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Macroecology of mangroves: large-scale patterns and processes in tropical coastal forests

Received: 10 July 2001 / Accepted: 1 October 2001 / Published online: 13 November 2001
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Abstract Macroecology is an emerging subdiscipline within ecology that explores effects of large-scale processes on local, regional, and global patterns of species diversity and taxon-independent scaling of structural and functional relationships. Statistical analysis of these patterns yields hypotheses concerning the processes determining population, community, and ecosystem-level patterns, which have been the historical focus of most ecological research, including that done in mangroves. The majority of studies of mangrove forests have aimed to better understand the causes of local (within-forest) ecological patterns (e.g. zonation, tolerance to salinity and hypoxia, litterfall and production), with little attention to the larger environmental, historical and evolutionary contexts that can influence local processes. I argue that a focus on the larger-scale contexts that constrain local processes (a “macroecology of mangroves”) will provide us with new insights into the structure and function of mangrove ecosystems. Further, such analyses can be used to determine if mangroves follow similar general rules that have been identified for upland forested ecosystems. I consider two examples: relationships between local species richness and latitude, longitude and regional diversity; and structural coordination of leaf traits. I present data and analyses of these macroecological patterns in mangrove forests, and illustrate points of agreement and disagreement between these and upland ecosystems. I suggest that ecological theory developed in upland forests can be readily applied to mangrove forests. Such a conclusion should lead to advances in ecological research of mangroves and better predictions of how they will respond to global climate change.

Keywords Biogeography · Leaf traits · Macroecology · Mangroves · Zonation

“To do science is to search for repeated patterns, not simply to accumulate facts...”

(R.H. MacArthur 1972)

Introduction

“Macroecology” is concerned with the statistical analysis of large-scale patterns of the distribution, abundance and diversity of species (Brown and Maurer 1989; Brown 1995), and with the scaling among species of structural and functional relationships (e.g. Enquist et al. 1999, 2000; Enquist and Niklas 2001; Niklas and Enquist 2001). Many ecological patterns that are observed and measured on one or a few species at single study sites are controlled or constrained by general processes common to many taxa or operating at much larger spatial and temporal scales. However, it is rarely possible to conduct replicated, manipulative experiments on many species simultaneously at large scales. Humans are affecting ecosystems at regional and global scales but responses of ecosystems to small-scale perturbations at single study sites are not easily extrapolated to large-scale impacts on whole ecosystems. Guidance is needed on how to scale the results of studies conducted on single species at single sites for short periods of time, to multiple species at large spatial and temporal scales (Farnsworth 1998).

Mangrove forests are distributed worldwide on sheltered, tropical coastlines (Ellison and Farnsworth 2001), and consist of 50–75 species in 20–26 genera in 16–20 families (contrasting numbers from different circum-spections of “mangrove” by Tomlinson 1986; Duke 1992; Kathiresan and Bingham 2001). Mangroves are a good ecological group to use for macroecological investigations because they include a large number of taxonomically unrelated species in which convergent properties have been well documented (Ellison and Farnsworth 2001). Further, mangroves are restricted to a small number of habitat types (intertidal eutrophic to oligotrophic estuaries) constrained by geomorphology (Thom 1982; Twilley 1995), so dramatic differences in “habitat com-

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plexity” – a common bugbear of macroecology – are minimized among mangrove forests. Thus, large-scale patterns in the structure and function of mangrove forests should be readily apparent and straightforward to interpret.

Here, I illustrate two examples of macroecological analyses of mangroves. First, I describe relationships among species richness patterns of mangroves at local, regional, and global scales. Understanding the relationships between small- and large-scale patterns of species richness is the starting point for any macroecological analysis. Second, I examine relationships among mangrove leaf traits and compare these relationships to those seen for plant taxa across a range of temperate and tropical biomes. Such relationships can be used to model regional- and global-scale patterns of productivity, distribution, and dynamics of vegetation (Leuning et al. 1995; Aber et al. 1996; Reich et al. 1999).

I illustrate how macroecological analyses of mangroves can provide inferences about large-scale processes from small-scale patterns and simultaneously yield new insights regarding the structure and dynamics of mangrove forests. These analyses also illustrate that the many processes that structure mangroves are similar to those that structure upland forests, and that general ecological theory is applicable to mangrove forests. Mangroves do not exist in isolation, but occur at the boundary between terrestrial and marine environments. Integrating regional and global patterns of mangrove species richness with general ecophysiological processes into a comprehensive “macroecology of mangroves” could lead to more reliable predictions of the responses of mangrove and upland forests to global climate change. This integration is a major challenge for mangrove ecologists.

Large amounts of existing data on mangrove ecosystems can be brought to bear in macroecological analyses, and new data are being published at an exponential rate (Fig. 1). A cynical mangrove macroecologist could observe that at the current rates of deforestation (1–2%/year; Farnsworth and Ellison 1997a; Ellison and Farnsworth 2001), and in response to rising sea levels (Ellison 1993, 1994; Ellison and Farnsworth 1996b, 1997) mangrove forests will be virtually gone by the year 2100, and during that same year 4.3 million papers will be published about them.

Developers of ecological databases and models of responses of ecosystems to global change are not drawing on available data from mangrove forests. For example, recent compilations of data on forest species diversity (Waide et al. 1999), leaf-level trait, phenology, and climate relationships (Reich et al. 1992, 1999; Reich 1995), global ecosystem net primary productivity (Esser et al. 2000), and tropical forest production (Clark et al. 2001) do not include data from any mangrove forest, despite the existence of these data in the published, indexed literature. The absence of mangroves in these databases may be related to the observation (Fig. 1) that studies of mangroves appear to contribute little to developing fundamental ecological theories or applied ecological

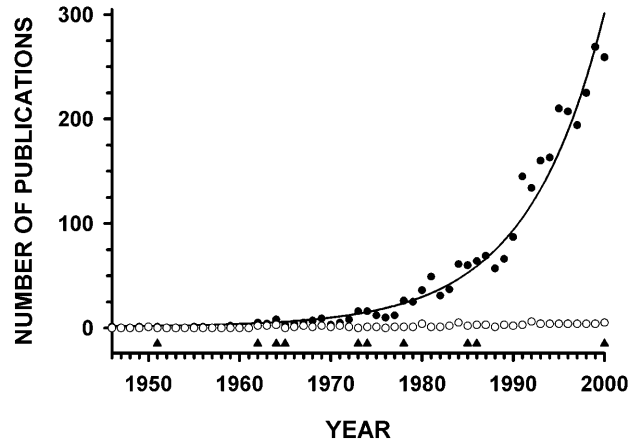


Fig. 1 Publication rate of papers on mangroves. *Solid circles* illustrate total number of papers per year with the word “mangrove” or “mangroves” in the title, abstract, or keywords that occurred in ISI’s Science Citation Index of >5,700 peer-reviewed scientific journals (ISI, Philadelphia). The line is the best-fit non-linear regression ($r^2=0.97$). *Open circles* are the total number of papers per year published in international “high-impact” ecological journals (*Ecology*, *Ecological Monographs*, *Ecological Applications*, *Journal of Ecology*, *Journal of Animal Ecology*, *Journal of Applied Ecology*, *Oecologia*, *Oikos* and *American Naturalist*). The annual number of high-impact mangrove papers is roughly constant over the 55-year period surveyed and never exceeds 5 per year. *Triangles* indicate years in which a single mangrove-related letter or paper (two in 1974) was published in *Science*, *Nature*, or *Proceedings of the National Academy of Sciences, USA*

models. The macroecological analyses described here show that mangrove forests and upland forests are structured similarly. However, relationships among ecophysiological leaf traits of mangroves are different enough to suggest that current models of responses of global vegetation to climate change may need to be adjusted to account for unique properties of woody halophytes.

Example 1: patterns of mangrove species richness

Describing and interpreting species distributions of mangrove trees has preoccupied mangrove researchers for centuries (see reviews in Ball 1988; Smith 1992; Duke et al. 1998; Ellison et al. 1999). These studies have focused either on the local (within stand or forest) patterns of mangrove species “zonation” (e.g., Snedaker 1982) or on the biodiversity “anomaly” of global mangrove species richness (e.g., Ricklefs and Latham 1993). In contrast, regional patterns of species richness have received significantly less attention (but see Schaeffer-Novelli et al. 1990; Duke 1992; Duke et al. 1998). In this review, a region is the area whose species complement (or species pool, Caley and Schluter 1997) could contribute to local species richness. This lacuna is curious, since in general, regional richness can strongly influence local richness (see review in Srivastava 1999), and is the raw information that is used for determining global diversity patterns.

Local patterns of mangrove species richness

Species zonation patterns – the predictable and discrete ordering of species with respect to one or several environmental gradients – have been described for dozens of individual mangrove swamps (reviews in Macnae 1968; Snedaker 1982; Smith 1992; Bunt 1996). Virtually all such descriptions are based in some way on the classification first presented in Watson's (1928) monograph on mangroves of the Malaysian peninsula, in which he suggested that restrictions of given mangrove species to certain portions of a swamp are determined by their tolerance to tidal inundation. Tidal inundation is a nearly ideal proxy for the wide variety of environmental conditions that affect plant growth, including soil salinity, redox potential, and waterlogging (Adams 1963; Snow and Vince 1984; Bertness and Ellison 1987; Ukpong 1994), and degree of tidal inundation largely derives from local geomorphology (Thom 1967, 1982). Nevertheless, Watson's proposed inundation classes were "entirely arbitrary" (Watson 1928, p 130) and the species distribution map he produced (Watson 1928, p 128) is "entirely imaginary" (Watson 1928, p 130). Smith (1992, p 103) reprints this map, but claims it represents Watson's "synthesis of zonation" rather than the "typical, but by no means inevitable distribution of the more important mangrove species" (Watson 1928, p 128). Finally, the "imaginary" zonation and "arbitrary" inundation categories described by Watson (1928) were, he stated, only applicable for the west coast of Malaysia, in the neighborhood of Port Swettenham.

Watson's description of local patterns of species distributions in mangroves epitomize those that follow: they are qualitative, not quantitative, and they are site-specific. Although Watson did not discuss succession of mangroves (the concept of succession being relatively young in 1928), he did consider mangroves to be land-builders (cf. Davis 1940), and zones to be (in modern terms) equilibrium communities. An evaluation of ≈50 years of observations on zonation and succession in mangrove forests reviewed by Lugo (1980) led to the conclusion that zonation represents an equilibrium, steady-state condition, but not a successional one. Studies on disturbance and gap dynamics in mangrove forests (Wadsworth and Englerth 1959; Roth 1992; Ellison and Farnsworth 1993, 1996a; Smith et al. 1994; Imbert et al. 1996; McCoy et al. 1996), however, often fail to support even the idea that they are equilibrium communities.

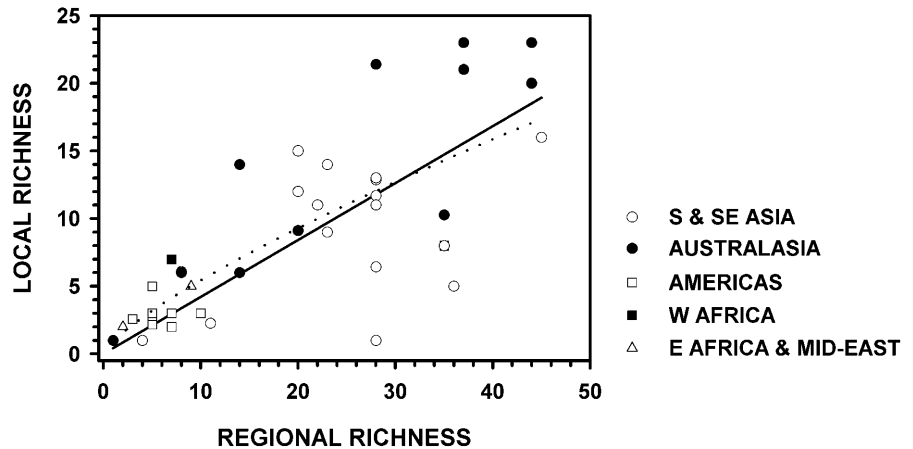
This qualitative, site-specific approach to documenting zonation, and the implicit assumption that mangroves are equilibrium communities (whether successional or not) permeated many subsequent studies of the associations between mangrove distribution patterns and local edaphic conditions (summarized in Macnae 1968; Smith 1992; Ellison and Farnsworth 2001). Despite the availability since the early 1970s of statistical tests for zonation (reviewed by Dale 1999), the fundamental assumption that species in mangrove forests are, in fact, zoned

with respect to these edaphic conditions, has been tested explicitly only in the last 5 years (Bunt 1996, 1999; Bunt and Bunt 1999; Bunt and Stieglitz 1999; Ellison et al. 2000). These studies, conducted in the species-rich forests of northeastern Australia and the Sundarbans of Bangladesh, have failed to support the hypothesis that species occur in distinct (or even indistinct) zones.

Why was zonation not detected quantitatively? Possible explanations for the lack of zonation observed in these studies include: (1) the use of inappropriate statistical methods for testing for zonation in mangrove forests; (2) these investigators focused on an inappropriate spatial scale of observation and analysis for detecting zonation; (3) human impacts on the forests have disrupted zonation patterns; and (4) the "null hypothesis" that zonation does not actually exist in mangrove forests. Explanation 1 is unlikely, as statistical methods for testing species distributions across environmental gradients are well-developed (Dale 1999), and different statistical tests have yielded similar results (see comparison of methods in Ellison et al. 2000). Explanation 2 is contradicted by Ellison et al.'s (2000) study that explicitly looked at species distributions as a function of spatial scale. Human impacts (explanation 3) were minimized at all sites studied in Australia and Bangladesh, but it is virtually impossible to find a mangrove swamp anywhere on the planet that has not been altered substantially by human activities. Jackson (1997) has warned about drawing conclusions about ecological (especially marine) systems based on a "shifting baseline" of assumptions. Current intensive studies of mangrove swamps are being conducted on fragmented remnants of these forests that may bear little structural or functional resemblance to the mangrove forests of centuries past, yet we often consider our study sites to be "representative". Thus, we cannot rule out that these forests were once zoned, but are no longer because of previous, undocumented anthropogenic disturbance(s).

Researchers should consider seriously the last explanation, however: the "null" hypothesis that true zonation does not occur in mangrove forests. Profile diagrams based on dominant species do not reflect distributions of all the species in a given forest, and so generally are not usable to test hypotheses regarding zonation. Without statistical testing, such diagrams convey only the investigator's idealized notion of forest structure, a pattern little changed since Watson (1928). Considering the distribution of mangrove species across the intertidal in terms of overlapping species arrayed along an environmental gradient(s) (cf. Whittaker 1956; Ball 1998; Ball and Sobrado 1998) may lead to a better understanding of mechanisms promoting species segregation and coexistence in mangrove forests. In addition, alternative hypotheses generated by applying basic theory regarding the relationship between regional richness (availability of species) and local richness (Srivastava 1999) can suggest mechanisms determining mangrove forest structure. Relationships between regional and local richness fall within the domain of macroecology.

Fig. 2 Local-regional richness plot for mangrove swamps around the world. Solid line is the best-fit linear regression ($r^2=0.592$; $P=1\times 10^{-9}$), and dotted line is the best-fit saturating (power) function ($r^2=0.595$; $P=1\times 10^{-9}$). No significant improvement in fit ($P=0.15$, F -test) is provided by the power function, which suggests that these forests are not saturated with species



A macroecology of local richness

A macroecological analysis of local richness begins with the axiom that species that occur at a given site are a subset of a regional pool of species that are available to colonize the site (Caley and Schluter 1997; Grace 2001a). For example, of the 22 mangrove species that are known from Bangladesh (Spalding et al. 1997), a maximum of 11 occurred in any of the sites described in Ellison et al. (2000). The absence of the full complement of 22 species at any given site could result from edaphic conditions that favor some species over others, but it could also result from: (1) the failure of some species to colonize the site (e.g., Rabinowitz 1978a); (2) the competitive exclusion of some species by others at the site (e.g., Ball 1980; Ellison and Farnsworth 1993); or (3) preferential predation of propagules (e.g., Smith et al. 1989). A simple correlation analysis could support the hypothesis that species occurrences result from associations with edaphic factors, but this result would not rule out propagule sorting, competition, or preferential predation as mechanisms causing species to occur or not occur in a given site.

An appropriate null hypothesis is that any species that is available in the regional pool could be found in the local assemblage (Caley and Schluter 1997). This is the appropriate null hypothesis because only after species have colonized a site could edaphic sorting, competitive interactions, or propagule predation occur. One way to test this null hypothesis is to examine the relationship between regional and local species richness (Srivastava 1999). A linear relationship between total regional richness and the number of species in a given forest implies that local areas are “unsaturated”. That is, local species richness is controlled by ecological factors such as colonization ability and dispersal, and evolutionary factors such as speciation and fixation of mutations that allow species to establish at a given site. A curvilinear (or asymptotic) relationship between regional and local richness implies that there is an upper limit to local species richness that is set by ecological factors such as niche availability (edaphic tolerance), niche partitioning (competition), or exclusion (due to competition or predation).

Thus, if species richness is determined by random colonization and evolutionary diversification, then the number of species in a given swamp should increase consistently with the number of species available for colonization. Alternatively, if species richness is limited by niche availability, as implied by zonation models that restrict species to particular edaphically or competitively determined niches, then the number of species in a given swamp should be independent of the total number of species available in the region.

I examined the relationship between local and regional species richness for 44 study sites around the world for which I could obtain complete species lists from the literature.¹ Local species richness values were determined from these species lists, which were based on 100–200 m transects, 0.1 ha, or 1.0 ha plots. Regional species richness values were taken from Spalding et al. (1997), with additions for China from Li and Lee (1997). Country-wide richness totals were used as regional species pools for all sites except for those in Australia and India, which were divided into sub-regions by Spalding et al. (1997), and for countries in the Neotropics that have both Pacific and Atlantic (or Caribbean) coastlines. A common difficulty with analyzing local versus regional patterns of species richness is an independent measure of the species pool (Grace 2001b). However, the existence of independent lists of regional species (Spalding et al. 1997), and data on the long-range dispersability of mangrove propagules (Rabinowitz 1978a; Steinke 1986; Komiyama et al. 1992; Smith 1992; Clarke 1993; McGuinness 1997) suggests that the species pools used are appropriate for these analyses. Linear and non-linear (power) functions were fit to the data using S-Plus version 6.0 (Insightful, Seattle, Wash., USA). Relative fits of the models were compared using an F -test (Draper and Smith 1981; Hilborn and Mangel 1997).

Regional species richness explains nearly 60% of the variance in within-site species richness (Fig. 2), and a linear relationship provides as good a fit to these data as

¹ The full dataset and literature citations are available on request from the author

does an asymptotic saturating relationship. Since the saturating relationship has one more parameter than the linear relationship and there is no significant difference in fit, parsimony suggests that we accept the linear relationship as the true relationship between local and regional species richness. Such a linear relationship implies that mangrove forests are unsaturated with species, and that controls on local species richness are best looked for at regional scales. This relationship is independent of biogeographic province [as defined by Spalding et al. (1997): South and Southeast Asia, Australasia (including the eastern Pacific), the Americas, West Africa, and East Africa and the Middle East; Fig. 2].

Global distribution of mangrove species

Species richness of mangrove forests is highest in the Indo-West Pacific and declines relatively smoothly with distance from $\approx 100^\circ\text{E}$, the longitude of peak species richness (Fig. 3; Ellison et al. 1999). This distribution pattern is similar to that seen in reef-building corals and seagrasses, (McCoy and Heck 1976), reef-fishes (Bellwood and Hughes 2001), and mangrove-inhabiting snails (Ellison et al. 1999). After nearly 100 years of discussion, a consensus is emerging that for mangroves, this pattern is best explained by a combination of continental drift and in situ species diversification (reviews in Ellison et al. 1999; Ellison and Farnsworth 2001). The extent and structure of mangrove ecosystems in geological time have been determined by tectonic activity (Ellison et al. 1999) and changing sea levels (Woodroffe and Grindrod 1991; Ellison 1993, 1994).

Less has been written about latitudinal patterns of mangrove species richness (but see Schaeffer et al. 1990; De Lange and de Lange 1994; Duke et al. 1998). In contrast to their “anomalous” longitudinal distribution pattern, latitudinal gradients in mangrove species richness are quite similar to those seen for other taxa. Species richness is highest at the equator and tails off smoothly to the north and south (Fig. 3). There is a vast literature on such patterns, and hundreds of mechanisms have been hypothesized to explain them (Huston 1994; Palmer 1994; Colwell and Lees 2000).

The “mid-domain effect” provides one appropriate null model for such patterns (Colwell and Lees 2000). The mid-domain model accounts for the joint effects of observed latitudinal midpoints and extents of species’ geographic ranges and their potential geographic ranges as determined by biogeographic barriers [winter seawater isotherm $\approx 20^\circ\text{C}$ and winter minimum air temperature $>0^\circ\text{C}$; Duke et al. (1998)]. This model depends on a geometric constraint: species whose range midpoints occur towards the edge of a geographic boundary (here the northern and southern climatic boundaries) must have relatively smaller latitudinal ranges than species whose range midpoints occur towards the center of a groups’ distribution (here, the equator). Colwell and Lees (2000) showed that these geometric constraints on range size

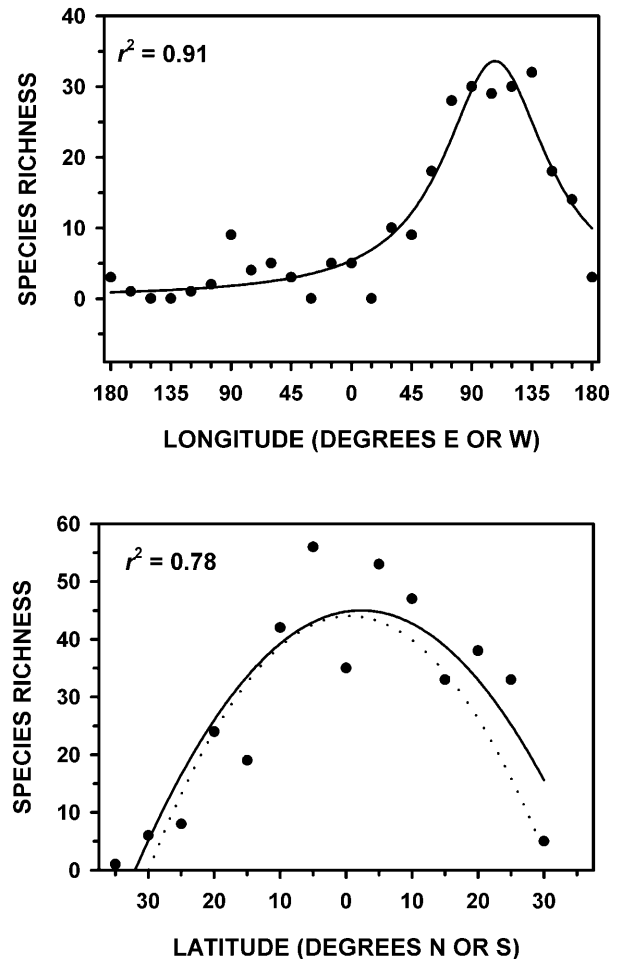


Fig. 3 Species richness of mangroves as a function of longitude (*upper panel*) and latitude (*lower panel*). Lines are best fit non-linear regressions. On the richness vs. latitude plot (*lower panel*) the solid line is the observed relationship, and the dotted line is the expected relationship for all mangrove species with observed latitudinal midpoints and randomized latitudinal ranges. The expected distribution was generated using RangeModel 3.0 (Colwell 2000)

lead to a peak in species richness at the center, even in the absence of environmental gradients correlated with latitude. By comparing the observed pattern of species richness with that expected under the mid-domain (“null”) model (Lees et al. 1999; Lyons and Willig 1999; Veech 2000), one can test whether global patterns of species distribution can be explained simply by spatial geometry, or whether other processes need to be considered.

I used RangeModel 3.0 (Colwell 2000) to generate, using Monte Carlo simulations, 1,000 distributions of all mangrove species [those listed Spalding et al. (1997) along with the Chinese endemics listed in Li and Lee (1997)]. Country-by-country data (Spalding et al. 1997) were used to determine latitudinal mid-points and ranges of these mangroves. The observed distribution (Fig. 3, solid line) was compared with a null distribution in which latitudinal midpoints were those actually observed and range sizes were chosen at random (Fig. 3, dotted

line). This is a reasonable null model if modern species essentially evolved in situ (Ellison et al. 1999). The actual latitudinal distribution did not differ from this null distribution ($P=0.26$, two-sample Kolmogorov-Smirnov test), and explained nearly 80% of the variance in latitudinal species richness. Thus, simple geometric constraints, notably habitat area, perhaps interacting with regional climatic variables, are sufficient to explain latitudinal patterns in mangrove species richness.

What determines regional richness of mangrove species?

The analysis of the local-regional richness plot (Fig. 2) suggests that regional processes are critical determinants of local species richness. Similarly, a null model analysis indicates that regional variables, especially available habitat area, also play a significant role in determining global patterns of species richness with respect to both latitude and longitude (Fig. 3). These results illustrate that a macroecological approach can lead to better understanding of factors that control species richness of mangroves at intermediate (regional) scales.

In the most complete study to date of regional species richness patterns, Duke and his colleagues (Duke 1992; Duke et al. 1998) concluded that environmental factors such as rainfall, tidal variation, estuary length, and catchment area contribute significantly to observed intra-regional differences in species richness. Similarly, Schaeffer-Novelli et al. (1990) attributed intra-regional differences in species composition of Brazilian mangroves to local topography and edaphic factors operating within the constraints set by climate and hydrology.

Because habitat area has a strong effect on species richness (Connor and McCoy 1979), it is important to remove its effects before attributing observed patterns of species richness to edaphic factors, topography, and rainfall. Using geographic data in Spalding et al. (1997), I examined the relationship between regional species richness and area occupied by mangroves. Area alone explains 28% of the variance in species richness across regions (Fig. 4A). Stepwise multiple regression analysis further indicates that annual rainfall (Fig. 4B) and biogeographic province (categories of Fig. 2) explain an additional 23% and 13%, respectively, of the overall variance in inter-regional species richness, but there is no additional significant effect of either latitude or longitude. Thus, variables identified by Schaeffer-Novelli et al. (1990) and Duke (1992; Duke et al. 1998) do affect regional species richness, but less so than available area.

The lack of discrete latitudinal or longitudinal effects also is observed at global scales (Ellison et al. 1999). The latitudinal pattern shown in Fig. 3 is due almost entirely to total mangrove area at a given latitude, which accounts for 78% of the variance in latitudinal species richness patterns (Fig. 4C). Similarly, mangrove area explains 88% of the variance in species richness across the five large biogeographic provinces (South and Southeast

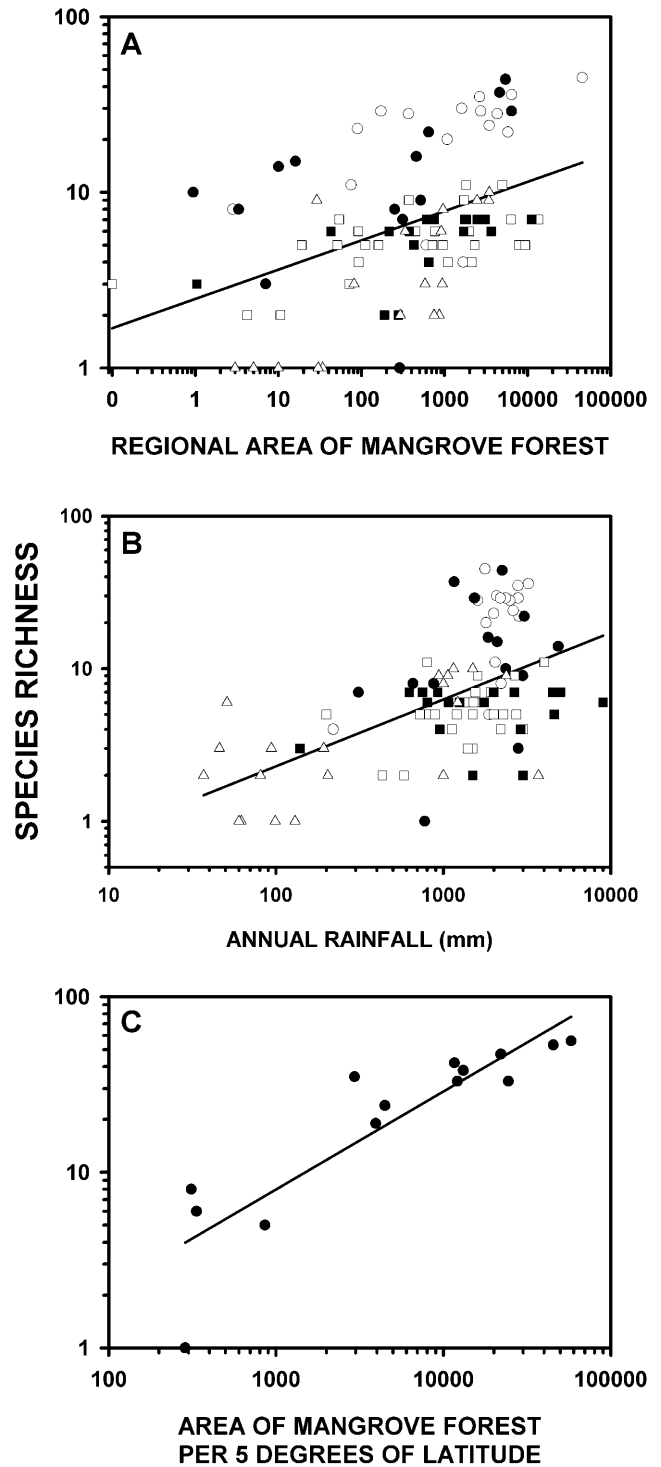


Fig. 4A–C Species richness of mangroves as a function of area and rainfall. **A** Richness as a function of regional (country or region within country) area (symbols as in Fig. 2); **B** richness as a function of regional rainfall (symbols as in Fig. 2); **C** richness for a given 5° interval of latitude as a function of area at that latitude

Asia, Australasia and the Pacific Islands, the Americas, West Africa, and East Africa and the Middle East) in which mangroves occur (Ellison et al. 1999). A similarly large effect of habitat area in these regions was found for coral reef fishes (Bellwood and Hughes 2001), which

have latitudinal and longitudinal patterns of species richness nearly identical to that of mangroves.

This macroecological analysis of mangrove species richness leads to three conclusions. First, we can identify regional species pools and use them to predict local species richness. This alone may help us to determine whether a given forest is or has been impacted by anthropogenic activities. Second, we can construct more accurate models of large-scale forest compositing that can be used in models of forest productivity and nutrient cycling. Third, this approach can be used for mangrove associates such as invertebrates (Ellison et al. 1999), fish, birds, or fungi. As more taxa are studied, the global pattern of mangrove species distribution becomes less anomalous.

Considering species within mangroves to be distributed broadly among overlapping gradients as opposed to in discrete zones can inform our understanding of how local processes filter regional species pools to result in the structure and composition of a specific forest. Within individual swamps, it is as important to ask why available species do not occur as it is to determine edaphic limits of currently occurring species. For example, predation of propagules prior to dispersal (Farnsworth and Ellison 1997b) may reduce significantly the colonization of some mangroves to a given site. Similarly, dispersed propagules are consumed in large numbers, and often in density- or frequency-dependent numbers once they wash up on shore (Smith 1987; Smith et al. 1989; Sousa and Mitchell 1999). Data available on post-predation recruitment and early seedling success (Ellison and Farnsworth 1993; Clarke 1995; McKee 1995; Kathiresan et al. 1996; O'Grady et al. 1996; Koch 1997; Osunkoya and Cresse 1997) have focused on locally-occurring species (as opposed to the entire species pool). Only Rabinowitz (Rabinowitz 1978b) experimentally examined the interaction of seedling growth, dispersal, and local distribution patterns, and her results are not applicable to the Indo-West Pacific, where within- and between-forest diversity is much higher (Smith 1992). Interspecific interactions – notably interspecific competition – have been little studied in mangroves (Ball 1980; Smith 1988; Rey 1994), despite their overwhelming importance in determining plant species distributions in terrestrial uplands (Gurevitch et al. 1992), freshwater wetlands (Keddy 2000), and salt marshes (Bertness and Ellison 1987).

Example 2: functional relationships among mangrove leaf traits

Local species richness by itself is not the same as zonation. Edaphic conditions vary across the intertidal creating environmental stressors that are linked to species distributions through their effects on plant physiological processes (Ball 1988; Ball and Sobrado 1998). Mangroves are a model system for studying effects of hypoxia and salinity on water relations and photosynthesis in

stressful habitats. Yet, as with the studies of mangrove distributions described above, there have been few attempts to integrate mangrove ecophysiology with broader patterns and trends across the plant kingdom (but see notable exceptions in Ball 1996; Farnsworth and Farrant 1998; Farnsworth 2000).

Recent research has shown that relationships among key ecophysiological traits of leaves – lifespan, specific area, nitrogen content, photosynthetic and diffusive conductance rates – are similar across a taxonomically diverse range of plants in upland biomes ranging from the Arctic tundra to the tropical rain forests (Reich et al. 1992, 1997, 1999). This generality could allow for the modeling of regional- and global-scale productivity, distribution, and dynamics of vegetation given a small set of easily measured leaf traits (Leuning et al. 1995; Aber et al. 1996; Reich et al. 1999). Many of these leaf traits may be measurable for mangroves using remote-sensing technologies (Ramsey and Jensen 1996; Green et al. 1997; Blasco et al. 1998; Mumby et al. 1999), leading to better predictions of the responses of mangroves to global climate change and other large-scale stressors. In light of this potential, and to determine if existing models might need adjustments to account for the unique ecophysiological traits associated with adaptations for dealing with hypoxia and salinity, I compared relationships among mangrove leaf traits with those published for upland biomes (Reich et al. 1999) and temperate wetlands (Shipley and Lechowicz 2000).

Data of the kind used by Reich et al. (1999) and Shipley and Lechowicz (2000) to examine the generality of relationships among leaf-trait never have been collected simultaneously from a single mangrove plant. Therefore, for comparative exploratory analyses, I extracted values for leaf lifespan (months), specific leaf area (SLA: cm^2/g), photosynthetic rates [either area-based (A_{area} : $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) or mass-based (A_{mass} : $\text{nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$), foliar nitrogen content [either area-based (N_{area} : g/m^2) or mass-based (N_{mass} : mg/g)], and leaf diffusive conductance (G_s : $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) from the published literature and created “composite mangrove” leaves by pooling traits across studies (Table 1)². In general, published photosynthetic rates for mangroves are area-based, and I derived A_{mass} as $A_{\text{area}} \times \text{SLA}$ ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1} \times \text{cm}^2 \text{ g}^{-1} / 10 = \text{nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$). I then plotted the “composite mangrove” data alongside field data published by Reich et al. (1999) for 105 species from six upland biomes in the Americas and data published by Shipley and Lechowicz (2000) for 40 species of freshwater wetland herbs from eastern North America that were grown in a common garden. Regression analyses were done separately for the mangrove species, the wetland herbs, and the upland species (in S-Plus). Model I and model II regressions gave similar results, and for consistency with Reich et al. (1999), I report the results of the model I regressions.

² The full dataset from which these “composite mangroves” were created, along with literature citations, is available on request from the author

Table 1 Leaf traits of “composite mangroves” used in the comparative analysis of leaf-trait relationships (Fig. 5). Variables used and their units are: leaf lifespan (months); specific leaf area (SLA) (cm²/g); mass-based photosynthetic rate (A_{mass}) (nmol CO₂ g⁻¹ s⁻¹); mass-based leaf nitrogen content (N_{mass}) (mg/g); leaf diffusive conductance (G_s) (mmol H₂O m⁻² s⁻¹). (n.a. no data available)

Species	Leaf lifespan	SLA	N_{mass}	A_{mass}	G_s
<i>Aegiceras corniculatum</i>	24	n.a.	n.a.	n.a.	138.00
<i>Avicennia germinans</i>	10	64.80	16.00	41.15	270.00
<i>Avicennia marina</i>	13.7	42.20	13.54	54.31	200.00
<i>Bruguiera gymnorrhiza</i>	32.7	75.13	6.50	71.37	160.00
<i>Ceriops tagal</i>	36.5	52.85	7.72	15.58	43.75
<i>Cocoloba uvifera</i>	n.a.	n.a.	9.60	n.a.	300.00
<i>Conocarpus erectus</i>	5	65.80	8.55	32.70	196.67
<i>Kandelia candel</i>	12	n.a.	14.95	n.a.	n.a.
<i>Laguncularia racemosa</i>	4	67.50	8.85	50.56	182.00
<i>Rhizophora apiculata</i>	19.5	67.20	15.30	51.41	69.25
<i>Rhizophora mangle</i>	9	80.00	18.00	74.05	163.25
<i>Rhizophora mucronata</i>	17	n.a.	10.50	n.a.	44.00
<i>Rhizophora stylosa</i>	19	59.07	9.22	62.02	114.00

Table 2 Summary of Model I regression analyses for leaf traits illustrated in Fig. 5. Reich et al.’s (1999) dataset includes field data from six biomes of the Americas: alpine tundra-subalpine forest ecotone, cold temperate forest-prairie ecotone, montane cool temperate forest, desert shrubland, subtropical forest, and tropical rainforest. The data for eastern North American wetlands are from plants grown in a common garden by Shipley and Lechowicz

(2000). Species used in the mangrove analysis are: *Avicennia germinans*, *Avicennia marina*, *Bruguiera gymnorrhiza*, *Ceriops tagal*, *Conocarpus erectus*, *Laguncularia racemosa*, *Rhizophora apiculata*, *Rhizophora mangle*, and *Rhizophora stylosa*. Variables and units as in Table 1. All regressions were done on log₁₀-transformed data. Shipley and Lechowicz do not provide data for leaf lifespan. (n.a. no data available)

Upland biomes of the Americas		Mangroves		Eastern North American Wetlands	
Regression equation	r^2	Regression equation	r^2	Regression equation	r^2
SLA=2.42–0.46×Leaf lifespan	0.57	SLA=1.85–0.05×Leaf lifespan	0.05	n.a.	
A_{mass} =2.56–0.66×Leaf lifespan	0.78	A_{mass} =1.77–0.10×Leaf lifespan	0.03	n.a.	
N_{mass} =1.57–0.34×Leaf lifespan	0.59	N_{mass} =1.18–0.12×Leaf lifespan	0.06	n.a.	
G_s =2.8–0.33×Leaf lifespan	0.30	G_s =2.65–0.49×Leaf lifespan	0.31	n.a.	
A_{mass} =–0.20+1.06×SLA	0.74	A_{mass} =–0.11+0.99×SLA	0.15	A_{mass} =1.24+0.44×SLA	0.13
N_{mass} =0.13+0.56×SLA	0.55	N_{mass} =–0.91+0.07×SLA	0.001	N_{mass} =1.09+0.08×SLA	0.01
G_s =2.03+0.23×SLA	0.06	G_s =1.28+0.48×SLA	0.03	G_s =4.40–0.95×SLA	0.28
N_{mass} =0.31+0.49× A_{mass}	0.68	N_{mass} =0.65+0.23× A_{mass}	0.09	N_{mass} =0.87+0.18× A_{mass}	0.13
G_s =1.65+0.44× A_{mass}	0.30	G_s =1.11+0.62× A_{mass}	0.26	G_s =1.63+0.31× A_{mass}	0.04
G_s =2.05+0.35× N_{mass}	0.07	G_s =1.81+0.30× N_{mass}	0.02	G_s =1.06+0.98× N_{mass}	0.12

Reich et al. (1999) also performed a principal components analysis (PCA) to determine if species from different functional groups (forbs, shrubs, deciduous broad-leaved trees, evergreen broad-leaved trees, coniferous needle-leaved trees) clustered together in multivariate space. After re-entering the data from Table 2 of Reich et al. (1999), I performed a PCA on those data to recover their trait loadings and species ordination. I used those loadings to predict where the “composite mangroves” would be expected to occur in multivariate space if the leaf-trait relationships observed for upland species by Reich et al. (1999) were the same for mangroves. I then performed a PCA on all the data (Reich et al.’s and the “composite mangroves”) combined to see if the results would differ if mangroves were included in the overall analysis. Only the nine mangrove species for which I had values for all five leaf traits in Table 1 were used in the PCA.

Principal axis scores for the predicted mangroves were compared with those observed in the combined analysis using a matched-pairs *t*-test. PCAs were done using S-Plus on untransformed data that were first standardized into standard deviation units [(observation – mean) / SD]. Because Shipley and Lechowicz (2000) did

not provide leaf lifespan data, their wetland herb dataset was not used in the PCA.

Correlations among mangrove leaf traits were similar in direction to those observed by Reich et al. (1999), but differed in magnitude (slopes of the regressions) (Table 2, Fig. 5). With respect to leaf lifespan, G_s declined 48% faster, but N_{mass} , A_{mass} , and SLA declined 64%, 85%, and 91% slower for mangroves than were predicted by Reich et al.’s (1999) general leaf-trait equations. Similarly, with respect to SLA of mangroves, G_s increased 109% faster while N_{mass} increased 88% slower than predicted, but A_{mass} was nearly identical to that predicted. Across the observed range of mangrove A_{mass} rates, G_s increased 41% faster while N_{mass} decreased 53% faster than predicted. G_s also increased 14% faster with N_{mass} than predicted (Table 2, Fig. 5). Fits of the regression lines for mangroves were generally poorer than those for upland biomes, principally because of the small sample size ($n=9$).

Leaf trait relationships among SLA, N_{mass} , A_{mass} , and G_s of wetland herbs (Shipley and Lechowicz 2000) differed from those observed both for upland biomes and mangroves (Table 2, Fig. 5). As for mangroves, slopes of

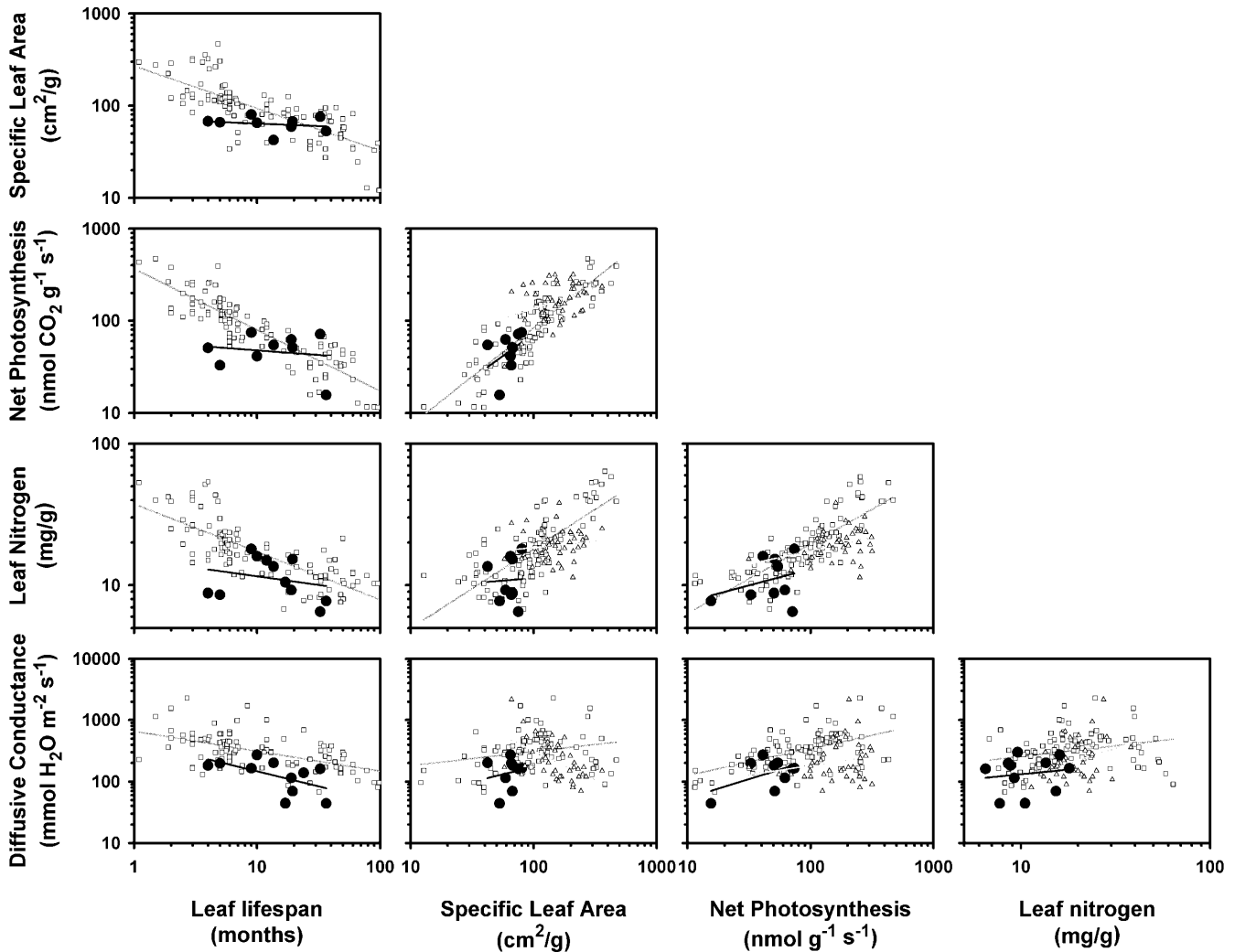


Fig. 5 Scatterplot matrix of the relationship among five leaf traits: leaf lifespan, diffusive conductance, nitrogen content, photosynthetic rate, and specific leaf area. *Small open squares* and *dark grey regression lines* are data from Reich et al. (1999) for 105 species from six upland biomes. *Small open triangles* and *light grey regression lines* are data from Shipley and Lechowicz (2000) for 40 species of wetland herbs. No data on leaf lifespan are provided in Shipley and Lechowicz (2000). *Large black symbols* and *black regression lines* are data for the “composite mangroves” in Table 2

the regression lines relating leaf traits of wetland herbs were lower than those for upland plants. In general, the slopes of the regression lines relating leaf traits of the wetland herbs were also lower than those for mangroves, but intercepts were higher. Thus wetland herbs, with their relatively small ranges of SLA, N_{mass} , A_{mass} , and G_s fell within the cluster of points representing upland plants in Fig. 5 (with the exception of the relationship between N_{mass} and G_s which is more similar to that of mangroves). The regression lines of the wetland herbs also fit the data relatively poorly, despite somewhat larger sample sizes ($n=40$) than was available for the mangroves.

Applying the loadings of the PCA of Reich et al. (1999) to the nine “composite mangrove” species for

which complete data were available predicted that mangroves would not form a natural grouping, and would not be distinguishable from the non-mangrove species (Fig. 6, predicted mangrove plot). However, the PCA that included not only the non-mangrove species but also the “composite mangroves” did not qualitatively re-shape the arrangement of non-mangrove species in multivariate space, but did cluster together the “composite mangroves” more tightly (Fig. 6, observed mangrove plot). In the latter PCA, the “composite mangroves” clustered closely with evergreen (tropical) broadleaved trees of tropical and subtropical forests. The scores of the nine mangrove taxa on principal axis 1 differed slightly ($P=0.08$) between those predicted by the first PCA and those observed in the second PCA. No difference ($P=0.27$) was observed between predicted and observed locations on principal axis 2. Loadings on each axis did not differ by more than a few percent in magnitude, and were similar in direction between the two PCAs (Table 3). In both PCAs, principal axis 1 primarily reflected (left to right) increasing leaf lifespan and decreasing leaf SLA and A_{mass} . Principal axis 2 reflected (bottom to top) primarily decreasing G_s and N_{mass} .

Table 3 Loadings of the five variables on the two principal axes shown in Fig. 6 for the Reich et al. (1999) data set alone, and for that dataset together with the “composite mangroves”. Variable names as in Table 1; PCAs were conducted on variables standardized to standard deviation units

Variable	Biomes of the Americas		Biomes of the Americas plus “composite mangroves”	
	PC-1	PC-2	PC-1	PC-2
Leaf lifespan	0.473	0.092	0.464	0.049
SLA	-0.528	0.267	-0.531	0.220
N_{mass}	0.318	-0.593	0.302	-0.694
A_{mass}	-0.553	-0.109	-0.557	-0.137
G_s	-0.303	-0.746	-0.318	-0.694

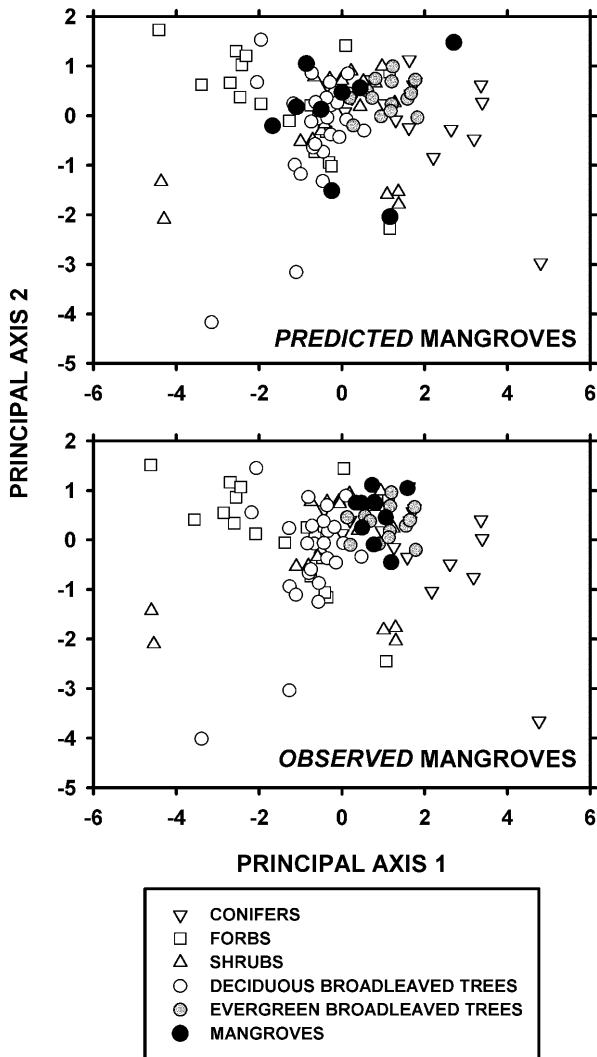


Fig. 6 Principal components analysis (PCA) of leaf traits of mangrove and of 96 species from six upland biomes. The “predicted mangroves” plot (*top*) illustrates the placement of the 9 “composite mangrove” species expected from the ordination of the 96 upland species. The “observed mangroves” plot (*bottom*) illustrates the placement of the mangrove species when they are included in the PCA along with the upland species

Are mangroves really different?

The macroecological analysis of mangrove leaf traits suggests that for pairwise relationships (Fig. 5), mangroves respond differently from upland plants to envi-

ronmental stressors. Mangroves have thicker leaves that live longer, photosynthesize more slowly, and have lower nitrogen content than upland species. Because of the generally higher y-intercepts for the leaf-trait relationships of wetland herbs (except for the G_s vs N_{mass} relationship), differences between mangroves and wetland herbs appear to be in the same direction as between mangroves and upland plants (Fig. 5). The qualitative conclusion from Fig. 5 is that in terms of leaf traits and their relationships, freshwater wetland herbs are more like upland plants than they are like mangroves. This interpretation argues for the relatively large importance of salinity in determining mangrove leaf traits (Ball 1988, 1996). This appears to be a convergent property among mangroves, not a species- (or genus-) specific (Table 1) characteristic. Mangroves cluster together in multivariate ecophysiological space, a result not predicted by leaf-trait relationships of upland plants (Fig. 6), but not unexpected given the restriction of these diverse taxa to a habitat with a common set of severe environmental stressors. In multivariate leaf-trait space (Fig. 6), mangroves are most similar to evergreen trees of tropical wet forests (cf. Ball 1996).

The results for these woody halophytes need to be taken with a large grain of salt, however. Reich et al. (1999) and Shipley and Lechowicz (2000) measured all leaf traits simultaneously on single plants. Therefore, in their data there is a true link between, for example, leaf N content and net photosynthetic rate because these values were measured on the same leaf. In contrast, the mangrove leaf trait data are from “composite” plants; for example, leaf N data and photosynthetic rates for *Bruguiera gymnorhiza* come from different plants and different studies, albeit in the same country. True tests of the hypotheses suggested in Figs. 5 and 6, that mangroves have unique sets of leaf-trait relationships, require long-term data collection on individual leaves of individual plants. Further, the large dataset of Reich et al. (1999) has broad taxonomic diversity and the results are supported even after phylogenetic relationships have been accounted for (Ackerly and Reich 1999). I did not apply phylogenetically independent contrasts to the “composite mangroves” because the sample size for which complete data were available was only nine species, five of which are in the Rhizophoraceae (Table 1). However, the large number of mangrove species, and their representation in many plant families would allow for independent contrast analysis, once more data were amassed.

A research agenda for mangrove macroecology

The two examples presented illustrate that for fundamental questions in mangrove ecology – determinants of diversity and its relationship to ecophysiology – that there is much yet to be done, and much to be learned from the macroecological approach. In presenting a research “agenda” for mangrove macroecology, I suggest only the first steps and the list is not meant to be exhaustive.

Documenting zonation

Although there now are comprehensive regional lists of “true” (*sensu* Tomlinson 1986) mangrove species (e.g. Spalding et al. 1997), data on within-swamp distributions (i.e. zonation) are surprisingly unreliable. Most publications report only dominant species, and describe zones without quantifying them. The minimum data required to assess zonation (or gradients) are:

- A complete list of species in a given forest;
- A measure of the abundance of each species where it occurs;
- Measurements of edaphic parameters and topographic relief wherever composition and abundance data are taken;
- Ideally, data should be taken in contiguous quadrats along transects (Dale 1999).

Quantitative analyses of zonation should begin with testing the null hypothesis of no zonation, and then precede to describe zonation only if the null hypothesis is rejected (cf. Ellison et al. 2000). The analysis should also include an assessment of why available species in the regional species pool do not occur at the study site. Explicit consideration of dispersal probabilities (local current regimes) and biotic factors (especially pre- and post-dispersal propagule predation, competition, facilitation) would improve significantly our understanding of the interplay of local and regional processes in determining within-forest patterns of distribution and abundance.

Global diversity of mangrove ecosystems

Even fewer data are available or organized on the distribution and abundance of mangrove associates, including plants, animals, and microorganisms. Ellison et al. (1999) illustrated that collation and analysis of published data of a single faunal group associated closely with mangroves – littorinid snails – led to stronger inferences about processes leading to global diversification of mangroves. I expect similar increases in our understanding of these forests to come from detailed analysis of distribution patterns of other tight associates, notably vascular epiphytes (Gomez and Winkler 1991; Ellison and Farnsworth 2001), macroalgae (Littler 1989), sessile invertebrates (Rützler 1969; Farnsworth and Ellison 1996), insects (Murphy 1990), crabs (Jones 1984), fish

(Krishnamurthy et al. 1984), and fungi (Kohlmeyer 1984; Hyde and Lee 1995). The long-standing debate on the importance of mangroves as nursery grounds for fish (reviewed in Ellison and Farnsworth 2001) could be clarified if we had a more complete global assessment of the diversity of fish associated with mangroves. If nothing else, a comprehensive assessment of the diversity of mangroves would illustrate the importance of these threatened forests as ecosystems of high diversity, in contrast to their current perception as ecological deserts.

Initially, existing data should be collated to identify geographical gaps in coverage and to determine common methods for subsequent collections. As for analyses of zonation, analyses of global diversity patterns require both distribution and abundance data. Ideally, collection of such diversity data also should include size measurements of associated trees and determination of key ecosystem properties (e.g. salinity, water and soil temperatures, litterfall, so that the data could be used to associate measurements of mangrove productivity (Saenger and Snedaker 1993) with heterotrophic diversity.

Functional traits and ecosystem dynamics

Renewed interest in the relationship between plant functional traits and ecosystem dynamics has been spurred by the recognition that traits that are easily measured, such as SLA, are well-correlated with traits that are more difficult to measure, including rates of photosynthesis and diffusive conductance (Reich et al. 1992, 1997, 1999; Shipley and Lechowicz 2000). Scaling relationships that appear to be independent of species identity (Enquist et al. 1999, 2000; Enquist and Niklas 2001; Niklas and Enquist 2001) should allow these leaf-level traits to be used to develop robust predictions of the responses by mangrove ecosystems to increases in global temperature and sea level. The existing data for mangroves, however, are weak. Only four *Rhizophora* spp. are included in the dataset (Cannell 1981) analyzed by Niklas and Enquist (2001), and the data I culled from the literature (Table 1) to compare with those of Reich et al. (1999) and Shipley and Lechowicz (2000) are “composites”.

Besides needing better, replicated data on correlated leaf traits of individual mangrove trees, more data on measurements of mangrove stand productivity are needed. Saenger and Snedaker (1993) compiled existing data (through 1992) on standing biomass and litterfall of mangroves throughout the world. Their salient result, that the litterfall of individual species increases with plant height and towards the equator, cannot be scaled easily to either mixed-species stands or whole forests. In particular, general allometric theory predicts that overall ecosystem productivity should be independent of plant size (Enquist et al. 2000; Enquist and Niklas 2001; Niklas and Enquist 2001). This theory, like that of Reich et al. (1992, 1997, 1999) on the scaling of leaf traits could be tested independently using data from mangroves. This would be a major contribution to general

ecological theory, and would also let us really decide whether mangroves are different from other biomes in their ecosystem properties. I suspect that they are not, and an integration of “mangrove ecology” into “ecology” would help advance both.

Acknowledgements This paper was presented as a plenary lecture at the International Symposium on Mangroves, 10–12 July 2001, Tokyo. I thank Zvy Dubinsky and Nobutaka Hanagata for inviting me to present this work at the symposium. Peter Reich and Bill Shipley are commended for publishing raw data, without which the analyses on leaf-trait relationships could not have been done. Elizabeth Farnsworth and I have collaborated on mangrove research for many years, and discussions with her of the ideas presented herein have substantially improved this work. Data collection, collation and analysis were supported by grants from the US NSF (DEB 91-07195, 92-53743) and Mount Holyoke College.

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