Effects of storm frequency on dune vegetation

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Abstract

In the Gulf of Mexico, barrier islands absorb the majority of wind and wave action from storms, which modifies their dune morphology and vegetation dynamics. Storm frequency is predicted to increase as a result of climate change, yet the effects of this change on coastal ecosystems remain poorly understood. Using estimates of plant growth in storm and nonstorm years from long-term census data describing the dynamics of dune vegetation on St. George Island, FL, we built a first-order model that predicts how dune communities will respond to a change in storm frequency. It predicts that an increasing frequency of storms will result in a change in the vegetation across the dunes. The fore- and interdune communities are predicted to become more similar to one another through the dominance of a small number of common storm-resilient species. Alternatively, the backdune community is predicted to become more distinct through an increase in rare species that represent primary succession. Finally, the model predicts that many species will not respond to an increase in the number of storms per year in the same manner in which they respond to current storm frequency. This model is beneficial both for the development of more complex approaches to predicting effects of climate change and for informing preventative management techniques.

Keywords: barrier islands, climate change, ecological model, hurricanes, storm frequency, succession

Received 24 August 2009 and accepted 8 November 2009

Introduction

Changes in tropical cyclone and hurricane activity are an increasingly important component of global climate change (Emanuel, 2007). Despite intense debate concerning the mechanisms responsible (Elsner *et al.*, 2006; Vecchi & Soden, 2007), most models show that the frequency (Webster *et al.*, 2005; IPCC, 2007) and intensity (Emanuel, 2005; Trenberth, 2005) of tropical storms and hurricanes is increasing and is projected to continue doing so for at least the next 50–100 years. Coastal systems in tropical and subtropical climates are especially vulnerable to the effects of storms, yet surprisingly little information is available on how climate change might affect these areas (Alley *et al.*, 2003; Fagherazzi *et al.*, 2003; Harley *et al.*, 2006; Prato, 2010), partly because few long-term studies (Johnson, 1997) directly measure recovery within coastal vegetation communities after damaging events (but see Grootjans *et al.*, 1991).

Predicting vegetation response to storms is difficult, as the habitats that make up coastal systems are regulated by different types and gradients of stress (da Silva *et al.*, 2008; Houle, 2008), resulting in both disturbance and recovery that can differ significantly in different habitats (Helmer *et al.*, 2000). Storms also differ in intensity, making recovery hard to predict (Sousa,

1984; Pickett & White, 1985). The influence of disturbance frequency on plant communities is well known (Johnson & Miyanishi, 2007), and the differential response of dune species to storms has been identified as an important characteristic driving vegetation dynamics and succession across barrier islands (Miller *et al.*, 2010), but the ways in which the predicted increase in storm frequency might change the future composition of coastal plant communities is not well understood.

Using a succession framework to understand the effects of storms could be useful because individual species, suites of species, and habitats can be isolated for investigation of storm response (see, e.g., Mulhouse *et al.*, 2005). Studies of succession after severe damaging events in long-term plots (Hibbs, 1983) or reconstructions (Henry & Swan, 1974) highlight the importance of considering both the response of individual species to these events and how the behaviour of a species contributes to changes in community structure.

The fore-, inter- and backdune habitats that characterize a barrier island represent successively older stages of long-term (500 + years) succession on the island (Gleason, 1927; Dahl *et al.*, 1975). Primary succession occurs on newly exposed bare sand adjacent to the shoreline that gradually builds to form foredunes. Wind moves these dunes inland while winds and waves create newer dunes on the generally progressing shores. The foredunes eventually degrade and the vegetation found there slowly gives way to secondary succession

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in flatter interdune areas (Johnson, 1997). These interdune areas are particularly subject to saltwater flooding from storm surge and freshwater flooding from heavy rains, which create very different conditions for vegetation. Finally, the interdune habitat becomes low dunes and troughs in the backdunes, where a higher diversity of longer-lived species stabilizes the habitat.

On a much shorter time scale of months to a few years, these habitats also undergo succession when they recover from climatic disturbances. The plant communities within each dune habitat change in response to environmental stresses like sand movement, drought, and, particularly, heavy precipitation and storm surge resulting from hurricanes (Miller *et al.*, 2010). These short-term responses from storm events can be used to make predictions about the effects of increasing storm frequency within each dune habitat. Storms can denude large swaths of habitat across a barrier island in a single event, and succession may then be restarted within each dune habitat.

We used long-term data of dune vegetation from a barrier island to quantify vegetation dynamics in storm and nonstorm years and then used this information to create a model of vegetation dynamics on the island under different storm frequencies. Identifying long-term vegetation change in coastal regions allows a better understanding of the relationships among barrier-island geomorphology, vegetation, and climate and in turn provides an opportunity to develop conservation techniques.

This first-order model uses the long-term census to predict patterns of species occurrence and plant communities that might be created by the disturbance and subsequent recovery that occurs in each dune habitat (Feagin *et al.*, 2005). The model also predicts how community patterns such as diversity, richness, and average abundance will change with storm frequency. So far as we know, this is the first model parameterized by long-term data that identifies how Gulf coastal plant communities may be expected to change with storm frequency.

Methods

The model was created from data collected from 1999 to 2008 on St. George Island, Florida, a typical long and narrow microtidal barrier island (Hayes, 1979) in the Gulf of Mexico, off the coast of Florida. On average, a named tropical storm passes within 125 nautical miles of the island every four years, and approximately every third storm is a category 3–5 hurricane (about every 11 years; National Hurricane Center, http://www.nhc.noaa.gov/). The data document the vegetation dynamics on the island since 1999. The census that generated the data was initiated by one of us (T. E. M.), has

been conducted annually since 1999, and has documented the distribution and abundance of dune-plant species over a 2.5 ha area in St. George Island State Park. The census determines species presence and abundance on 98 1m² plots in each of the three dominant habitats on the island: foredunes, interdunes, and backdunes. For a complete description of the census methods, see Miller *et al.* (2010); the data are publicly available at http://bio.fsu.edu/∼ miller/stgeorge). Briefly, a 1-m² quadrat is placed over each plot and all vegetation is counted by # individuals, # clumps, and/or % cover by species. Any unknown plants are sampled off the plots in replicate, given an ID number and identified later. Other aspects of each plot are also noted, such as dead plants or evidence of flooding or sand movement.

For each species, percent occurrence (hereafter referred to as occurrence) is the percentage of the 98 plots in each of three habitats (foredunes, interdunes, and backdunes) in which that species was present. Species occurrences were used to parameterize a vegetation model in which each species begins at its ambient nonstorm occurrence and then is allowed to increase or decrease through time, on the basis of frequency of storms and species-specific changes in occurrence in storm and nonstorm years. Separate models were created for foredune, interdune, and backdune habitats. The model was built in the freeware R version 2.5.1 (R Development Core Team, 2007).

The model simulates the occurrence of each species within a particular dune habitat through time. Models for each dune habitat include only those species that were observed in that habitat at least three times during the period of 1999–2008. Species were defined as 'common' if present in a particular dune habitat more than three times since the first census. Distributions of occurrence and growth for common species were described as either normal (Gaussian), uniform (unimodal), or skewed (beta), on the basis of patterns exhibited by each species in the census. Species were defined as 'rare' if present in a particular dune habitat only three times since the first census. Distributions in occurrence for rare species were defined as uniform. The initial occurrence value of each common species was randomly chosen from the species-specific distribution of occurrence within that habitat in nonstorm years, but only values >1% were used. Initial occurrence of all rare species was 0. Nonabsorbing occurrence boundaries for the model were 0% and 100%.

Occurrence values for common species in each time step were derived from growth rates in either nonstorm years (R_n; 1999–2003, 2006–2008) or storm years (R_s; 2004, 2005). R_n was chosen at random from a species- and habitat-specific distribution of change in occurrence in nonstorm years. For storm years, the R_s of each common species was taken from a uniform distribution bounded by the values of the change in occurrence observed after storm years. The occurrence (P_t) of a common species in time step t is:

$$P_t = P_{t-1} + (P_{t-1}R).$$

$R = R_n$ if a hurricane does not occur in time step t; $R = R_s$ if a hurricane does occur in time step t.

The occurrence of a rare species was a value chosen at random from a uniform distribution, bounded by 0 and maximum occurrence values from the long-term data. Rare

species that were documented in the long-term census only after a storm event became extinct in non storm time steps but had the chance to recolonize in storm time steps. Rare species documented as extinct in the long-term data after storm events became extinct in storm time steps but had the chance to recolonize in nonstorm time steps. At every time step, common species with occurrence values of 0 had a random chance to recolonize the habitat with an occurrence between 0% and 5%. The model included no density-dependent regulation.

The model for each habitat was run for 100 years, and 100 replicate runs were conducted for each of the following storm probabilities: 0.16, 0.20, 0.25, 0.33, 0.5, and 1 per year (respectively, storms approximately every 6, 5, 4, 3, 2, and 1 years). Occurrence of each species was determined for every run of the model, and the mean of these 100 replicates became the single occurrence value for each species at each combination of time step, habitat, and storm frequency. The predicted directional changes of occurrence for each species at different storm frequencies were compared. Changes could be positive (increases in occurrence), negative (decreases in occurrence), or zero (unchanged occurrence). We compared model results to current storm-response values (storm frequency = 0.25), derived from the long-term census data, to determine whether increasing storm frequency resulted in a departure from current values.

At the community level, effects of changing storm frequency were quantified by comparison of species richness (number of species), alpha diversity (determined by the Shannon–Weiner diversity index, $H' = \Sigma$ proportion of species in the habitat $\times \ln$[proportion of species in habitat]), and average species occurrence at each level of storm frequency. Biotic similarity between dune habitats was also determined, with the Jaccard similarity index, by ESTIMATES version 8 (Colwell, 1999). The strength of relationships between resulting habitat characteristics and storms was tested with Pearson's product moment correlations for normally distributed data; otherwise, Spearman's rank-order correlation analysis was used.

Nonmetric multidimensional scaling (NMDS) was used to identify similarities between species and community scores as hurricane frequency increased (Clarke, 1993) to infer the representation of each species within sites, across hurricane frequencies. NMDS is a robust, nonparametric ordination approach for similarity analysis that uses occurrence values of each species, time step, and habitat to calculate a community score (Torgerson, 1958). This analysis takes into account the independent vegetation dynamics occurring within each dune habitat (Miller et al., 2010) and facilitates comparisons within and among dune habitats across all storm frequencies. NMDS analysis was conducted in R (Vegan package), and a final solution for two dimensions was reached after 20 iterations. Community scores for the last 10 time steps of each model simulation were averaged to produce a centroid value that represented the equilibrium community of that habitat in a particular storm frequency. Communities were compared within and among dune habitats at different storm frequencies. Dune species also received a score at each time step for each parameter value in each habitat. This score was a function of the individual species' occurrence, compared with the occurrences of all other species in that habitat in that time step.

Results

Species patterns

Model results predicted that 63% of foredune species will decrease in occurrence as hurricane frequency increases, consistent with the results of the long-term census. Foredune species that were negatively affected by increasing storms included some common species (e.g., *Phyla nodiflora* and *Eragrostis lugens*), but the negative effects were most pronounced in relatively rare species (e.g., *Heterotheca subaxillaris, Hydrocotyle bonariensis,* and *Ipomea imperati*). A small number of the more common species, mostly grasses, were predicted to increase with storm frequency (*Fimbristylis* spp., *Sesuvium maritimum,* and *Sporobolus virginicus*), but the overall result was lower species diversity and average occurrence in the foredunes (Fig. 1).

Seventy-three percent of the species in the interdune habitat were predicted to decline with increasing storm frequency, resulting in an overall decrease in average occurrence and species diversity in this habitat (Fig. 1). The model predicted that species with both lower (e.g., *E. lugens, I. imperati,* and *Oenothera humifusa*) and higher (e.g., *Cyperus croceus, Juncus megacephalus,* and *Paspalum vaginatum*) than average occurrence will decline as hurricanes increase in frequency. Many of the species that were predicted to decrease in occurrence in the interdune area are not specialists in this habitat and can be found across the island (Table 1). A small group of more common species, mostly grasses, were predicted by the model to increase in occurrence (e.g., *Panicum amarum, Physalis angustifolia,* and *Uniola paniculata*).

Sixty-four percent of plant species in the backdune habitat were predicted to decline in occurrence in response to increasing hurricane frequency. More than half of the common species in this habitat were predicted to decrease greatly in occurrence (e.g., *I. imperati, P. angustifolia, Schizachyrium maritimum,* and *Smilax auriculata*) as storms increase in frequency. A few common species were predicted to respond positively to increased storm frequency (*Aristida purpurascens, Cynanchum angustifolium,* and *S. virginicus*), but the model generally predicted a change in dominance in the backdune habitat to species that are currently rare (e.g., *Andropogon gyrans, Cenchrus incertus, P. amarum,* and *Paronychia erecta*), resulting in a relatively small effect of increasing storm frequency on average occurrence and diversity (Fig. 1).

The three dune habitats did not differ significantly in the percentage of species that were predicted to respond negatively to storms. Rare species were predicted to be more likely to decline as storms increase ($P = 0.04$).

Community patterns

Species richness in the foredune ($P = 0.02$), interdune ($P = 0.01$), and backdune ($P = 0.03$) habitats were negatively correlated with hurricane frequency (Fig. 1a; Spearman's rank
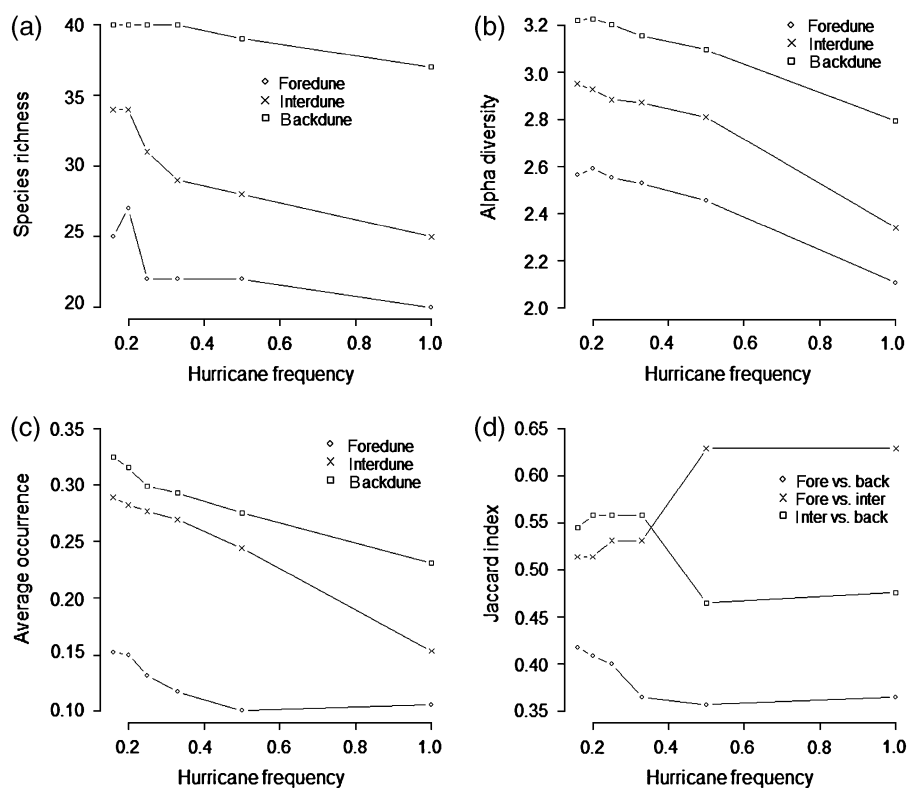
Fig. 1 (a) Species richness, (b) alpha diversity, (c) average occurrence, and (d) similarity index in each dune habitat along a hurricane-frequency gradient.

correlations, foredune $\rho_s = -0.88$, backdune $\rho_s = -0.84$; Pearson's product moment correlations, interdune $r = -0.91$). Alpha diversity was also ($P < 0.001$ for all habitats) negatively correlated with storm frequency in all habitats (Fig. 1b; Pearson's product moment correlations, foredune $r = -0.99$, interdune $r = -0.98$, backdune, $r = -0.99$), but the effect of increasing frequency on diversity was relatively small, except at the highest storm frequency. For all dune habitats, average occurrence was also negatively correlated ($P = 0.08$ for foredune and $P < 0.001$ for interdune and backdune) with hurricane frequency (Fig. 1c; Spearman's rank correlation, foredune $\rho_s = -0.75$; Pearson's product moment correlations, interdune $r = -0.99$, backdune, $r = -0.98$). An increase in storm frequency caused the foredune and interdune habitats ($P = 0.003$) to become more similar (Fig. 1d; Spearman's rank correlations, $\rho_s = 0.96$), whereas the similarities between the other habitat pairs decreased (Spearman's rank correlations, interdune and backdune $\rho_s = -0.52$; Pearson's product moment correlations, foredune and backdune $r = -0.67$).

NMDS illustrated that the plant communities in the foredune habitat were predicted to change continuously as a result of increased hurricane frequency (Fig. 2a). The responses of these communities at low frequencies were influenced most by declines in the occurrence of rare species. At high storm frequencies, more common species responded positively to an increased frequency of storms, leading to significant changes in community structure. These patterns were in contrast with those predicted for the interdune and backdune habitats (Fig. 2b and c). Plant communities in these habitats remained relatively similar at any storm frequency lower than one storm per year, but the habitats differed in the characteristics of species maintaining these dynamics. In the interdune habitat, no clear pattern was apparent in the types of species having the largest influence on the community predicted to exist at the highest storm frequency. Many of the species that appeared to make up a large portion of the plant communities in the interdune habitat at lower storm frequencies responded negatively to storms and occurred less often than average. The vegetation communities in the backdune habitat exhibited yet another pattern. All the species that characterized the community at high storm frequencies had lower than average occurrence and responded favourably to increasing storm frequency. The species that maintained the plant communities of the backdune habitat when storms were less frequent were a mixture of those with lower and higher than average occurrence and positive and negative responses to increasing storm frequency.

Discussion

Our model uses the St. George Island long-term census data to make first-order predictions of how changing storm frequencies will affect the vegetation in different dune habitats. The model predicted that increasing storm frequency would bring about changes in the

Table 1 Predictions of response rate to increasing storm frequency from the succession model in each dune habitat

Species	Foredune	Interdune	Backdune
Andropogon gyrans			+
Aristida purpurascens	+		+
Baccharis spp.			−
Cenchrus incertus		0	+
Centella asiatica	+	−	−
Chamaesyce maticulata			−
Cnidoscolus stimulosus			−
Cynanchum angustifolium	−	+	+
Cyperus croceus	0	−	−
Dichromena colorata			−
Eragrostis lugens	−	−	+
Fimbristylis spp.	+	−	+
Heterotheca subaxillaris	−	−	−
Hydrocotyle bonariensis	−	−	−
Ipomea imperati	−	−	−
Juncus megacephalus		−	−
Muhlenbergia capillaris		−	−
Oenothera humifusa	−	−	−
Panicum aciculare			−
Panicum amarum	−	+	+
Paronychia erecta			+
Paspalum vaginatum		−	
Phyla nodiflora	−	−	0
Physalis angustifolia		+	−
Polypremum procumbens		−	−
Sabatia stellaris		−	
Schizachyrium maritimum	−	−	−
Sesuvium maritimum	+	0	
Smilax auriculata			−
Sporobolus virginicus	+	−	+
Uniola paniculata	−	+	−

0 = no change in occurrence, + = increased occurrence in response to increased storm frequency, and − = decreased occurrence in response to increasing storm frequency. An empty cell indicates the species was not included in the model for the particular habitat.

occurrence of many individual species, and each dune habitat was predicted to exhibit turnover in dominant species. The model also predicted only slight declines in dune plant diversity in all habitats, except at the highest storm frequencies. The foredune and interdune habitats were predicted to become more similar to one another and less similar to the backdunes. Finally, species' predicted responses to increasing annual storm number were sometimes different from those observed at the current storm frequency.

The foredune habitat is expected to be most affected by increasing storms (Fig. 1) and to decline in species richness and average occurrence. Interestingly, species diversity was predicted to peak at low to intermediate storm frequencies. Increasing storm frequency seemed

to have a more continuous effect on plant communities in the foredunes than in the other two habitats. The storm-resilient species that come to dominate when hurricanes occur frequently (e.g., *Fimbristylis* spp., *S. maritimum*, and *S. virginicus*) appear integral to the primary succession that occurs in the foredune habitat after storms. Species documented in the long-term census to have average occurrence in this habitat were predicted to become less dominant when hurricanes are more frequent (e.g., *E. lugens*, *H. bonariensis*, *I. imperati*, and *S. maritimum*). These species are probably secondary or climatic succession species that are more prevalent in years following storms.

In the interdune habitat, the model predicted that alpha diversity and average occurrence will decrease primarily at high storm frequencies, whereas species richness was predicted to decline more continuously. The lack of a consistent pattern describing how species will change their occurrence in response to increasing storm frequency might be a result of the intermediate characteristics of the interdune habitat itself. The interdune habitat can be considered the secondary stage of succession in the chronological sequence from foredunes to backdunes (Gleason, 1927; Dahl *et al.*, 1975). As such, it may include species from a variety of successional stages. The interdune habitat has the smallest number of endemic species and shares the most species with other dune habitats (Gornish, 2009). Species found in the interdune habitat are likely to have a greater variance in morphological, life-history, and stress-tolerance traits.

The model predicted that the backdune habitat would be least affected by increasing storm frequency, showing minimal declines in species richness and comparatively smaller declines in alpha diversity and average occurrence, except at very high storm frequency. This result may be due to competition: the backdunes have higher percent cover of older, potentially more competitive species (Gornish, 2009). Competition in this habitat probably occurs for water, which is limiting in all three habitats (Ehrenfeld, 1990), and storms are almost always accompanied by significant, sometimes extreme, precipitation – the average rainfall recorded for Apalachicola during hurricane season between 1996 and 2006 is 144 mm (http://www.nhc.noaa.gov/). The increased moisture in the backdune habitat might release the backdune species from competitive stress by making more water available. A reduction in competitive stress could mitigate the negative effects of hurricanes, minimizing changes in the backdune habitat as a result of increasing hurricane frequency.

The model predicts that increased storm frequency will result in an increase of similarity between the vegetation communities in the foredune and interdune
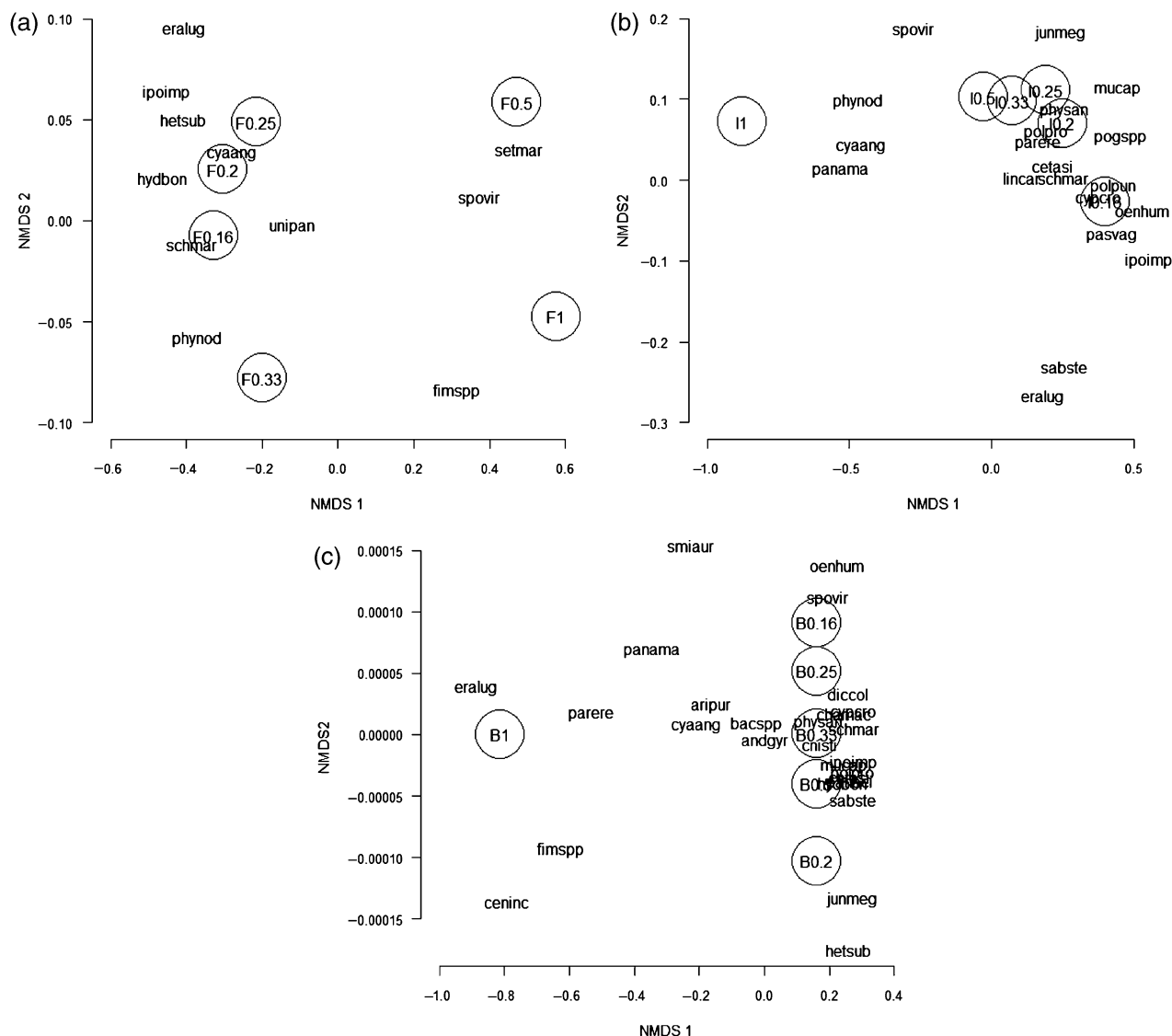
Fig. 2 Community non metric multidimensional scaling scores for each habitat (a = foredune, b = interdune, c = backdune) for each storm frequency (approximate frequencies represented are 1, every year; 0.5, every 2 years; 0.33, every 3 years; 0.25, every 4 years; 0.2, every 5 years; 0.16, every 6 years) are circled. Species codes (each consisting of the first three letters of the genus name and first three letters of the specific epithic; see Table 1) are also plotted.

habitats. Species that appear to be responsible for the composition of the plant communities within these two habitats at high storm frequencies (i.e., *P. nodiflora* and *S. virginicus*; Fig. 2) are similar. Alternatively, many of the backdune species that decrease in abundance in response to storms appear to be being replaced by rare species. This maintenance of backdune diversity (Fig. 1a) is probably responsible for the backdune community's decreasing in similarity to both the foredune and interdune habitats. Species responsible for backdune community characteristics at high storm frequencies, like *C. incertus, E. lugens,* and *P. erecta* (Fig. 2), are not important for the remaining habitats at these frequencies.

Overall, species with higher occurrences within dune habitats are more likely to respond positively to an increase in the frequency of storms, but more generalist species (those that occur in more habitats) are more likely to respond with decreasing occurrences, a seemingly confounding result as prevalent species on St. George Island often have the largest average occurrence in each dune habitat (Miller *et al.*, 2010). Perhaps, among the common species, generalists are less well equipped to deal with the hurricane effects that are unique to each habitat.

Model results predicted vegetation change within each dune habitat that could not have been predicted

from simple observation of which species do well after storms. The results of the model balance the dynamics of storm years and nonstorm years: species that responded well to environments with low hurricane frequency (0.25; about every four years, as documented in the long-term census) do not necessarily do well when exposed to more frequent storm events. The model predicted that 25% of the species on St. George will respond to more storms with a change in occurrence that is different from that observed at the current storm frequency. Knowledge of the types of dune species that are disproportionately responsible for community-level patterns of response to increasing storm frequency is only accessible from model simulations.

The results of these simulations were constrained by the assumptions inherent in the model. Storm behaviour in the model was simplified by the assumptions that increasing storm frequency had only additive effects, the use of a single hurricane intensity, and the back-to-back sequence of the two storm years used for parameterization. These assumptions probably reduced variance associated with individual species' storm response and minimized stochasticity associated with model results. The absence of density dependence and competition in the model could obscure the occurrence of species that can take advantage of empty niche space in lieu of adequate storm response; some annuals such as *Sabatia stellaris* and short-lived perennials such as *H. subaxillaris* may use such a strategy. Finally, the 2 years of storm-response data used in the model may not be representative of average response; storms can clearly differ in intensity, amount of accompanying precipitation, time of year, etc. This limitation is associated with most models for which sufficiently complete sets data of data do not yet exist. This concern should encourage more researchers to initiate and continue long-term studies of vegetation response to damaging events. Despite its simplicity, the model provides insight into some nonlinear, unexpected patterns that might otherwise have remained unrecognized.

Although each habitat responds to an increasing frequency of storms independently, implications of these community changes are not restricted to an individual habitat. The three habitats are inextricably linked, and changes that occur in the vegetative community of any one dune habitat will affect all other habitats and, ultimately, the succession of the entire coastal system. Establishing a preliminary understanding of how organisms will respond to damaging events as a result of climate change can be useful for estimating the dynamics of species of concern (Thomas *et al.*, 2004), designing restoration methods (Prach & Pysek, 2001), and selecting conservation approaches (Palmer *et al.*, 2008).

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