

Climate and coastal dune vegetation: disturbance, recovery, and succession

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Abstract The sand dune habitats found on barrier islands and other coastal areas support a dynamic plant community while protecting areas further inland from waves and wind. Fore-dune, interdune, and backdune habitats common to most coastal dunes have very different vegetation, likely because of the interplay among plant succession, exposure, disturbance, and resource availability. However, surprisingly few long-term data are available describing dune vegetation patterns. A nine-year census of 294 plots on St. George Island, Florida suggests that the major climatic drivers of vegetation patterns vary with habitat. Community structure is correlated with the elevation, soil moisture, and percent soil ash of each 1 m² plot. Major storms reduce species richness in all three habitats. Principle coordinate analysis suggests that changes in the plant communities through time are caused by climatic events: changes in fore-dune vegetation are correlated with temperature and summer precipitation, interdune vegetation with storm surge, and backdune vegetation with precipitation and storm surge. We suggest that the plant communities in fore-dune, interdune, and

backdune habitats tend to undergo succession toward particular compositions of species, with climatic disturbances pushing the communities away from these more deterministic trajectories.

Keywords Dune habitats · Succession · Disturbance · Coastal vegetation · Hurricane · Tropical storm

Introduction

Sand beaches, dunes, and swales create a common set of coastal formations found worldwide (e.g., Labuz and Grunewald 2007; da Silva et al. 2008; Forey et al. 2008; Judd et al. 2008). Sandy coasts, especially on barrier islands, are particularly dynamic environments because of interactions among geology, climate, and vegetation (Ehrenfeld 1990; Stallins and Parker 2003). A typical barrier island is composed of a series of dunes, the newest and largest of which, the fore-dunes, are created on the more exposed ocean side where sediments are deposited. Interdune areas behind the fore-dunes are lower and more level because of overwash and flooding from storms. Backdune areas include both dunes and swales in older, less disturbed areas, which are often slowly eroding into the back, or bay, side of the island.

The factors that control dune formation are often attributed to two sets of forces: the relatively constant

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actions of wind and waves (e.g., Hayes 1979; da Silva et al. 2008), and disturbance from rare but intense storms (Masetti et al. 2008; Houser et al. 2008). Normal wave and wind action generally act to build foredunes slowly, ultimately producing regular dunes and swales. Less frequent but intense storms, with heavy rainfall and overwash, tend to break down dunes and cause sediment deposition over interdune areas. Both of these habitats tend to protect the backdune areas from major damage. A third factor that also controls dunes is time; new dunes are formed on the ocean sides of islands, then gradually move inland as they become older and lower, generally over a relatively long time-scale (100–1,000 years; Hayden et al. 1991)

The vegetation on dunes and the dune and swale geomorphology interact reciprocally, as plants stabilize and promote their own preferred environmental conditions. At least three important groups of dune plants have been described: dune builders, burial-tolerant stabilizers, and burial intolerant stabilizers (see Ehrenfeld 1990; Stallins 2005). Dune builders grow upward rapidly after burial, and their stems and roots help to stabilize growing foredunes. Burial-tolerant stabilizers must withstand overwash and flooding and have a lattice network of rhizomes that stabilize low-lying areas affected by storm surge and heavy rain. Finally, burial-intolerant stabilizers are generally longer-lived species that are found in stable dunes and swales in more protected inland areas.

The feedback between vegetation and dunes has been hypothesized to result in the characteristic vegetation found in different dune habitats—the vegetation and morphology are predicted to converge toward particular species assemblages (stability domains; Stallins 2005) appropriate for each habitat (Ehrenfeld 1990). Of course, since the dunes themselves are aging, these assemblages can be viewed as short-term stable points or points along a more continuous longer-term successional trajectory. In particular, a suite of dune-builder plants may establish on new foredunes, promoting high dunes that reduce the effects of wind and waves associated with storms. In interdune areas, burial-tolerant plants may stabilize sediments and contribute to a flat topography that promotes or allows further overwash or flooding by heavy rain. Finally, the more stable backdune areas accumulate the highest diversity through time and may reflect a longer sere, from

initial dune stabilizing species to more burial intolerant species, and ultimately to woody shrubs and trees.

In this view, feedback between vegetation and geomorphology is the mechanism promoting different vegetation assemblages on foredunes, interdunes, and backdunes. Disturbances such as severe storms push the communities away from these assemblages; short-term succession returns dunes to their previous vegetation patterns. On a longer-time scale, the geomorphology of the dunes also changes with age resulting in a longer-term succession trajectory.

Surprisingly, there are few available data on vegetation patterns through time to study the dynamic pattern between disturbance and short-term succession for dune environments (see Day et al. 2001; Martinez et al. 2001; Snyder and Boss 2002). Studies of vegetation and climate through time can document the effects of disturbance by storms and other climate factors, while providing evidence for feedback mechanisms, the relative stability of different dune habitats, and the convergence of vegetation following disturbance. Here, we present the first results from a 9-year study of the vegetation of St. George Island, Florida, USA.

Materials and methods

Study site

St. George Island in north Florida is the largest of four islands fronting Apalachicola Bay. It is a typical wave-dominated microtidal barrier island (Hayes 1994) with a single fronting line of foredunes, an interdune area of overwashed flats, and a low ridge-and-swale topography in the backdunes. Geologically, it is a typical Holocene barrier island with 5–10 m of fine quartz sand over a thin Pleistocene layer of sandy-silt, silt, or clay.

The study area is in St. George Island State Park on a dune and beach ridge plain that has been forming on an active spit platform. Although St. George Island probably began forming about 4,000 years ago or later (Donoghue and Tanner 1992; Donoghue and White 1995), the study site on the growing eastern tip of the island is certainly much younger. Repeated beach profile surveys by the Florida Department of Environmental Protection over the past 30+ years

indicate that the shoreline at our site is prograding at an average rate of 5.5 m/year (Foster and Cheng 2001).

Field methods

We established permanent locations in 1999 where we have since monitored the vegetation annually (no data were collected in 2002). Six large grids (60 m × 60 m), each consisting of a 7 × 7 array of 1-m² plots, 10 m apart, were marked out with large wooden stakes, for a total of 49 censused plots per grid. Two grids were placed across foredunes, two in the interdune area, and two across ridges and swales in the backdunes, for a total of 294 plots. In the fall of each year (late October or early November), a 1-m² quadrat is placed over each plot, and all vegetation within it is censused. Different measures of abundance are used for plants with different growth forms (discrete individuals, number of individuals; clonal plants, number of ramets; bunch grasses, number of clumps; rhizomatous grasses, percentage cover); in this article, the analyses were conducted on presence/absence of each species in each 1-m² plot.

Data on several environmental variables associated with each plot were also collected. We determined soil moisture gravimetrically in 2001 by collecting a 2-cm diameter × 15-cm column of sand from a corner of each plot. Each sample was placed in an airtight bag in the field and later weighed, dried at 60°C, and reweighed. We determined percent ash using the same dried samples by reweighing the samples after they were heated in a combustion furnace. The elevation of each plot relative to mean sea level was determined in 2007 with a TopCon Total Station (Topcon Positioning Systems, Livermore, CA).

Analyses

Patterns through time for individual species were quantified as average species occurrences in plots within grids in each year ($n = 2$) in each of the foredune, interdune, and backdune habitats. Species richness was also determined as a function of time and habitat. Communities were initially described in terms of the rank-abundance patterns within each habitat, as determined from the presence and absence data for each plot within the habitat.

To quantify differences in community composition across the grids and through time, we created a distance matrix among plots using the Steinhaus similarity coefficient, then used principal coordinate analysis (PCoA) as an exploratory ordination tool (LabDSV package in R version 2.8; <http://www.r-project.org>). To reduce the influence of rare species on the analysis, only the 22 most abundant species were included in the analyses based on an inflection point in the rank-curve (see “Results” section). The contributions of environmental factors to community composition were explored by fitting a surface for each factor on the ordination using GAM (“surf” function in the LabDSV library in R version 2.8). Spearman correlations were then determined between PCoA sites scores for the first two axes in 2007 and environmental factors measured that year (percent soil moisture and ash, and elevation). To illustrate how species occurrences were associated with PCoA scores, axes scores for plots were averaged for all plots where the species was present.

To investigate changes in each grid through time, centroids for grids in each year were created by averaging the PCoA scores for plots from the first two axes (see Fukami et al. 2005). Patterns across years in different habitats could then be observed as changes in the PCoA scores for each grid. Changes from year to year in first and second axes of the PCoA for each grid were correlated ($n = 8$ years in each case) with climate patterns that occurred during that year, including precipitation, temperature, and total storm surge (defined as the water height above astronomical normal tide levels). For example, differences in PCoA1 scores between 1999 and 2000 were correlated with climate data for 2000. Climate data were obtained from the National Oceanic and Atmospheric Administration for weather (<http://www.noaa.gov/>) and storm surge (<http://www.nhc.noaa.gov/pastall.shtml>) for Apalachicola, Florida. When data were missing, additional climate data were obtained from the nearby Apalachicola National Estuarine Reserve (<http://cdmo.baruch.sc.edu/>) in Eastpoint, Florida. As the weather in the study area is strongly affected by a relatively dry period in the spring from March to June, followed by a summer storm season from July to October, precipitation and temperatures during these periods were also correlated with changes in PCoA axis scores.

Results

Species and habitat patterns

Over 60 vascular plant species have been identified in the study area, although many species were restricted to particular habitats and years (see <http://bio.fsu.edu/~miller/StGeorge/> for a complete species list). Species richness and species abundance patterns differed with habitat; 32 species were found in the foredunes, 41 in the interdunes, and 48 in the backdunes. The foredunes were dominated by the grass *Uniola paniculata* and the prostrate vine *Ipomoea imperati* on the dune tops; the sedge *Fimbristylis* spp. (we cannot distinguish between non-reproductive individuals of *Fimbristylis caroliniana* and those of *Fimbristylis spadicea* in the field) occurred in lower areas. The interdunes were dominated by large monocultures of the grass *Paspalum vaginatum* and the perennial ground herb *Phyla nodiflora*, which are likely tolerant of flooding and saline conditions. The highest plant diversity was in the backdunes, where *U. paniculata* was again a dominant, along with another grass, *Schizachyrium maritimum*, and a number of herbaceous perennials including *Physalis angustifolia* and *Heterotheca subaxillaris*.

Species associations varied somewhat continuously across the dunes (Fig. 1a; the first and second PCoA axes explain 20 and 9% of the variance, respectively). Plots from the flat interdune habitat had relatively high PCoA 1 and low PCoA 2 scores. One interdune grid in particular stands out with low PCoA2 scores; this area has a high frequency of plots dominated by the flood- and salt-tolerant *Paspalum vaginatum* (e.g., Cantero et al. 1998). Foredunes and backdunes grids are composed of plots spread among higher and drier dunes, as well as low, wet swales; this is reflected in the higher variation in PCoA 1 scores for these two habitats (Fig. 1a).

The first PCoA axis has a relatively high (and negative) correlation with elevation ($r^2 = 0.60$, $P < 0.001$), but is also positively correlated with percent soil moisture and ash ($r^2 = 0.26$ and 0.25 , respectively, both $P < 0.001$). Environmental correlates with the second PCoA axis were much weaker; the second axis was significantly negatively correlated with soil moisture ($r^2 = 0.29$, $P < 0.001$), but not elevation or percent ash ($r^2 = 0.07$ and 0.13 , respectively). The effects of these three correlated

environmental variables cannot be separated in this study; we show the patterns associated with the best correlated factor, elevation, in Fig. 1b. Plots in the right side of Fig. 1b (high PCoA1 value) are dominated by species common to lower, wetter areas with higher organic material (high soil ash), including *P. vaginatum*, *P. nodiflora*, *Sporobolus virginicus*, and *Fimbristylis* spp. Plots with low PCoA1 values are dominated by species found primarily in high, dry areas with low organic material, including *U. paniculata*, *I. imperati*, and *Schizachyrium maritimum*.

Temporal patterns and climate

Of particular interest are community patterns through time. Although the highest species richness always occurred in the backdunes and the lowest in the foredunes, species richness changed consistently across all plots from 1999 to 2007 (Fig. 2), regardless of habitat. Species richness increased from 1999 to 2001, decreased sharply in 2004 and 2005 then gradually returned to higher values in 2007. The declines in richness coincide with major storms. In 1998, St. George Island was in the path of Hurricanes Earl and Georges (storm surges of 1.81 and 1.41 m, respectively). The more recent declines are correlated with Hurricanes Ivan (2004, 1.60 m storm surge) and Dennis (2005, 2.45 m storm surge).

The PCoA values averaged within grids and years also suggest that the communities differed among in the three habitats but changed in similar ways through time. Most of the six grids, regardless of habitat, showed an increase in PCoA2 from 1999 to 2003, then a decrease in 2005. The correlations between the two PCoA axes and climate variables suggest that each habitat was affected by different combinations of climate variables (Table 1). Changes in the foredune vegetation were significantly correlated with annual and seasonal temperatures and the precipitation associated with summer storms. The lower interdune grid dominated by *P. vaginatum* was affected by storm surge, but the vegetation on the other interdune grid was uncorrelated with any of the measured climate variables. Finally, vegetation on the backdune grids was correlated with precipitation and storm surge.

The changes in PCoA scores in each of the habitats can be attributed to changes in the abundances of particular species. For example, in the foredunes, the

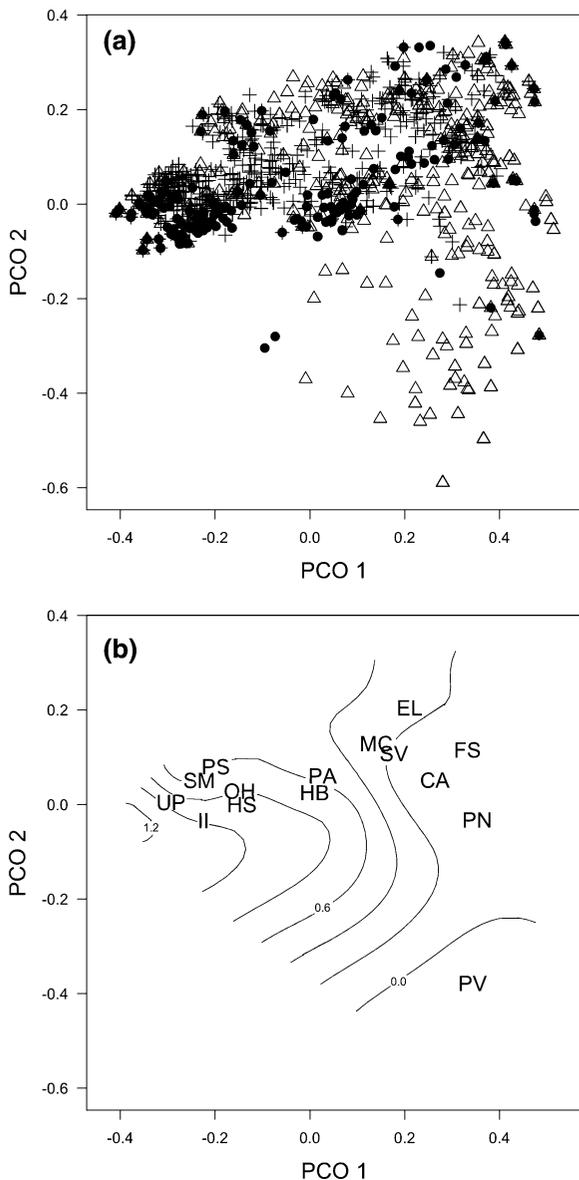


Fig. 1 Variation in plant species composition among St. George Island plots, based on first two axes (PCoA1 and PCoA2) from a principle coordinates analysis. **a** Results from individual plots in each year across the three habitats. Foredune plots are *filled circles*, interdune plots are *open triangles*, and backdune plots are *crosses*. **b** The associations among the PCoA scores, species, and elevation. The locations for selected dominant species were determined by averaging PCoA scores for all plots containing a given species. The distribution of elevation on the ordination is illustrated by isoclines derived using the LabDSV surf function in R, with elevation increasing from lower right to the left. Species is represented include *Centella asiatica* (CA), *Eragrostis lugens* (EL), *Fimbristylis* spp. (*F. caroliniana* and *F. spadicea*; FS), *Heterotheca subaxillaris* (HS), *Hydrocotyle bonariensis* (HB), *Ipomoea imperati* (II), *Muhlenbergia capillaries* (MC), *Oenothera humifusa* (OH), *Panicum amarum* (PA), *Paspalum vaginatum* (PV), *Physalis angustifolia* (PS), *Phyla nodiflora* (PN), *Schizachyrium maritimum* (SM), *Sporobolus virginicus* (SV), and *Uniola paniculata* (UP)

H. subaxillaris but also others, such as *O. humifusa* and *Hydrocotyle bonariensis*) after the storms of 2004 and 2005, and increases in other species such as *P. nodiflora* in the interdunes (Fig. 3b) and the grasses *Eragrostis lugens* and *S. maritimum* in the backdunes (Fig. 3c), appears to be responsible for the community patterns observed in Table 1.

Discussion

This study describes the vegetation patterns across three major coastal habitats, as well as the effects of climatic disturbances and subsequent vegetation recovery over a nine year period. The general spatial pattern of vegetation across St. George Island is consistent with other studies of sandy coasts (e.g., Ehrenfeld 1990; Stallins 2005; Forey et al. 2008). The foredunes are more highly disturbed, have the lowest species richness (Fig. 1), and are dominated by the dune stabilizer *U. paniculata*. The low-lying interdunes immediately behind the foredunes are dominated by clonal grasses (especially *P. vaginatum*) and clonal forbs (especially *P. nodiflora*). These species are tolerant of the saltwater overwash brought by storms and of freshwater flooding from heavy rainfall. The highest diversity is found on the low dunes and swales of the relatively protected backdunes, which have a more stable geomorphology. The backdune swales do flood with heavy rain and storm surge, but also harbor long-lived woody species.

abundance of *U. paniculata* stayed relatively constant, while that of both *H. subaxillaris* and *Oenothera humifusa* increased from 1999 until 2003 (Fig. 3a), then dramatically declined after storms in 2004 (Hurricane Ivan) and 2005 (Hurricane Dennis), perhaps because of sensitivity to saltwater inundation. *O. humifusa* has since started to recover, but *H. subaxillaris* remained rare through 2007. Other species, such as *P. nodiflora*, have become more common in the low areas behind the foredunes since these storms. The decline in some species (especially

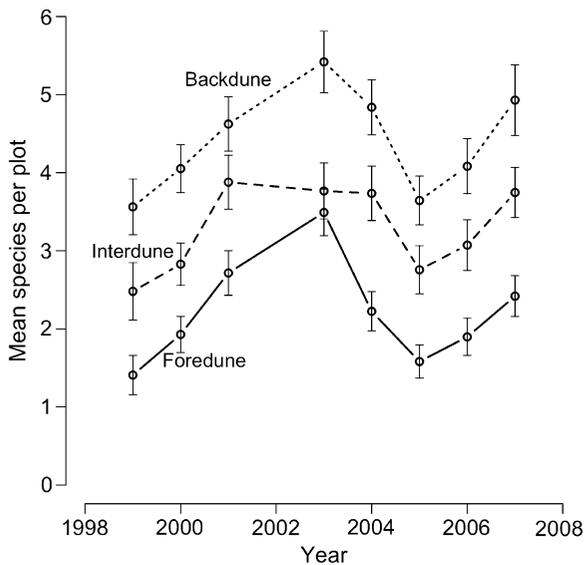


Fig. 2 Patterns of plant species richness on St. George Island from 1999 to 2007. *Solid lines*, mean number of species per plot on the 98 foreddune plots each year; *dashed lines*, interddune plots; *dotted lines*, backddune plots. *Error bars* show the 95% confidence intervals for the mean

Water, nutrients, and disturbance have all been proposed to limit dune vegetation in similar habitats

worldwide (e.g., Dech and Maun 2005; Houle 2008; Forey et al. 2008; Lane et al. 2008). While our vegetation patterns are best correlated with elevation, the analyses of elevation, soil moisture, and percent ash do not reveal which is limiting because these factors necessarily covary—elevation is inversely correlated with soil moisture, which is, in turn, usually correlated with soil organic content. Other unmeasured factors may also be correlated with these factors, including nutrients such as nitrogen, disturbance, and even herbivory. Our work will help to design more direct experiments that may determine which factors actually drive the documented vegetation patterns.

The temporal patterns across habitats from 1999 to 2007 show that the dune communities are quite dynamic through time. The changes in vegetation from year to year suggest that the temporal variation within grids can be substantial, but relatively similar patterns are seen among habitats. Two questions particularly interested us: what are the effects of storms and other climate factors, and is there any evidence to support short-term stability or long-term successional patterns?

Correlations among changes in PCoA scores and known climate factors strongly suggest that each

Table 1 For principal-components axes (PCoA) 1 and 2, Pearson coefficients of correlation between changes in the axis from year to year and climate variables

	Foreddune		Interddune		Backddune	
	1	2	1	2	1	2
PCoA axis 1						
Mean annual temperature	0.929**	-0.250	-0.464	0.286	-0.250	-0.571
Mean spring temperature	0.250	0.857*	0.429	0.571	-0.571	-0.250
Mean summer temperature	0.321	-0.714	-0.214	-0.179	-0.214	-0.107
Annual precipitation	-0.643	-0.143	-0.071	-0.179	0.857*	0.321
Spring precipitation	-0.714	-0.143	0.000	-0.429	0.857*	0.536
Summer precipitation	-0.286	0.607	0.321	0.143	0.429	0.357
Storm surge	-0.670	-0.394	-0.158	-0.906**	0.729†	0.709†
PCoA axis 2						
Mean annual temperature						
Mean spring temperature	0.250	-0.036	0.250	0.607	-0.286	-0.286
Mean summer temperature	0.929**	0.643	0.071	0.429	0.571	0.321
Annual precipitation	-0.536	-0.857*	-0.036	-0.357	-0.536	-0.429
Spring precipitation	-0.214	0.214	-0.429	-0.321	0.429	-0.107
Summer precipitation	-0.250	0.071	-0.179	-0.393	0.536	0.143
Storm surge	0.393	0.857*	0.143	0.429	0.536	0.464

Columns 1 and 2 are the first and second sampling grid within each dune area. $N = 8$ years in each case; † $P < 0.10$, * $P < 0.05$, ** $P < 0.01$

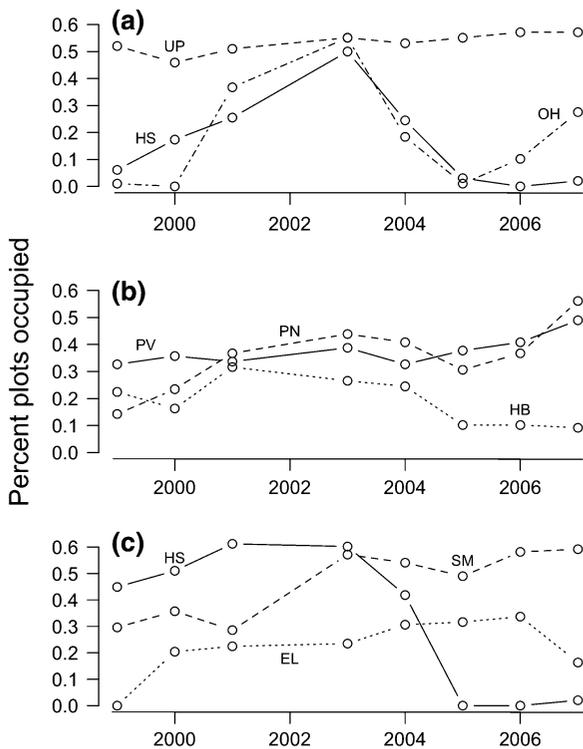


Fig. 3 Abundances of selected plant species on **a** foredune plots, **b** interdune plots, and **c** backdune plots across years. Values are the average number of the 98 plots in each habitat that contained individuals of each species. Species abbreviated as in Fig. 1

habitat and grids within habitats are affected by different climate factors (Table 1). While our two replicate grids within each habitat were initially chosen because they were in similar locations and contained similar vegetation, they have often revealed interesting differences. Changes in the foredunes, which bear the brunt of storms, were not strongly correlated with storm surge, but these exposed and often very dry dunes were affected by temperature. The second foredune grid is located in a prograding portion of the island and is now behind several more recently developed foredunes; this dune was also affected by precipitation. The low-lying interdunes were expected to be subject to flooding from rains and storms. However, the first interdune grid is also in an area where the island is prograding, and is less subject to storm surge. This area was not found to be affected by any of the measured climate variables (Table 1). Conversely, the second interdune is immediately behind active foredunes and some

flooding was observed almost every year of the study: not surprisingly, vegetation changes in this plot were correlated with storm surge. Finally, the backdune grids differ slightly, with the first being slightly higher and further from the backside of the island. While changes in the vegetation in both backdune grids were correlated with storm surge, the first grid did appear much drier and was also significantly affected by rainfall (Table 1).

It appears that two periods of large storms may have affected all of our plots, either through precipitation or surge: 1998 and 2004–2005. Although we do not have data from 1998 when Hurricane Georges occurred, most of the plots showed a relatively large increase in PCoA1 from 1999 to 2003, followed in 2004 and 2005 by a significant decrease correlated with the occurrence of Hurricanes Ivan (2004) and Dennis (2005). Some of the grids are now showing a return to an increase in PCoA values in 2007. These patterns are consistent with the idea that relatively stable or slowly changing assemblages will prevail in the absence of extreme storms and that the communities will tend to return to these assemblages after storms.

Storms do not explain all the observed vegetation changes, and processes other than storm recovery are likely to occur on different time scales. For example, over the long term, St. George Island will continue to build on the eastern tip. This process will produce shifts from one dune habitat type to another, like that exhibited by the second foredune grid that is now far from the beach. Other differences may simply be the result of succession in more stable areas such as the backdunes, where more woody species become established and even slash pines (*Pinus elliotii*) may later occur. These processes, island accretion and succession, may occur on much longer time scales than the 3–5 years apparently necessary for recovery from storms (see Sykora et al. 2004).

Dune vegetation patterns hold particular interest for ecologists since Henry Cowles's work in 1898, in part because of their dynamic interaction with the dune geomorphology (see Cowles 1911), but dune vegetation is also important in providing a barrier that protects inland areas. We have shown that storms can have strong effects on coastal vegetation, and that the communities recover over a 3–5 year period. Long-term vegetation studies are critical to formulation of predictions about the effects of both intrinsic (e.g.,

succession) and extrinsic (e.g., climate) factors on vegetation over significant time scales. Understanding and monitoring dune vegetation dynamics may also be important for predicting the effects of predicted climate-change events, such as increased storm frequency and ocean-level rise.

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