirsuta Lag.
Buchnera americana L.
Bumelia celastrina Kunth
Bursera simaruba (L.) Sarg.
Caesalpinia bonduc (L.) Roxb.
Cakile lanceolata (Willd.) O. Schulz
Callicarpa americana L.
Canavalia rosea (L.) DC.
Capparis cynophallophora L.
Capsicum frutescens L.
Cassytha filiformis L.
Celtis pallida Torr.
Cenchrus incertus M.A. Curtis
Centrosema virginianum (L.) Benth.
Cereus gracilis Mill.
Chamaecrista fasciculata (Michx.) Greene
Chamaecrista nictitans (L.) Moench
Chamaesyce blodgettii (Engelm. ex Hitchc.) Small
Chamaesyce hypericifolia (L.) Millsp.
Chamaesyce hyssopifolia (L.) Small
Chamaesyce mesembryanthemifolia (Jacq.) Dugand
Chiococca alba (L.) Hitchc.
Chrysobalanus icaco L.
Cirsium horridulum Michx.
Cladium jamaicense Crantz
Cnidioscolus stimulosus (Michx.) Engelm. & Gray
Coccoloba uvifera (L.) L.
Commelina erecta L.
Conocarpus erectus L.
Conyza canadensis (L.) Cronq.
Coreopsis leavenworthii Torr. & Gray
Crinum americanum L.
Crotalaria rotundifolia (Walt.) Gmel.
Croton glandulosus L.
Croton punctatus Jacq.
Cynanchum angustifolium Pers.
Cynanchum scoparium Nutt.
Cyperus compressus L.
Cyperus ligularis L.
Cyperus planifolius L. Rich.
Cyperus polystachyos Rotth.
Dalbergia ecastophyllum (L.) Taub.
Dichantherium dichotomum (L.) Gould
Dichantherium portoricense (Dfv. ex Ham.) B. F. Hansen & Wunderlin
Dichantherium strigosum (Muhl. ex Ell.) Freckmann
Digitaria villosa (Walt.) Pers.
Distichlis spicata (L.) Greene
Dodonaea viscosa (L.) Jacq.
Encyelia tampensis (Lindl.) Small
Eragrostis ciliaris (L.) R. Br.
Erechtites hieracifolia (L.) Raf.
Erigeron quercifolius Lam.
Ernodea littoralis Sw.
Erythrina herbacea L.
Eugenia axillaris (Sw.) Willd.
Eugenia foetida Pers.
Eupatorium mikanioides Chapm.
Eustachys petraea (Sw.) Desv.
Evolvulus alsinoides L.
Ficus aurea Nutt.
Fimbristylis caroliniana (Lam.) Fern.
Fimbristylis castanea (Michx.) Vahl
Fimbristylis spathacea Roth
Flaveria linearis Lag.
Forestiera segregata (Jacq.) Krug & Urban
Galium hispidulum Michx.
Gaura angustifolia Michx.
Genipa clusiifolia (Jacq.) Griseb.
Gnaphalium obtusifolium L.
Hedyotis nigricans (Lam.) Fosberg
Hedyotis procumbens (J.F. Gmel.) Fosberg
Hedyotis uniflora (L.) Lam.
Heliotropium angiospermum Murr.
Heliotropium curassavicum L.

- Heliotropium polyphyllum* Lehm.
Herissantia crispa (L.) Briz.
Heterotheca subaxillaris (Lam.) Britt. & Rusby
Hydrocotyle umbellata L.
Hymenocallis latifolia (Mill.) Roem.
Ipomoea alba L.
Ipomoea indica (Burm. f.) Merrill
Ipomoea pes-caprae (L.) R. Br.
Ipomoea sagittata Poir.
Ipomoea violacea L.
Iresine diffusa Humb. & Bonpl. ex Willd.
Iva frutescens L.
Iva imbricata Walt.
Jacquinia keyensis Mez
Kosteletzkya virginica (L.) Presl ex A. Gray
Laguncularia racemosa (L.) Gaertn. f.
Lantana involucrata L.
Lasiacis divaricata (L.) Hitchc.
Lepidium virginicum L.
Leucaena leucocephala (Lam.) de Wit
Licania michauxii Prance
Limonium carolinianum (Walt.) Britt.
Ludwigia microcarpa Michx.
Ludwigia repens Forst.
Lycium carolinianum Walt.
Malvastrum corchorifolium (Desr.) Britt.
Mastichodendron foetidissimum (Jacq.) H.J. Lam
Maytenus phyllanthoides Benth.
Melanthera nivea (L.) Small
Melothria pendula L.
Merremia dissecta (Jacq.) Hall. f.
Mikania scandens (L.) Willd.
Monarda punctata L.
Muhlenbergia capillaris (Lam.) Trin.
Myrica cerifera L.
Oenothera humifusa Nutt.
Opuntia humifusa (Raf.) Raf.
Opuntia stricta Haw.
Panicum amarum Ell.
Panicum virgatum L.
Parietaria floridana Nutt.
Parthenocissus quinquefolia (L.) Planch.
Paspalum distichum L.
Passiflora suberosa L.
Pectis glaucescens (Cass.) Keil
Pedilanthus tithymaloides (L.) Poit.
Petiveria alliacea L.
Phlebodium aureum (L.) Sm.
Phyla nodiflora (L.) Greene
Phyllanthus abnormis Baill.
Phytolacca americana L.
Pinus elliotii Engelm.
Pisonia aculeata L.
Pithecellobium unguis-cati (L.) Benth.
Pluchea odorata (L.) Cass.
Pluchea rosea Godfrey
Poinsettia cyathophora (Murr.) Kl. & Gke.
Polygala boykinii Nutt.
Polygala grandiflora Walt.
Polygala incarnata L.
Polygonum hydropiperoides Michx.
Polypodium polypodioides (L.) Watt
Polypremum procumbens L.
Portulaca pilosa L.
Portulaca rubricaulis HBK.
Psilotum nudum (L.) Beauv.
Psychotria nervosa Sw.
Pteridium aquilinum (L.) Kuhn
Pterocaulon pycnostachyum (Michx.) Ell.
Ptilimnium capillaceum (Michx.) Raf.
Quercus virginiana Mill.
Randia aculeata L.
Rapanea punctata (Lam.) Lundell
Rhizophora mangle L.
Rhynchospora colorata (L.) Pfeiffer
Rivina humilis L.
Sabal palmetto (Walt.) Lodd. ex Schult.
Salicornia virginica L.
Salix caroliniana Michx.
Samolus ebracteatus Kunth
Samolus valerandi L.
Sarcostemma clausum (Jacq.) Roem. & Schult.
Scaevola plumieri (L.) Vahl
Scoparia dulcis L.
Serenoa repens (Bartr.) Small
Sesuvium portulacastrum L.
Setaria geniculata (Lam.) Beauv.
Setaria macrosperma (Scribn. & Merrill) Schum.
Sida acuta Burm. f.
Smilax auriculata Walt.
Solanum americanum
Solidago gigantea Ait.
Solidago sempervirens L.
Sophora tomentosa L.
Spartina bakeri Merr.
Spartina patens (Ait.) Muhl.
Spermacoce prostrata Aubl.
Sporobolus virginicus (L.) Kunth
Stenotaphrum secundatum (Walt.) Kuntze
Suaeda linearis (Ell.) Moq.
Suriana maritima L.
Thelypteris kunthii (Desv.) Morton
Tillandsia balbisiana Schult.
Tillandsia flexuosa Sw.
Tillandsia paucifolia Baker
Tillandsia recurvata (L.) L.
Tillandsia setacea Sw.
Tillandsia usneoides (L.) L.
Tillandsia utriculata L.
Toxicodendron radicans (L.) Kuntze
Trichostema dichotomum L.
Triplasis purpurea (Walt.) Chapm.
Typha domingensis Pers.
Uniola paniculata L.
Verbesina virginica L.
Vicia acutifolia Ell.
Vigna luteola (Jacq.) Benth.
Vitis munsoniana Simpson
Vittaria lineata (L.) Smith
Waltheria indica L.
Zanthoxylum clava-herculis L.
Zanthoxylum fagara (L.) Sarg.

Appendix 2. Native Vascular Plant Species on Cayo-Costa Island But Not on Sanibel Island

- Agalinis filifolia* (Nutt.) Raf.
Apium leptophyllum (Pers.) F. Muell.

- Asclepias verticillata* L.
Bulbostylis barbata (Rottb.) Clarke
Cenchrus gracillimus Nash.
Chamaesyce cumulicola Small
Chrysopsis scabrella Torr. & Gray
Dalea feayi (Chapm.) Barneby
Desmodium marilandicum (L.) DC.
Eupatorium leptophyllum DC.
Galactia parvifolia A. Rich.
Gnaphalium purpureum L.
Gratiola virginiana L.
Helianthemum corymbosum Michx.
Hieracium megacephalon Nash.
Lantana depressa Small
Launaea intybacea (Jacq.) Beauv.
Lechea sessiliflora Raf.
Mecardonia acuminata (Walt.) Small
Nephrolepis cordifolia (L.) Presl
Panicum anceps Michx.
Persea borbonia (L.) Spreng.
Physalis walteria Nutt.
Rhynchosia reniformis DC.
Rhynchospora grayi Kunth
Rhynchospora microcarpa Baldw. ex A. Gray
Sagittaria lancifolia L.
Salvia coccinea Buchoz ex Epling
Scleria triglomerata Michx.
Setaria corrugata (Ell.) Schult.
Sisyrinchium miamiense Bickn.
Sonchus asper (L.) Hill
Sonchus oleraceus L.
Sporobolus jacquemontii Kunth
Thelypteris palustris Schott
Vitis aestivalis Michx.
Woodwardia virginica (L.) Smith
Ximenia americana L.
Xyris elliottii Chapm.
Zamia pumila L.

Appendix 3. Native Vascular Plant Species on Sanibel Island But Not on Cayo-Costa Island

- Acacia pinetorum* (Small) Herm.
Aeschynomene americana L.
Agalinis fasciculata (Ell.) Raf.
Amaranthus hybridus L.
Amaranthus spinosus L.
Amaranthus viridus L.
Ampelopsis arborea (L.) Kohne
Amphicarpum muhlenbergianum (Schult.) Hitchc.
Anagallis minima (L.) Krause
Annona glabra L.
Argemone mexicana L.
Asplenium abscissum Willd.
Aster bracei Britt. ex Small
Aster simmondsii Small
Axonopus furcatus (Fluegge) Hitchc.
Baccharis glomeruliflora Pers.
Berlandiera subacaulis (Nutt.) Nutt.
Boerhavia erecta L.
Bothriochloa pertusa (L.) A. Camus
Capraria biflora L.
Capsicum annuum L.
Cardamine hirsuta L.
Cardiospermum microcarpum Kunth
Carex albolutescens Schwein.
Celosia nitida Vahl
Celtis iguanaea (Jacq.) Sarg.
Cenchrus echinatus L.
Centella asiatica (L.) Urban
Cephalanthus occidentalis L.
Cereus pentagonus (L.) Haw.
Chamaesyce bombensis (Jacq.) Dugand
Chamaesyce hirta (L.) Millsp.
Chamaesyce maculata (L.) Small
Chamaesyce ophthalmica (Pers.) Burch
Chamaesyce thymifolia (L.) Millsp.
Chenopodium ambrosioides L.
Chromolaena odorata (L.) King & Robins.
Cissus trifoliata L.
Cissus verticillata (L.) Nicols. & Jarvis
Commelina diffusa Burm. f.
Commelina elegans Kunth
Cuscuta pentagona Engelm.
Cyperus brevifolius (Rottb.) Hassk.
Cyperus globulosus Aubl.
Cyperus odoratus L.
Cyperus retrorsus Chapm.
Cyperus surinamensis Rottb.
Cyperus tetragonus Ell.
Desmodium incanum DC.
Desmodium scorpiurus (Sw.) Desv.
Desmodium tortuosum (Sw.) DC.
Dichantherium aciculare (Desv. ex Poir.) Gould & Clark
Dichantherium commutatum (Schult.) Gould
Dichondra carolinensis Michx.
Dicliptera assurgens (L.) Juss.
Digitaria ciliaris (Retz.) Koel.
Digitaria longiflora (Retz.) Pers.
Diodia teres Walt.
Diodia virginiana L.
Diospyros virginiana L.
Drymaria cordata (L.) Willd. ex Roem. & Schult.
Duranta repens L.
Echinochloa colonum (L.) Link
Echinochloa paludigena Weig.
Echinochloa walteri (Pursh) Heller
Eclipta prostrata (L.) L.
Eleocharis albida Torr.
Eleocharis atropurpurea (Retz.) Kunth
Eleocharis flavescens (Poir.) Urban
Eleocharis geniculata (L.) Roem. & Schult.
Eleocharis montevidensis Kunth
Emilia fosbergii Nicols.
Eragrostis elliottii F. Wats.
Eragrostis spectabilis (Pursh) Steud.
Eragrostis tracyi Hitchc.
Erianthus giganteus (Walt.) Muhl.
Eriochloa michauxii (Poir.) Hitchc.
Eryngium baldwinii Spreng.
Eugenia confusa DC.
Eupatorium capillifolium (Lam.) Small
Eupatorium serotinum Michx.
Euphorbia inundata Torr. ex Chapm.
Eustachys glauca Chapm.
Eustoma exaltatum (L.) Griseb.
Euthamia tenuifolia (Pursh) Greene

- Evolvulus sericeus* Sw.
Fimbristylis autumnalis (L.) Roem. & Schult.
Flaveria floridana J.R. Johnston
Flaveria trinervia (Spreng.) Mohr
Froelichia floridana (Nutt.) Moq.
Fuirena breviseta (Cov.) Cov.
Fuirena pumila (Torr.) Spreng.
Fuirena scirpoidea Michx.
Gaillardia pulchella Foug.
Galactia striata (Jacq.) Urban
Galactia volubilis (L.) Britt.
Galium tinctorium L.
Geranium carolinianum L.
Gnaphalium falcatum Lam.
Gnaphalium pensylvanicum Willd.
Gossypium hirsutum L.
Habenaria odontopetala Reichb. f.
Hamelia patens Jacq.
Haplopappus phyllocephalus DC.
Hedyotis corymbosa (L.) Lam.
Helenium amarum (Raf.) H. Rock
Hemicarpha micrantha (Vahl) Pax
Hexalectris spicata (Walt.) Barnh..
Hydrocotyle verticillata Thunb.
Hypoxis juncea Smith
Ipomoea triloba L.
Juncus marginatus Rostk.
Juncus megacephalus M.A. Curtis
Lantana camara L.
Lemna obscura (Austin) Daubs
Leptochloa dubia (Kunth) Nees
Leptochloa fascicularis (Lam.) A. Gray
Linaria canadensis (L.) Dun.
Lindernia crustacea (L.) F. Muell.
Linum medium (Planch.) Britt.
Lipocarpa maculata (Michx.) Torr.
Lobelia feayana A. Gray
Ludwigia curtissii Chapm.
Ludwigia erecta (L.) Hara
Ludwigia octovalvis (Jacq.) Raven
Ludwigia palustris (L.) Ell.
Ludwigia peruviana (L.) Hara
Lythrum alatum Pursh
Malvastrum americanum (L.) Torr.
Melochia villosa (Mill.) Fawc. & Rendle
Mentzelia floridana Nutt.
Micranthemum glomeratum (Chapm.) Shinnners
Mitreola petiolata (J.F. Gmel.) Torr. & Gray
Mollugo verticillata L.
Morinda royoc L.
Najas guadalupensis (Spreng.) Magnus
Najas marina L.
Nephrolepis biserrata (Sw.) Schott
Neptunia pubescens Benth.
Nymphaea mexicana Zucc.
Oenothera laciniata Hill
Opizia stolonifera Presl
Oxalis corniculata L.
Oxalis florida Salisb.
Panicum adpersum Trin.
Panicum chapmanii Vasey
Panicum dichotomiflorum Michx.
Panicum hians Ell.
Panicum repens L.
Panicum rigidulum Bosc ex Nees
Parietaria praetermissa Hinton
Paspalum blodgettii Chapm.
Paspalum boscianum Fluegge
Paspalum caespitosum Fluegge
Paspalum floridanum Michx.
Paspalum setaceum Michx.
Pectis linearifolia Urban
Pectis prostrata Cav.
Physalis angulata L.
Physalis angustifolia Nutt.
Physalis pubescens L.
Pilea herniarioides (Sw.) Lindl.
Pilea microphylla (L.) Liebm.
Piriqueta caroliniana (Walt.) Urban
Piscidia piscipula (L.) Sarg.
Plantago virginica L.
Plumbago scandens L.
Poinsettia heterophylla (L.) Kl. & Gke.
Polygonum setaceum Baldw. ex Ell.
Pyrrhopappus carolinianus (Walt.) DC.
Reimarochloa oligostachya (Munro) Hitchc.
Rhabdadenia biflora (Jacq.) Muell.-Arg.
Rhus copallina L.
Rhynchosia michauxii Vail
Rhynchosia minima (L.) DC.
Rudbeckia hirta L.
Rumex pulcher L.
Rumex verticillatus L.
Ruppia maritima L.
Sabatia stellaris Pursh
Sagittaria graminea Michx.
Salvia riparia Kunth
Sambucus canadensis L.
Scirpus robustus Pursh
Scirpus validus Vahl
Scleria reticularis Michx.
Scleria verticillata Muhl. ex Willd.
Senecio glabellus Poir.
Senna occidentalis (L.) Link
Sesbania emerus (Aubl.) Urban
Sesbania vesicaria (Jacq.) Ell.
Sesuvium maritimum (Walt.) BSP.
Setaria magna Griseb.
Sida rhombifolia L.
Sisyrinchium atlanticum Bickn.
Spartina alterniflora Loisel.
Spermacoce assurgens Ruiz & Pavon
Spiranthes vernalis Englem. & Gray
Sporobolus domingensis (Trin.) Kunth
Sporobolus junceus (Michx.) Kunth
Stillingia sylvatica L.
Stylosanthes hamata (L.) Taub.
Thalassia testudinum Banks & Solander ex Koenig
Thelypteris interrupta (Willd.) Iwatsuki
Tillandsia fasciculata Sw.
Tribulus terrestris L.
Triglochin striata Ruiz & Pavon
Tripsacum dactyloides (L.) L.
Typha latifolia L.
Urena lobata L.
Verbena scabra Vahl

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□ RÉSUMÉ □

Examine, en fonction des flores indigènes vasculaires, une théorie de l'équilibre biogéographique de deux îles barrière, différentes par leur taille et par leur éloignement du SW de la Floride. Sur Cayo-Costa (5,6 km² de surface et localisée à 12,8 km de la terre), 261 espèces ont été identifiées. Sur Sanibel (43,6 km² de surface et située à 3,2 km de la terre) un inventaire des années 50 a identifié 266 espèces, ce dernier étant incomplet par rapport à celui de Cayo-Costa. Un inventaire a identifié de 1965 à 1985 432 espèces indigènes sur Sanibel. Cette différence doublant presque le nombre d'espèces à Sanibel par rapport à Cayo-Costa est cohérente par rapport à une théorie de l'équilibre qui prédit significativement un nombre plus grand d'espèces sur une île plus vaste et plus proche de la Terre. Comparée à d'autres études de flore insulaire, Sanibel a pu avoir davantage d'espèces. Le développement urbain et l'éparpillement d'espèces allogènes qui résulta de la création d'une chaussée reliant Sanibel à la terre en 1963 a pu y réduire le nombre de plantes autochtones.—*Catherine Bressolier (Géomorphologie EPHE, Montrouge, France)*.

□ ZUSAMMENFASSUNG □

Die Gleichgewichtstheorie in Arbeiten zur Biogeographie von Inseln wurde untersucht bei der Aufnahme der einheimischen Gefäßpflanzenflora von zwei Barriereinseln unterschiedlicher Größe und unterschiedlicher Entfernung vom Festland Südwest-Floridas. Auf der Insel Cayo-Costa, die 5,6 km² groß und 12,8 km vom Festland entfernt ist, konnten 261 Arten gefunden werden. Auf der Insel Sanibel, die 43,6 km² groß ist und in 3,2 km Entfernung vom Festland liegt, konnten in einer Aufnahme in den 50er Jahren 266 Arten identifiziert werden. Die vergleichbare Anzahl von Arten, ungeachtet der Unterschiede in Entfernung zum Festland und Größe der Inseln, wurde auf die Unvollständigkeit der Florenaufnahme in den 50er Jahren auf Sanibel zurückgeführt. Eine Aufnahme, die zwischen 1965 und 1985 durchgeführt wurde, erbrachte ein Vorhandensein von 432 einheimischen Arten. Die fast doppelt so große Anzahl von Arten auf Sanibel im Gegensatz zu Cayo-Costa stimmt mehr mit der Gleichgewichtstheorie überein, die eine signifikant größere Anzahl von Arten auf der fröheren und näher zum Festland gelegenen Insel voraussagt. Vergleicht man die Arten-Gebiets-Relationen von Sanibel und Cayo-Costa mit anderen Studien zur Florenausstattung von Inseln, müßte Sanibel eigentlich eine noch größere Anzahl von Arten aufweisen. Wahrscheinlich hat aber die Stadtentwicklung und die Verbreitung von nicht einheimischen Arten im Zuge des Dammbaus zwischen Sanibel und dem Festland die Anzahl einheimischer Arten auf Sanibel reduziert.—*Ulrich Radtke, Geographisches Institut, Universität Düsseldorf, F.R.G.*