

Hurricane Andrew and Upland Forest Succession in Biscayne National Park

Report to the U. S. National Park Service

by

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Abstract:

A tree species replacement sequence for dry broadleaved forests (tropical hardwood hammocks) in the Florida Keys was inferred from species' abundances in a series of stands abandoned from agriculture or other anthropogenic activities at different times in the past. Using a weighted averaging regression procedure, species' positions within the sequence were then used to analyze within-stand structure in two forests impacted by Hurricane Andrew in Biscayne National Park. Species characteristic of the earliest stages of post-agricultural stand development remain a significant component of the forest for many years, but are gradually replaced by taxa not present, even as seedlings, during the first few decades.

This compositional sequence of a century or more in length is characterized by the replacement of deciduous by evergreen species, which is hypothesized to be driven by increasing moisture storage capacity in the young organic soils. Despite passing directly over Biscayne National Park, Hurricane Andrew created limited opportunities for the successful establishment of early-successional species. Establishment of pioneers like *Solanum bahamense*, *Guettarda elliptica*, *Bourreria ovata*, and *Piscidia piscipula* were largely restricted to large openings in the older of the two stands examined. Geostatistical analyses indicated that the same stand also exhibited a spatial structure in Inferred Successional Age, which was interpreted to result from a long history of partial disturbances similar to the most recent hurricane.

Introduction:

Major hurricanes are catastrophic events from the human perspective, but their effects in many ecosystem types may be ephemeral to the casual observer, and spatially variable. For instance, functional recovery of upland forests from some Caribbean hurricanes is rapid (e.g., Whigham et al. 1991), though changes in species composition may continue for several decades or more (Crow 1980). By producing large openings in the forest canopy --- thereby increasing overall structural heterogeneity --- hurricanes and other high-wind events may create some limited opportunities for rapid accession to the forest canopy by seedlings of post-hurricane origin. Species successful at this opportunistic strategy are apt to be the same that dominate the early stages of stand development following more comprehensive disturbances, e.g., fire or anthropogenic landclearing activities. Elsewhere in the same stand, the hurricane may create less open conditions, where increase in species dominance occurs primarily through crown expansion by large trees that survived the storm, or by growth into the overstory by pre-storm advance regeneration or subcanopy trees. Species successful at the latter two mechanisms are likely to be most abundant during the mid- and late-successional stages, respectively, following fire or other catastrophic disturbance. In the studies reported below, we describe the mosaic of post-hurricane forest stand structure and successional status within two upland forests ("hardwood hammocks") in Biscayne National Park four growing seasons after the passage of Hurricane Andrew (August 24, 1992). To do so, we employ relationships derived from observed species' abundances along a chronosequence of time since abandonment from anthropogenic disturbance in nearby Key Largo.

Study Area:

The upland forests of the Upper Florida Keys, including Key Largo and the islands of Biscayne National Park (BNP), comprise a diverse mixture of deciduous and evergreen broadleaved tree species that is predominantly West Indian in origin (Tomlinson 1986; Robertson 1955). Canopy height in these low-branching hardwood hammocks is quite low, averaging about 8-12 meters, with few emergents (Ross et al. 1992; Hilsenbeck 1976). However, basal area in well-developed Upper Keys hardwood hammocks is typically high in comparison to other dry tropical forests, ranging from about 25 m²/ha to more than 40 m²/ha. Total aboveground biomass usually exceeds 100 Mg/ha, and estimated net annual aboveground production is ca 3 Mg/ha/year (L. Coultas and M. Ross unpublished manuscript). The relatively high productivity of these ecosystems is in sharp contrast to the skeletal organic soils on which they grow. The soils rarely exceed 20 cm in depth (Ross et al. 1992; L. Coultas and M. Ross unpublished manuscript), and develop directly on a Pleistocene limestone bedrock with elevations ranging from about 1.5 to more than 5 meters above sea level.

As a result of its maritime setting, climatic conditions in the study area are tropical despite a location several degrees north of the Tropic of Cancer ([Figure 1](#)). Based on thirty-year averages from the nearest Florida Keys weather station in Tavernier (mean annual temperature 25.1°C, mean annual precipitation

1178 mm), the climate is characterized in Walter's (1985) Zonobiome II (tropical with summer rain), and the ecosystems in Holdridge's (1967) Tropical Dry Forest Life Zone. Periodic freezes which affect forests in mainland South Florida (Olmsted et al. 1993) are extremely rare in the Keys, although a brief freeze in northern Key Largo in December 1989 did cause some mortality and premature leaf abscission among susceptible species in exposed areas (Ross pers. obs.). Occasional devastating ground fires, which kill virtually all stems and incinerate the shallow organic soils (Craighead 1981), are more important components of the natural disturbance regime impacting Florida Keys hardwood hammocks, as are frequent windstorms ranging up to major hurricanes, which are less all-consuming in effect. Based on data from Neumann et al. (1981), the 190-km stretch from Key West to Key Largo has been affected by 14 major hurricanes (highest winds > 125 mph) during the period 1895-1994. Assuming an average path width for maximum winds of 50 km, and an equal likelihood of experiencing a hurricane throughout the Keys, the expected return interval is approximately 27 years. Because the frequency of hurricanes in the Florida Keys (and elsewhere in the Caribbean) is well within the maximum longevity of most resident tree species, adaptations which contribute to resistance, recovery, and/or regeneration in their aftermath are likely to have evolved.

Aerial photos indicate that much of Key Largo was under cultivation as recently as 1926, with pineapple, lime, and sapodilla among the major crops. Agricultural activities slowed after the 1935 Labor Day hurricane, which spelled the end for the Overseas Railroad, the major shipping conduit for Keys produce. Landclearing in subsequent years was associated with a wide range of purposes, including roads, residential development, oil exploration, and military installations. As in Key Largo, farming was the primary source of human disturbance in the current Biscayne National Park (established 1980). Agricultural activities were more extensive in the northern islands, especially Elliott Key, than further south (e.g., Totten and Old Rhodes Keys).

Following a westward track, Hurricane Andrew crossed the Florida Keys in the early morning of August 24, 1992 ([Figure 1](#)). The storm's compact path was centered on northern Elliott Key in BNP; our BNP sites were in its southern eyewall, which also passed over the northernmost portions of the Key Largo study area. Peak 5-second gusts at the BNP sites have been estimated at 70 meters per second, or 157 miles per hour (Powell and Houston 1996). A maximum storm surge of 14 feet was recorded on the mainland coast north of the hurricane eye. While water levels were not much more than 2 meters above sea level in our study sites in southern BNP, this was enough to inundate all but the highest locations in the forest.

Methods:

Field Methods:

Key Largo sites. In the course of examining initial damage from Hurricane Andrew in Key Largo hardwood hammocks (Ross et al. unpublished report), we sampled the composition and size structure of living and hurricane-killed trees at 23 upland locations in the Crocodile Lakes National Wildlife Refuge and the Key Largo Hammocks State Botanical Area ([Figure 1](#)). Sample sites were evenly distributed along a 20-km stretch of the narrow upland ridge, mostly within 200 meters of a road that followed the crest of the uplands. Between November 1993 and June 1994, we established a set of nested belt transects 60-100 meters in length at each site. For both live and dead trees less than 25 cm in diameter, we recorded species and DBH (diameter at 1.45 m height) of all trees rooted within one meter (stems 1.0-9.9 cm DBH) or two meters (stems 10.0- 24.9 cm DBH) of the center line of the transect. Live trees ≥ 25 cm DBH were sampled within 5 meters of the line, and hurricane-killed trees of the same size within 10 meters. For the present purposes, data were summarized as basal area of each species in the pre-hurricane stands.

We also estimated the elevation, distance from the southern edge of the study area, and time since abandonment from anthropogenic disturbance for each sampling location. Elevation of the midpoint of each transect was interpolated from 5-foot contours on USGS topographic surveys. Date of site abandonment was estimated on the basis of its appearance on black and white aerial photos from 1985, 1971, 1959, 1940, and 1926, supplemented by reliable anecdotal information for several sites. Five stands which appeared undisturbed in all photos were assigned an age of 100 years. The presence of several cut stumps in a few of these forests indicated that they had not been entirely free of human impacts, but these did not appear extensive enough to have substantially altered overall species composition.

Biscayne National Park sites. Sampling areas were chosen in the southern portion of BNP, where human impact has generally been less than in other portions of the Park. The two areas selected --- one near the northern terminus of Old Rhodes Key, and the second at the southern end of Totten Key --- were extensive stands of mature or oldgrowth structure in upper slope positions, relatively homogeneous in species composition, and lacking evidence of recent human disturbance. At Totten Key, we gridded a 1.05 ha square plot into 421 5 x 5 meter cells, flagging the center of each cell. Because of the irregularity of the uplands at northern Old Rhodes Key, our plot at that site was an L-shaped area of 0.97 ha, gridded into 388 cells. In October- November 1996 (Old Rhodes) and April-June 1997 (Totten), we recorded the species and height interval(s), in 1-meter increments, of each crown which intercepted a cylinder of 30 cm radius centered on a level height pole extended upward from the midpoint of each cell. With a few exceptions, the grid spacing of 5 meters was sufficient that the same large tree was not sampled in adjacent plots. When several conspecific individuals intercepted the cylinder within the same height interval, the species was recorded once only. We also recorded species represented by seedlings (beyond the cotyledon stage, but < 0.5 m height) rooted within 30 cm of the cell center.

In October 1997 we used a canopy analyzer (CI-100 Digital Plant Canopy Imager, CID Inc., Vancouver, WA, USA) to estimate diffuse site factor (Anderson 1964; Rich et al. 1993) at 57 grid points in the Totten Key forest. Sampling locations were randomly selected within two disturbance categories (described below) in each quarter of the plot network. Hemispherical photographs were taken at 1.5 m above the ground, and as close to the selected grid coordinate as possible, such that there were no leaves within 30 cm of the lens. Camera orientation was checked with a compass and a bubble level.

Analytical Methods:

The covariation of overall Key Largo stand composition with time since disturbance, location, and elevation was examined by plotting each of the environmental variables on the detrended correspondence analysis (DCA) site ordination (ter Braak 1987), based on species that occurred in three or more stands. Indirect gradient analysis was chosen over direct gradient analysis (e.g., canonical correspondence analysis) because of its simplicity and because of the small number of physical factors to be assessed.

Weighted averaging (WA) regression and calibration (WACALIB version 3.3; Line et al., 1994) was used to estimate the successional status of each sample plot in the two BNP stands from relationships exhibited in Key Largo. The latter procedures are frequently employed in paleoecological studies whose objectives are to reconstruct past environments from fossil assemblages (e.g., Birks et al., 1990; Gaiser et al., in press). In WA regression, species optima are determined by abundance-weighted averaging in a calibration data set (i.e., 23 North Key Largo sites) in which the environmental variable of interest (i.e., time since disturbance) is known. Following Birks et al. (1990), we calculated the WA estimate of a species Successional Age Optimum, or u_k , as:

$$\hat{\mu}_k = \sum_{i=1}^n y_{ik} x_i / \sum_{i=1}^n y_{ik}$$

and its tolerance (weighted standard deviation), or τ_k , as:

$$\hat{\tau}_k = \left[\sum_{i=1}^n y_{ik} (\hat{x}_i - \hat{\mu}_k)^2 / \sum_{i=1}^n y_{ik} \right]^{1/2}$$

where x_i is the time since disturbance in stand i and y_{ik} is the abundance of species k in stand i ($i=1, \dots, n$ stands and $k=1, \dots, m$ tree species).

In WA calibration, the environment value of each site in the calibration data set is inferred from the weighted species optima, and the relationship of these scores with observed environmental values is used to "deshrink" estimates for the unknown data set (i.e., BNP sites). Deshrinking corrects for a systematic contraction in the range of inferred values (i.e., overestimates at the low end and underestimates at the high end of the environmental scale) that results from the double averaging associated with the above process (ter Braak and van Dam, 1989). The occurrence of inferred values outside the range of the calibration data set is a byproduct of all deshrinking procedures. We used classical deshrinking (ter Braak 1988), a method in which initial environmental predictions are adjusted on the basis of their linear regression on known values in the calibration set. Inferred stand ages for the calibration data set were calculated with and without weighting of species on the basis of tolerance. The logic for tolerance weighting is that species with narrow environmental tolerances may supply more information about site conditions than less exacting species, and therefore should be weighted more heavily. Following Birks et al. (1990) again, we calculated the unweighted site estimate, WA, as:

$$\hat{x}_i = \sum_{k=1}^m y_{ik} \hat{\mu}_k / \sum_{k=1}^m y_{ik}$$

and the tolerance-weighted estimate, WA(tol), as:

$$\hat{x}_i = \left(\sum_{k=1}^m y_{ik} \hat{\mu}_k / \hat{\tau}_k \right) / \left(\sum_{k=1}^m y_{ik} / \hat{\tau}_k \right)$$

The predictive capacity of WA and WA(tol) were compared on the basis of the root mean square error (RMSE) of predicted and observed values generated by a bootstrapping procedure in WACALIB 3.3, described in Birks et al. (1990). The method which yielded a smaller RMSE was then used to calculate an Inferred Successional Age (ISA) from the species composition found at each point in the Totten Key and Old Rhodes Key stands.

Analyses of overall forest composition in Key Largo and BNP were based on relativized species abundances --- relative basal areas within the 23 Key Largo stands, and relative lengths of crown intercepted within individual plots at Totten and Old Rhodes Key. In addition to summarizing species Successional Age Optima, we also characterized species in terms of (a) leaf longevity, and (b) canopy position. We characterized species as deciduous or evergreen, depending on their tendency to experience

a leafless period each year during the dry season. Classification was based on descriptions in Tomlinson (1986), supplemented by site- and species- specific data from Key Largo in 1991-92 (L. Flynn and M. Ross unpublished data). We characterized species as occupants of the canopy, midstory, or subcanopy based on structural data collected in hardwood hammocks throughout the Keys in 1989-91, and summarized in part in Ross et al. (1992).

We applied geostatistical techniques to evaluate spatial structure in canopy height and in our composition-based point estimates of ISA within the two BNP stands. We used the PREVAR2D module (Version 2.3) of VARIOWIN 2.1 (Y. Pannatier 1994) to create the distance matrix and calculate a standardized semivariance statistic for groups of points falling within 3-meter band widths, beginning at 5 meters (our shortest distance) and continuing up to a distance of 70 meters, which was approximately 50% of the maximum distance between points. We based our conclusions on omnidirectional variograms, after examining a series of directional variograms and finding no evidence of significant anisotropy for either variable in either stand. We fit the data according to an exponential model

$$\gamma_h = C_0 - C \cdot \exp(-3h/a),$$

where γ_h is standardized semivariance, h is lag distance in meters, and C , C_0 , and a are best-fit constants determined via the STATISTICA Non-linear Curve-fitting module (StatSoft Inc, 1995). Our analysis applies the terminology of Isaaks and Srivastava (1989), defining the *nugget* as the value indicated by the exponential model at a lag spacing of 5 meters, the *sill* as the model value at the maximum lag distance (70 meters), and the *practical range* as the lag at which the model semivariance equaled the nugget plus 95% of the difference between nugget and sill. A semivariogram that is well-fit by an exponential model has a *transitional* structure, i.e., spatial effects are strong at short distances but approach an asymptote as point-to-point distances increase. Our evaluation of the relative degree of such spatial structure in the four data sets was based on the coefficient of determination (R^2) of the best-fit exponential model.

Further analysis of within-stand variation in BNP composition focused on hurricane- related disturbance, as reflected in forest structure. Two groups of plots were distinguished on the basis of current tree stature: those with maximum canopy heights of 5.5 meters or less, and those supporting higher canopies. Five years after Hurricane Andrew, these groups roughly represented (A) locations that had sustained heavy structural damage, releasing a mixture of stems that had been present in the pre-hurricane understory or that had germinated shortly after the storm, and (B) locations that had suffered less complete damage among larger trees, characterized by the reiteration and resprouting of survivors of the pre-hurricane midstory and overstory. We designated Group A points as "Heavily Disturbed" (HD) and Group B points as "Less Heavily Disturbed" (LHD). We were aided in determining the 5.5 meter height criterion by two sources: (1) architectural reconstructions in one Key Largo and one BNP hammock (plot sizes 2.5 x 50 meters and 5 x 20 meters, respectively) (Oosterhuis et al. unpublished manuscript), and (2) the 1997 heights of trees known to be of post-hurricane origin (e.g., were rooted in pits formed by the uprooting of large trees during the hurricane). Besides the disturbance classification detailed above, each interior point was characterized according to the number of HD points included among its eight nearest neighbors. Isolated and Extensive HD subcategories were recognized, depending on whether HD points were surrounded by 0-4 or 5-8 HD neighbors.

Finally, we examined patterns of stratification with respect to successional status within the forest canopy. We calculated the mean Successional Age Optimum of the 1-3 species occupying the uppermost meter in each plot, and the mean SAO of all other species occupying subordinate height strata. These optima were compared, and each plot was characterized as "upper canopy earlier-successional" or "upper canopy later-successional". Within each of the three disturbance types in each

stand, we used a G-test (Sokal and Rohlf 1981) to assess the hypothesis that the number of plots in "canopy earlier-successional" and "canopy later-successional" categories were equal.

Results:

Key Largo sites: the calibration data set. 42 tree species were encountered in the 23 Key Largo transects. The distribution of abundances among stands indicated considerable compositional structure, with 32% of total variation in species composition accounted for by the first two axes of the DCA ordination. Additional axes accounted for 4% or less. There were strong associations between ordination Axis 1 and Age ($r=0.62$), and between Axis 2 and Distance ($r=0.72$), but Elevation was not strongly correlated with either axis (Figure [2A](#), [2B](#), & [2C](#)). Correlations among the three environmental variables were weak ($r<0.38$).

Successional Age Optima for Key Largo tree species are listed in [Table 1](#). Five species exhibited a preference for the early stages of stand development. Except for *Solanum bahamense*, which occurred in only one stand, tolerances in this group approximated or exceeded the mean for all species (21.5 years). Such broad tolerances demonstrate that typical early- successional species in Key Largo forests persist for several decades or more after establishment. While both large and small trees are included in this group, all five species are characterized by a short leafless period during the dry South Florida spring ([Table 1](#)).

Eighteen species in [Table 1](#) had optima in the 50-75 year age class. This group included both species with wide and narrow tolerances. Among the latter, *Eugenia foetida* is a common subcanopy tree which appears to be a good indicator of intermediate developmental stages. This diverse group is composed primarily of evergreen species, but its deciduous members (*Swietenia mahogani*, *Ficus* spp., *Metopium toxiferum*, *Piscidia piscipula*, and *Bursera simaruba*) are very prominent in the upper levels of the forest canopy.

Twelve species were associated with the later stages of stand development ([Table 1](#)). The four with the highest optima (*Drypetes lateriflora*, *D. diversifolia*, *Calyptanthus pallens*, and *Simarouba glauca*) all had relatively narrow tolerances, and therefore appeared to be excellent indicators of advanced stand age. The absence of deciduous species in this late-successional group is notable.

The WA model was superior to the WA(TOL) model, based on a higher coefficient of determination for uncorrected predictions vs. observed ages in the calibration data set itself ($R^2=0.72$ and 0.65 , respectively), and on a lower root mean square error of prediction in the bootstrapped predictions (RMSE=19.6 and 21.1 years, respectively). A plot of observed vs. corrected WA predictions presented no evidence of systematic under-or over-estimation at stand age extremes ([Figure 3](#)).

Biscayne National Park canopy structure. Mean canopy heights at Totten and Old Rhodes Keys were approximately equal (5.8 and 6.0 meters, respectively), but the standard deviation of height was almost 30% higher at the former site. Furthermore, the two distributions differed in their direction of skew, with a strong tail to the left at Totten Key and a mild right tail at Old Rhodes Key ([Figure 4](#)). The relatively high abundance of grid points with low canopy heights at Totten Key was indicative of more extensive hurricane damage in that stand.

The variograms of canopy height from both BNP sites exhibited a transitional spatial structure ([Figure 5A and 5B](#)). The pattern was more pronounced at Totten Key, where the exponential model accounted for 75% of the variation among lag spacings; the corresponding value for Old Rhodes Key was 31% ([Table 2](#)). The distance beyond which spatial effects on canopy height were undetectable was slightly

higher at Totten than Old Rhodes Key (practical ranges of 15.0 and 11.6 meters, respectively).

Table 2: Features of omnidirectional standardized semivariograms of canopy height and successional index at Totten and Old Rhodes Keys, fitted using an exponential model. Nugget, sill, and range are defined in text.

Variable	Island	Nugget	Sill	Range	Coefficient of determination of exponential model
Height	Totten	0.782	1.008	15.0	74.3
Height	Old Rhodes	0.902	1.006	11.6	30.9
Successional Index	Totten	0.822	1.009	13.9	56.8
Successional Index	Old Rhodes	0.989	1.004	8.6	0.4

Analysis of digital canopy photos from Totten Key suggested that the spatial pattern in height described above is mirrored by a similar patterning in understory light conditions. Diffuse site factor averaged 0.16 in Heavily Disturbed locations and 0.10 in Less Heavily Disturbed ones. For both disturbance types, diffuse site factor was positively correlated with the number of HD neighbors, and the effect did not differ between HD and LHD data sets ([Figure 6](#)).

Biscayne National Park species composition. Compositional data suggest that the Totten Key site had been more extensively or more recently disturbed than had the Old Rhodes Key plot. Mean Inferred Successional Age was 114 years at the former and 81 years at the latter ([Figure 7](#)), with ISA differentials of 29-33 years carrying across all three disturbance categories ([Table 3](#)). Two-way analysis of variance, with Site and Disturbance Category as fixed factors, indicated that only the Site effect was significant. However, for Heavily Disturbed sites at Totten Key, ISA decreased with an increase in the number of HD neighbors. A similar effect of opening size was not observed at Old Rhodes Key.

Table 3: Inferred Successional Ages in three disturbance types in Biscayne National Park. HD=heavily damaged; LHD=less heavily damaged. In Isolated HD plots, 0-4 of 8 nearest neighbor plots were See text for definitions of disturbance types.

Island	Distribution Type	Mean	S.D.	n
Totten Key	Extensive HD	108.4	41.3	118
	Isolated HD	125.0	30.5	48
	LHD	114.0	41.1	192
	Extensive HD	78.7	27.2	13
Old Rhodes Key	Isolated HD	85.8	32.2	91
	LHD	79.0	24.3	212

The more advanced successional condition at the Totten Key site was accompanied by higher overall

point-to-point variation in ISA (standard deviation 40.1 and 27.0 at Totten and Old Rhodes Keys, respectively), and a spatial structure that contrasted with Old Rhodes Key's. As had been its pattern with respect to canopy height, the Totten Key stand clearly exhibited a transitional spatial structure in Inferred Successional Age, with a nugget/sill ratio of 0.82, an R^2 for the exponential model of 0.57, and a practical range of 14 meters (Figure 9A, Table 2). In contrast, the ISA variogram for the Old Rhodes Key site followed a pure nugget model, i.e., there was no relationship between proximity and successional status within the range of distances considered (Figure 9B, Table 2).

In LHD and Extensive HD points at Totten Key, the occurrence of plots characterized as "canopy earlier-successional" and "canopy later-successional" did not differ, but in Isolated HD plots in the same stand, species whose crowns were highest in each plot tended to have later-successional optima than species below them in the forest canopy (Table 4). At Old Rhodes Key, a different pattern was observed. Here, LHD plots were usually "canopy earlier-successional", but neither Extensive HD points (which were relatively uncommon) nor Isolated HD points exhibited significant stratification with respect to Successional Age (Table 4).

Table 4: Percentage of plots of three disturbance types in which successional optimum of dominant species was earlier/later than the mean optimum of subordinate species in the same plot. See text for definitions of disturbance types.

Island	Plot Structure	n	Dominant Species Earlier-successional	Dominant Species Late-Successional	Statistical Significance ¹
	Less Heavily Disturbed	187	53.5	46.5	n.s.
Totten Key	Isolated Heavily Disturbed	79	39.2	60.8	$0.05 < p < 0.10$
	Extensive Heavily Disturbed	61	47.5	52.5	n.s.
	Less Heavily Disturbed	207	80.2	19.8	$p < 0.001$
Old Rhodes Key	Isolated Heavily Disturbed	76	50.0	50.0	n.s.
	Extensive Heavily Disturbed	12	41.7	58.3	n.s.

¹Probability that percentage differ from 50:50 within each structural type.

Discussion:

The results presented above are derived from two studies focused at distinct scales of variation: relatively coarse-scale variation in species composition among 23 stands representing a chronosequence of time since abandonment in Key Largo, and fine-scale variation in composition and structure within two hurricane-affected stands in Biscayne National Park. Together, these studies were designed to shed light on three interrelated hypotheses:

Hypothesis A: Florida Keys tropical hardwood hammocks undergo a predictable sequence of species

replacement following catastrophic disturbance,

Hypothesis B: By freeing space in the upper canopy, damage from storms like Hurricane Andrew create a range of opportunities, some of which favor early invaders in the post-catastrophe species replacement sequence.

Hypothesis C: Hurricanes therefore result in within-stand spatial patterning with respect to position within the successional sequence.

Hypothesis A: species replacement following catastrophic disturbance. In our examination of upland tree species composition in Key Largo, time since abandonment was strongly associated with the first axis of the DCA ordination, a geographic variable related to position within the study area was associated with the second DCA axis, and elevation was unrelated to either of the first two axes (Figure [2A](#), [2B](#), & [2C](#)). Previously, Ross et al. (1992) found that variation in plant species composition among Florida Keys terrestrial ecosystems was most strongly correlated to elevation, and secondarily to a geographic factor associated with climatic and substrate variables. In the earlier study, an extensive geographic range and a wide array of ecosystems were considered, but sites were limited to those which had not undergone significant anthropogenic disturbance during the previous 50 years. In the current study, temporal variation was the primary focus; sampling locations varied in time since disturbance from about a decade to a century or more, while geographic and ecologic range were intentionally restricted. Thus, neither study in itself allows the assessment of the relative effects of physical factors and successional relationships on hammock species composition, but in combination they provide a more multi-dimensional view of hammock development.

Long-term successional dynamics have not often been studied in dry tropical forest ecosystems. Using a chronosequence of five dry forest sites in the U. S. Virgin Islands, Ray and Brown (1995) inferred a tree species replacement series that extended for at least 150 years. Our own data, derived from a time sequence of 23 Upper Florida Keys forests, likewise indicate a directional change in species composition that continues through most or all of the first century following the cessation of agricultural or other anthropogenic activities (Figure [2A](#), [2B](#) & [2C](#), [Table 1](#)). These patterns represent the most extensive evidence to date regarding the course of secondary succession in South Florida. Other information on the topic is found in a series of papers that document compositional change at a single site in southern Dade County over a 46-year period (Phillips 1940; Alexander 1967; Molnar 1990; Mack 1992). Between 1940 and 1986, some portions of the Castellow-Ross tract were relatively unchanged in species composition, but in others, mortality among large trees (primarily *Lysiloma bahamense*) created large gaps which were reoccupied by a different set of tree species, including a number of exotic taxa (Molnar 1990).

In its absence of non-native species, the Key Largo species replacement series contrasts with the sequence in recovering agricultural fields on rockplowed uplands on the South Florida mainland, where the exotic Brazilian pepper (*Schinus terebinthifolius*) achieves canopy dominance within 5-10 years after abandonment, and subsequently resists replacement by native hardwoods (Ewel et al. 1982). With the integration of the rockplow into mainland agricultural practices in the 1940's, a pulverized mineral soil was created on which *Schinus* was apparently better-adapted than the native early-successional species. In contrast, agriculture in the Keys never recovered following the 1935 destruction of the railroad, and therefore never advanced beyond low-intensity practices that had relatively little effect on the underlying substrate. The non-agricultural purposes (residential, military, etc.) for which many of our more recent sites were cleared required scraping to bedrock, piling the scraped material, and perhaps burning it, but likewise did not involve significant disruption to the rock substrate itself.

In fact, the post-disturbance surfaces on many of our sites probably resembled those which are found

in South Florida pine rocklands after wildfire: a combination of exposed limestone bedrock, rock fragments of all sizes, mounds of coarse unconsolidated materials associated with old treefalls, and micro-karst features filled with organic-rich sediments. It is therefore not surprising that a number of species with optima during the early and intermediate stages of post-abandonment stand development in Key Largo are among the first invaders of South Florida pine forests in the absence of fire. Of the species included in [Table 1](#), *Lysiloma bahamense*, *Metopium toxiferum*, *Bumelia salicifolia*, *Bursera simarouba*, and *Coccoloba diversifolia* were early invaders of pine forests on Long Pine Key (Robertson 1955), and *L. bahamense* was the most abundant of several tree species that replaced *Pinus elliottii* var *densa* in pine forest portions of the Castellow tract (Alexander 1967). *Guettarda scabra* is an extremely fire-tolerant shrub in pine forest fragments in urban Dade County, and *Piscidia piscipula* is a common invader in pine forests of the Lower Florida Keys (Ross pers. obs.).

For the most part, the first trees to capture disturbed uplands in the Upper Florida Keys are fast-growing, deciduous species capable of surviving for several decades or more after establishment ([Table 1](#)). A few of these species --- most prominently *Swietenia mahogani* and *Metopium toxiferum* --- persist in low numbers in the upper levels of old stands. In general, however, late seral stages in Upper Keys forests are characterized by a suite of evergreen trees, most of which are not present even as seedlings during the early years of stand development. Swaine (1992) presented profile diagrams that show a stratification between a deciduous upper canopy and an evergreen lower canopy in some Ghanaian dry forests, but the temporal development of this structure was not described. However, Janzen (1986) noted an increase in evergreenness with time in several forest types in Guanacaste Province, northwestern Costa Rica. This wholesale transition from one functional group to another in the course of stand development suggests a distinct change in the underlying physical environment. We postulate that the replacement of deciduous by evergreen species during stand development reflects an increase in buffering from periodic moisture stress associated with the development of hammock soils.

Florida Keys hammock soils are predominantly organic, with a very minor mineral component (Coultas and Ross unpublished manuscript). As such, they are dynamic biogenic entities whose development parallels and is intertwined with that of the forest above. In the absence of human landclearing activities, both forest and soil development ends and begins with fire, which occurs infrequently, but can and often does consume virtually everything down to the limestone surface (Craighead 1981). We are familiar with one hammock area in Key Largo which burned more than two decades ago; in the areas between clumps of tree regeneration, the surface remains rubbly today, without significant soil cover. During the time required for the species replacement sequence illustrated in Figure 2 ([A](#), [B](#) & [C](#)) to take place, the barren, rocky post-disturbance surface becomes blanketed by a spongy, organic substrate of 10-20 cm depth. Thin as it is, such a soil provides markedly different seedbed conditions and enhanced rooting volume in comparison to the rockland substrate over which it formed, and is able to soak up many times its weight in water. This augmentation of soil moisture-holding capacity is particularly important to species which acquire most of their water from surface sediments rather than deeper groundwater sources (Ish-Shalom et al. 1992), and may directly influence the relative success of deciduous and evergreen species.

The deciduous habit is generally considered to be an adaptation to periodic moisture stress in dry tropical forests (Murphy and Lugo 1986; Gerhardt and Hytteborn 1992). In part, this hypothesis is based on research detailing the phenology of leaf fall and leaf production in relation to moisture stress (Reich and Borchert 1984; Borchert 1994; Olivares and Medina 1992). Of course, avoiding transpirational water loss by shedding leaves is only one way plants regulate their internal water economy during dry periods. Species which retain their leaves during such times may avoid water loss by increasing their internal osmotic potential or through more effective stomatal control. The association of deciduousness and moisture stress is also supported by studies of the distribution of deciduous and evergreen species along known moisture gradients (e.g., Kapos 1986; Reich and Borchert 1984; Swaine 1992; van

Rompaey 1993). Given the arrangement of deciduous- and evergreen-dominated forests toward the dry and wet poles, respectively, of spatial gradients in moisture availability throughout the tropics, it is not surprising to find these two leaf life history strategies distributed similarly along a temporal moisture gradient.

Hypothesis B: establishment of early-successional species. In Hurricane Andrew's passage over BNP, most surviving trees suffered some form of severe structural damage, through branch or bole breakage, partial uprooting, or bending under the weight of falling debris. Five years after the storm, even the highest portions of the canopy were therefore in the building phase of development (*sensu* Whitmore 1975). Geostatistical analyses identified a spatial structure in canopy height in the recovering BNP stands that was more clearly expressed at Totten Key than at Old Rhodes Key. This structure was rather fine-scaled, that is, points that were within ten meters of each other were frequently similar in height, but spatial effects dissipated rapidly beyond this small distance. Similar small-scale spatial variation in canopy height has also been observed in undisturbed rainforest in Costa Rica (Clark et al. 1996). However, in BNP the observed height structure seems to reflect the small size and diffuse nature of openings created by the hurricane. Most hardwood hammock tree mortality associated with Hurricane Andrew resulted from the snapping of boles. In Key Largo 71% of direct mortality (on a basal area basis) resulted from broken stems, while only 27% was attributable to wholesale uprooting (Ross et al unpublished report). Though hurricane mortality was not quantified in BNP, we observed that many of the larger openings at both sites were created by the uprooting of large trees; these frequently caused a chain reaction that toppled or bent numerous neighbors. Broken tops do damage or kill adjacent individuals, but their effects are not usually as extensive or forceful as the toppling of entire trees.

The concept of gap-partitioning (Ricklefs 1977; Denslow 1980) predicts that different groups of tree species will be successful in colonizing large v. small openings, as well as the center v. the edges of the larger gaps. Whitmore (1978) observed that small gaps were generally reoccupied by seedlings and saplings that had been present in the pre-disturbance understory, while large gaps were freshly colonized by seedlings of ruderal tree species. More generally, gap partitioning is a manifestation of species' responses to spatial variation in the light or rooting environment of the forest understory. One objective of our study was to determine whether such patterns, usually associated with scattered openings in an otherwise relatively undisturbed forest matrix, were paralleled in stands impacted by a severe hurricane, where the level of damage was so extensive that gaps were difficult or impossible to delineate. In other words, does patterning in species composition coincide with level and extent of damage within the storm-impacted forest? Following the terminology outlined in the Methods, higher representation of early-successional species in Extensive than Isolated HD locations would constitute evidence of a phenomenon akin to gap-partitioning, which may be described as "disturbance-partitioning". Whereas gap-partitioning is usually examined with respect to species that contrast in their purported shade-tolerances, we take a multivariate, community-based approach in searching for patterns among local species assemblages that differ with respect to Inferred Successional Age, as determined via our Key Largo chronosequence.

While damage due to Hurricane Andrew produced a broad spectrum of disturbance conditions, our data were equivocal with respect to the prediction that early- and late-successional species were distributed differently across this range during the early recovery period. When combined with Site in a 2-way ANOVA, Disturbance Type was not significantly related to Inferred Successional Age (Table 3). However, as predicted, the ISA of assemblages in Heavily Disturbed locations in the Totten Key stand decreased with an increase in the number of adjacent HD plots (Figure 8); only 17 locations had ISA's below 60 years, all in Extensive HD settings. In Isolated HD plots on Totten Key, upper canopy strata were more frequently occupied by late-successional species, which were therefore in a favorable position to increase their dominance in the future. Neither of the latter two patterns were observed at Old Rhodes Key, where large openings were less frequent and canopy heights less clearly structured. These

mixed results apply only to the early stages of post-hurricane recovery, and do not necessarily reflect stand structure at a later stage of development. They indicate that Hurricane Andrew create relatively few opportunities for successful colonization by early-successional species, but those it did provide were located in relatively open portions of the stand.

We suggest that the limited establishment of early-successional species described above reflects the rapid recovery of leaf area associated with resprouting and reiteration of surviving stems from all levels of the pre-hurricane canopy. Along a moderately damaged forest transect in Key Largo, where median PPFD in the forest understory (1 m height) increased from 4% of above-canopy values prior to Hurricane Andrew to 57% immediately afterward, recovery to the pre-hurricane median occurred within 28 months (Ross unpublished data). However, recovery was not uniform (in part because of patchy vine incursion), and open conditions continue to persist locally. With respect to effects on plant growth or establishment, direct measures of canopy openness or % PPFD are superior to, and not necessarily well-correlated with, measurements of canopy height alone (Whitmore 1996). In their study of the rainforest understory, Clark et al. (1996) detected a strong and predictable relationship between the light environment at 1-3 meters and the occurrence of saplings of seven species of known successional affinity, but found only a weak negative correlation between understory light condition and the height of the canopy immediately above. Unfortunately, our research in BNP was not initiated until four years after Hurricane Andrew, so environmental conditions during the critical first few years after the hurricane were entirely unknown to us. Given this limitation, our approach was to hindcast three disturbance categories based on the current local distribution of canopy heights, from which a resource gradient capable of shaping current species composition might reasonably be inferred.

Hypothesis C: Successional patterning. The strong transitional spatial structure in ISA at Totten Key (Figure 9A) suggests that even in the untidy aftermath of a major disturbance, some South Florida hardwood hammocks may be effectively viewed as a patchwork of successional- related compositional units. This finding may be interpreted as a stand-level expression of Oldeman's (1983, 1990) "silvatic mosaic", composed of developmentally-related "eco-units" ("...unit of vegetation which started its development at the same moment and on the same surface."). The fine-scale spatial structure illustrated in Figure 9A is entirely encompassed within the range 5-15 meters. It is important to note that these analyses address neither spatial effects at shorter distances, nor the distinctness of boundaries between adjacent units. Eco-units may be delineated clearly through analyses of forest architecture (Oldeman 1990); such examinations are currently underway for the Totten Key forest, as well as other hammocks affected by Hurricane Andrew (Oosterhuis et al. in prep.).

Architectural studies could also clarify further how much the successional structure identified at Totten Key reflects vegetation responses to Hurricane Andrew, and how much to earlier disturbances. Based on the relatively restricted opportunities for establishment of early- successional species documented above, we suggest that Totten Key's compositional structure may reflect a long history of partial disturbances akin to the most recent hurricane, while the absence of similar structure at Old Rhodes Key is a result of its more abbreviated stand history. The two stands differed dramatically in their distributions of point estimates of ISA (Figure 7). The Old Rhodes Key stand (mean ISA 81 years, with few estimates > 120 years) is apparently second growth, or has been through some sort of stand-initiating disturbance (e.g., fire) during the last century. Its Totten Key neighbor (mean ISA 114 years, with point estimates ranging to more than 200 years) was probably never cleared for agricultural purposes, and has not been impacted by catastrophic disturbance for at least a few decades longer. Perhaps spatial structure in Inferred Successional Age is a characteristic of old-growth, one that develops over many years, taking on momentum as the stand begins to include trees of large size. When periodic hurricanes strike such stands, mortality of individual trees can create openings of sufficient size to allow the establishment of early-succesional species. Our study of two stands affected by Hurricane Andrew is obviously not adequate to verify the postulated connection between stand history and spatial

structure, but justifies further investigation.

Conclusion:

Examination of 23 stands ranging in time since abandonment from anthropogenic disturbance (primarily agriculture) yielded good evidence for species turnover through a period of at least a century, and documented species' positions within the sequence. Hurricane Andrew provided some opportunities for establishment of early-successional species, but these were for the most part confined to large openings in one of the two stands studied. Given the limited occurrence of such openings, evidence of spatial structure in the same stand could not be entirely attributed to the most recent hurricane. Certainly, factors like dispersal limitation, topographic variability, and a wide array of inter- and intra-specific relationships may contribute to a generalized compositional structure. However, patterning *among species groups associated with different stages in stand development* would seem to require an underlying patch structure in disturbance history. Based on spatial analysis of the canopy of post-Andrew forests, patch structure of the appropriate scale may be supplied by hurricanes. Following a single storm, only a few of the largest of these openings may be successfully colonized by early-successional species. Over time, however, the establishment and development of such hurricane-derived eco-units may constitute much of the variation in composition and structure within old-growth tropical hardwood hammocks.

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