

## FLORISTIC ZONATION, VEGETATION STRUCTURE, AND PLANT DIVERSITY PATTERNS WITHIN A CARIBBEAN MANGROVE AND SWAMP FOREST ON THE BAY ISLAND OF UTILA (HONDURAS)

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*Abstract.* Utila is a small island off the north coast of Honduras. More than two-thirds of its surface are covered by swamp forests and mangroves, since large areas of the topographically flat island are frequently inundated, favoring vegetation tolerant to the influence of brackish and/or salt water. These wetlands provide important ecosystem services and are the habitat of some endangered and well-studied narrow endemic reptiles. From a botanical point of view, however, the swamp forests of Utila have not received much scientific attention. Using quantitative data along a line-transect, we try to provide insight into the vegetation zonation and intrazonal structures, as well as into the diversity patterns and ecotonal complexity of the swamp forests on Utila.

We found an apparent zonation pattern, but edges between units differ in terms of statistically significant distinctiveness and depth, resulting in either sharp boundaries between rather discrete communities or broad ecotonal transitions affecting whole sequences along the transect. While zonation is controlled by a factorial complex of physiochemical gradients, topography, and species competition, structural features seem to be related to large-scale disturbances. The variety of functional types, structural characteristics, and evenness patterns found in Utila's coastal forests far exceed species richness in terms of diversity.

*Keywords:* *Conocarpus erecta*, *Islas de la Bahía*, *Laguncularia racemosa*, *line transect*, *mangroves*, *Rhizophora mangle*, *swamp forests*, *Utila*, *zonation*.

### INTRODUCTION

Swamp forests and mangroves are characteristic azonal ecosystems of the (sub)tropics. While mangroves occupy either shores with low wave action or lagoons and estuaries draining the interior in varying brackish and salty environments, many different types of moist forests occur in freshwater environments according to site conditions, inundation, and floral history (for Central American wetlands see Ellison 2004).

Besides being of unique and characteristic beauty, swamp forests, and in particular mangroves, provide

important direct and indirect ecosystem services (Ewel *et al.* 1998, Saenger 2002, Nagelkerken *et al.* 2008). Also, even if not standing comparison with other tropical ecosystems, such as rainforests or coral reefs, in terms of species richness, swamp forests and mangroves are highly diverse ecological communities regarding structural and functional attributes (see e.g. Ricklefs & Latham 1993, Farnsworth & Ellison 1996, Saenger 2002, Ellison 2004). Nevertheless, wetland forests and mangroves all over the world are in great danger of degradation or extinction due to the overexploitation of their natural resources (e.g. Saenger 2002).

The high ecological value of these systems and the urge for their protection are recognized by many

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authors, and there is no shortage of regional wetland species lists (see Spalding *et al.* 1997, Saenger 2002, Ellison 2004) or of descriptive studies on mangrove zonation (see e.g. Lugo 1980 or Saenger 2002). Most of these publications focus on the dominant species, and the support or rejection of an intracommunal zonation is primarily based on qualitative data with an *a priori* assumption that a zonation exists (Ellison *et al.* 2000, Ellison 2002). However, when dealing with questions like floristic zonation and significant boundaries of possible zones, quantitative data are crucial. In this paper, we present a quantitative description of the zonation, vegetation structure, and diversity patterns of the swamp forests, mangroves, and adjacent back-beach forests on Utila.

METHODS

*Study area.* The archipelago of the Bay Islands (or Islas de la Bahía) is located off the north coast of Honduras between 16°24'–16°42'N and 86°07'–

86°35'E. It consists of three major islands as well as some 70 smaller cays. Utila is the westernmost and smallest of the three main islands next to Roatán and Guanaja (see Fig. 1) and possesses a tropical climate, dominated by trade winds for most of the year. Climate data of neighboring Roatán (Fig. 2) show an average annual temperature of 27.3°C and a mean precipitation of about 1750 mm per year (Bak & Gallner 2002) with an obvious peak in winter, when polar-continental cold fronts (*nortes*) advance far south into the Gulf of Honduras. Due to its lower relief, precipitation on Utila might be slightly less. During the “hurricane season” between May and October tropical waves regularly move in from the Atlantic, but Utila has gotten off lightly so far with only four hits/near-hits of class 2 hurricanes within the last century and a half (Dankewich 2006).

The Bay Islands are part of the Bonacca Ridge, a submerged continuation of the Sierra de Omoa on the Central American mainland, dropping into the Caribbean Sea at Puerto Cortes (Banks & Richards

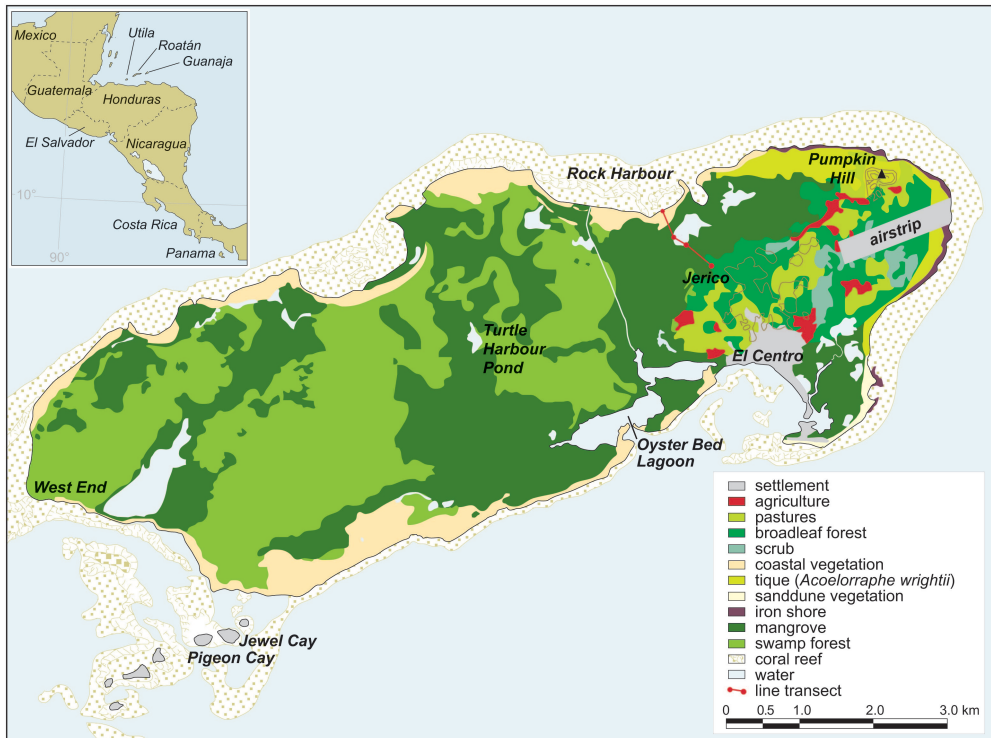


FIG. 1. Vegetation map of Utila (modified from [www.islasdelabahia.org/estudios\\_ed\\_mapas.html](http://www.islasdelabahia.org/estudios_ed_mapas.html))

1969). The volcanic knoll of Pumpkin Hill (74 m a.s.l.), forming the highest point of Utila, is surrounded by flat coralline limestone platforms (McBirney & Bass 1969). Combined with the high phreatic water table, the seasonal rainwater accumulation in depressions, and the occasional ocean water influx, the slightly undulating terrain is the basis for a spatio-temporal mosaic of varying brackish conditions.

Here, Utila hosts not only the most extensive mangrove area of the Bay Islands (with 669.4 ha covering more than 1/3 of the total island surface of 42 km<sup>2</sup>, see Fig. 1), but also “one of the largest, contiguous and most unique mangroves in the Caribbean” (Lemay *et al.* 2003). These mangrove forests differ in some respects from others within the Caribbean because they mostly do not have direct contact to the sea, but are separated from ocean water by sandy beaches of various widths, covered by coastal forest vegetation (Fig. 1). Despite occasional (illegal) hunting of *Ctenosaura bakeri*, an endemic reptile occurring exclusively within the mangroves and swamp forests of Utila (e.g. Gutsche & Streich 2009), anthropogenic impacts on the wetlands are still minor due to the inland’s low land-use potential (see Kaiser & Grismer 2001, Currin 2002). However, Utila’s forests are at high risk, as realty and tourism on the island grow rapidly and large stretches of the recently undeveloped northern coast are planned to be opened up for infrastructure in the near future (Clauss & Wild 2001, Currin 2002). Besides the on-going destruction of forest areas, many additional negative impacts on the functionality of the remaining wetland ecosystems can be expected from the extension of forest edges, selective wood cutting, drainage, and water contamination.

*Sample design and field measurements.* Referring to Ellison’s (2002) recommendation of minimum data required to assess zonation or gradients within mangrove forests, quantitative data on vegetation was sampled along a 1250-m line-transect employing the “line-intercept method” (see Mueller-Dombois & Ellenberg 1974). Located in the eastern half of the island, the transect runs roughly at a right angle to potential environmental gradients (Cintrón & Schaeffer Novelli 1984) from Jericho to Rock Harbour on the northern shore of Utila (see Fig. 1). The center of the transect features a 200-m gap at Rock Harbour Pond devoid of vegetation. Along the transect, all vascular plant species (taxonomy following Balick *et al.* 2000), along with life-form and height class affiliation (< 2 m, 2-5 m, 5-10 m, 10-15

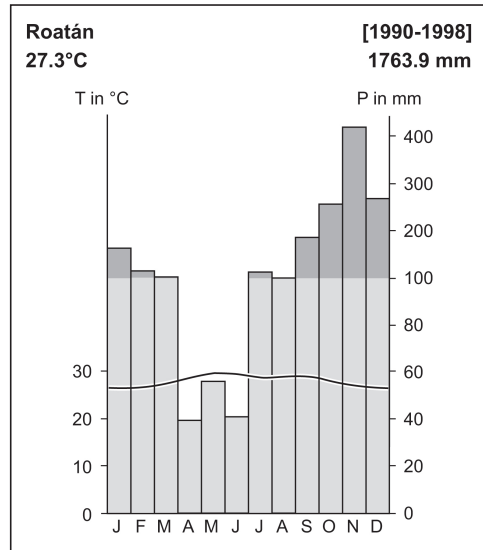


FIG. 2. Climate diagram of Roatán, the neighboring island to the east of Utila (source Bak & Gallner 2002).

m, >15 m), were recorded with a resolution of 10 cm. For statistical analyses concerning floristic zonation, boundary detection, vegetation structure and diversity patterns, these raw data were merged to give adjoining 10-m segments and the accumulated length measured for any one species within these segments was converted to ground cover values in %. In addition, diameter at breast height (dbh) was obtained for all woody plants taller than 2 m (excluding lianas).

Along the transect, measurements of some important physiochemical soil parameters (pH, salinity, and redox potential) were carried out using a multi-parameter measuring device (Eijkelkamp 18.28, Agrisearch Equipment). Sample points were located at regular intervals of 25 m, resulting in a total of 43 measurements. Redox potential was measured *in situ* at topsoil level (10-cm depth) with a platinum Ag/AgCl 3 mol/l KCL electrode after equilibration for 30-60 minutes, when stable values were reached. Salinity and pH values were measured in a suspension of soil material taken at 10-cm depth in interstitial water taken from the water filling the hole (H<sub>2</sub>O dest. for the dry back beach forests samples) mixed in a sample bottle at a ratio of 1:5. Salinity values were derived by an automated translation of the measured conductivity values to values in g/l by the

measuring device. The pH values were determined with a standard KCl pH electrode ( $T = 25^{\circ}\text{C}$ ) after calibration in 4.0 and 7.0 standards (NIST scale). At ten locations within homogeneous sections of the transect, soil samples were taken at 10-cm depth for laboratory analyses of organic matter and particle size composition.

*Soil texture and organic matter analyses.* Grain size determination for the ten samples was carried out by a combined sieving and pipetting procedure (see Schlichting *et al.* 1995). Only a rough estimation of organic matter content was possible. For equipment reasons, the hydrogen peroxide ( $\text{H}_2\text{O}_2$ ) digestion method had to be adopted, which destroys the organic matter in the soil sample through oxidation. The gravimetrically determined difference between the original sample weight and the weight after treatment can roughly be considered as organic matter content. The authors are fully aware of the limitations of this procedure (Schumacher 2002), but for a tentative estimation of differences between sample groups it might still be useful.

*Statistical analyses.* Different structural measures, such as relative density ( $\text{Den}_r$ ), relative dominance ( $\text{Dom}_r$ ), relative frequency ( $\text{Freq}_r$ ) and Importance Value Index (IVI) of all tree species (Cintrón & Schaeffer Novelli 1984), as well as Complexity Index (CI) of forest types (modified from Holdridge 1967, see below) were calculated:

- $\text{Den}_r$  in % = (no. of individuals of a species / total no. of individuals)  $\times$  100
- $\text{Dom}_r$  in % = (total basal area of a species / basal area of all species)  $\times$  100
- $\text{Freq}_r$  in % = (frequency of a species / sum-frequency of all species)  $\times$  100
- $\text{IVI} = \text{Den}_r + \text{Dom}_r + \text{Freq}_r$
- $\text{CI} = S \times D \times B \times H$ , where S is the species number, D the stand density (no. of tree stems of or over 10-cm diameter), B the basal area, and H height (total mean). Density in our study was calculated per transect segment and not per 0.1 ha as done by Holdridge (1976), and so the above formula was not divided by  $10^3$ . Our CI values are therefore not comparable with those of other studies; for a comparison of the relative complexity of segments, however, this modified CI is still a valuable measure.

In addition, evenness values (E) to describe the dominance ratios within plant community samples

independent of their species richness (see Pielou 1966) were calculated for the 10m-transect segments:

- Evenness  $E = (H'/H_{\text{max}}) \times 100$ , where  $H'$  is Shannon's entropy (Shannon & Weaver 1949) and  $H_{\text{max}}$  (maximum diversity) =  $\log n$  (with  $n$  = total species number).

For a rough overview on the possibility of floristic zonation along the transect, agglomerative hierarchical cluster analyses were employed. Similarities of the quantitative sample segment data were calculated using the Van der Maarel coefficient (a quantitative modification of the Jaccard index); the cluster agglomeration rule followed minimum variance clustering (or Ward's) method. All calculations were performed with MULVA 5 (Wildi 1994).

The presence of significant boundaries was tested by split moving window distance (dissimilarity) analyses (SMWDA, see also Hennenberg *et al.* 2005). SMWDA is a direct boundary detection tool that focuses on significant discontinuities within the transect data, or their principal components, by calculating distance values from covariance matrices of paired moving data-windows, thus averaging a specified amount of samples on the sides of each tested boundary location to reduce the influence of outlier samples. These analyses were carried out using different packages in the R environment for statistical computing (R Development Core Team 2008, R-script for SMWDA by Rossiter 2009).

Constrained unimodal ordination models (here canonical correspondence analyses, CCA) were employed to show the plant species information as a function of the measured environmental factors (as the ordination axes here are weighted sums of the environmental variables used), and also to allow an interpretation of the samples' interrelations (see Lepš & Šmilauer 2003). Segments without related environmental data were handled as "passive" samples, with no influence on the ordination axes, and are integrated in the CCA by means of their floristic relation to the "active" samples. Significance of the environmental factors was tested by Monte Carlo permutation tests, with permutations restricted in respect of the transect data. Semi-parametric regression models (here Generalized Additive Models, GAMs) were used to model the performance of important species along the measured environmental variables. Models, relevant statistics, and graphics were carried out in CANOCO 4.5 (Ter Braak & Šmilauer 2002)

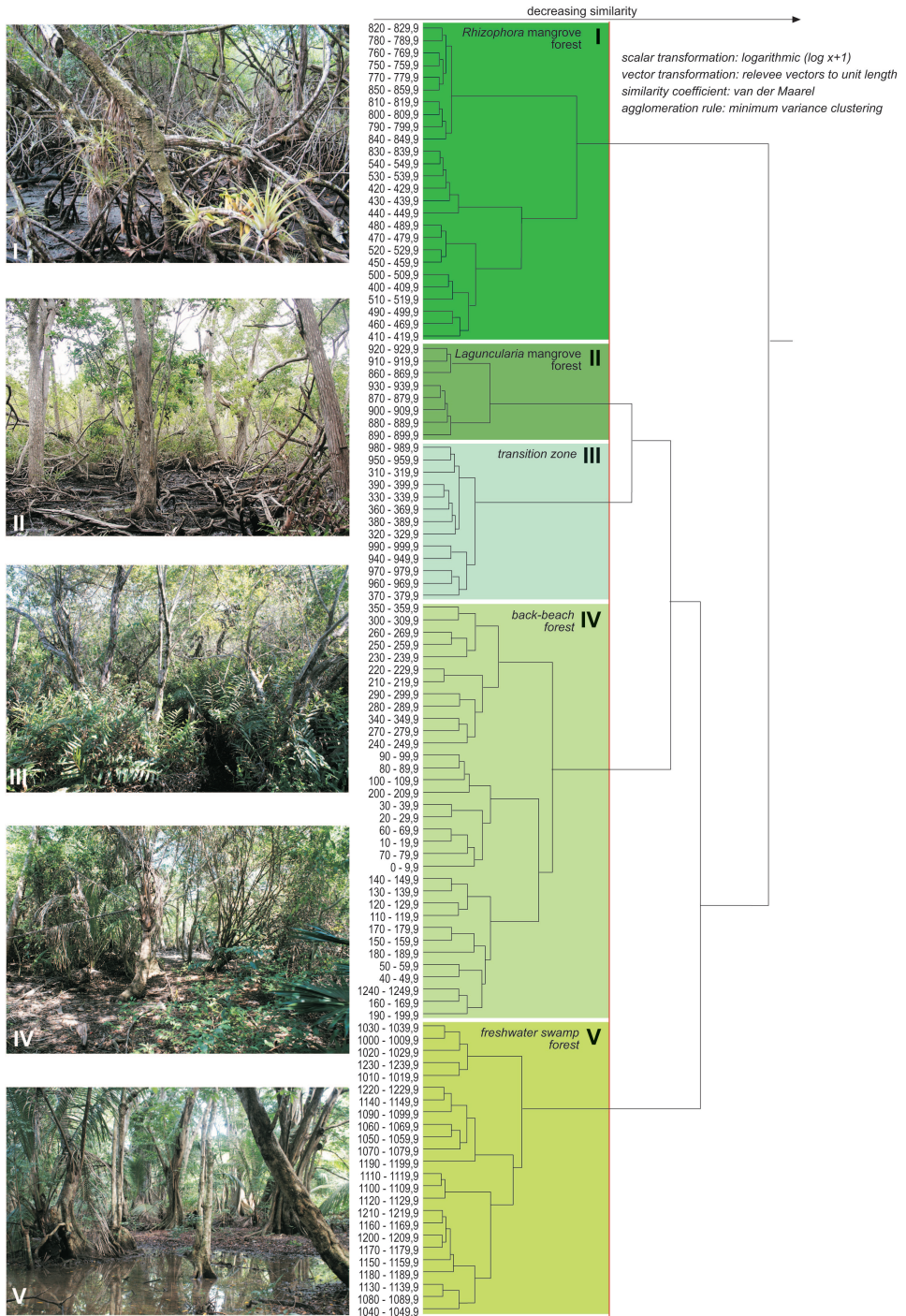


FIG. 3. Classification of 10-m sample segments; the photographs show characteristic aspects of the respective sample groups.

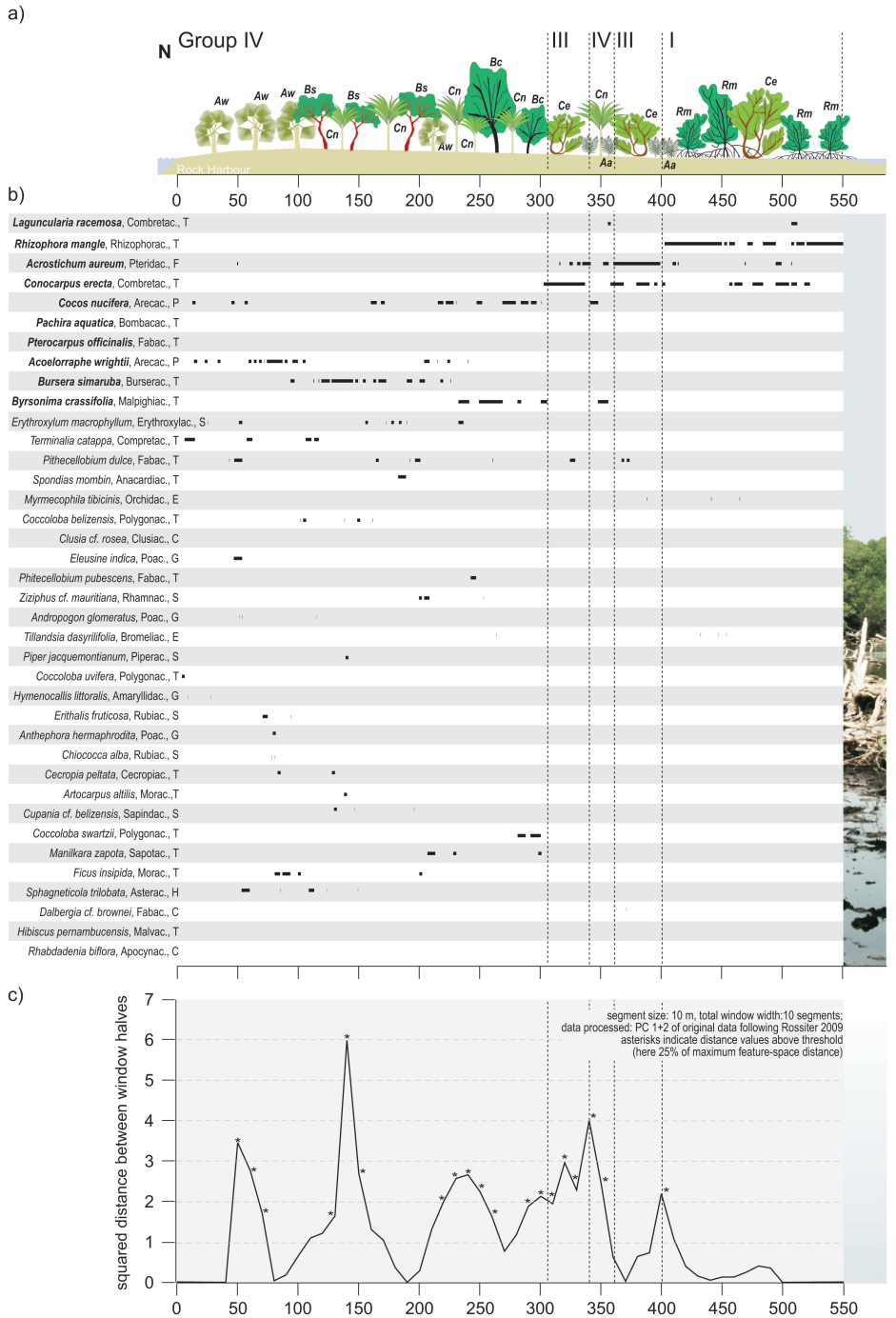
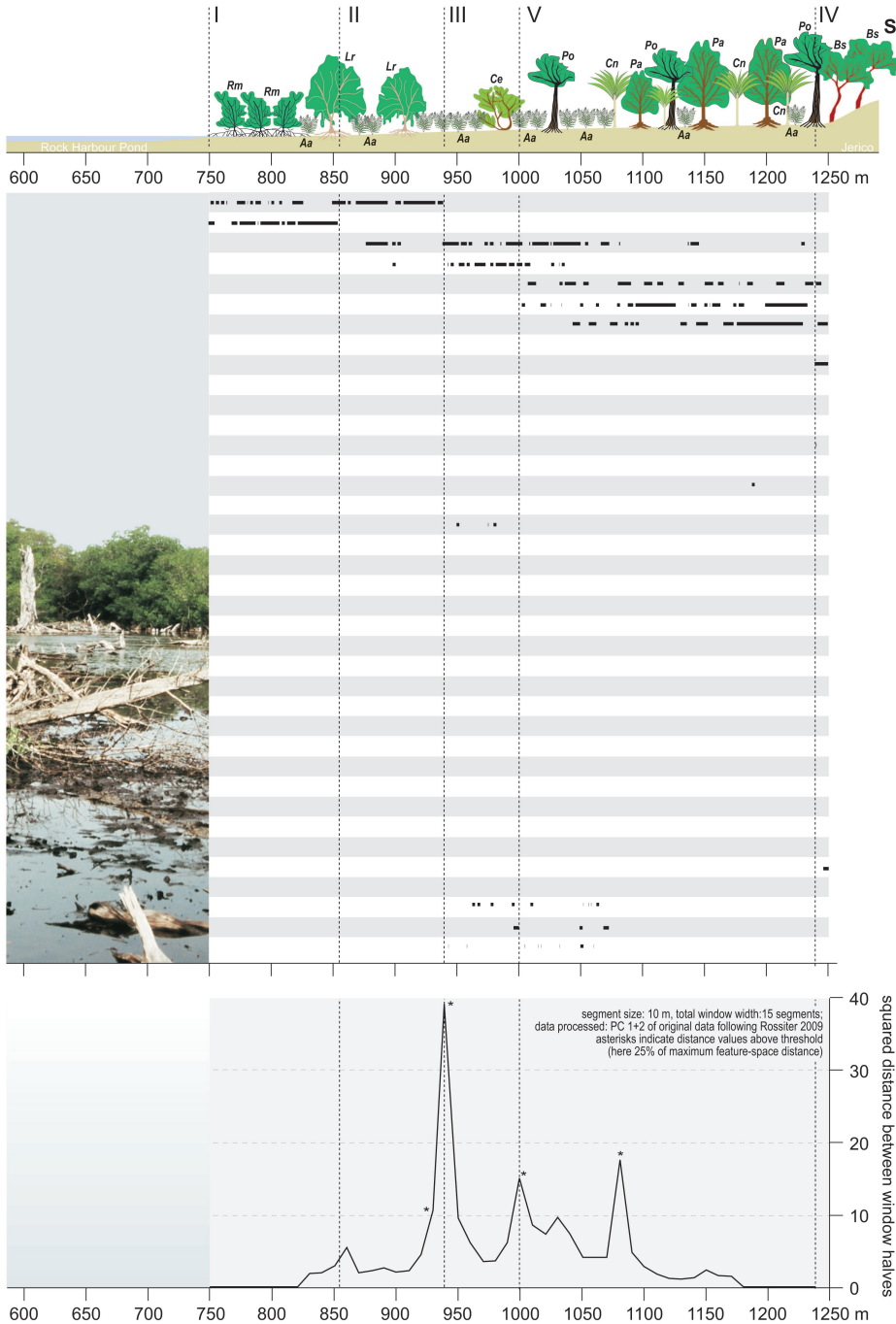
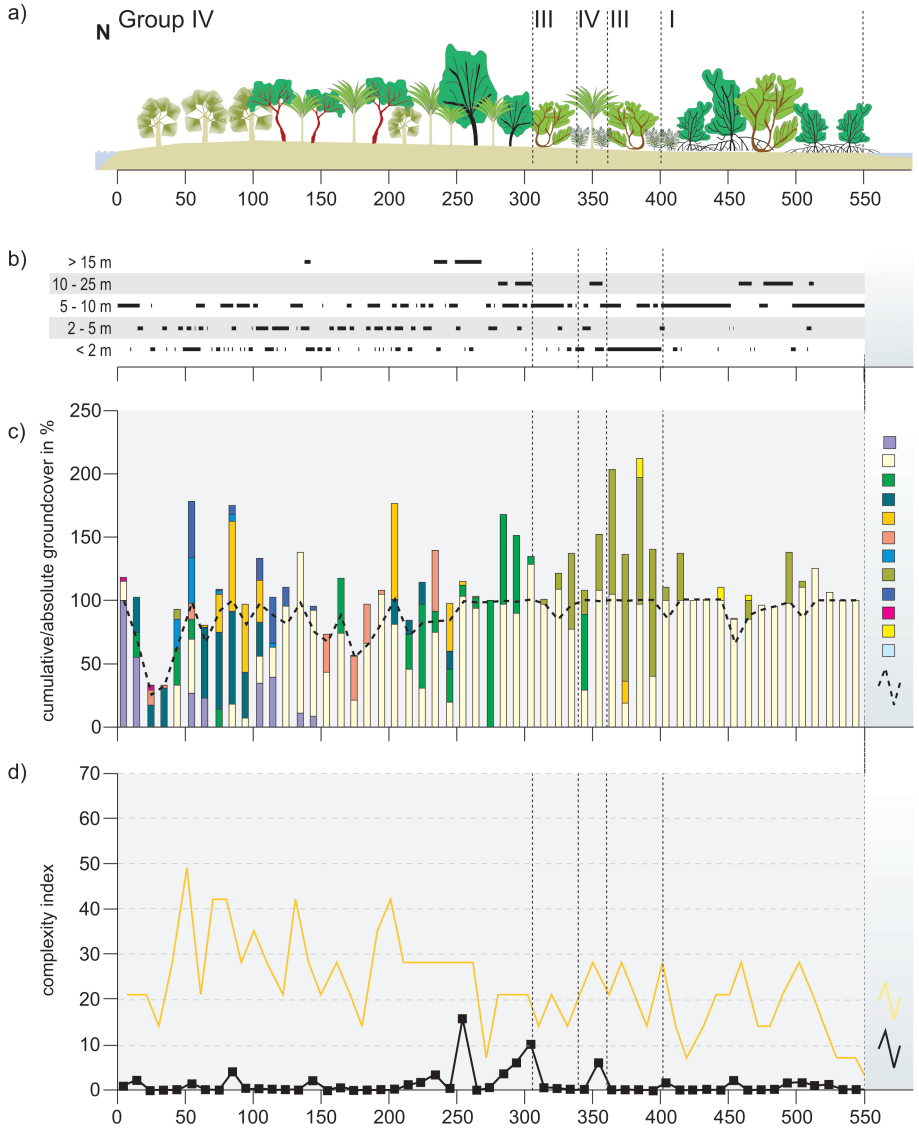


FIG. 4. (a) profile, (b) species list with life-form assignment (C = climbers/vines, E = epiphytes, F = ferns, G = graminoids, H = herbs, P = palms, S = shrubs, T = trees) and distribution of species along the transect studied; important taxa are shown with initials in (a) and are printed in bold in (b); (c) the results of a split



moving window distance analysis; note the different scale and analysis characteristics to the north and south of Rock Harbour Pond.



## RESULTS

A total of 38 species belonging to 26 different plant families was encountered along the transect. The Fabaceae are represented by 4 species in 3 genera, the Combretaceae, Poaceae, and Polygonaceae families by three species each, none belonging to the same genus. Nineteen families occur with just one species each. About half of the species belong to the life-form “tree” (meso- and macrophanerophytes). At parti-

cular sites fern and palms prevail. All other life-forms are not well represented. While many minor associates tend to occur patchily along the transect, several common taxa exhibit a distinct distribution pattern, as presented below.

*Floristic zonation.* The cluster analysis of the transect segments in Fig. 3 reveals five discrete groups, indicating a distinct zonation pattern. The calculated level of dissimilarity between the groups is indicated



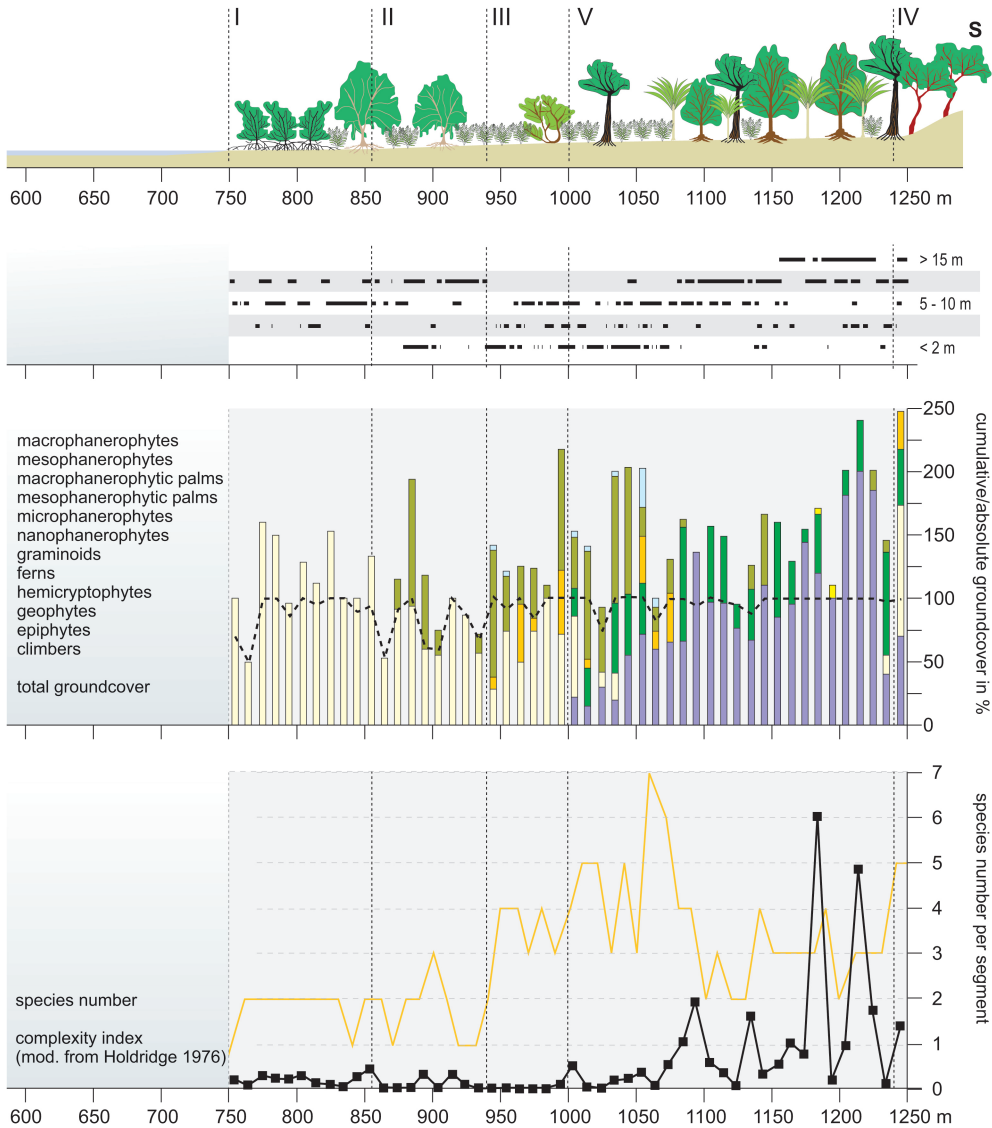


FIG. 5. (a) profile, (b) stratification, (c) life-form composition, (d) species number and complexity index per segment.

by the linkages connecting the cluster. The photographs on the left side of the classification in Fig. 3 are representative of the assigned groups, while their distribution along the transect and species composition are visible in Fig. 4. Due to the slightly bowl-shaped topography the zonation is twofold, with a more or less symmetrical arrangement of different forest belts to the north and south of Rock Harbour

Pond. This brackish inland water body is surrounded by forests dominated by *Rhizophora mangle* (group I, Fig. 4). *Conocarpus erecta* and *Laguncularia racemosa* are minor associates on the southern and northern side respectively. These forests comprise mesophanerophytic trees with the mangrove fern (*Acrostichum aureum*) being the only non-arboreal understory plant present, primarily in canopy gaps (Fig. 5). The

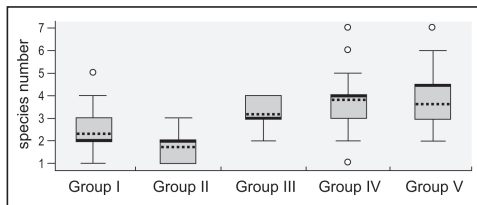


FIG. 6. Boxplots of species numbers in the different forest types encountered along the transect. Diagrams show median (solid line), mean (dashed line), the middle half of the sample (= interquartile range IQR between the 25% and 75% percentile, i.e. box), whiskers (which extend to lowest and highest values inside a "reasonable" [ $< 1.5$  IQR] distance from the end of the box), and outliers (between 1.5 IQR and 3 IQR from the end of the box).

epiphytic flora includes *Tillandsia dasyrifolia* (Bromeliaceae) and *Myrmecophila tibicinis* (Orchidaceae). This group is floristically most different from all other sample groups. Restricted to the south of Rock Harbour Pond, *Laguncularia racemosa* forms its own distinct belt (group II), associated again with *Acrostichum aureum* and *Conocarpus erecta* as exclusive associates, but *Rhizophora mangle* is entirely lacking. Segments assigned to group III are again found on both sides of Rock Harbour Pond. This group is dominated by *Acrostichum aureum* and *Conocarpus erecta*, while the true mangrove taxa *Rhizophora mangle* and *Laguncularia racemosa* are missing. Thus group III can be regarded as transitional to the adjacent non-mangrove forest communities, the back-beach forest on the one hand (group IV) and the freshwater swamp forest on the other (group V). The latter is dominated by *Pterocarpus officinalis*, *Pachira aquatica*, and *Cocos nucifera*, while locally *Acrostichum aureum* forms a dense understory. The most diverse (both floristically and structurally, see below) forest type encountered along the transect is the back-beach forest (group IV), best developed on dry sandy coralline soils. Common tree species are *Bursera simaruba* and *Byrsonima crassifolia*, as well as the palms *Cocos nucifera* and *Acoelorrhaphe wrightii*.

**Vegetation structure.** In general, the canopy of the different forest types reaches heights between 8 and 15 m, occasionally overtopped by tall individuals of *Byrsonima crassifolia* or *Pterocarpus officinalis* (Fig. 5). More obvious than changes in growth height, however, are variations in the degree and complexity of

stratification between the different forest types. The true mangrove forests (groups I and II), dominated by medium-sized *Rhizophora*- and *Laguncularia*-trees are characterized over wide areas by just one stratum at any given place, i.e. there is rarely a joint occurrence of plants belonging to different height classes. Locally, *Acrostichum aureum* patches provide an understory layer, which however is much more pronounced in the transitional forests of group III.

Stratification of the swamp forest (group V) and the back-beach forest (group IV) is spatially much more heterogeneous and multi-layered (Fig. 5). The former formation, with tree individuals reaching heights of 20 m and more, are structurally dominated by macrophanerophytic trees and palms, two life-forms entirely absent within the mangroves and their transitional borders (group I to III). The high floristic heterogeneity within group IV is reflected in the vegetation structure, with many co-occurring species belonging to several different functional types (Fig. 5).

**Diversity patterns.** The distinct plant associations (i.e. groups) do not only differ in species composition and vegetation structure but also in particular diversity patterns. Regarding species richness (Fig. 6), a total of six different species was encountered within the *Rhizophora mangle*-dominated mangroves (group I), with the maximum species richness in an outlier segment ( $S_{\max}$ ) being five, the median of species per segment ( $S_{\text{med}}$ ) being just two. The *Laguncularia*-dominated mangrove community of group II is the least diverse along the transect ( $S_{\max}$ : 3,  $S_{\text{med}}$ : 2). The transitional character of group III is affirmed by its higher species richness, with a total of 10 taxa present within the whole community and a slightly increased species diversity per segment ( $S_{\max}$ : 4,  $S_{\text{med}}$ : 3). With just nine different species encountered in the freshwater swamp forests (group V), the total species number is again slightly lower, but significantly higher than in the mangrove forest. While floristically still rather species-poor, this forest type possesses a higher number of co-occurring species per segment ( $S_{\text{med}}$ : 4.5,  $S_{\max}$ : 7) than the previous types. In contrast, the back-beach forest (group IV) is floristically quite heterogeneous, with a total of 28 species encountered ( $S_{\max}$ : 7,  $S_{\text{med}}$ : 4).

Regarding the diversity measure of evenness in Fig. 7, there is a great deal of variance within and between forest types. The median of evenness values in all groups is high ( $> 0.75$ ), but wide within-group variations become obvious within the true mangrove

forests: particularly in group II, monodominant stretches (see also Fig. 5d) create evenness values of 0 and thus cause the lower quartile threshold to reach a value of zero. In contrast, within the terrestrial and freshwater swamp forests (groups IV and V) several co-occurring taxa with significant ground cover result in a high median as well as a high lower quartile threshold evenness value, and also a much lower within-group variance.

Relative dominance, density, and frequency, as well as the derived Importance Value Index for the tree species within the sample groups are given in Table 1. *Conocarpus erecta* is the only species occurring in all sample groups but is of highest importance in group III. All other taxa show a restricted distribution in one or in only a few sample groups.

*Edaphic parameters.* In Fig. 8, the results for the soil chemical properties analyzed at 43 locations, as well as the grain size spectra including organic matter content taken at ten locations along the transect are given. Salinity stays well below mean sea strength in all places, with highest values being found in the

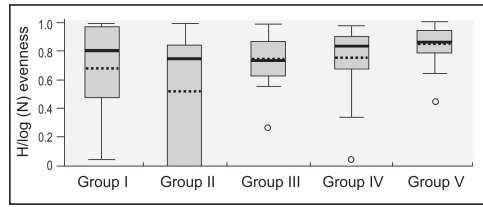
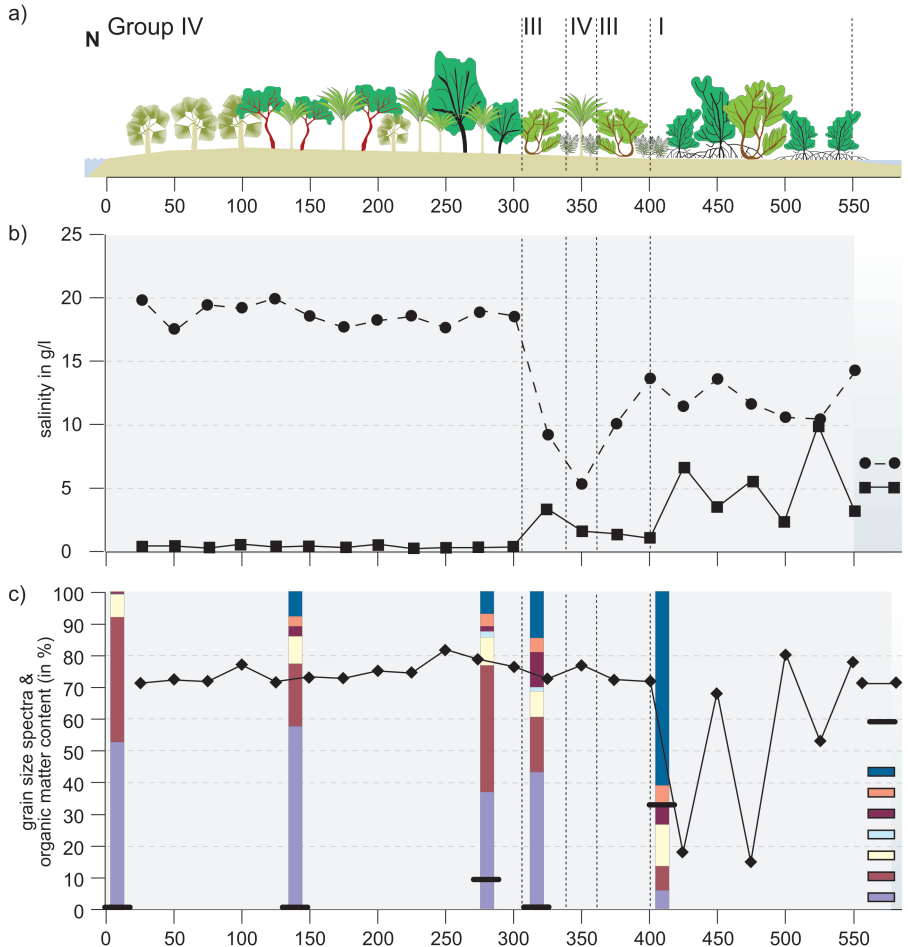


FIG. 7. Boxplots of evenness values of the different forest types encountered along the transect. Diagrams show median (solid line), mean (dashed line), the middle half of the sample (= interquartile range IQR between the 25% and 75% percentile, i.e. box), whiskers (which extend to lowest and highest values inside a "reasonable" [ $< 1.5$  IQR] distance from the end of the box), and outliers (between 1.5 IQR and 3 IQR from the end of the box)

middle of the transect in the vicinity of Rock Harbour Pond. The pH values indicate near-neutral to slightly acidic conditions, with the exception of the first 300 m of the transect (group IV) where slightly

TABLE 1. Structural characteristics of all tree species encountered along the transect.

	<i>Accolarraphie wrightii</i>	<i>Artocarpus altilis</i>	<i>Byrsonima crassifolia</i>	<i>Bursera simaruba</i>	<i>Cecropia peletata</i>	<i>Coccoloba belizensis</i>	<i>Coccoloba swartzii</i>	<i>Coccoloba uvifera</i>	<i>Cocos nucifera</i>	<i>Conocarpus erecta</i>	<i>Ficus insipida</i>	<i>Hibiscus pernambucensis</i>	<i>Laguncularia racemosa</i>	<i>Manilkara zapota</i>	<i>Pachira aquatica</i>	<i>Pithecellobium dulce</i>	<i>Pithecellobium pubescens</i>	<i>Pterocarpus officinalis</i>	<i>Rhizophora mangle</i>	<i>Spondias mombin</i>	<i>Terminalia catappa</i>	sum of tree species
<b>Rel. Dominance</b>																						
group 1										20.47			37.10						42.43			3
group 2										0.01			99.99									2
group 3										94.94		2.34				2.72						3
group 4	3.41	10.09	46.15	5.05	1.74	0.21	3.11	0.21	13.17	1.63	3.99		1.99	1.75		1.02	0.02			0.66	5.79	17
group 5									5.55	0.82		0.03		24.79			68.82					5
<b>Rel. Density</b>																						
group 1										10.26			33.33						56.41			3
group 2										7.14			92.86									2
group 3										88.46		7.69				3.85						3
group 4	15.66	1.20	6.02	15.66	2.41	3.61	2.41	1.20	22.89	2.41	7.23		1.20	3.61		6.02	1.20			1.20	6.02	17
group 5									22.67	6.67		2.67		44.00			24.00					5
<b>Rel. Frequency</b>																						
group 1										18.18			27.27						54.55			3
group 2										11.11			88.89									2
group 3										80.00		13.33				6.67						3
group 4	11.94	1.49	7.46	13.43	2.99	2.99	2.99	1.49	20.90	2.99	7.46		1.49	4.48		7.46	1.49			1.49	7.46	17
group 5									23.08	5.77		3.85		40.38			26.92					5
<b>Import. Value</b>																						
group 1										48.91			97.70						153.38			3
group 2										18.26			281.74									2
group 3										263.40		23.36				13.24						3
group 4	31.01	12.79	59.64	34.15	7.13	6.81	8.51	2.91	56.96	7.03	18.68		4.69	9.85		14.50	2.71			3.36	19.28	17
group 5									51.30	13.25		6.54		109.17			119.74					5



alkaline values were measured in coralline sand (Fig. 8b). The redox potential given in Fig. 8c remains relatively stable and positive around +300 mV for the first 400 m, but fluctuates heavily further inland, the negative values indicating waterlogged soils and oxygen deficiency. The grain size spectra reflect the alteration in topographic conditions and proximity to the sea, with a high percentage of the sandy grain sizes in the back-beach forests and a significantly higher proportion of finer grain sizes in all interior swamp forest types. Here, the considerably higher organic matter content indicates a slower decomposition rate, while low organic matter content in the back-beach forest soils might occur because of shorter nutrient cycles, with rapid decomposition of the dead biomass and leaf litter.

## DISCUSSION

**Floristic zonation.** The existence of floristic zonation within swamp and coastal forests has been controversially discussed. For old world mangroves at different locations, Bunt (1996), Bunt & Stieglitz (1999), Ellison *et al.* (2000) or Ellison (2002) showed that species distribution is highly variable and basically unpredictable. However, studies by Smith (1992), Matthijs *et al.* (1999), and Sherman *et al.* (2000) show clear zonation, and at least in the species-poor Western mangroves zonal patterns are apparently rather common (see e.g. Watson 1928, Lugo & Snedaker 1974, Snedaker 1982, Smith 1992, Duke *et al.* 1998, Ball & Sobrado 1999, and Sherman *et al.* 2000). Our classification in Fig. 3 confirms this,

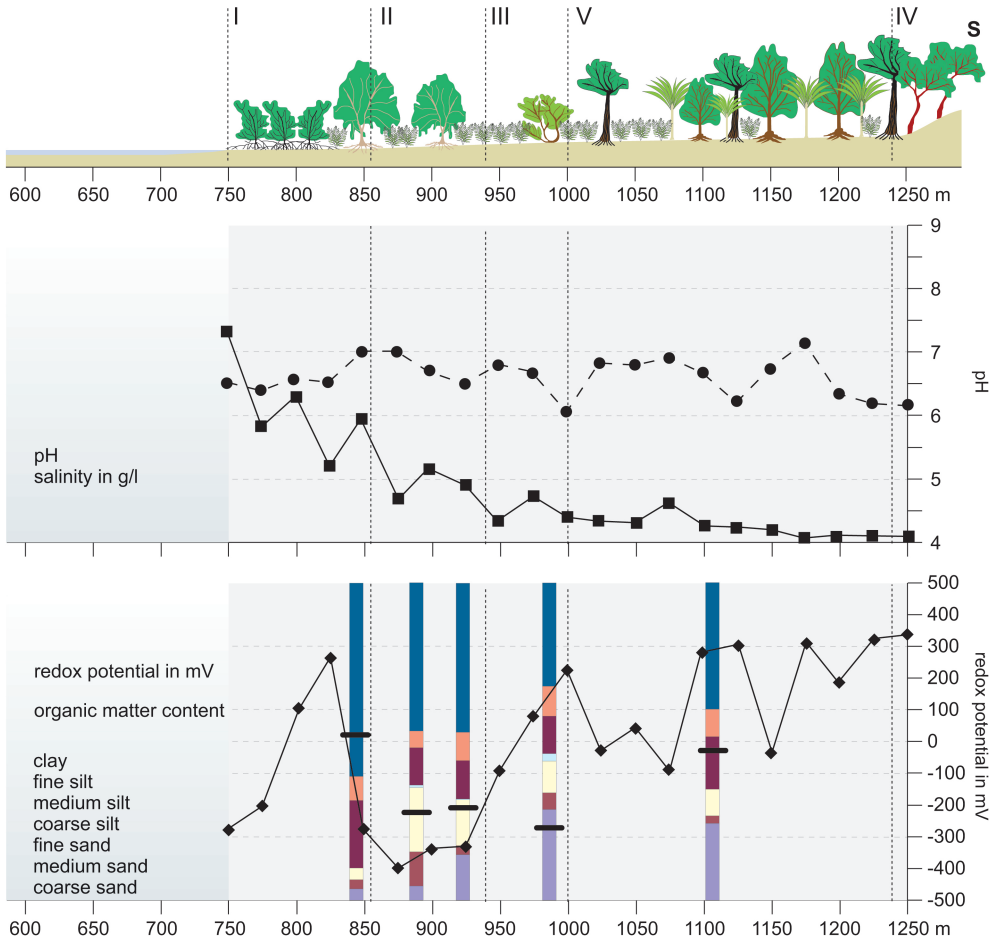


FIG. 8. (a) profile, (b & c) variation in soil chemical properties ( $n = 43$ ), (c) grain size spectra and organic matter content of soil samples ( $n = 10$ ).

even if the banded Caribbean shoreline zonation from true mangroves through swamp forest to terrestrial forests is modified by the topographic situation on Utila.

The creation of discrete groups in ecological data, as by agglomerative cluster analyses, is a well-established and helpful indirect method of detecting zonation patterns. Nevertheless, these methods focus on the internal composition and structure of the clustered groups and on the characteristics of the dissimilarities between species, samples, and the created sample groups. Underlying explanatory variables, as well as the significance and depth of detected

discontinuities in the data, remain hidden (see also Choesin & Boerner 2002). The application of ordinations and SMWDA proved to be useful for the exploration of these features and will be discussed next.

Within the flat interior of Utila, gradual or sudden changes of physiochemical soil properties correlate well with species distribution. A canonical correspondence analysis in Fig. 9 shows a high eigenvalue of 0.718 for the 1st axis and of 0.413 for the 2nd axis. The variance in the species-environment relationship explained by the strongest environmental factors salinity and pH value accounts for 86% of

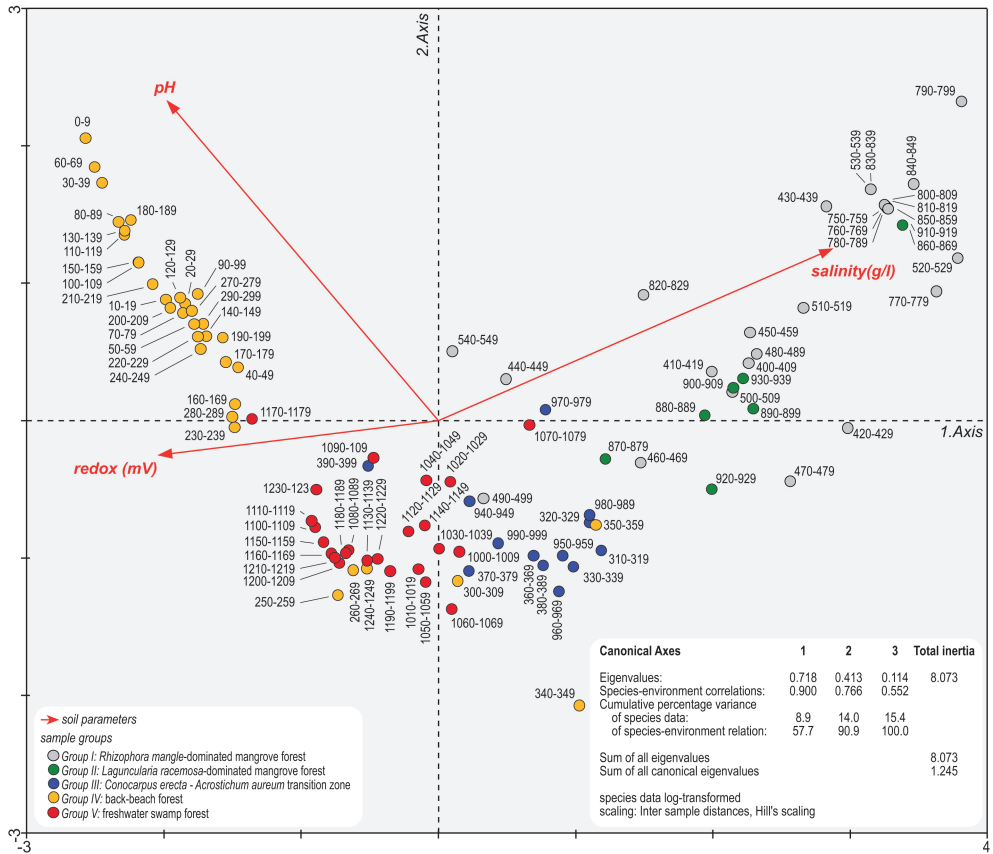


FIG. 9. CCA graph of axes 1 and 2, showing all active and passive 10-m sample segments (color coded according to the classification groups in Fig. 3), environmental variables, and statistics; segment labels exclude decimal places for space-saving reasons (e.g. segment “0–9.9 m” is labeled “0–9” in ordination).

the total variance of the three variables included (Monte Carlo test lambda-A values of 0.67,  $P = 0.03$  for salinity and 0.41,  $P = 0.1$  under reduced model for pH value).

The 1st axis of the CCA show the highest correlation with salinity, whereas the 2nd axis is mainly correlated with pH value. The “true” mangrove forests of groups I & II in Fig. 9 are located in the upper right quadrant of the ordination space under high salinity and near neutral pH values, as dissolved salts like  $\text{Na}^+$  and  $\text{Mg}^{2+}$  have a high buffering potential (see Hseu & Chen 2000) and prevent acidification. *Rhizophora mangle*, considered a facultative halophyte, dominates group I around Rock Harbour Pond and shows the highest response to the (modest)

maximum salinity values in the GAM models of Fig. 10. Due to its ability to aerate by prop roots overtopping even the highest water levels (Gill & Tomlinson 1972), *Rhizophora* is highly competitive in areas with long inundation periods and low nutrient availability. *Laguncularia racemosa* (group II) is also quite salt-tolerant, but in contrast to *Rhizophora* is a shade-intolerant species with a fast growth rate and low competitiveness (Sousa *et al.* 2003, Piou *et al.* 2006). It depends on ground-level pneumatophores for aeration and therefore relies on shortened inundation times. Thus highest dominances are achieved on slightly elevated terrain patches along the undulating topography of the transect. This indistinct separation is documented by the superimposed

group colors in Fig. 9, revealing the weak group separation by quite similar sample scores for some segments of groups I and II, indicating low species turnover. The SMWDA in Fig. 4c also produces no significant distance between groups I and II because of the non-linear floristic distribution of the dominant species. The boundary between groups I and II detected by the classification is therefore rather indistinct.

In contrast, the segments of the ecotonal sequence of group III from mangrove forests to terrestrial forest types are positioned in the lower right quadrant, near the origin of the diagram, indicating intermediate conditions along the environmental gradients processed (see Fig. 9). *Conocarpus erecta*, with the highest IVI of group III tree species (see Table 1), is considered a mangrove ally rather than a mangrove species *sensu strictu* (Tomlinson 1986), illustrating this by its shallow unimodal response regarding salinity and redox potential in Fig. 10. As elsewhere within vital mangrove forests of the Greater Caribbean, *Acrostichum aureum* is a major associate. This shade-tolerant and edaphically undemanding fern develops best under full light conditions (see Medina *et al.* 1990), and along our transect it shows high abundance on sites where canopy gaps occur (Figs. 4 and 5). The SMWDA in Fig. 4 gives considerable distances and thus sharp boundaries between the central mangrove groups and group III. To the north, the SMWDA reveals a broad ecotonal sequence towards the back-beach forests. Especially between 360 and 300 m, short segments of the

floristically quite different groups III and IV alternate and cause high distance values over the whole range.

Within the freshwater swamp forests (group V) salinity is further reduced (see Fig. 9 and response of *Pterocarpus officinalis* as species with highest IVI [Table 1] in Fig. 10). The soils show a high content of fine grain sizes (clay and silt), are rich in organic matter, and possess slightly higher pH values than the mangrove sites (see also Medina *et al.* 2007). The back-beach forests of group IV differ in many ways from the previous forest types. As they grow on coral debris, soil texture is dominated by sandy grain sizes and the pH values ( $\text{pH}_{\text{mean}} = 7.5$ ) are significantly higher than the mean values in groups 1, 3, and 5. In addition, the coarser grain sizes and slightly higher terrain account for the continuously high redox-potential values (see Fig. 8).

Soil salinity and organic matter content, by contrast, are lower, indicating the lack of inundation by seawater on the one hand and a short nutrient cycle with rapid decomposition of the dead biomass and leaf litter on the other. Due to sudden changes in the dominance ratios of co-occurring species, sharp intrazonal boundaries (like those at 140 m or 1080 m) might be detected within the apparently homogeneous non-mangrove forest groups by the SMWDA in Fig. 4c.

In accordance with the findings discussed above, zonation patterns in the coastal forests of Utila are verifiable, but the intrazonal variety in species composition might exceed the interzonal one, at least in our transect study. Furthermore, the zonal edges

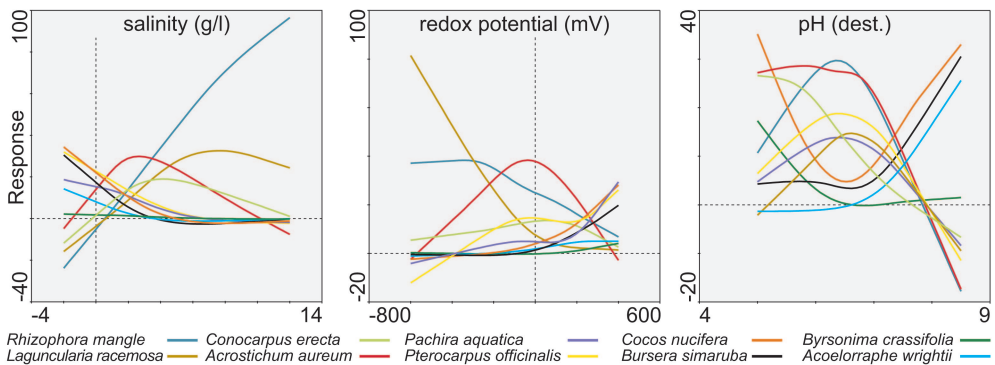


FIG. 10. Species response curves (GAM model) along the first species axis. Shown are the responses of important tree species and the mangrove fern (*Acrostichum aureum*) to the edaphic variables salinity, redox potential, and pH.

differ considerably in distinctiveness and depth, some even affecting the whole zone and creating a broad ecotonal sequence rather than a discrete vegetation unit. Several hypotheses exist to explain the floristic zonation patterns of coastal forests. Considering our available data, we find a combination of the following drivers applicable to the mangrove zonation on Utila: (1) zonation patterns as a consequence of topography and geomorphologic variation (see also Thom 1967, Woodroffe 1982); (2) zonation as a consequence of physiochemical gradients (see also Watson 1928, McKee 1993); (3) zonation as a consequence of competition between mangrove species (see also Ball 1980).

*Vegetation structure.* The different forest types identified along the transect are characterized by particular structural features such as canopy height, stratification, and life-form composition (Fig. 5). Forest structure in general is controlled by many different factors, depending on forest type, location, stand age, edaphic variables, or on type, frequency, and intensity of disturbances.

The *Rhizophora mangle* stands along the transect show rather uniform canopy heights of roughly 8 m. These could indicate more or less constant underlying unfavourable site conditions. But, as the measured edaphic variables are well within the common range for the mangrove taxa present (see Lacerda *et al.* 2002, Saenger 2002), strong edaphic stress commonly triggering growth performance (Lin & Sternberg 1992, Koch 1997, Feller *et al.* 1999, 2003) does not seem to control vegetation structure here. Rather, the uniform canopy height here simply reflects uniform age structures, which commonly are the result of earlier large-scale disturbances with subsequent auto-succession processes. The frequent hurricanes (and associated high wind and/or wave action, flooding, and input of terrestrial sediments) are known to be important drivers controlling the structure of Caribbean ecosystems in general and of coastal and swamp forests in particular (see Lugo 1980, 2008, Roth 1992, Smith *et al.* 1994). According to Roth (1992), the periodic destruction of Caribbean mangrove forests by cyclonic storms might be responsible for their low structural complexity. The observed even-aged growth pattern within the mangroves on Utila might be a result of hurricane Fifi, which hit Utila in September 1974 as a category 2 hurricane and caused great devastation to infrastructure. Al-

though there is no information available about the destruction of the forests on the island, the height and uniform structure of the *Rhizophora* stands sampled fit the pattern of a late auto-successional stage following a major disturbance (Lugo 1980, Roth 1992). *Rhizophora mangle* is highly susceptible to wind damage, and large older trees regularly do not survive major storms (Imbert *et al.* 1996, Vanse-low *et al.* 2007). However, high propagule production coinciding with the hurricane season in the Caribbean seems able to compensate for storm damage (Roth 1992), and mass establishment of propagules presumably accounts for the even-aged, even-structured *Rhizophora* forest present today. Several thick-stemmed, oblique-growing individuals of *Laguncularia racemosa* in group II support our assumption of a former storm impact.

*Diversity patterns.* As already stated, swamp forests and mangroves are rather simple and species-poor biocoenoses compared with other tropical ecosystems like rainforests or coral reefs. This is also reflected in a generally low complexity as expressed by the Complexity Index (CI) according to Holdrige (1967, see Fig. 5), and even holds true for the terrestrial back-beach forests. Only where tall-trunked, thick-stemmed tree individuals (*Byrsonima crassicaulis*, *Pterocarpus officinalis*) in comparatively species-rich segments occur, does the CI locally rise.

Nevertheless, the swamp forests are highly diverse ecological communities due to their multitude of structural and functional attributes (see e.g. Ricklefs & Latham 1993, Farnsworth & Ellison 1996, Ellison 2004, Mumby *et al.* 2004). Thus rather than by species numbers, diversity in these forests is expressed by the physiological and physiognomic adaptations to specific environmental conditions (e.g. by root types), by different structural characteristics such as stratification patterns, growth height and life-form composition (see above), or by changes in the equitability or dominance of species within these forests. The generally low yet slightly increasing species number from the true mangrove forest through the ecotonal *Conocarpus* stands to the freshwater swamp and terrestrial forests was addressed earlier (Figs. 5 & 6). More favorable site conditions potentially allow more non-specialized species to grow and co-occur.

*Prospect.* The tremendous value of coastal forests is recognized today and they are protected in many parts (Bliss-Guest & Rodriguez 1981). Nevertheless,



Caribbean mangroves are – as all over the world – in great danger from both direct and indirect anthropogenic impacts (Linden & Jernelov 1980, Ellison & Farnsworth 1996, Ellison 2004). The unique and ecologically invaluable forests on Utila are no exception. Predicted climate changes may cause local alterations in precipitation and temperature patterns and probably an increase in frequency and/or intensity of tropical storms (IPCC 2007). Subsequent changes in soil chemical properties resulting from altered duration of inundation, salinity or O<sub>2</sub> availability, as well as modified disturbance regimes, will result in fundamental shifts within existing forest types.

Due to the very flat and low-lying terrain on Utila, sea level rise may cause major changes in current species composition, vegetation structure, and functioning of the forest ecosystems. According to Doyle *et al.* (2003), mangrove habitats are expected to advance over the next century into higher terrain freshwater marshes and swamp forest. Even if there is controversy about the magnitude of sea level rise that mangrove forests can withstand – Ellison & Stoddart (1991) consider a sea level rise of >12 cm/100 cal years as a critical value, while Snedaker (1995) reports that the mangrove forests of southern Florida have survived a mean rate of sea level rise of 23 cm/100 cal years since 1925 – such shifts will definitely occur, or rather are already taking place.

Anthropogenic interference intensifies the pressure on mangroves and swamp forest ecosystems. These direct and indirect anthropogenic impacts are considered to surpass the influence of natural disturbances on the structure and species composition of mangroves (Ong 1995). The actions may vary from low impact practices to the point of complete conversion; while small-scale wood extraction rarely causes major impacts, pollution by industries, human settlements, and oil spills, as well as realty and expansions within the tourism sector, clearly do. On Utila, the latter two are of particular concern. Of course climate-change-related aspects are phenomena extending over the globe and are hard to overcome by the local communities. However, governmental guidance concerning tourist developments on the island is a feasible and necessary action to avoid uncontrolled coastal development, deforestation, and disruption of hydrological cycles, and to conserve the precious ecosystem services provided by the swamp forests of the island.

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