Spatio-temporal Analysis of the Effects of Hurricane Ivan on Two Contrasting Epiphytic Orchid Species in Guanahacabibes, Cuba

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ABSTRACT

Hurricanes represent the dominant type of disturbance in many tropical coastal forests. Here, we focus on mortality of epiphytic orchids caused by hurricane Ivan in the Guanahacabibes National Park (Cuba) and subsequent population recovery. We analyzed different aspects of hurricane damage on two contrasting epiphytic orchids, *Broughtonia cubensis* and *Dendrophylax lindenii*, as observed in three plots of coastal vegetation and in three plots of semi-deciduous forest, respectively. First, we quantified the damage to host trees and orchids and explored if hurricane damage depended on height, size, or identity of the host tree. Second, we used mark connection and mark correlation functions to conduct a detailed analysis of small-scale spatial patterns in hurricane damage for host trees and orchids. Finally, we analyzed the degree of recovery after Ivan during the 6 yr following the storm. Damage of *B. cubensis* host trees was independent of height and size, but Ivan severely affected larger and higher host trees of *D. lindenii*. Spatial analysis revealed non-random structure in damage that differed between species. *Broughtonia cubensis* exhibited small-scale spatial correlation in the proportion of damaged orchids, whereas *D. lindenii* did not. *Dendrophylax lindenii* showed 'patchy' damage patterns, correlated with height, but *B. cubensis* did not. The relative growth rate of *B. cubensis* for the 5–17 mo following Ivan was only moderately reduced and fully recovered in subsequent years, whereas that of *D. lindenii* was severely reduced the first year and did not fully recover thereafter. We hypothesize that differences in the host, vegetation type, and the traits of the two orchids contribute to the different responses to the hurricane.

Abstract in Spanish is available in the online version of this article.

Key words: Biodiversity; Cuba; epiphytic orchids; hurricanes; mark correlation function; phorophytes; relative growth rate.

HURRICANES REPRESENT THE DOMINANT TYPE OF DISTURBANCE IN MANY TROPICAL COASTAL FORESTS. For example, the Caribbean Basin is characterized by high cyclonic activity (Landsea *et al.* 1999), with over 2000 hurricanes recorded from 1851 to 2008 (http://hurricane.csc.noaa.gov/hurricanes/) that have affected ecosystems (Walker *et al.* 1991), plant population dynamics (Lugo *et al.* 1983), food webs (Spiller & Schoener 2007), and nutrient cycling (Sanford *et al.* 1991). The cumulative or interactive effects of a sequence of such disturbance events play a dominant role in determining the abundance and distribution of organisms (Tanner *et al.* 1991, Boose *et al.* 2004, Uriarte *et al.* 2005).

Epiphytic orchid communities are especially threatened by the effects of hurricanes because hurricane damage can result in the loss of a large component of the community (*e.g.,* Rodríguez-Robles *et al.* 1990, Migenis & Ackerman 1993, Tremblay 2008), in addition to strong pressures from human activity and habitat changes (Salazar 1996, Morales 2000). In sessile organisms, such as epiphytic orchids, space is an important determinant for some aspects of their dynamics (Raventós *et al.* 2011), playing a fundamental role in the specialization and realization of high diversity

in epiphytic orchids (Winkler *et al.* 2009). For example, epiphytic orchids show often a patchy distribution where clusters of plants growing on individual trees are spatially separated and may function as metapopulations (Winkler *et al.* 2009).

Spatially structured hurricane damage, superimposed to spatially clustered orchid distributions, may therefore change critical aspects of the spatial structure of the orchid populations, for example causing extinction of clusters, or hindering (re)colonization of unoccupied phorophytes. Studying the small-scale pattern of hurricane damages on both the level of host trees and the level of the associated epiphytic orchids may help us to better understand such effects. A detailed spatial analysis should also allow us to hypothesize on the possible processes that influence the dynamics of orchids (Jacquemyn *et al.* 2007, 2009; Raventós *et al.* 2011).

Hurricanes vary strongly in intensity, both spatially within individual storms and temporally between storm events. Some of this variation can be attributed to topography and storm dynamics (Boose *et al.* 2004). The trees of different species may also show spatial clustering because of environmental filtering or limited dispersal, and differences among tree sizes and tree species in their response to wind also accounts for smaller scale spatial variation in damage (*e.g.,* Boucher *et al.* 1994, Zimmerman *et al.*

1994, Cooper-Ellis *et al.* 1999, Ostertag *et al.* 2005, Canham *et al.* 2010). In addition, differences in the physiological response of each species to water stress may enhance such differences (Zoltz & Tyree 1996). The smaller scale spatial effects of hurricane damages on both, the level of the host tree and the orchids can be detected using techniques of spatial point pattern analysis (Wiegand & Moloney 2004, Illian *et al.* 2008, Raventós *et al.* 2011).

In this study, we focus on mortality of two epiphytic orchids caused by hurricane Ivan, which struck the Guanahacabibes peninsula on 13–14 September 2004. Our ultimate goal was to collect basic information that could be used to manage orchid populations in this area. To this end, we analyzed different aspects of hurricane damage on two contrasting epiphytic orchids, *Broughtonia cubensis* and *Dendrophylax lindenii*, as observed in several fully mapped plots of coastal vegetation and semi-deciduous forest, respectively, located in the Guanahacabibes National Park, Cuba. First, we quantified the damage of host trees and orchids and explored if hurricane damage depended on height, diameter at breast height (dbh), or the identity of the host tree. Second, we conducted a detailed spatial analysis of hurricane damage on the levels of the host tree and the orchids. Finally, as hurricane damage may also affect the temporal dynamics of the epiphytic community, we analyzed the degree of recovery after Ivan on the abundance of these orchids during the following 6 yr.

To structure our analysis, we developed the following guiding hypotheses. First, hurricane damages should be more severe in the semi-deciduous forest, especially on exposed trees, compared with the more homogeneous coastal vegetation characterized by xeromorphic scrubs. Second, we expect a spatial correlation in hurricane damage on the level of the host tree and the epiphytic orchids. The smaller sized and leafless species *D. lindenii* is more vulnerable to changes and disruptions in its habitat than the larger species *B. cubensis* (see section 'Species' below). *Dendrophylax lindenii* may therefore show a tendency to patchy damage patterns, and damage should tend to be higher on more exposed sites (*i.e.,* higher locations in the tree). Such a pattern is also likely because the structure of the semi-deciduous forest may create a patchier pattern of protected sites compared with the more homogeneous coastal vegetation. Third, *B. cubensis*, which has a well-developed leaf system and therefore a larger photosynthesis capacity, should recover more quickly from the hurricane damage than the smaller and leafless orchid *D. lindenii*. This expectation is based on the general scaling relationship between photosynthesis and plant size (Ozane *et al.* 2003), which has been documented for all major epiphyte groups (orchids, bromeliads, aroids, and ferns) (Schmidt *et al.* 2001).

MATERIALS AND METHODS

SPECIES.—The epiphytic *B. cubensis* is endemic to Cuba, and commonly found in xerophytic coastal vegetation of Guanahacabibes (Pinar del Río province) and in low range elevations of La Coca (Havana province). It has well-developed leaves and blooms between January and March (Mújica *et al.* 2000). *Dendrophylax*

lindenii is a large-flowered epiphytic species that can be found in some Cuban provinces and the Everglades, Florida (U.S.A.). It inhabits the semi-deciduous forest and elevations close to sea level and flowers mainly from October to December (Mújica *et al.* 2000). *Dendrophylax lindenii* has extremely small leaves that are only present at the seedling stage. Its leafless habit makes it very vulnerable to changes and disruptions in its habitat (*e.g.,* due to hurricanes), which is why it is considered to be an ecological indicator species. The small *D. lindenii* plants are easily pulled out by strong winds (whereas *B. cubensis* plants are better fixed on its host tree), and once their roots are damaged they have no reserves to recover (whereas pseudobulbs supply *B. cubensis* after leave damage with water and nutrients). In addition, *D. lindenii* depends on shady and humid forest sites (whereas *B. cubensis* is heliophile), which decline in suitability after defoliation by hurricanes.

STUDY SITE AND DATA COLLECTION.—The study was carried out on xeromorphic coastal vegetation and semi-deciduous forest in Cape San Antonio, located in Guanahacabibes National Park (21°59′ N, 84°50′ W), Pinar del Río province, Cuba (Fig. S1) (Herrera *et al.* 1987). The climate is strongly seasonal, with a dry period from November to April. Mean annual rainfall yields 1333 mm/yr (Lopetegui *et al.* 1999). This area is surrounded by the Gulf of Mexico and is protected from commercial epiphyte collectors.

Six 20 × 20 m plots were established in January/February 2005 approximately 4–5 mo after hurricane Ivan; three plots in xeromorphic coastal vegetation to map *B. cubensis*, and three plots in a semi-deciduous forest to map *D. lindenii* (Fig. S1). The plots were selected to show similar vegetation characteristics with no obvious differences in topography, orientation or elevation. Because of the close proximity of the plots, the exposed location of Cape San Antonio, and the high intensity of Ivan (270 km/h), we can assume that the intensity of Ivan did not greatly vary among plots and did not create systematic differences among vegetation types. Within each plot, all woody plants with a dbh larger than 2.5 cm were identified (Migenis & Ackerman 1993) and each tree examined for epiphytes; the orchid species were also identified, individuals, including seedlings, were counted and the height above ground recorded for each orchid. In addition, we recorded for each orchid (also others than our study species) signs of hurricane damage (*i.e.,* fallen down plants, uprooting, loss of leaves, and pseudobulbs, lesions due to wind or sunburn after forest defoliation). Our data set comprised in total 181 individuals of *D. lindenii* (99 affected and 82 non-affected) and 290 individuals of *B. cubensis* (101 affected and 189 non-affected). Dead, occupied trees could not be identified and these were tallied as a separate group. We also examined hurricane damage of the host trees and defined a host tree as severely affected if it was knocked down or if the degree of damage in its structure was larger than 90 percent. All identified occupied trees, and orchid plants were marked using aluminum tags and mapped using X and Y coordinates (Fig. S1). All orchids, including newly recruited orchids were monitored the 6 yr following hurricane Ivan (*i.e.,* 2005–2010).

NON-SPATIAL ANALYSIS OF HURRICANE DAMAGE.—The non-parametric Mann–Whitney U-test was used to compare the height and dbh of affected and non-affected trees with *B. cubensis* and *D. lindenii* at the plot level, and between affected and non-affected individuals of the more important phorophytes species. In all cases, we used a P value based on Exact Sig. ($2*[1$-tailed Sig.]), because our data were small, unbalanced and did not meet the assumption of normality (Quinn & Keough 2002). We also used logistic regression analysis to test if the height at which orchids grow influenced the probability of being damaged.

SPATIAL PATTERN OF AFFECTED VS. NON-AFFECTED PHOROPHYTES.—To assess the small-scale spatial pattern of damaged orchids, we used marked point pattern analysis (Stoyan & Stoyan 1994, Raventós *et al.* 2011). In this analysis, a host tree was termed 'affected' if it hosted at least one orchid showing signs of damage. We used the random labeling null model (Wiegand & Moloney 2004) to find out if the 'affected' labels were randomly distributed among all host trees. To quantify the spatial patterns, we used mark connection functions (Stoyan & Stoyan 1994, Jacquemyn *et al.* 2010, Raventós *et al.* 2010) as summary statistics. A mark connection function $p_{ij}(r)$ gives the conditional probability that, from two host trees, which are separated by distance r, the first is type i and the second type j (Illian *et al.* 2008).

SPATIAL PATTERN OF AFFECTED VS. NON-AFFECTED ORCHIDS.—To assess the small-scale spatial pattern of affected and non-affected orchids caused by hurricane Ivan we used mark correlation functions (Illian *et al.* 2008, Getzin *et al.* 2011, Raventós *et al.* 2011). Mark correlation functions can be estimated for data sets that comprise additional quantitative information (*i.e.*, marks) characterizing the objects (*e.g.*, number of orchids hosted by tree). For example, nearby trees may host more orchids that trees separated by larger distances. This allowed us to consider the information on the number of affected and non-affected orchids on a phorophyte. Each host tree has two quantitative marks: the number of orchids with damage (m_1) and number of orchids without damage (m_2). We used (1) the total number of orchids as a quantitative mark (*i.e.*, $m = m_1+m_2$) to find out if the orchids were distributed in a spatially correlated way, conditionally on the locations of the host trees; (2) the proportion of damaged orchids as a quantitative mark (*i.e.*, $m = m_1/(m_1+m_2)$) to find out if the hurricane damage acted in a spatially correlated way; and (3) the two marks m_1 and m_2 in a bivariate analysis to find if the specific combination of affected and non-affected orchids (m_1, m_2) are spatially correlated.

EFFECT OF HEIGHT ON ORCHID DAMAGE.—We tested if damage was associated with the height at which an orchid was located. For this analysis, we used one qualitative mark (pattern 1: affected orchid vs. pattern 2: non-affected orchid) and one quantitative mark m (height).

MARK CORRELATION FUNCTIONS.—Univariate mark correlation functions consider only pairs of host trees that are distance r apart. They are estimated as the mean value of an appropriate test function $t(m^0, m^r)$ taken over all pairs that are located at distance r, normalized with the test function calculated for all pairs of trees). The mark m^0 is the mark of focal tree and m^r is the mark of a tree at distance r from the focal tree. Appropriate test functions are (Illian *et al.* 2008):

$$
\begin{aligned}
t_1(m^0, m^r) &= m^0 \times m^r \\
t_2(m^0, m^r) &= m^0 \\
t_3(m^0, m^r) &= m^r
\end{aligned}
\tag{1}
$$

The mark correlation function $k_{mm}(r)$ is associated with test function t_1 and yields the mark product of pairs of host trees that are distance r apart, relative to the corresponding non-spatial expectation. To test for non-random correlation structures in the quantitative marks, we used the independent marking null model, which shuffled the marks randomly over all host trees (Illian *et al.* 2008). If $k_{mm}(r) > 1$, there is mutual stimulation, which means that the mark product is larger than expected by the null model of independent marking. Conversely, if $k_{mm}(r) < 1$, there is inhibition. The mark correlation functions $k_{m.}(r)$ and $k_{.m}(r)$ related to test functions t_2 and t_3, respectively, are called r-mark correlation functions (Illian *et al.* 2008). The $k_{m.}(r)$ uses test function t_2 and gives the mean mark of host trees that are located distance r away from another host tree relative to its non-spatial expectation.

To assess whether the affected and non-affected orchids (m_1, m_2) are spatially correlated, we used the test function 4

$$
t_4(m_1^0, m_2^r) = (m_1^0 - m_2^r)^2/2
\tag{2}
$$

where m_1^0 is the first mark of a focal tree (*i.e.*, number of affected orchids) and m_2^r the second mark (*i.e.*, number of non-affected orchids) of a tree at distance r from focal tree. This test function yields a bivariate mark variogram $\gamma_{m1m2}(r)$ and tests if the number of affected orchids at the focal tree and the number of non-affected orchids at nearby trees tended to be relatively similar or dissimilar (compared to those of pairs of trees taken at random). We contrasted the observed summary statistics to a null model that shuffled the mark pairs (m_1, m_2) attached to the given host tree together over all host trees.

In testing whether damage was associated with orchid height, we also used test function t_4, but now the mark m_1^0 represents the damaged focal orchid (*i.e.*, height) and m_2^r the height of a damaged orchid located at distance r away (in the univariate case) and the height of a non-damaged orchid located at distance r away (in the bivariate case). It tests whether the heights of nearby orchids tend to be relatively similar or dissimilar (compared with those of pairs of orchids taken at random). In this analysis, we used the null model of independent marking that shuffled the mark height randomly over all (damaged and non-damaged) orchids.

We performed 999 simulations of the null models and used the 25 lowest and highest values of the test statistic as simulation envelopes with an approximate error rate of 0.05. To assess the overall fit of null models for a given test statistic, we also used a

Goodness-of-Fit, which is described in detail in Loosmore and Ford (2006). If the rank of the test was larger than 950 (990), the data showed a significant departure from the null model with an error rate $\alpha = 0.05$ ($\alpha = 0.01$). We combined the test statistics of the three replicate plots (for each orchid species) into a single test statistic (Raventós *et al.* 2011). All the spatial analyses were carried out using Programita software (Wiegand & Moloney 2004). More detail on the technical aspects of the spatial pattern analysis is provided in Appendix S1.

TEMPORAL ANALYSIS.—To assess the resilience of the two orchid species after the impact of Ivan, we evaluated changes in the relative growth rate (RGR) after the impact on their populations. This index is a good indicator of population size and can be influenced by environmental parameters on plants in general (Valladares *et al.* 2006) and on orchids in particular (Agosto & Tremblay 2003). To calculate the RGR, we included the new individuals from each year. To avoid bias in calculation of RGR, we followed the advice of Hoffmann and Poorter (2002) and used the following formula:

$$RGR = \left(mean(\ln N_{t_2}) - mean(\ln N_{t_1})\right)/(t_2 - t_1) \qquad (3)$$

where $mean(\ln N_{t_2})$ and $mean(\ln N_{t_1})$ are the means of natural log-transformed number of individuals in two successive years. Note that the first period where we determined RGB was 5–17 mo after Ivan. To compare the evolution of the RGR, we used a Kruskal–Wallis Non-parametric one-way analysis of variance (ANOVA).

RESULTS

NON-SPATIAL ANALYSIS OF HURRICANE DAMAGE.—The effect of hurricane Ivan on the phorophytes differed, depending on the hosted orchid species. For phorophytes hosting *B.cubensis,* the mean percentage of severely affected hosts was 10.8 percent, ranging from 7.3 percent on *Plumeria tuberculata* to 22.2 percent on *Chascoteca neopeltandra*. Ivan affected mainly medium size phorophyte species (*i.e., P. tuberculata, Erythroxylum aerolatum* and *C. neopeltandra*), which represent 67.5 percent of the host trees for *B.cubensis* (Table S1). At the level of plots, there were no significant differences between the height (U = 4.5; $P = 0.57$) or the dbh (U = 4.5; $P = 0.56$) of affected and non-affected host trees. At the phorophyte species level, there were also no significant differences between height or dbh: *E. areolatum* (height [U = 6.5; $P = 0.24$]; dbh [U = 15.0; $P = 0.93$]); *C. neopeltandra* (height [U = 6.0; $P = 0.89$]; dbh [U = 4.0; $P = 0.50$]); and *P. tuberculata* (height [U = 41.0; $P = 0.1$]; dbh [U = 76.5; $P = 0.40$]).

The percentage of phorophytes that were affected by hurricane Ivan and hosted *D. lindenii* individuals was more than four times (59.1%) that of phorophytes hosting *B. cubensis* individuals (10.8%) (U = 17,63; $P < 0.006$). Damage by Ivan on phorophytes hosting *D. lindenii* ranged from 66.7 percent for dead unidentified trees to 100 percent on *Echafferia frutescens* (Table S2). Contrary to *B. cubensis,* we found on *D. lindenii* plots significant differences between the height (U = 25.00; $P = 0.025$) and dbh (U = 27.00; $P = 0.036$) of affected and non-affected host trees. Hurricane Ivan severely affected larger, taller individuals, leaving the smaller, shorter ones with little or no damage at all. By and large, the host tree most affected was *Comocladia dentata*, a late, slow growing tree.

The second level of damage by hurricane Ivan was on the orchid species. Mújica (2007) found that approximately 30 percent of *B. cubensis* orchids were lost on transects that were installed before Ivan. The degree of negative impact of Ivan on *D. lindenii* was almost twice as large (59%) as on *B. cubensis*. Logistic regression analysis did not detect a significant impact of height on the probability of being damaged (*B. cubensis*: $P = 0.26$; *D. lindenii*: $P = 0.11$).

SPATIAL PATTERN OF AFFECTED VS. NON-AFFECTED PHOROPHYTES.— The univariate mark connection function $p_{11}(r)$ did not detect significant spatial differentiation among the affected host trees (Figs. 1B and D). Similarly, the bivariate mark connection function $p_{12}(r)$ indicated that affected and non-affected host trees did not show any non-random pattern on any spatial scale (Figs. 1A and C).

SPATIAL PATTERN OF AFFECTED VS. NON-AFFECTED ORCHIDS.—We found a weakly significant, small-scale inhibition among the total number of orchids (Fig. 2A), which means that two phorophytes separated by approximately 0.4 m hosted fewer *B. cubensis* orchids than the average phorophyte pair. Essentially, the same result was found for the r-mark correlation function (Fig. 2B). *Dendrophylax lindenii* showed a similar tendency of inhibition, but this was not significant (Figs. 2C and D).

The proportion of damage of *B. cubensis* orchids was positively correlated for phorophytes that were 1 m apart (Fig. 3A). There was also a second peak, with positive spatial correlation for trees separated 7–8 m (Fig. 3A). As stated earlier, we could not detect any non-random effect for *D. lindenii* orchids (Figs. 3C and D).

We did not detect with the mark variogram significant effects for *B. cubensis* orchids (Figs. 4A and B). For *D.lindenii,* however, there was a significant effect for the univariate $\gamma_{m1m1}(r)$ (Fig. 4C), which means that the difference in the number of damaged orchids on phorophytes separated by 4.5 m was larger than would be expected by chance. In addition, there was a non-significant tendency that two nearby (< 3.5 m) phorophytes showed a more similar number of damaged orchids than expected. These two findings point to a patchy pattern of damage for this species. The results of the bivariate analysis using $\gamma_{m1m2}(r)$ (Fig. 4D) resembled that of the univariate $\gamma_{m1m1}(r)$ (Fig. 4C), but they were not significant ($P = 0.085$).

EFFECT OF HEIGHT ON ORCHID DAMAGE.—For *B. cubensis*, we found that damaged nearby orchids showed a tendency to be more similar in height than expected (Fig. 5A; rank = 865, $P = 0.1360$), and undamaged orchids close by (< 5 m) damaged orchids showed a tendency to be more similar in height than
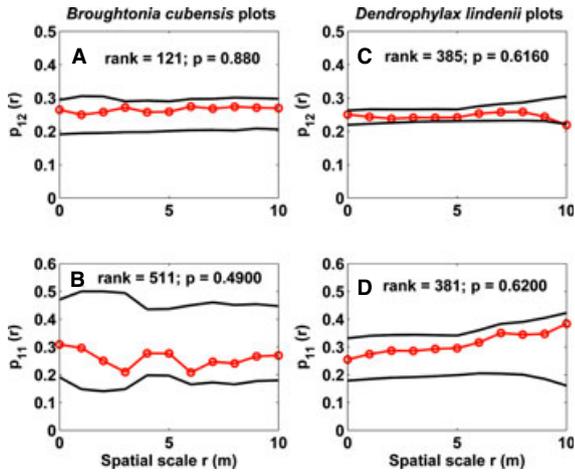
FIGURE 1. Test for spatial differentiation between affected and non-affected phorophytes using the random labeling null model and univariate and bivariate mark connection functions as test statistics. Mark connection functions $p_{ij}(r)$ give for bivariate patterns with i, j = 1, 2 the probability that the first point is of type i and the second of type j, given that the two points are separated by distance r. (A) and (C): analysis with i = 1 (damaged) and j = 2 (not damaged), (B) and (D): analysis with i = j = 1 (damaged). Red: observed mark connection function, black: simulation envelopes of the random labeling null model where the mark 'damaged' was randomly shuffled over the phorophytes.
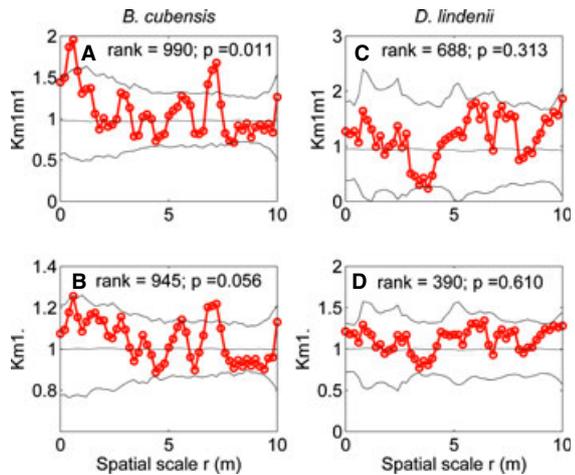

FIGURE 2. Analysis using mark correlation functions to determine if orchids are distributed in a spatially correlated way over the host trees. We used the total number of epiphytic orchids (m = m_1+m_2) as a mark where m_1 and m_2 are the number of damaged non-damaged orchids, respectively. The mark correlation function $k_{m1m1}(r)$ gives the mean (normalized) mark product of two phorophytes, which are separated by distance r, whereas the r-mark correlation function $k_{m.}(r)$ considers only the mark of the first (focal) phorophytes. If $k_{m1m1}(r) < 1$ and/or $k_{m1.}(r) < 1$, there is inhibition, the marks of a host tree, which have a neighbor at distance r are smaller than the average mark. Significance was tested against the independent marking null model, where mark m was randomly shuffled over the phorophytes. Other conventions as in Fig. 1.
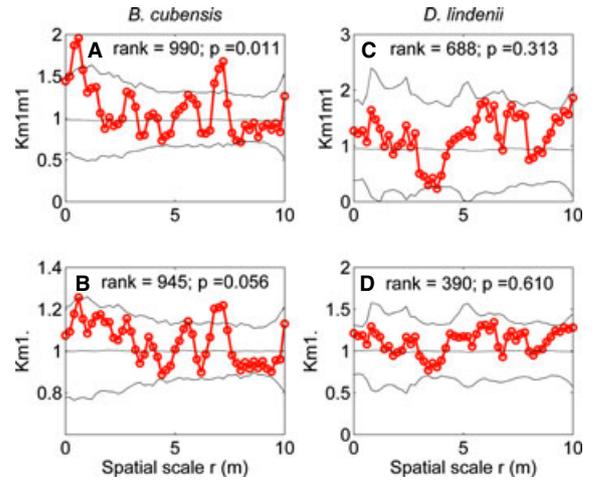

FIGURE 3. Same as Fig. 2, but using the proportion of damaged orchids (i.e., $m = m_1/(m_1 + m_2)$) as a quantitative mark.
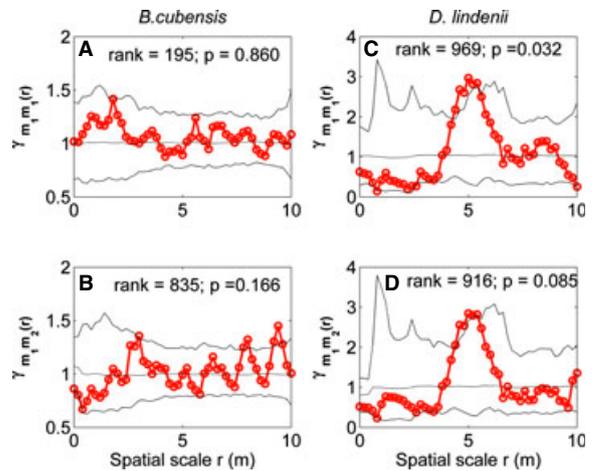

FIGURE 4. Analysis using the mark variograms $\gamma_{11}(r)$ and $\gamma_{12}(r)$ to find out if the number of damaged and non-damaged orchids showed a patch distribution over the phorophytes. In this case, we expected a large value of the variogram at the spatial lag r separating low and high damage. The univariate mark variogram $\gamma_{m1m1}(r)$ returns the mean squared difference between the number of damaged orchids (= m_1) on phorophytes, which are separated by distance r. The bivariate mark variogram $\gamma_{m1m2}(r)$ returns the mean squared difference between the number of damaged orchids on the focal phorophytes (= m_1) and the number of non-damaged orchids (= m_2) on phorophytes located distance r away. Significance was tested against a null model, where the marks m_1 and m_2 were randomly shuffled together over the phorophytes. Other conventions as in Fig. 1.

expected (Fig. 5B; rank = 994, $P = 0.007$). For *D. lindenii*, we found that damaged nearby orchids ($r < 0.7$ m) were more similar in height than expected, but this did not translate in a significant departure over the entire distance interval (Fig. 5C; rank = 765, $P = 0.236$). Undamaged orchids two meters away from damaged orchids, however, showed a much larger difference in height than expected (Fig. 5D; rank = 999, $P = 0.002$).
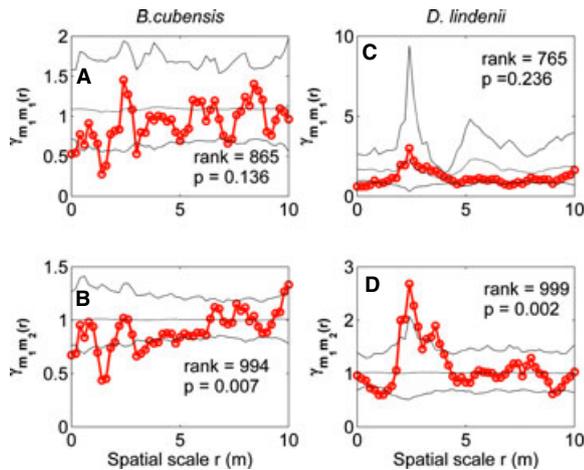
FIGURE 5. Analysis to find out if the height of damaged and non-damaged orchids was spatial correlated. In this case, we expected a small height difference for nearby and damaged orchids and larger height differences between damaged and non-damaged orchids located further away. The univariate mark variogram $\gamma_{m1m1}(r)$ returns the mean squared height difference between the damaged orchids separated by distance r. The bivariate mark variogram $\gamma_{m1m2}(r)$ returns the mean squared height difference between damaged focal orchids (and non-damaged orchids located distance r away. Significance was tested against a null model, where the mark height was randomly shuffled over all orchids. Other conventions as in Fig. 1.
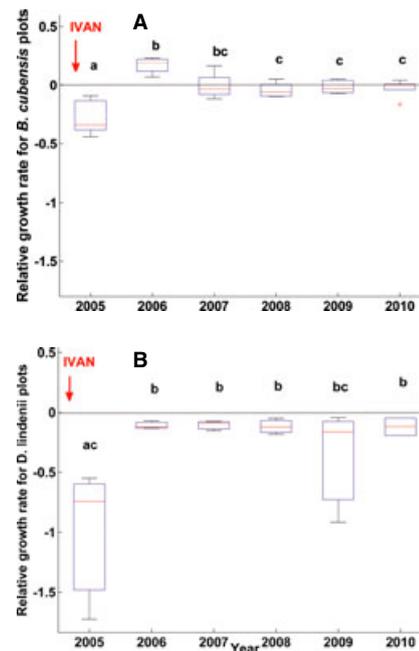

FIGURE 6. A–B. Change in the Relative Growth Rate (RGR) of *B. cubensis* and *D. lindenii* during the post-hurricane Ivan period 2005–2010 as observed on the Guanahacabibes peninsula, Cuba.

TEMPORAL ANALYSIS.—The relative growth rate (RGR) of the *B. cubensis* population for the first 2005–2006 period (*i.e.,* 5–17 mo after hurricane Ivan) was significantly lower than that of the following 5 yr (χ^2 = 18.27; P = 0.0026). The initially negative value of RGR in 2005 turned into a transient positive value in 2006, but over the following 4 yr, the RGR remained basically close to zero (Fig. 6A). The impact of Ivan on the population of *D. lindenii* was more severe than on *B. cubensis*. The initial reduction in RGR in the *D. lindenii* populations was almost seven times greater than on *B. cubensis*. The RGR in the first year after hurricane Ivan was significantly smaller than that of the following 5 yr, except 2009, which always showed a negative growth rate (χ^2 = 10.29; P = 0.049) (Fig. 6B).

DISCUSSION

In this study, we analyzed different aspects of the ecological consequences of hurricane Ivan on two epiphytic orchids, *B. cubensis* and *D. lindenii* that showed contrasting life histories. First, approximately 11 percent of the host trees of *B. cubensis* and 59 percent of the host trees of *D. lindenii* were severely affected by the hurricane. As a consequence, 30 percent of the individuals of *B. cubensis* and 59 percent of *D. lindenii* were lost. Damage of *B. cubensis* host trees was independent on height and dbh, but Ivan severely affected larger and taller host trees of *D. lindenii*, leaving the smaller, shorter ones with little or no damage at all. Second, two nearby trees hosted fewer *B. cubensis*

orchids than expected, the proportion of damage of *B. cubensis* orchids showed positive small-scale (< 1 m) correlation; *D. lindenii* damage occurred in a 'patchy' way, and damaged nearby orchids showed a tendency to be located at more similar heights on their host tree than expected. Third, the relative growth rate of *B. cubensis* 1 yr after Ivan was only moderately reduced, recovered in the second year, and stabilized around zero in the following years, whereas that of *D. lindenii* was severely reduced in the first year, but did not fully recover the following years.

OVERALL HURRICANE DAMAGE.—Studies evaluating the loss of diversity after hurricanes in Cuba are scarce (Ferro *et al.* 2006, Mújica 2007, González 2010). Given the importance of hurricanes to the forest dynamics in the region and the likelihood that these effects will increase, our study is therefore a valuable contribution to the documentation and understanding of hurricane effects on epiphytic orchids and their host trees. Hurricane damage on orchid communities have been quantified before in other areas (*e.g.,* Migenis & Ackerman 1993, Bayman *et al.* 2002). González (2010) compared the effect of hurricane Ivan on four different size classes of the species *B. cubensis* and found that the two pre-reproductive individual classes were more severely affected, whereas the same study showed generally high damage on all four classes of *D. lindenii*. We found that the hurricane damaged substantially more host trees of *D. lindenii* than of *B. cubensis* (59% vs. 11%) and that it damaged selectively the larger and higher host trees of *D. lindenii*. This result is consistent with

Ostertag *et al.* (2005) who found that the degree of hurricane damage increased with tree size. For example, heavy branch damage was less common than expected for smaller trees (< 20 cm), but higher than expected for trees in larger size classes.

The different degree of damage (30% vs. 59%) suffered by the two orchid populations is likely to be a consequence of the larger damage suffered by their respective host trees (11% vs. 59%) and consistent with our expectation. Indeed, we found that more exposed larger trees in the semi-deciduous forest showed a higher degree of damage, whereas the (overall lower) damage in the scrubland did not show such effects. Defoliation in the forest may also create less favorable habitat conditions for surviving orchids and cause additional loss (Shefferson *et al.* 2006).

SPATIAL PATTERNS IN THE HURRICANE DAMAGE.—Our detailed spatial analysis revealed non-random structures in the damages caused by Ivan on the two orchid species, but the effects were not very strong. This is understandable because the intensity of hurricane damage is often highly variable at smaller scales of tens to hundreds of meters (Boose *et al.* 2004). In addition, our study plots are relatively small and relatively low sample sizes in single plots introduced additional stochastic effects. Our methodology to combine the results of several replicate plots could alleviate this restriction to a certain extent by increasing the sample size, but we were restricted to spatial scale below 10 m. We studied spatial patterns of damaged orchids, however, which are small organisms and expected to show small-scale spatial effects.

Despite these limitations, it is interesting that our detailed spatial analysis was able to reveal signals of non-random smaller scale effects on orchids. First, both species showed a tendency to small-scale inhibition (Fig. 2), which means that two nearby trees (< 1 m) hosted fewer orchids than the average pair of host trees. This is somewhat surprising because processes, such as dispersal limitation, should generate clustering of orchids on nearby host trees (Raventós *et al.* 2011). Such a pattern, however, could be counteracted by size effects if host trees occurring close together would be smaller and may therefore host fewer orchids. Indeed, the size of the host trees was spatially correlated and the number of *D. lindenii* individuals at neighbored host trees (weakly) positively correlated with the size of the focal tree (result not shown).

The two orchid species showed a contrasting pattern of spatial correlation in damage. *B. cubensis* showed a small-scale correlation in the proportion of damaged orchids (Fig. 3A) not found in *D. lindenii* (Fig. 3C), whereas *D. lindenii* showed indications of 'patchy' damage, but not *B. cubensis*. The latter was indicated by the finding that the difference in the number of damaged orchids tended to be smaller than expected on nearby (< 3 m) host trees, but was larger than expected at host trees separated by 5 m (Fig. 4C). The patchy damage of *D. lindenii* can be explained with the findings that Ivan affected smaller and shorter host trees of *D. lindenii*, which were arranged in clusters, with little or no damage at all. This result is strengthened by the finding that damaged nearby *D. lindenii* individuals showed a tendency to be more similar in height than expected (Fig. 5C) and

undamaged orchids 3 m away from damaged orchids showed significantly larger height differences than expected (Fig. 5D). This finding is also consistent with the more sensitive life style of *D. lindenii* (*i.e.*, it is smaller sized and leafless which make it more vulnerable to changes and disruptions in its habitat) compared to the larger species *B. cubensis*.

TEMPORAL PATTERNS OF RECOVERY.—The relative growth rate of *B. cubensis* recovered quickly, reached 2 yr after Ivan positive values, and stabilized thereafter around zero. However, the relative growth rate of *D. lindenii* was severely reduced in the first year and remained negative. González (2010) found similar results based on a matrix model. Thus, the species *B. cubensis* that has a well-developed leaf system, and therefore a larger photosynthesis capacity, recovered, whereas the smaller leafless species *D. lindenii* did not. The better recovery of *B. cubensis* may also be related with the characteristics of the vegetation type. Orchid species, such as *B. cubensis* that inhabit vegetation characterized by the coastal xeromorphic scrubs are less affected because the levels of humidity, temperature, and sunlight after hurricane damage vary to a lesser extent than that in the semi-deciduous forest inhabited by *D. lindenii*. Defoliation caused by the hurricane in the forest increases temperature and sunlight levels, causing a decrease in relative humidity which, in turn, becomes less favorable to epiphytic growth.

Other factors affected by hurricane Ivan, however, such as presence of mycorrhizal fungi and/or pollinators, might explain the differences in recovery. Ackerman and Moya (1996) pointed out that not only are organisms affected by these extreme events, but the dynamics of interaction might also be altered. These disturbances can also alter resource availability and heterogeneity, providing opportunities for regeneration, species invasion, and alteration of successional pathways (Harrington *et al.* 1997). In the years following the hurricane, we also detected few pollinarium removals and pollinia depositions and, consequently, very low fruit production, and almost no pollinator presence (Ernesto Mujica, unpubl. data).

The strong stochasticity of hurricane disturbances makes the planning of conservation actions, such as population relocalization difficult. Although we found a signal of spatial structure in the hurricane damage, it was not very strong and overlaid by stochastic effects. Other results of our study, however, might be useful for conservation strategies. For example, Tremblay (2008) examined if relocation of the protected orchid *Lepanthes eltoroensis* Stimson from trees felled by Hurricane George to standing trees would be a viable management tool. He found that most relocated individuals (73%) survived the first year, and that survival was not influenced by presence of other orchids on the new host trees or the species of the host tree. In the coastal forest, we found that hurricane Ivan severely affected larger or higher host trees, whereas smaller trees showed lower degree of damage. This suggests that possible relocation of orchids from felled trees to standing trees may be a viable management tool in this environment if smaller trees are selected that additionally provide shady sites not directly exposed to the sun and drying winds resulting from the canopy opening after the hurricane.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. Map of the study site.
APPENDIX S1. Detailed description of the spatial pattern analysis.
TABLE S1. *Frequency and degree of damage to trees and their epiphyte load in B. cubensis plots on the xeromorphic coastal vegetation in Cape San Antonio, Cuba.*
TABLE S2. *Frequency and degree of damage to trees and their epiphyte load in D. lindenii plots on the xeromorphic coastal vegetation in Cape San Antonio, Cuba.*

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