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Testing patterns of zonation in mangroves: scale dependence and environmental correlates in the Sundarbans of Bangladesh

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Summary

1 Associations between abiotic variables and patterns of species distribution and abundance are a major preoccupation of community ecologists. In many habitats, this association is manifest in discrete zones of vegetation.

2 We used statistical methods to examine tree species distribution patterns in relatively undisturbed regions of the Sundarbans of Bangladesh. We tested the hypothesis that mangroves occur in discrete zones with respect to elevation. These data were gathered with explicit attention to local and regional differences in edaphic characteristics so that species-environment relationships could be analysed at several spatial scales.

3 Correlations were also assessed between mangrove species composition and edaphic variables that co-vary with elevation, i.e. salinity, field capacity, cation exchange capacity, percentage silt, and mangrove physiognomic category (slope, basin, levee and flat).

4 Quantitative statistical analysis using randomization techniques failed to detect species zonation along any of 33 individual 200-m transects, within 1-km^2 blocks, or within 1200-km^2 regions.

5 Canonical correspondence analysis relating edaphic variables to species distributions accounted for a total of only 24% of the variance in species composition.

6 Our data suggest that the absence of zonation in the Bangladesh Sundarbans reflects the underlying biology of the system and is not an artefact of long-term human disturbance.

Key-words: Bangladesh, canonical correspondence analysis, *Excoecaria agallocha*, *Heritiera fomes*, management, mangroves, randomization tests, salinity, Sundarbans, zonation

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Introduction

Identifying patterns of species distribution and abundance and determining the mechanisms underlying these patterns have been, and continue to be, major preoccupations of community ecologists (e.g. Connell 1961; Pielou 1977; Bertness & Ellison 1987). It has been asserted repeatedly that the halophytic trees and shrubs of tropical coastal forests (typically mangroves) exhibit pronounced zonation of species (e.g. Watson 1928; Chapman 1944, 1976; Macnae 1968; Snedaker 1982). Strong zonation – defined as the ordering of species, or groups of species, at a given location (after Chapman 1979) with respect to elevation being predictable, with the lower limit of one species (or group of species) marking the upper limit of a second – is rarely met in the field. Instead, vegetation composition usually shows some overlap between zones (Whittaker 1967).

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Zonation in mangrove forests often has been attributed to the responses of individual species to variation in degree of tidal inundation, salinity or other measurable edaphic gradients that vary predictably across the intertidal (reviewed by Snedaker 1982; Smith 1992), although it may be at least partially determined by biotic factors (e.g. Ball 1980; Smith 1987). Quantification or statistical testing of mangrove zonation patterns (which are usually presented as vegetation profile diagrams) is rare, despite the availability of statistical tests for zonation (reviewed in Dale 1999). Bunt and colleagues (Bunt *et al.* 1991; Bunt 1996, 1999; Bunt & Bunt 1999; Bunt & Stieglitz 1999) have failed however to detect clear-cut zonation of mangrove distribution patterns in any of their quantitative studies of 17 riverine estuaries in eastern and northern Australia and along 60 transects in 953 sites on Hinchinbrook Island, north-eastern Australia. The patterns, and processes controlling, distribution of mangrove species may warrant careful reconsideration, as suggested by Duke *et al.* (1998). However a method for hypothesis testing, which is needed to analyse Bunt's measures of species overlap and zonation has not been presented. Here, we assess statistically the distribution patterns across the intertidal zone in the Sundarbans, the largest mangrove forest in the world, and develop an explicit, quantitative method to test the hypothesis that mangrove species are zoned.

The Sundarbans mangrove forest covers *c.* 10 000 km^2 in the Ganges Delta of India and Bangladesh (Chaudhuri & Choudhury 1994; Hussain & Acharya 1994). Despite its relatively high species richness (for mangrove forests) and considerable historical interest in its forest resources, most of the few data that exist on its physical environment, species composition, or possible relationships between them, concern areas of active management (as opposed to stands that have been impacted minimally), cover relatively small spatial scales, and are difficult to obtain outside India or Bangladesh. Recent uses of remote-sensing technology have increased our understanding of forest structure (Khan *et al.* 1990; Choudhury *et al.* 1994) and response to flooding (Blasco *et al.* 1992) of the Sundarbans mangroves, but ground-level studies are required for interpretation of relationships between stand structure and edaphic variables. Here, we present an analysis of the distribution of mangrove species with respect to elevation, salinity, soil physico-chemical characteristics and topography at 11 stations distributed evenly across *c.* 3600 km^2 of the Sundarbans of Bangladesh.

We collected data with explicit attention to local, landscape- and regional-level differences in elevation and edaphic characteristics, and consequently analysed species-environment relationships at several spatial scales. Distribution and abundance of mangroves and associated faunal species are affected by physical and biotic parameters that operate on varying spatial scales (reviewed by Farnsworth 1998; see also Farnsworth & Ellison 1996). For example, landscape-scale geomorphological processes are known to regulate the extent and structure of mangrove forests (Thom 1967, 1982) and these factors may mask the local importance of spatial or temporal variation in salinity by limiting distribution or abundance of individual species (e.g. Ball 1980, 1988a,b; Ball & Pidsley 1995). Such large-scale geomorphological processes may lead to the occurrence of species at different locations being predictable within a large geographical region, but they may also alter local factors and thereby reduce the predictability of species composition at a single study site (local or landscape scale). Our study takes advantage of the large size of the Sundarbans forest to investigate interactions between large- and small-scale factors that could control mangrove community structure.

Materials and methods

STUDY SITE

A complete description of the study site (location shown in Fig. 1), including its vegetation and underlying edaphic parameters (summarized in Fig. 2) was presented by Karim (1988, 1994), and only salient details are presented here. The Sundarbans mangrove forest lies within the Gangetic delta on the northern coast of the Bay of Bengal (Fig. 1). This delta is bounded on the west (in India) by the Hooghly River and on the east (in Bangladesh) by the Meghna River. The delta is created by continual deposition of weathered, sorted sediments carried by the Ganges, Brahmaputra and Meghna Rivers (Bagchi 1944). It is characterized by a complex network of branching and meandering distributaries and rivers varying from a few meters to several kilometers in width, and a collection of low-lying, shifting islands. The mangrove forest occurs on a geologically recent part of the delta (the Bengal basin), which is underlain by quaternary sediments deposited by the three aforementioned rivers (Morgan & MacIntire 1959). Subsidence of the Bengal basin is not uniform across the delta. Because of tectonic activity and uneven rates of sediment deposition, the eastern portion of the delta is subsiding more rapidly than the western side, resulting in an apparent west-to-east downward tilt of the Sundarbans (Deb 1956). At present, the Hooghly and Megna Rivers are the only perennial sources of freshwater that directly feed the Sundarbans mangrove forest, whereas the other rivers indicated in Fig. 1 are tidal (brackish) inlets of the Bay of Bengal. The drainage pattern has shifted eastward along with the west-to-east tilt of the Sundarbans,

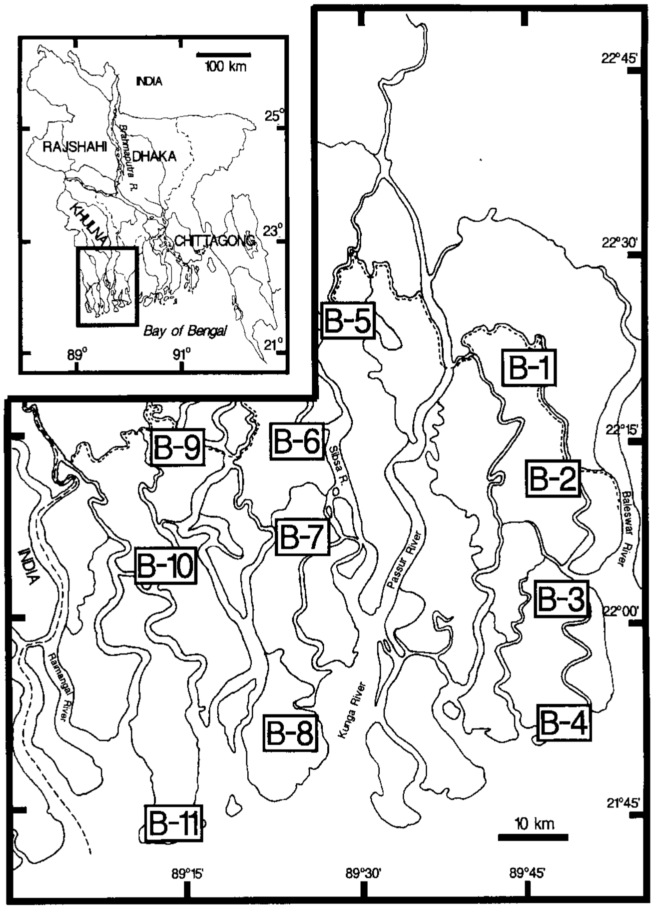

Fig. 1 Study sites in the Sundarbans of Bangladesh. Centres of boxed labels indicate locations of sampled blocks. Dotted line indicates the limit of the Sundarbans core forest area.

resulting in a substantial reduction in freshwater flow into the western side of the Sundarbans, and a natural west-to-east salinity gradient across the delta (Fig. 2).

Bangladesh (including the Sundarbans) has a tropical monsoonal climate, with average annual rainfall of 1800 mm, average annual maximum temperature of 30 °C, and average annual minimum temperature of 21 °C (Karim 1988). Tidal amplitude throughout the Sundarbans is 3–4 m.

STUDY SPECIES

The principal mangrove tree species encountered in this study are listed in Table 1 (nomenclature follows Tomlinson 1986). The Sundarbans itself is named for *Heritiera fomes* (known locally as sundri), an endemic that is the historical dominant of the forest. However, a combination of centuries of over-harvesting and the eastward movement of the Ganges that has reduced freshwater flow into the western section of the Sundarbans is thought to have led to the near-total extinction of *Heritiera* from its Indian sector (Mukherjee 1992).

SAMPLING

Vegetation, soil, and water sampling were conducted between 1983 and 1985 using a stratified random sampling design within 11 blocks, each *c.* 1 km^2, located between latitudes 21°30′ and 22°30′ N and longitudes 89°00′ and 89°55′ E (*c.* 3600 km^2). The entire forest was stratified by three roughly equidistant north–south lines and four roughly equidistant east–west lines, and the blocks were located at their intersections (Fig. 1). Sampled blocks had little or no recent history of logging (Karim 1988). Within each block, three 200-m transects were selected for sampling. Transects were spaced randomly along the shore, and extended from the shore inland and upwards through the intertidal and into the back mangrove. Vegetation, elevation, soil properties and elevation (m a.s.l.) were measured in 20 adjacent 10 × 10 m quadrats along each transect.

Density, frequency and basal area were measured within each quadrat for all woody species encountered. These data were used to calculate species richness (*S*, total number of species present), Shannon-Weiner diversity (*H*′), Shannon-Weiner evenness (*J*

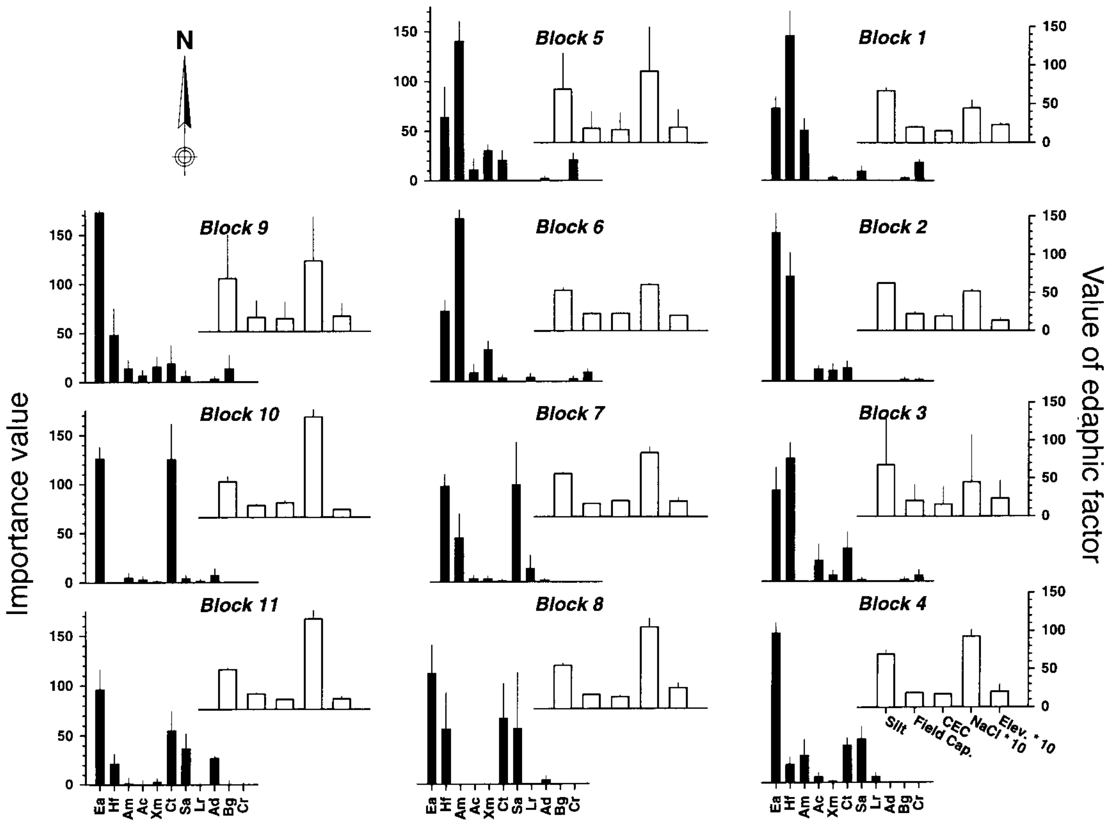

Fig. 2 Vegetation composition and edaphic characteristics in each of the 11 blocks. Bar charts with black bars illustrate mean (± SD) importance value within each block of the 11 most common species. Bar charts with white bars illustrate mean (± SD) values for percentage silt, field capacity, cation exchange capacity (CEC), salinity (parts per thousand × 10) and elevation (metres above sea level × 10). All values are means of 60 quadrats (20 quadrats per transect, 3 transects per block). From left to right along the x-axis, species abbreviations refer to: *Excoecaria agallocha*, *Heritiera fomes*, *Avicennia officinalis*, *Aglaia cucullata*, *Xylocarpus mekongensis*, *Ceriops decandra*, *Sonneratia apetala*, *Lumitzera racemosa*, *Aegiceras corniculatum*, *Bruguiera gymnorrhiza* and *Cynometra ramiflora*.

$= H'/\ln(S)$) and species importance values (IV) as the sum of each species relative density, relative frequency and relative basal area. Soil samples (one per quadrat, i.e. 20 per transect, located at random) were collected and analysed for pH, percentage organic matter, soil texture, field capacity, conductivity (salinity), available Na, K, Ca, and Cl, and cation exchange capacity (CEC) following standard methods (Davis & Freitas 1970; Molital *et al.* 1986). Elevation above mean low water was measured with surveyors' stadia rods and transits relative to nearby reference stations (BIWTA 1985). Topography was classified into four (unordered) physiognomic types – slope, basin, levee and flat – analogous to Lugo & Snedaker's (1974) fringing, basin, overwash and riverine mangrove forest types, respectively. Dwarf mangroves (*sensu* Lugo & Snedaker 1974) were not encountered in our study.

WITHIN-TRANSECT ZONATION

At the transect level, we tested for zonation across the intertidal using randomization tests developed for niche-overlap models (summarized by Gotelli & Graves 1996). Briefly, since each species in a zoned sequence should occupy a distinct portion of the intertidal, the intertidal gradient (expressed as elevation in metres a.s.l.) can be treated as a uni-dimensional 'niche axis'. Tidal elevation is a good measure to use because most edaphic parameters associated with species distributions in the intertidal are well-correlated with tidal elevation (e.g. Adams 1963; Snow & Vince 1984; Bertness & Ellison 1987; Ukpong 1994), and tidal inundation frequency is the most common variable used to illustrate species zonation patterns in mangrove forests (e.g. Watson 1928; Macnae 1968; Chapman 1976; Snedaker 1982).

If species along a transect exhibit zonation, then there should be less overlap or fewer co-occurrences of species at any given tidal elevation than expected by chance alone. Pianka's (1973) index was used as a measure overlap within the community, thus allowing us to test not only for single-species zones, but also for zones consisting of multiple species. The actual species distributions were then compared with

Table 1 Principal mangrove species encountered in the vegetation sample. Data given are the frequency of species occurrences in blocks, transects within blocks, and quadrats within transects

Species	Family	Percentage occurrence in		
		Blocks	Transects	Quads
Trees				
Excoecaria agallocha L.	Euphorbiaceae	100	100	83
Heritiera fomes Buch.-Ham.	Sterculiaceae	91	82	68
Avicennia officinalis L.	Avicenniaceae	73	36	10
Xylocarpus mekongensis Pierre	Meliaceae	72	47	12
Sonneratia apetala Buch.-Ham.	Sonneratiaceae	61	44	14
Bruguiera gymnorrhiza (L.) Lamk.	Rhizophoraceae	36	15	7
Sonneratia caseolaris (L.) Engler	Sonneratiaceae	27	8	1
Xylocarpus granatum Koenig	Meliaceae	18	6	1
Rhizophora mucronata Lamk.	Rhizophoraceae	18	6	1
Avicennia marina (Forsk.) Vierh.	Avicenniaceae	9	4	3
Small trees and shrubs				
Nypa fruticans (Thunb.) Wurmb.	Arecaceae	82	50	16
Aglaia cucullata (Roxb.) Pellegrin*	Meliaceae	73	56	30
Phoenix paludosa Roxbj.*	Arecaceae	73	35	8
Acanthus ilicifolius L.	Acanthaceae	72	44	8
Ceriops decandra (Griff.) Ding Hou	Rhizophoraceae	72	58	44
Lumnitzera racemosa Willd.	Combretaceae	46	18	6
Aegiceras corniculatum (L.) Blanco	Myrsinaceae	36	12	3
Cynometra ramiflora L.	Caesalpiniaceae	33	30	12
Brownlowia tersa (L.) Kosterm.	Tiliaceae	18	9	2
Kandelia candel (L.) Druce	Rhizophoraceae	10	6	3
Hibiscus tiliaceus L.	Malvaceae	9	6	2
Aegialitis rotundifolia Roxb.	Plumbaginaceae	9	3	3

*Not considered true mangroves or mangrove associates by Tomlinson (1986).

a null model generated using Randomization Algorithm 3 (RA3) developed by Lawlor (1980). Winemiller & Pianka (1990) evaluated the performance of different randomization algorithms using data sets with known structure, concluding that RA3 had the best power of detecting non-random patterns of overlap and was not vulnerable to Type I statistical errors (false positives). An illustration of how this test works is described below, and summarized in Fig. 3.

We first arranged our data in a species (rows) × tidal elevation (columns) matrix, where each cell contained the number of individuals of a given species occurring at a given tidal elevation (0.1-m increments). Patterns for three hypothetical mangrove communities – one in which each species occupies a distinct zone (albeit with minor overlap), one in which two or more species share a single zone, and one in which species are distributed completely at random – are shown at the left of Fig. 3. For each of these communities, we first calculated Pianka's (1973) index of community overlap. We then applied randomization algorithm RA3. The position of each species is reshuffled along the intertidal by row and this process results in a 'null' matrix in which no species has a preference for a given tidal elevation. This procedure is repeated 1000 times to generate a distribution for the values of Pianka's index (Fig. 3a–f) against which our observed measure of niche overlap can be compared (see Gotelli & Graves 1996 for analytical details).

For the first hypothetical community (one species per zone with minor overlap), the mean pairwise overlap is 0.097, which is significantly ($P = 0.048$) lower than that predicted by the randomization (Fig. 3a). In contrast, the variance in overlap of such a community (0.009) is not significantly different ($P = 0.24$) from that predicted by the randomizations (Fig. 3b). For the second hypothetical community (multiple species per zone), the mean pairwise overlap is high (not a surprising result as many species co-occur) and not significantly different from random ($P = 0.213$; Fig. 3c), but the *variance* in overlap is significantly higher ($P < 0.00001$) than that found from the randomizations (Fig. 3d). For the hypothetical community lacking any zoned structure, neither the mean overlap nor its variance are significantly different from that expected by chance alone (Fig. 3e & f). In summary, average overlap that is significantly lower than expected indicates that the community tends to have only a single species per zone, while variance in overlap that is significantly higher than expected indicates that zonation does occur, but with multiple species per zone. In a community lacking zonation, neither the mean overlap nor its variance would be different from that found for a community structured at random.

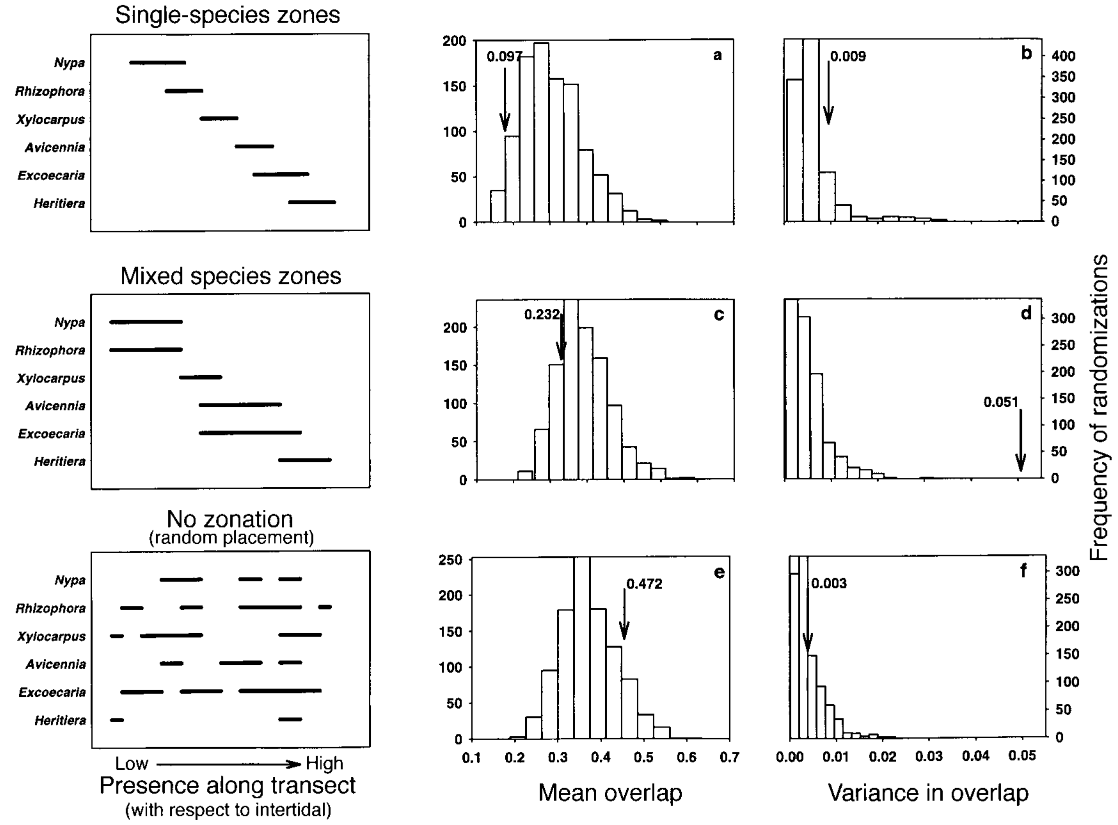

Fig. 3 Illustration of the use of Pianka's index and randomization algorithm 3 (RA3) for testing for zonation. The left panels illustrate hypothetical communities across an intertidal gradient with the corresponding left panels (a, c & e) showing Pianka's index of overlap and right panels (b, d & f) its variance for the hypothetical communities (numbers printed within each panel and arrows pointing to their location along the x-axis). Also shown are histograms of those values obtained from 1000 randomizations of the hypothetical communities using EcoSim version 1.1 (Gotelli & Entsminger 1997).

Despite these clear metrics, RA3 may be overly conservative (i.e. more likely to fail to reject the null hypothesis of no zonation) because it does not take into account known limitations on species distributions. It assumes that all possible positions along the intertidal could be occupied but, because lower elevational limits of species in mangroves may be set by physiological tolerances (Ellison & Farnsworth 1993), it may be more realistic to assume that the tidal ranges below those in which a species is found are unavailable for use in the 'null' communities. Accordingly, we modified RA3 so that the occurrence of each species in the 'null' communities could be no lower in the intertidal than the lower limit actually observed. The results of these runs with our hypothetical communities were not statistically different from those for the unmodified RA3, although the tails of the distributions of both the simulated means and variances in overlap were slightly longer.

As a visual test to determine if species occur in predictable sequences, we also plotted our data according to methods developed by Williams *et al.* (1991) and expanded by Bunt (1996). We emphasize that these plots (see Results) can be used for *qualitative* comparisons only, but the statistical significance of the data can be assessed quantitatively by examining the variance of Pianka's (1973) index of overlap (Gotelli & Graves 1996), as illustrated in Fig. 3b, d & f. A significantly higher than expected variance would indicate that groups of species are consistently found together, and associated with particular positions in the intertidal (Fig. 3d).

Randomization tests (using both original and modified versions of RA3) were carried out using the EcoSim software, version 1.11 (Gotelli & Entsminger 1997). EcoSim calculates significance tests both for the mean and variance of Pianka's index of overlap. One thousand randomizations were performed for each transect. Because there were 33 transects, we used a table-wide Bonferroni-adjusted α-level of 0.0015 for rejection of the null hypothesis of no zonation.

ZONATION AT LANDSCAPE AND REGIONAL SCALES

Similar randomization tests were conducted for data from all transects pooled within each 1-km^2 block (the 'landscape' level) and for data from all blocks pooled along each 80–100 km north–south line (the 'regional' level). This pooling increased statistical power and allowed us to determine whether or not species patterning at successively larger scales differed from that observed at smaller, within-block or within-landscape scales. In each case, we again asked if individual species or groups of species occurred at predictable positions in the intertidal.

VEGETATION-ENVIRONMENT RELATIONSHIPS

Relationships between vegetation structure and composition, soil characteristics and topographic type were assessed with canonical correspondence analysis (CCA) (Ter Braak 1986), using the software package PC-ORD version 3.0 (McCune & Mefford 1997). Ordinations were unconstrained. To determine which variables should be used in the CCA, we examined correlations among all the edaphic variables that we measured, and identified five variables (percentage silt, field capacity cation exchange capacity, salinity and topographic type) that were not correlated directly with each other. The four quantitative variables (percentage silt, field capacity, cation exchange capacity and salinity) were all significantly correlated within transects with tidal elevation ($r > 0.7$) and each of these variables was strongly correlated with some, if not all, of the other edaphic parameters that we measured (e.g. percentage silt is well correlated with percentage sand and percentage clay in a soil sample). Figure 2 illustrates how these edaphic factors varied across the 11 blocks.

Results

SPECIES COMPOSITION

Twenty-two species considered to be true mangroves or common mangrove associates (*sensu* Tomlinson 1986) were found in the 11 blocks (Table 1). *Excoecaria agallocha, Heritiera fomes, Avicennia officinalis* and *Xylocarpus mekongensis* were the most abundant and widespread tree species encountered. The mangrove fern *Acrostichum aureum* L. (Pteridaceae) occurred in half the blocks, but in < 2% of the quadrats. In addition, we encountered two non-halophytic trees and shrubs (*Sapium indicum* Willd., Euphorbiaceae, and *Pandanus foetidus* Roxb., Pandanaceae), as well as several climbers (*Dalbergia spinosa* Roxb., Papilioniaceae, *Derris trifoliata* Lour., Papilioniaceae, and *Sarcolobus globosus* Wall, Asclepiadaceae) and herbs (the grasses *Proterasia coarctata* L., *Phragmites karka* (Retz.) Tran. and *Saccharum* sp., and the sedge *Cyperus javanicus* Hoult). Within transects, the mean number of species $(S) = 5.1 \pm 0.28$, mean Shannon-Weiner diversity $(H') = 1.19 \pm 0.042$ and mean evenness $(J) = 0.76 \pm 0.013$. Within blocks, $S = 8.2 \pm 0.38$, $H' = 1.42 \pm 0.59$ and $J = 0.68 \pm 0.031$. Within north–south groups, $S = 13.0 \pm 1.00$, $H' = 1.71 \pm 0.067$ and $J = 0.67 \pm 0.028$.

WITHIN-TRANSECT ZONATION

For many transects, illustrations drawn using standard methods to show mangrove distribution patterns along gradients of tidal elevation (i.e. profile diagrams as in Fig. 4) gave the appearance of distinct zonation patterns. However, even for the clearest example (shown in Fig. 4), where species occurred in distinct patches, randomization tests suggest that these species are not zoned ($P = 0.96$) and may in fact show more overlap than expected by chance alone ($P = 0.03$). In this case, this is due to the overlap of *Ceriops and Excoecaria*, and the occurrence in two zones (3.05 and 3.2–3.3 m a.s.l.) of *Nypa*. Overall, randomization tests using either RA3 or its modification failed to identify a single transect in which individual species had significantly less overlap at a given tidal elevation than expected by chance alone. In other words, we could not sup-

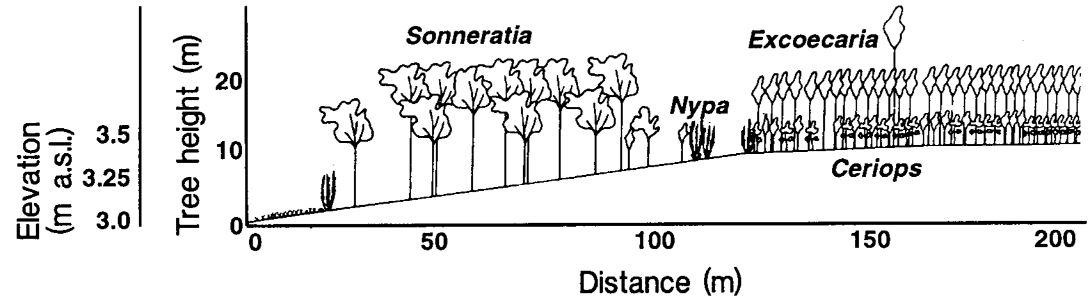

Fig. 4 Example of a profile diagram (block 7, transect 2): trees are drawn to represent average height and density within quadrats along the transect. There appears to be clear zonation with *Nypa fruticans* occurring both lowest in the intertidal and at 3.2–3.3 m a.s.l., *Sonneratia apetala* in a broad zone from approximately 3.1–3.2 m a.s.l., and *Ceriops decandra* and *Excoecaria agallocha* occupying the highest intertidal from 3.3 to 3.5 m a.s.l.

port statistically the occurrence of zonation in any of the 33 transects studied and, even if we ignored the table-wide Bonferroni correction, only three transects exhibited significant zonation ($P < 0.05$).

ZONATION AT THE LANDSCAPE SCALE

We pooled data from transects within blocks to increase our statistical power and to test for zonation patterns within each block. As with our transect-level analysis, however, we found little evidence for zonation. Although block 7 (which contained the transect illustrated in Fig. 4) exhibited significant zonation patterns ($P = 0.01$), those in block 8 had significantly *more* overlap than expected by chance alone ($P = 0.02$) as well as low variance in overlap, and no other block was significantly different from that expected by chance: the occurrence of 2 of 11 blocks with statistically significant patterns of species with respect to tidal elevation is likely to be due to chance alone.

Computation of normalized species scores using the method of Williams *et al.* (1991) similarly failed to detect zonation patterns in any block (Fig. 5): no species remains at a constant relative position within the intertidal, either across blocks or with respect to other species. We tested to see if the position remained constant using a Friedman's non-parametric ANOVA on species ranks within the intertidal. This analysis failed to reject the null hypothesis that there is no systematic response or pattern across the 11 blocks (Friedman's $\tau = 0.929$, $P = 1.0$).

There was extensive overlap among most species in most blocks, even in the only block (7) which showed statistical evidence of zonation. None of the randomization tests on the *variance* of Pianka's index of overlap found significant departures from that expected when there were no groups of species that co-occurred regularly ($P > 0.10$, all cases). In other words, neither qualitative nor quantitative examination of the data could identify discrete zones within the intertidal based either on single species or groups of species.

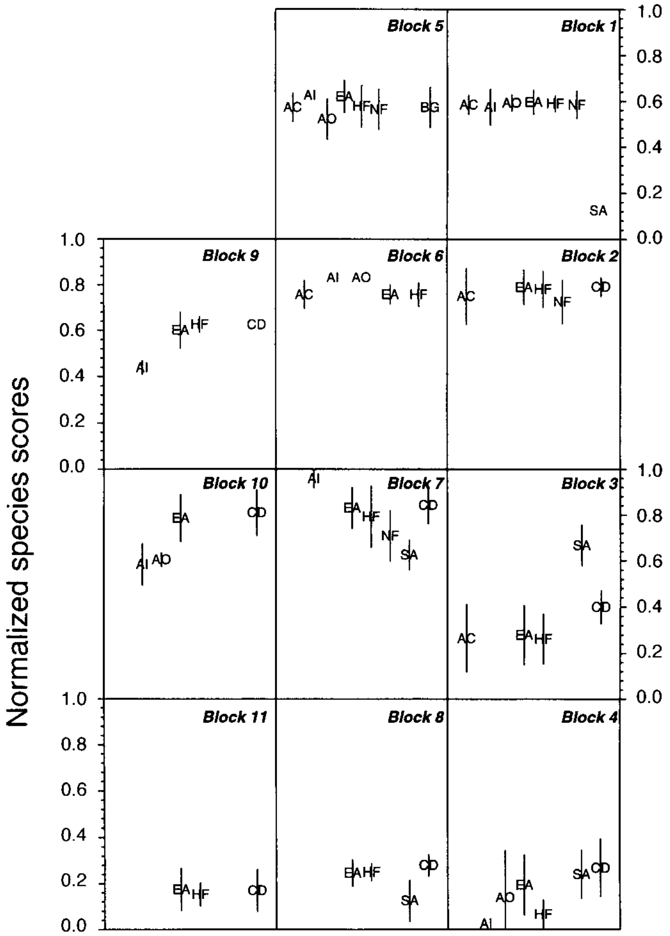

Fig. 5 Sequencing diagrams for the 11 sampled blocks, illustrating only those species common to at least two blocks. Letter pairs denote species and are centred on the mean standardized species score. Species scores range from 0 (lowest occurrence in the intertidal) to 1 (highest occurrence in the intertidal). Grey vertical lines indicate 1 SD. Species codes as in Fig. 2, with the addition of: AI, *Acanthus ilicifolius*; and NF, *Nypa fruticans*.

ZONATION ACROSS THE REGION

Finally, we pooled data from all blocks within each 80–100 km north–south line (see Fig. 1) to test for zonation among species at the regional level. Zonation was not apparent in either the eastern (blocks 1–4) or central (blocks 5–8) lines ($P = 0.82$ and 0.27, respectively). In the western line (blocks 9–11), species overlap was significantly *greater* than expected by chance ($P = 0.03$), opposite to that expected if species were zoned. No species patterning within or among north–south lines was visually apparent from normalized species scores (data not shown). Friedman's test failed to find a systematic ordering of species across the landscape, and randomization tests quantitatively failed to identify predictable groups of co-occurring species ($P > 0.3$, all cases).

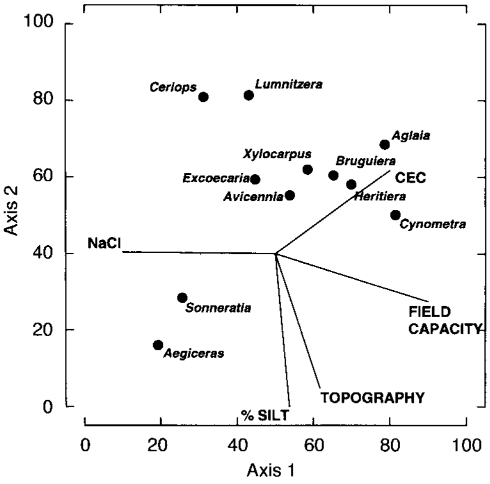

Fig. 7 Biplot illustrating the relative position of each of the 11 most common species in edaphic 'space'. Species references as in Fig. 2.

VEGETATION-ENVIRONMENT RELATIONSHIPS

Canonical correspondence analysis was used to examine multivariate relationships among edaphic factors, each transect and block, and the average within-transect importance value of each species (Figs 6 & 7; Table 2). Salinity and field capacity varied inversely with each other along axis 2, whilst on axis 2% silt and topographic class varied in parallel an in the opposite direction to cation exchange capacity (Table 2). Figure 6 illustrates the three transects from a block grouped together in the same area of the multivariate edaphic space.

The ordination of species with respect to the edaphic variables (Fig. 7) illustrates clearly why our randomization tests failed to identify zonation patterns with respect to tidal elevation. First, although these five edaphic variables are all correlated with tidal elevation, the correlations are not all in the same direction. Second, few species show clear relationships with more than one of these key edaphic variables. Only *Ceriops*, *Lumnitzera*, *Sonneratia apetala* and *Aegiceras* separate out clearly, whilst the other common species are clustered together in the multivariate edaphic space. Monte Carlo analysis (in PC-ORD; $n = 1000$ randomizations) suggested that at the scale of the entire Sundarbans, a real vegetation-environment correlation exists ($P = 0.001$) for axis 1 variables (primarily field capacity and salinity; see also Fig. 2), a possible vegetation-environment correlation exists ($P = 0.073$) for axis 2 variables (primarily cation exchange capacity, field capacity and topographic type), but little additional information is added by the third canonical axis ($P = 0.132$). Finally, the proportion of variability in species composition explained by these edaphic variables is low. The first two canonical axes accounted for only 24% of the variance in species composition.

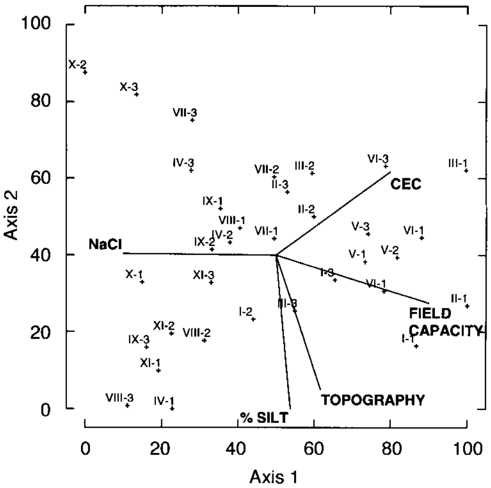

Fig. 6 Biplot illustrating the relative position of each sampled transect in edaphic 'space'. Block number is indicated by roman numerals and transect number is indicated by arabic numerals.

Table 2 Standardized canonical coefficients for the five edaphic characteristics used in the CCA (Figs 6 & 7). Each score represents the contribution of the individual variable to the ordination axis. Large absolute values indicate strong contributions to a given axis

Variable	Axis 1	Axis 2	Axis 3
Percentage silt	−0.167	−0.053	0.281
Field capacity	0.327	−0.394	−0.304
CEC	0.152	0.468	0.021
NaCl	−0.549	−0.161	−0.264
Topography	0.057	−0.348	−0.037

Discussion

Data from the Sundarbans of Bangladesh failed to support the hypothesis that mangroves exhibit zonation across the intertidal at any scale. Neither qualitative interpretation of species assortment across tidal elevation (Fig. 5) nor rigorous statistical analysis identified zonation patterns at the local (individual transect), landscape (within-block) or regional (within north–south lines) scales.

Although at the scale of the entire *c.* 3600-km^2 study area there is a significant vegetation-environment relationship, canonical correspondence analysis showed that this relationship only accounted for 24% of the variability in species composition. Only four species, *Aegiceras corniculatum*, *Ceriops decandra*, *Lumnitzera racemosa and Sonneratia apetala,* separate out clearly in multivariate edaphic space (Fig. 7), whilst the other common species do not sort along either single edaphic gradients (Fig. 5) or composite, multivariate edaphic axes (Fig. 7). Importance values of two of the other species, *Heritiera fomes* and *Excoecaria agallocha*, are, however, associated moderately with salinity (Fig. 2), but not with the other edaphic variables.

Overall large-scale, regional variation in salinity (Fig. 2) affects the regional occurrence of four species (cf. Duke *et al.* 1998). Salinity varies clearly with geography (Fig. 2) and the importance of *Heritiera fomes* generally declines with increasing salinity (Figs 2, 7). Although the importance of *Excoecaria agallocha* is less clearly tied to geography (Fig. 2), it is strongly and negatively associated with values of *Heritiera fomes*. *Ceriops decandra* has its highest importance at the highest levels of salinity (13‰), with a secondary peak at moderate salinity (*c.* 8‰), where *Sonneratia apetala* also predominates, although within-block variability in salinity obscures large-scale geographical predictability. Observed shifts in importance of *Heritiera fomes* and *Excoecaria agallocha*, and to a lesser extent *Ceriops decandra* and *Sonneratia apetala*, principally reflect the west-to-east and south-to-north gradient in salinity resulting from freshwater flow of the Ganges River, and differential subsidence across the Ganges Delta. Overall, these data suggest that edaphic variables are insufficient to predict with a high degree of confidence the local species distributions of mangroves in the Sundarbans, and that interspecific competition or propagule dispersal may be more important than edaphic variables in controlling the size and relative abundance of co-occurring species.

The apparent contradiction between the observed responses of individual species to edaphic variables (especially salinity; Fig. 2) and their lack of zonation (i.e. the absence of strong relationships between species distribution along an edaphic gradient; Figs 5 & 7) may result from a lack of concordance among edaphic characteristics across the intertidal (see also Youssef & Saenger 1999). Differential responses to independently varying edaphic factors result both in large variability in abundances among species at any given location in the intertidal and in high evenness (> 67%) across transects, blocks and regions.

Taken together, these results (especially Fig. 5 and those of the randomization tests) for the Sundarbans do not conform to expectations derived from decades of studies documenting local zonation in mangrove forests throughout the world (Watson 1928; Chapman 1944, 1976; Macnae 1968; Snedaker 1982; Smith 1992). We emphasize, however, that only recently have quantitative measures of zonation been applied to mangrove forests: the inability of Bunt (1996, 1999; Bunt & Bunt 1999; Bunt & Stieglitz 1999) to detect significant or consistent zonation patterns in 18 riverine mangrove forests in Australia, or along 60 transects at Hinchinbrook Island, one of the most well-studied mangrove forests in the world (Robertson & Alongi 1992), is similar to the results reported here.

Whilst we do not dispute that different species of mangroves respond differently to underlying edaphic gradients (e.g. Ball 1988a, b; Ellison & Farnsworth 1993; Ball & Pidsley 1995; Duke *et al.* 1998; see also Fig. 7), we suspect that many reports in the literature of species zonation in mangrove swamps do not reflect accurately the truly complex vegetation patterns found in these forests (see Smith 1992 for clear illustrations of such patterns in Australian mangroves). Rather, these reports rely on qualitative assessments of profile diagrams constructed with *a priori* assumptions of zonation. Observed patterns of species overlap (Fig. 5), where most species occur throughout the intertidal, and where the ordering varies from block to block, could result from random colonization by all species throughout the intertidal, from responses to edaphic variables that vary with tidal elevation in different ways, or from interspecific interactions occurring during the establishment phase. This conclusion is identical to that reached by Bunt & Stieglitz (1999) and hearkens back to general principles of plant distributions first expressed by Gleason (1926).

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