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Forest Succession in Tropical Hardwood Hammocks of the Florida Keys: Effects of Direct Mortality from Hurricane Andrew[1]

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ABSTRACT

A tree species replacement sequence for dry broadleaved forests (tropical hardwood hammocks) in the upper Florida Keys was inferred from species abundances in stands abandoned from agriculture or other anthropogenic acitivities at different times in the past. Stands were sampled soon after Hurricane Andrew, with live and hurricane-killed trees recorded separately; thus it was also possible to assess the immediate effect of Hurricane Andrew on stand successional status. We used weighted averaging regression to calculate successional age optima and tolerances for all species, based on the species composition of the pre-hurricane stands. Then we used weighted averaging calibration to calculate and compare inferred successional ages for stands based on (1) the species composition of the pre-hurricane stands and (2) the hurricane-killed species assemblages. Species characteristic of the earliest stages of post-agricultural stand development remains 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 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. Mortality from Hurricane Andrew was concentrated among early-successional species, thus tending to amplify the long-term trend in species composition.

Key words: Caribbean forests; chronosequence; disturbance; dry tropical forest; Florida Keys; hurricanes; Hurricane Andrew; leaf phenology; succession.

Natural disturbances frequently result in a temporary reversal of the directional stand development and species replacement processes associated with woody plant succession (Bormann & Likens 1979, Daniel *et al.* 1979). With respect to species dynamics, the reversal may stem from more effective resistance to the disturbance by taxa characteristic of early stages in the successional sequence. For instance, variable resistance explains why fires interrupt the encroachment of hardwoods into pine forests of the southeastern coastal plain of the United States (Stout & Marion 1993). Alternatively, variable resistance can be a mechanism that accelerates the successional process rather than interrupting it; cases in which pioneer species are especially disturbance-prone are included within the "inhibition" model of succession of Connell and Slatyer (1977). Examples include ice storms in Appalachian oak forests (Whitney & Johnson 1984) and spruce beetle outbreaks in the Colorado subalpine zone (Veblen *et al.* 1991).

Like most plant communities, the dry broadleaved forests of the Caribbean basin—of which the "hardwood hammocks" of the Florida Keys are one example—function in an environment characterized by several types of periodic disturbance, including fire, deforestation, and hurricanes. Wildfires, which recur at relatively long intervals in these forests, may result in high tree mortality and soil loss (Whigham *et al.* 1991). Moreover, anthropogenic burning and land clearing activities that have been carried out for centuries match or exceed

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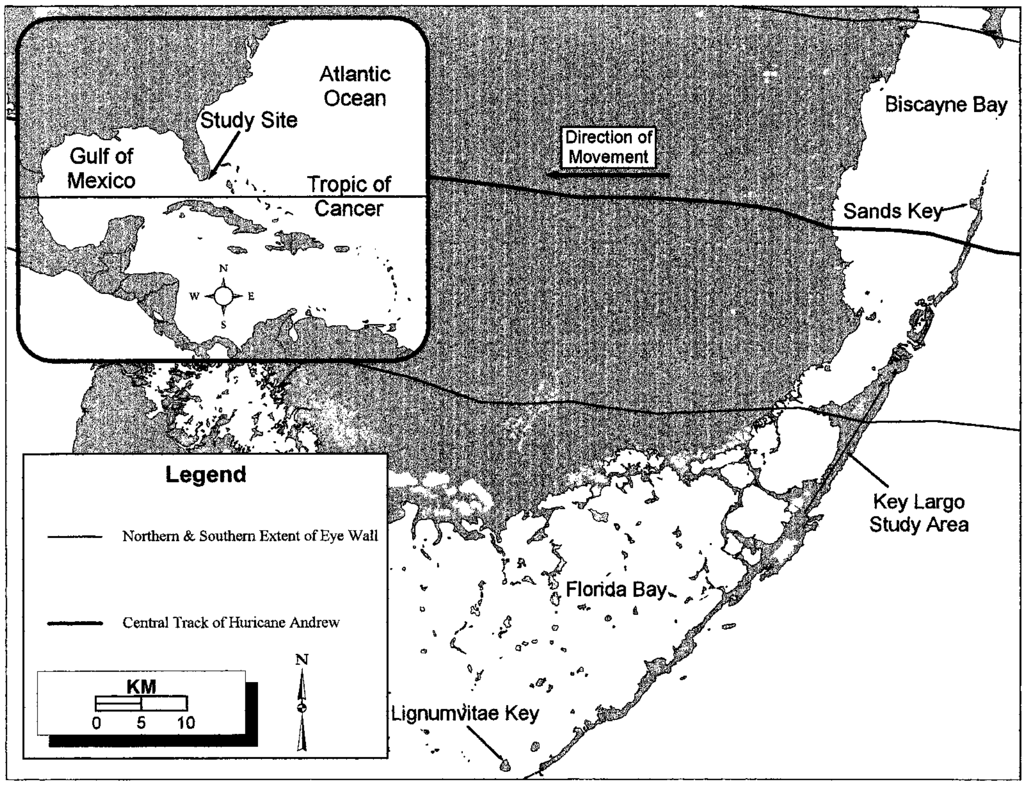

FIGURE 1. Location of study area, with track of Hurricane Andrew.

wildfires in their effects on the existing forests. Compared to these catastrophic disturbances, the impact of hurricanes on Caribbean hardwood forests is probably more frequent but also more ephemeral (*i.e.,* recovery of forest structure is relatively rapid; Turner *et al.* 1997). Hurricanes and less intense tropical storms therefore may play an important role in dry forest succession following fire or human disturbance, but probably do not initiate the successional process themselves, except on a small scale.

The ecological literature includes several accounts of long-term successional dynamics in Caribbean tropical forest ecosystems (Crow 1980, Ray & Brown 1995) and in the subtropical portions of peninsular Florida (Alexander 1967, Olmsted *et al.* 1980, Molnar 1990, Mack 1992); however, no published analyses of forest succession in the dry tropical forests of the Florida Keys are available. Our primary objective in the research described below was to describe the species replacement sequence, if any, that characterizes the forests of the Florida Keys. To do so, we determined tree species optima along a chronosequence of 23 stands abandoned from agriculture at different times in the past on a single island, Key Largo, in the upper Florida Keys. Furthermore, we also wished to assess the direct effects of hurricanes or less violent storms on species succession, since nearly all of the stands had experienced several such events since abandonment. We therefore compared the successional status of the assemblage of trees killed by Hurricane Andrew (1992) with that of the pre-hurricane tree community.

STUDY AREA

The upland forests of the upper Florida Keys (delineated in Fig. 1 as the islands between Sands Key in Biscayne Bay and Lignumvitae Key in southern Florida Bay) comprise a diverse mixture of deciduous and evergreen broadleaved tree species that is predominantly West Indian in origin (Robertson 1955, Tomlinson 1986). The 15-km stretch of continuous forest in northern Key Largo represents one of the most extensive remaining examples of these communities, which are locally referred to as “hardwood hammocks.” Canopy height in these low-branching forests is quite low, averaging *ca* 8–12 m, with few emergents (Hilsenbeck 1976, Ross *et al.* 1992); however, basal area in well developed upper Keys hardwood hammocks is typically high in comparison to other dry tropical forests, ranging from *ca* 25 to >40 m^2/ha. Total aboveground biomass usually exceeds 100 Mg/ha, and estimated net annual aboveground production is *ca* 3 Mg/ha/yr (L. Coultas & M. Ross, pers. obs.). 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 & M. Ross, pers. obs.), and develop directly on a Pleistocene limestone bedrock. Elevations range from a maximum of *ca* 2 m above sea level in the lower (westernmost) Keys to >5 m in the upper Keys.

As in much of the Florida Keys, the history of Key Largo hammocks includes a period of intensive agricultural disturbance. Aerial photos indicate that much of the island 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. In addition to causing great loss of life, this storm marked the end of the Overseas Railroad, the major shipping conduit for Keys produce. Land clearing in subsequent years became increasingly associated with nonagricultural purposes, including roads, residential development, oil exploration, and military installations.

As a result of a maritime setting, climatic conditions in Key Largo are tropical despite a location several degrees north of the Tropic of Cancer (Fig. 1). Based on 35-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 as tropical with summer rain (Walter 1985), and the ecosystems are classified within Holdridge's (1967) Tropical Dry Forest Life Zone. Periodic freezes that affect forests in mainland south Florida (Olmsted *et al.* 1993) are extremely rare in the Keys, although a brief freeze in December 1989 did cause some tree mortality and premature leaf abscission in exposed areas of northern Key Largo (M. Ross, pers. obs.).

Occasional devastating ground fires that kill virtually all stems and incinerate the shallow organic soils (Olmsted *et al.* 1980, Craighead 1981) are an important component of the natural disturbance regime impacting hardwood hammocks throughout south Florida. The same is true of frequent windstorms ranging up to major hurricanes, which are less all-consuming in effect. 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 (Neumann *et al.* 1981). 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 *ca* 27 years.

The most recent major hurricane to strike Key Largo was Hurricane Andrew, which passed over the northern half of the island in the early morning of 24 August 1992 (Fig. 1). The storm's compact path was centered on Biscayne National Park, but the southern eye wall also crossed over the northernmost portions of the Key Largo study area. Peak five-second gusts in Biscayne National Park were estimated at 70 m/sec, or 157 mph (Powell & Houston 1996). A maximum storm surge of >4 m was recorded on the mainland coast north of the hurricane eye; however, there was no evidence that storm waters rose high enough to inundate the ground surface in Key Largo upland forests.

METHODS

FIELD METHODS.—In May–June 1994, 21–22 months after Hurricane Andrew, we sampled the composition and size structure of living and hurricane-killed trees at 23 upland forest sites in the Crocodile Lakes National Wildlife Refuge and the Key Largo Hammocks State Botanical Area (Fig. 1). Sample sites were evenly distributed along a 15-km stretch of the narrow upland ridge, mostly within 200 m of a road that followed the crest of the uplands. We established a set of nested belt transects 60–100 m in length at each site. For both live and hurricane-killed trees <25 cm in diameter, we recorded species and DBH (diameter at 1.45 m height) of all trees rooted within 1 m (stems 1.0–9.9 cm DBH) or 2 m (stems 10.0–24.9 cm DBH) of the center line of the transect. Live trees ≥25 cm DBH were sampled within 5 m of the line, and hurricane-killed trees of the same size were sampled within 10 m. Data were summarized as basal area of each species in live and dead categories.

We also estimated the elevation in feet above sea level, distance from the southern edge of the study area, and time since abandonment from anthropogenic disturbance (hereafter referred to as "elevation," "distance," and "stand age") for each transect. Elevation of the midpoint for each transect was interpolated from 5-ft contours on USGS topographic surveys. Stand age was estimated on the basis of the appearance of the site on blackand-white aerial photos from 1985, 1971, 1959, 1940, and 1926, supplemented by reliable anecdotal information for several sites. Five stands that 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 the level of removal did not appear extensive enough to have substantially altered overall species composition.

Analytical methods.—The covariation of pre-hurricane Key Largo stand composition (*i.e.,* living trees + hurricane-killed trees) with stand age, distance, and elevation was examined through canonical correspondence analysis (CCA; ter Braak 1986), using PC-ORD version 3.11 for Windows (McCune & Mefford 1995). Compositional data used in the analysis were relative basal areas of species that occurred in 3 or more of the 23 stands.

Weighted averaging (WA) regression and calibration (WACALIB version 3.3; Line *et al.* 1994) were used to quantify the successional status of pre-hurricane and hurricane-killed tree assemblages in each sample plot. In WA regression, species optima are determined by abundance-weighted averaging in a calibration data set (*i.e.,* 23 pre-hurricane assemblages) in which the environmental variable of interest (*i.e.,* stand age) is known. Following Birks *et al.* (1990), we calculated the WA estimate for each species' successional age optimum, or SAO_k-hat, as

$$\widehat{SAO}_k = \sum_{i=1}^{n} y_{ik} x_i \Big/ \sum_{i=1}^{n} y_{ik}$$

and its tolerance (weighted standard deviation), or t_k-hat, as

$$\hat{t}_k = \left[\sum_{i=1}^{n} y_{ik}(x_i - \widehat{SAO}_k)^2 \Big/ \sum_{i=1}^{n} y_{ik} \right]^{1/2},$$

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

In WA calibration, the environmental 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 further refine, or "deshrink," estimates for both the calibration and test data sets (*i.e.,* 23 hurricane-killed assemblages). 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 & van Damm 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 (ISAs) 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, ISA_k, as

$$ISA_k = \sum_{k=1}^{m} y_{ik} \widehat{SAO}_k \Big/ \sum_{k=1}^{m} y_{ik},$$

and the tolerance-weighted estimate, $ISA_{k(\mathrm{tol})}$, as

$$ISA_{k(\mathrm{tol})} = \frac{\sum_{k=1}^{m} y_{ik} \widehat{SAO}_k}{\hat{t}_k^2} \Bigg/ \frac{\sum_{k=1}^{m} y_{ik}}{\hat{t}_k^2}.$$

The predictive capacity of the unweighted and tolerance-weighted models 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 that yielded a smaller RMSE then was used to calculate, for each site, separate ISAs on the basis of both pre-hurricane stand composition and the species composition of trees killed by Hurricane Andrew. The difference between the pre-hurricane and hurricane-killed ISAs was calculated for each stand, and the mean and 95 percent confidence interval of the differences calculated.

The successional sequence revealed by the above analyses was further examined by characterizing individual species with respect to (a) leaf longevity and (b) usual canopy position at maturity. We characterized species as deciduous or evergreen, depending on their tendency to experience a leafless period of any duration during the dry season. Classification was based on descriptions in Tomlinson (1986), supplemented by site- and species-specific data from Key Largo in 1991–1992 (L. Flynn & M. Ross, pers. comm.). We characterized species as occupants of the canopy, mid-story, or subcanopy based on structural data collected in hardwood hammocks throughout the Keys in 1989–1991, and summarized in part by Ross *et al.* (1992).

RESULTS

Immediate effect of Hurricane Andrew on forest structure.—For the study area as a whole, mean upland stand mortality resulting from Hurricane Andrew was 7.5 percent of pre-storm basal area, and 4.9 precent of pre-storm density. Mortality was concentrated among larger trees in most stands; in 15 of the 23 stands, the average stand diameter (ASD: diameter of a tree with the mean basal area; Daniel *et al.* 1979) of the assemblage of hurricane-killed trees was higher than the ASD of the pre-hurricane forest as a whole. The Wilcoxon's signed-ranks test however, indicated that the probability of no difference in ASD between the pre-hurricane and hurricane-killed assemblages was *ca* 9 percent, a nonsignificant result. On a basal area basis, bole breakage accounted for 71 percent of total hurricane mortality, uprooting for 27 percent, and other causes, 2 percent. Finally, orientation of fallen trees in the Key Largo study area was primarily toward the northeast, indicating that the most damaging winds occurred during the trailing half of the storm, when winds were from the southwest.

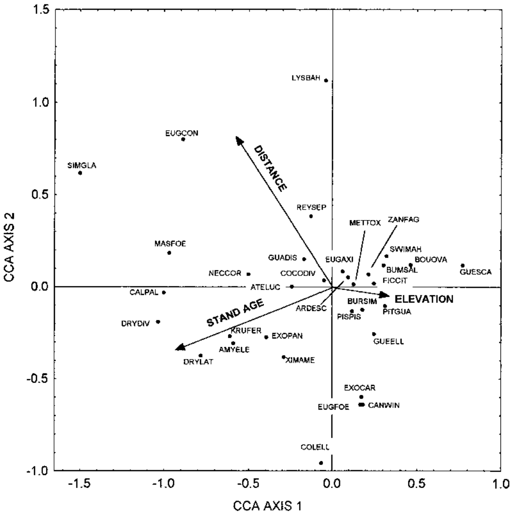

FIGURE 2. Species–environment bi-plot for CCA of pre-hurricane Key Largo hammocks, with ELEVATION, DISTANCE, and STAND AGE as environmental variables. Data labels are six-letter codes (first three letters of genus, first three letters of species) for species listed in Table 1.

Species composition and successional affinities in pre-hurricane forests.—Forty-two tree species were encountered in the 23 Key Largo transects. Axes 1 and 2 of the CCA (eigenvalues 0.238 and 0.228, respectively) accounted for > 25 percent of the total variance in the tree species data, while the third canonical axis explained only an additional 2 percent. The location variable distance was strongly correlated with the standardized site scores on Axis 1 ($r = 0.485$), and stand age was strongly correlated with Axis 2 ($r = 0.454$). Elevation, the third environmental variable, was weakly correlated with all three canonical axes ($r \leq 0.215$). Stand age was uncorrelated with the other two environmental variables, but distance and elevation were strongly correlated ($r = -0.42$; Fig. 2).

Based on calculated successional age optima, five Key Largo tree species exhibited an association with the early stages of stand development (Table 1). Except for *Solanum bahamense,* which occurred in only one stand, tolerances in this group approximated or exceeded the mean for all species (21.5 yr). Their broad tolerances demonstrate that characteristic early-successional species in Key Largo forests persisted for several decades or more after establishment. While both large and small trees were included in this group, all five species were characterized by a short leafless period during the dry south Florida spring (Table 1).

Eighteen species had optima in stands 50–75 years old. Tolerances within this group ranged from wide to narrow. Among the latter, *Eugenia foetida* was a common subcanopy tree that appeared to be a good indicator of intermediate developmental stages. The diverse group of mid-successional species was composed primarily of evergreen species, but its deciduous members (*Swietenia mahogani, Ficus citrifolia, Metopium toxiferum, Piscidia piscipula,* and *Bursera simaruba*) were very prominent in the upper levels of the forest canopy (Table 1).

Twelve species were associated with later stages of stand development (Table 1). The four with the highest optima (*Drypetes lateriflora, D. diversifolia, Calyptranthes 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.

Successional affinities of pre-hurricane versus hurricane-killed trees.—Among the five species that suffered above average hurricane mortality, three were early to mid-successional trees of the

TABLE 1. *Stand age optima of 35 Key Largo tree species. Canopy position categories: C = upper canopy; M = midstory; S = subcanopy. Leaf phenology categories: D = deciduous; and E = evergreen.*

Stand age group	Species	Optimum	Tolerance	*N*	Canopy position	Leaf phenology
Stands <50 years old	*Solanum bahamense*	14.0	—	1	C	D
	Guettarda scabra	38.1	27.1	7	S	D
	Bourreria ovata	43.0	29.6	10	S	D
	Lysiloma bahamense	46.9	21.6	10	C	D
	Guettarda elliptica	48.4	35.2	17	S	D
Stands 50–75 years old	*Swietenia mahogani*	55.3	22.1	16	C	D
	Ficus citrifolia	56.4	21.1	15	C	D
	Bumelia salicifolia	56.7	21.8	19	M	E
	Pithecellobium guadalupense	57.0	18.1	12	S	E
	Ardisia escallonioides	58.0	24.5	19	S	E
	Metopium toxiferum	58.4	18.4	23	C	D
	Piscidia piscipula	59.8	22.0	22	C	D
	Pithecellobium unguis-cati	60.0	—	1	S	E
	Zanthoxylum fagara	60.1	29.1	9	S	E
	Bursera simaruba	61.3	24.6	22	C	D
	Eugenia axillaris	61.9	26.1	23	S	E
	Exostema caribaeum	62.7	7.8	6	M	E
	Reynosia septentrionalis	62.9	6.2	4	S	E
	Guapira discolor	65.0	27.1	9	C	E
	Eugenia foetida	65.2	9.2	10	S	E
	Canella winterana	66.6	19.8	4	S	E
	Coccoloba diversifolia	71.4	25.6	23	M	E
	Ximenia americana	73.5	23.1	4	S	E
Stands >75 years old	*Colubrina elliptica*	77.4	23.9	6	M	E
	Amyris elemifera	78.3	23.3	11	S	E
	Ateramnus lucida	78.8	26.0	21	S	E
	Nectandra coriacea	82.7	27.6	8	S	E
	Krugiodendron ferreum	84.4	19.6	15	M	E
	Exothea paniculata	84.5	25.8	4	C	E
	Eugenia confusa	84.7	28.0	3	M	E
	Mastichodendron foetidissimum	85.9	20.5	4	C	E
	Drypetes lateriflora	86.9	18.0	5	S	E
	D. diversifolia	96.2	15.6	7	M	E
	Calyptranthes pallens	96.4	14.7	10	S	E
	Simarouba glauca	99.7	5.7	4	M	E

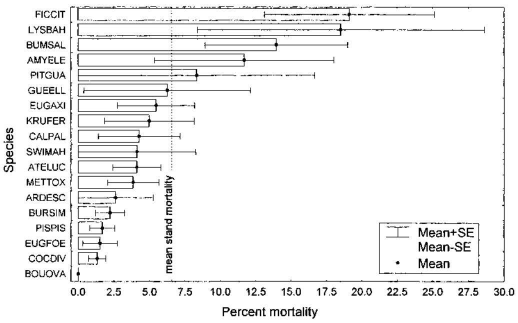

FIGURE 3. Mean (± SE) percent mortality (basal area basis) for species that occurred in ten or more sampled Key Largo hammocks. Species are coded as in Figure 2.

upper forest canopy (*F. citrifolia, Lysiloma bahamense,* and *Bumelia salicifolia*), while two (*Pithecellobium guadalupense* and *Amyris elemifera*) were mid- and late-successional subcanopy species, respectively (Fig. 3). Species exhibiting below average mortality ranged broadly in their successional age optima and canopy position.

The unweighted WA model was superior to the tolerance-weighted model, based on a higher coefficient of determination for uncorrected predictions versus 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 yr, respectively). No evidence of systematic underestimation or overestimation at stand age extremes was observed.

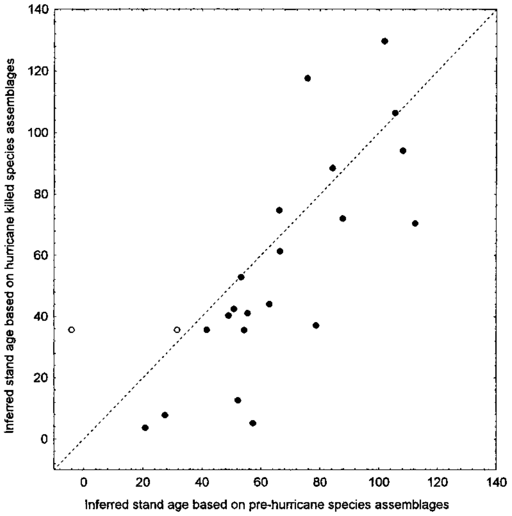

FIGURE 4. Scatterplot of inferred stand ages (ISAs) based on pre-hurricane and hurricane-killed species assemblages in 23 Key Largo forests. Open circles represent the two youngest stands with compositions consisting of pioneer species only; see text. The dashed line represents the set of points for which ISAs based on hurricane-killed and pre-hurricane assemblages were equal.

WA estimates of stand age based on pre-hurricane species composition exceeded those based on hurricane-killed species in 16 of 23 cases, with a mean difference across all sites of +6.4 years (Fig. 4). A paired *t*-test indicated that this difference was not significant at $P = 0.05$; however, the two youngest stands included in the above analysis had been abandoned only 14 years earlier, and their pre-hurricane composition was almost exclusively of pioneer species, with few mid- or late-successional trees. When these two stands were eliminated from the data set, the mean difference between estimates based on the two groups increased to +9.1 years, which was statistically different from zero. We take this result as a fairly strong indication that hurricane-induced mortality was concentrated among earlier-successional elements of the pre-hurricane stands.

DISCUSSION

Species replacement following catastrophic disturbance.—Our study is the first to describe a successional sequence of species in upper Florida Keys hardwood forests, and one of very few to address long-term successional dynamics of dry Caribbean 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 after release from intensive grazing activities. Our own data, derived from a time sequence of 23 upper Florida Keys forests, likewise indicated a directional change in species composition that continued through most or all of the first century following the cessation of agricultural or other anthropogenic activities (Table 1). Relevant information from south Florida is also found in a series of papers documenting compositional change in a single mainland forest (Phillips 1940, Alexander 1967, Molnar 1990, Mack 1992). Between 1940 and 1986, some portions of the Castellow-Ross hammock were relatively unchanged in species composition, but in others, mortality among large trees (primarily *L. bahamense*) created large gaps that were colonized by a different set of tree species, including several exotic taxa (Molnar 1990).

The Key Largo species replacement series contrasts with the sequence in recovering agricultural fields on rock-plowed uplands on the south Florida mainland, where the exotic Brazilian pepper (*Schinus terebinthifolius*) achieves canopy dominance within five to ten years after abandonment, and subsequently resists replacement by native hardwoods (Ewel *et al.* 1982). With the integration of the rock-plow into mainland agricultural practices in the 1940s, a pulverized mineral soil was created on which *S. terebinthifolius* was apparently better-adapted than the native early-successional species. In contrast, agriculture in the Florida Keys never advanced beyond low-intensity practices that had relatively little effect on the underlying substrate. The nonagricultural purposes (*e.g.,* residential or military) for which many of our more recent sites were cleared required scraping to bedrock, piling the scraped material, and perhaps burning it, but did not involve major disruption to the rock substrate itself.

In fact, the surfaces at many of our sites immediately after abandonment probably resembled those of south Florida pine rock lands 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 stand development in Key Largo hardwood forests also invade south Florida pine forests after fire, although establishment usually takes several years or more. Of the species included in Table 1, *L. bahamense, M. toxiferum, B.*

salicifolia, B. simarouba, and *Coccoloba diversifolia* were reported to be early invaders of pine forests on Long Pine Key (Robertson 1955), and *L. bahamense* was identified as the most abundant of several tree species that replaced *Pinus elliottii* var *densa* in pine forest portions of the Castellow tract (Alexander 1967). Our own observations indicated that *Guettarda scabra* resprouts aggressively after fire in urban pine forest fragments of urban Miami-Dade County, and *P. piscipula* is a common invader in pine forests of the lower Florida Keys.

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 *S. mahogani* and *M. 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 showed a stratification between a deciduous upper canopy and an evergreen lower canopy in some Ghanaian dry forests, but did not describe their temporal development. Janzen (1986) however, noted an increase in evergreen species 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. In the Florida Keys, this change may involve forest soil development.

Florida Keys hammock soils are predominantly organic, with a very minor mineral component (Coultas & Ross, pers. obs.). As such, they are dynamic biogenic entities having a development which is intertwined with that of the forest above. In the absence of human land clearing activities, both forest and soil development ends and begins with fire, which occurs infrequently but can and often does consume virtually all organic material down to the limestone surface (Craighead 1981). During the time required for the species replacement sequence illustrated in Table 1 to take place, the barren, rocky post-disturbance surface becomes blanketed by a spongy, organic substrate of 10 to 20 cm depth. Thin as it is, such a soil provides markedly different seedbed conditions and enhanced rooting volume in comparison to the rocky substrate over which it formed, and is able to absorb several times its weight in water. Augmentation of soil moisture-holding capacity may be especially important for Key Largo hammock species, which generally acquire most of their water from surface sediments rather than deeper groundwater sources that may be brackish in quality (Ish-Shalom *et al.* 1992).

We therefore suggest that the replacement of deciduous by evergreen species during stand development in the Florida Keys may reflect soil development through an increase in buffering from periodic moisture stress during the winter dry season. In tropical forests, the deciduous habit is considered to be a mechanism that minimizes transpirational water losses during periods of moisture stress (Reich & Borchert 1984, Murphy & Lugo 1986, Gerhardt & Hytteborn 1992, Olivares & Medina 1992, Borchert 1994). The association of deciduousness and moisture stress is further supported by studies of the distribution of deciduous and evergreen species along known moisture gradients (*e.g.,* Reich & Borchert 1984, Kapos 1986, Swaine 1992, van Rompaey 1993). Given the arrangement of deciduous- and evergreen-dominated forests toward the dry and wet extremes, respectively, of spatial gradients in moisture availability throughout the tropics, one may reasonably expect to find these two morphologic strategies distributed similarly along a temporal moisture gradient associated with stand successional age and soil development.

HURRICANE MORTALITY AND FOREST SUCCESSION.—In this study, we used an expression of species' positions along a temporal sequence initiated by one sort of disturbance, anthropogenic clearing, to assess community response to a second type of disturbance (*i.e.,* a hurricane). To accomplish that objective, we employed a weighted averaging procedure more frequently employed in paleoecological studies (*e.g.,* Birks *et al.* 1990, Gaiser *et al.* 1998). In the paleoecologic context, time is generally a background variable, while the observed modern relationships of species to environmental variables (*e.g.,* pH and hydroperiod) are used to reconstruct past environments on the basis of fossil assemblages. In our weighted averaging application, a retrospective analysis of the species-time relationship was the tool used to determine if the two disturbance types differed in their effects on community dynamics.

Our analyses indicated that species which responded most aggressively to anthropogenic clearing were the most negatively impacted by Hurricane Andrew, at least in terms of immediate damage. This pattern resembled that observed in a subtropical wet forest of Puerto Rico (Zimmerman *et* *al.* 1994), where several pioneer tree species experienced the highest level of mortality and stem breakage due to Hurricane Hugo (1989). In the face of substantial differences in climate, substrate, topography, species composition, and stand density between study areas, the similarity of results from Florida and Puerto Rico suggests that the vulnerability of early-successional species to immediate damage from hurricanes may be a general characteristic of tropical forests.

Interpretation of forest succession based on chronosequence data must be carefully qualified, in part because the overall pattern across sites may be colored by site history factors as well as by stand development (Fastie 1995, Lichter 1998). In the current case, compositional patterns interpreted as community responses to anthropogenic clearing also incorporated species responses to subsequent hurricanes (as well as other events). Nevertheless, the two disturbance types appeared to be opposite in their effect on species composition; *i.e.,* anthropogenic disturbance initiated a long successional sequence beginning with a narrow set of predominantly deciduous species, and hurricane disturbance selectively removed these trees in favor of a different set of evergreen taxa.

These responses may be better understood by considering the intensity and frequency of the two disturbance types during the evolutionary history of the Florida Keys. Disturbance intensity associated with hurricanes is variable within a forest; trees may be defoliated, snapped off, uprooted, killed, or not affected, and soil disturbance is local. On average, major hurricanes recur at intervals of two to three decades throughout the Keys. In contrast, anthropogenic clearings are characterized by extensive soil disturbance and high tree mortality. Historically, anthropogenic clearings occurred on a large spatial scale (*i.e.,* widespread clearings for agricultural or development purposes), but probably only occurred once during evolutionary history. The only natural disturbance in the upper Keys that also occurs with high intensity and at extremely low frequency is fire. Because of the humid microclimate, low wind speed, and absence of ignitable fuels that characterize upper Keys hardwood hammocks, the interval between fires under natural conditions is expected to be very long. Fires that do occur have profound effects on the ecosystem, typically consuming all of the organic soil and killing most trees (Robertson 1955).

Based on the patterns described above, we suggest that hurricanes and anthropogenic clearing should have different selective consequences for plant species. Since hurricanes have a return time shorter than the life spans of many tree species, their occurrence should act as a selective pressure to increase the short-term fitness of species (*sensu* Harper 1977). We believe that this mechanism helps explain the low hurricane-related mortality of later-successional tree species. These species had evolved under conditions of frequent hurricanes, and may be abundant in older stands in part because of their adaptations to such events. Adaptations may involve responses during the post-hurricane period, or resistance to the storm itself. With respect to the latter, resistance to wind damage has been attributed by several authors to high wood density (Putz *et al.* 1983, Zimmerman *et al.* 1994). Published wood densities for most Key Largo trees are not available, but it would be interesting to know if there is a positive relationship between wood specific gravity and species' successional age optima.

Late-successional tree species of the upper Florida Keys should be less likely to evolve life history characteristics in response to anthropogenic clearings or fires than to hurricanes. Adaptation to the extremely infrequent occurrence of such disturbances would likely decrease the short-term fitness of these species (Harper 1977). In our study, anthropogenic clearing resulted in a virtually complete replacement of tree species. The species that dominated the early years after clearing tended to be generalist pioneers on a broad range of uncolonized substrates. Many (*e.g., L. bahamense, M. toxiferum, B. salicifolia, B. simaruba,* and *C. diversifolia*) are among the first to colonize recently burned areas in the upper Florida Keys (M. Ross, pers. obs.) and pine forests in Everglades National Park (Robertson 1955), and are also early colonizers of sandy berms on Florida Bay mangrove islands (Carrington, pers. obs.). Early-successional species like *B. salicifolia* may be inherently short-lived and therefore susceptible to any agency of disturbance. Trees like *L. bahamense* or *F. citrifolia* may emerge substantially from the forest canopy, thereby exposing themselves to higher winds than their neighbors.

The results reported here address only one element of community response to hurricanes. During the period of relative canopy openness following a hurricane, surviving trees and smaller stems may rapidly expand their canopies, and new individuals may become established (Horvitz *et al.* 1995). Opportunities for germination and establishment of most early-successional species are rare in undisturbed forests, and are largely confined to short intervals following hurricanes or other damaging storms. Even then, seedlings of these species are uncommon outside of large, multiple-tree gaps (Ross, pers. obs.). More comprehensive analysis of the role of windstorms in the long-term succession of tropical hardwood forests may be achievable through matrix model approaches (*e.g.,* Batista *et al.* 1998, Pascarella & Horvitz 1998), but these transition models will need to include all stages of the hurricane recovery cycle.

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