chapter 16

Mangrove Communities

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Mangrove forests are excellent systems in which to study ecological processes at the community and the ecosystem level. Coastal environments uniquely shape plant physiology, ecological interactions, and patterns of biological diversity, all of which in turn strongly affect dynamics of ecological communities. Occurring at the interface of land and sea, mangroves encompass elements of both terrestrial and marine environments—providing double the fun for the inquiring ecologist. Although mangroves have fascinated natural historians since the days of Theophrastus (Rollet 1981), much remains to be learned about how mangrove communities form, cycle, and exchange materials and energy and withstand and recover from disturbance. Ignored by ecotourists and maligned in literature (Steinbeck, for example, vilified them as "salt-water-eating bushes" full of "quiet, stalking murder" [1941: 123]), their relative inaccessibility has discouraged both extensive resource exploitation and intensive ecological experimentation until quite recently. A comprehensive understanding of community-level processes in mangrove forests becomes all the more critical as the need to conserve, manage, and restore these systems intensifies throughout the world. This chapter reviews facets of the ecology of mangrove communities, with particular attention to their biogeography and physiological ecology; interactions among their plant and animal associates; community-wide responses to disturbance; and the maintenance and regeneration of mangrove ecosystems in the face of anthropogenic stresses. Despite 600 years of research, our understanding of these ecosystems is still far from complete, and new phenomena remain to be discovered.

WHAT ARE MANGROVES?

Authors have used the word *mangrove* to denote both a type of plant and a type of ecosystem. For clarity here, we distinguish the individual "mangrove" species from the wetland community ("mangal") of which it is the defining feature. Simply put, the term *mangrove* refers to any woody, tropical halophyte that is an obligate inhabitant of mangal (Tomlinson 1986). Around the globe, some 54–70 species (including hybrids) in 20–27 genera and 16–19 families fit comfortably into this broad category (the lower values according to Tomlinson [1986]; upper values according to Cronquist [1981] and Duke [1992]). Some generalist species are more challenging to classify using this definition—the Neotropical tree *Conocarpus erectus* (Combretaceae) or some of the rattan palms (*Calamus* spp.; Arecaceae), for example. These species frequently occur in mangal, but do not appear to be *restricted* to saline areas and may penetrate into freshwater swamps. Certain true mangrove species also may opportunistically occur in freshwater swamps, but this is a rare phenomenon. Mangroves vary both in their salinity tolerance and the degree to which salinity may be necessary to maintain their growth and competitive dominance—an important focus of research that we discuss later in this chapter.

BIOGEOGRAPHY OF MANGROVES

Global Distribution and Diversity

Mangroves grow throughout the tropics wherever the average monthly minimum air temperature is 20°C (Chapman 1976). The winter 20°C seawater isotherm generally limits the poleward extension of mangroves, although prevailing warm currents and a broader tolerance of environmental extremes allow the extension of *Avicennia marina* (Avicenniaceae) southward to the north island of New Zealand (Duke et al. 1998a), whereas its congener *A. germinans* ranges northward to the southern coast of Louisiana (U.S.). Overall species richness of mangroves declines from a peak of about 30 species (per 15° longitude) in Southeast Asia to < 5 species in the Caribbean (Figure 16.1). Explaining this anomalous (sensu Ricklefs and Latham 1993) biogeographic pattern has preoccupied biogeographers since the turn of the century (see Ellison et al. 1999 for a review).

Early researchers hypothesized that all mangrove taxa originated in the Indo-West Pacific (e.g., Schimper 1903; Aubréville 1964; Ricklefs and Latham 1993), but more recent studies have emphasized the role of continental drift and vicariant events in determining global patterns of mangrove species diversity (McCoy and Heck 1976; Duke 1995; Duke et al. 1998a; Saenger 1998; Ellison et al. 1999). These latter studies hypothesize a Cretaceous-Tertiary origin of most mangrove genera (and some modern species) on the shores of the Tethys Sea. Modern distributions are then thought to result from: in situ diversification following dispersal across the proto-Atlantic and Pacific; continental drift; the closure of the Tethys Sea and global cooling (in the late Miocene ~18 Mya); and finally, the uplift of the Panamanian Isthmus (~3 Mya), which isolated the Pacific mangrove flora from the Atlantic flora. The mangrove fossil record (reviewed in Ellison et al. 1999), biogeographic comparisons of associated fauna (McCoy and Heck 1976; Saenger 1998; Ellison et al. 1999), biochemical studies (Dodd et al. 1995; Rafii et al. 1996), and genetic analyses (Duke et al. 1998b) all support the vicariance model. Current debates focus on the direction(s) of dispersal of mangroves from the Tethys into the proto-Atlantic and Pacific regions (e.g., van Steenis 1962; Specht 1981; Mepham 1983; Duke 1995; Plaziat 1995; Saenger 1998; Ellison et al. 1999). Similar analyses have been applied to global biogeographic patterns of coral diversity (McCoy and Heck 1976; Veron 1995) and seagrass diversity (Heck and McCoy 1979; Specht 1981) with parallel results. These methods can be used to analyze global biogeographic patterns of most species assemblages.

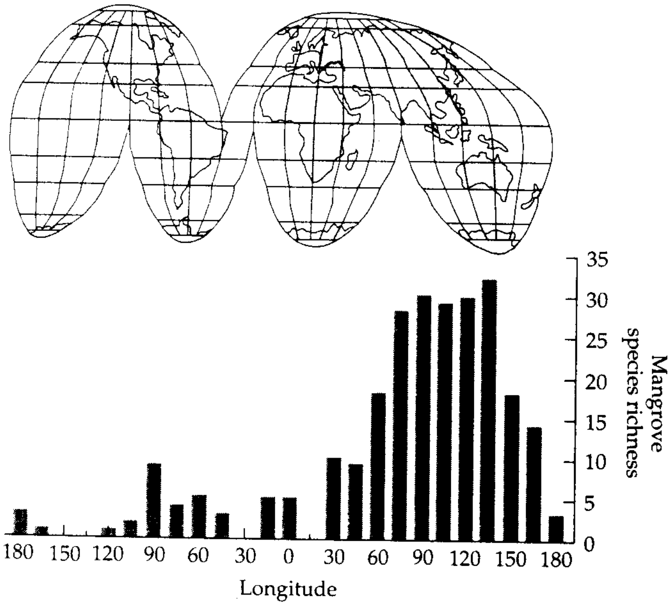


Figure 16.1 A map of the world showing mangrove distribution, adapted from Tomlinson 1986, as well as gradients of species richness illustrating the biodiversity anomaly.

Continental and Regional Diversity

The global patterns illustrated above (Figure 16.1) belie substantial continental and regional variation in mangrove species richness. For example, the Indo-West Pacific as a whole has 40–50 species of mangroves, of which 39 are found in Australia. Within Australia, however, species richness ranges from 25 species in northernmost Queensland to only 5–10 species in Western Australia (Duke 1992). On the western coasts of Africa and Australia, aridity (< 30 mm rainfall per month) dramatically reduces mangrove occurrences (Duke 1992; Saenger 1998), but species richness of mangroves does not vary with rainfall patterns in Central and South America (Ellison, in press). In the Neotropics, species richness is highest on the Pacific coasts of Columbia, Panama, and Costa Rica and declines with latitude (Duke et al. 1998a). Limits to waterborne dispersal of mangrove propagules likely constrain mangrove distribution within regions, but data addressing this hypothesis are sparse (Rabinowitz 1978a; Steinke 1986; Ellison 1996; Sun et al. 1998). Overall, when compared with studies of patterns of both global species richness (above) and local species distributions (below), there is a surprising lack of analysis of continental and regional-scale patterns of mangrove diversity (Duke et al. 1998a).

Local Diversity and Zonation

Within a site, individual mangrove species appear on first glance to occupy distinct and discrete zones of tree species along a presumed tidal gradient (MacNae 1968; Chapman 1976; Smith 1992). Certain species are noted to occupy the seaward fringes of swamps, whereas others occur more commonly in the upland reaches, albeit with considerable overlap (Watson 1928; Smith 1992). Such zonation has been variously attributed to: interspecific differences in tolerance of edaphic factors that co-vary with tidal elevation (Watson 1928; MacNae 1968; Ellison and Farnsworth 1993; McKee 1993, 1995); sorting of dispersed propagules during stranding (Rabinowitz 1978b); interspecific competition (Ball 1980); and frequency-dependent preferences of seed predators (Smith 1987; Smith et al. 1989; but see Sousa and Mitchell 1999). However, the identity and taxonomic affiliation of these species shifts between locales in the Neo- and Paleotropics (e.g., different *Avicennia* species occur low in the intertidal in Australasian mangal, but high in the intertidal of Caribbean mangal). In a critical review of available data bearing on hypotheses controlling mangrove zonation, Smith (1992) says that "there appear to be many papers which give specific examples of mangrove zonation and few papers which provide rigorous experimental tests of the hypotheses which attempt to explain why mangrove zonation occurs." Recent experimental work (cited above) provides conflicting results and does not yet allow for generalizations about the existence of zonation and the ecological mechanisms maintaining such zonation.

Other intertidal communities have provided fertile ground for testing hypotheses of species zonation (e.g., Connell 1961; Bertness and Ellison 1987) and developing statistical tests for zonation (Pielou 1977; Underwood 1978; Dale 1988), but species zonation in mangal rarely has been quantified. Recent statistical analyses have failed to detect significant, repeatable patterns of discrete zonation in Australian riverine mangal (Bunt 1996) or the Sundarbans of India (Ellison et al. 2000). Because different mangrove species vary in their tolerances to underlying edaphic gradients, considerable overlap among species occurs, and discrete zones are difficult to identify. Rather than focusing on the description of discrete vegetation zones in mangal, investigators should focus on the variation of patterns of species co-occurrence across tidal gradients (Ball 1998). Experimental work demonstrates that, as in other coastal communities, multiple physiological (Ball 1998) and biotic factors (McKee 1995) *in combination* influence recruitment of mangrove seedlings into the adult canopy and their patterns of occurrence within mangal. Patterns of and processes controlling mangrove distributions at local scales warrant careful and critical re-appraisal (Duke et al. 1998a), especially as we begin to characterize mangal at ever-larger scales using remote-sensing and other technologies for spatial analysis and community classification (Blasco et al. 1998). Furthermore, the role of human land-use history (e.g., selective harvesting and alteration of substrate) in determining mangrove profiles has been all but ignored in the majority of studies that take place in apparently pristine or protected mangrove swamps; realistic ecological paradigms must incorporate this ubiquitous force on communities.

CONVERGENT PROPERTIES OF MANGROVES AND MANGAL

When we think of "mangroves," we typically envision peculiar trees with tangled prop roots that spend much of their time inundated by tides. However, mangroves assume a variety of life forms reflecting the diversity of their origins: palms, shrubs, and ferns are all represented in mangal. Likewise, mangals exhibit a range of physiognomies that reflect the dynamic geomorphology, storm frequency, and nutrient status of the substrate that they inhabit: from squat, scrubby stands on exposed, hypersaline carbonate flats to 40-meter-tall gallery forests lining the rich alluvium of river mouths (Figure 16.2; Lugo and Snedaker 1974; Twilley 1995; Feller 1996; Lugo 1997). Even single mangrove species can display an impressive range of appearances depending on the edaphic and biotic conditions in which they are found.

Across this diversity in phenotypes and species, mangroves share certain notable commonalities in physiology, architecture, and life history that appear to reflect convergent "solutions" to evolutionary "challenges." Such characters have important implications for mangrove community interactions and may lead to convergences in ecosystem-level properties. For example, physiological traits can affect local, regional, and global patterns of distribution; plant-plant and plant-animal interactions may be mediated by architecture; and plant life-histories can determine the timing and effectiveness of responses to disturbance. Mangroves afford such a species-rich model system in which to identify and study convergent (pleisiomorphic) traits. It is tempting to interpret many shared mangrove characters as "adaptive." However, as others have admonished in the evolutionary literature (Gould and Lewontin 1979; Harvey and Pagel 1991), we caution that such traits must be evaluated critically with respect to their benefits and costs to fitness, their pleiotropic interactions with other traits, and the phylogenetic constraints under which they may have evolved.

Physiological Convergence

Within and among mangrove species, subtle physiological adjustments regulate responses to salinity, bright tropical sun, variable and often low nutrient availability, flooding, soil anoxia, and tidal action. All of these responses further influence community- and ecosystem-level processes in mangal.

RESPONSES TO SALINITY. Despite living in a saline environment, mangroves require fresh water. In order to obtain the fresh water required for growth, mangroves must maintain a tissue water potential below the osmotic potential of the very salty substrate (Naidoo 1985; Sperry et al. 1988; Sternberg et al. 1991). Ball (1996) provides a comprehensive recent review of many of the mechanisms by which mangroves achieve such a balance. All mangrove species exclude most of the sodium chloride and other dissolved salts in sea and soil interstitial water at the roots via a poorly understood ultrafiltration process (Scholander et al. 1962; Scholander 1968), even as transpiration rates increase (Ball 1988). Typical of other halophytes, mangroves accumulate what sodium and chloride ions do enter the transpiration stream in leaf vacuoles (where they are sequestered away from sensitive metabolic centers in the cell) and also may synthesize compatible solutes in other cellular compartments to maintain osmotic equilibrium (Popp et al. 1993). Some mangrove species possess salt glands in the leaves from which they excrete excess sodium (Dschida et al. 1992; Fitzgerald et al. 1992). Those without glands can accommodate rising sodium concentrations by exchange with potassium ions (Werner and Stelzer 1990), cell expansion (leaf growth), and increased leaf succulence (Camilleri and Ribi 1983; Ball 1996; see also Feller 1996 on leaf schleromorphy as an adjustment to nutrient availability). Anatomical differences in leaves may also be accompanied by differences in xylem anatomy—especially shorter and thicker vessels—that resist cavitation and embolism under very negative water potentials (Sperry et al. 1988). The solute content of leaves, together with other water-conserving foliar characteristics like succulence, pubescence, and the presence of a thick cuticle, may in part select for specializations on the part of insect folivores that result in niche-parti-

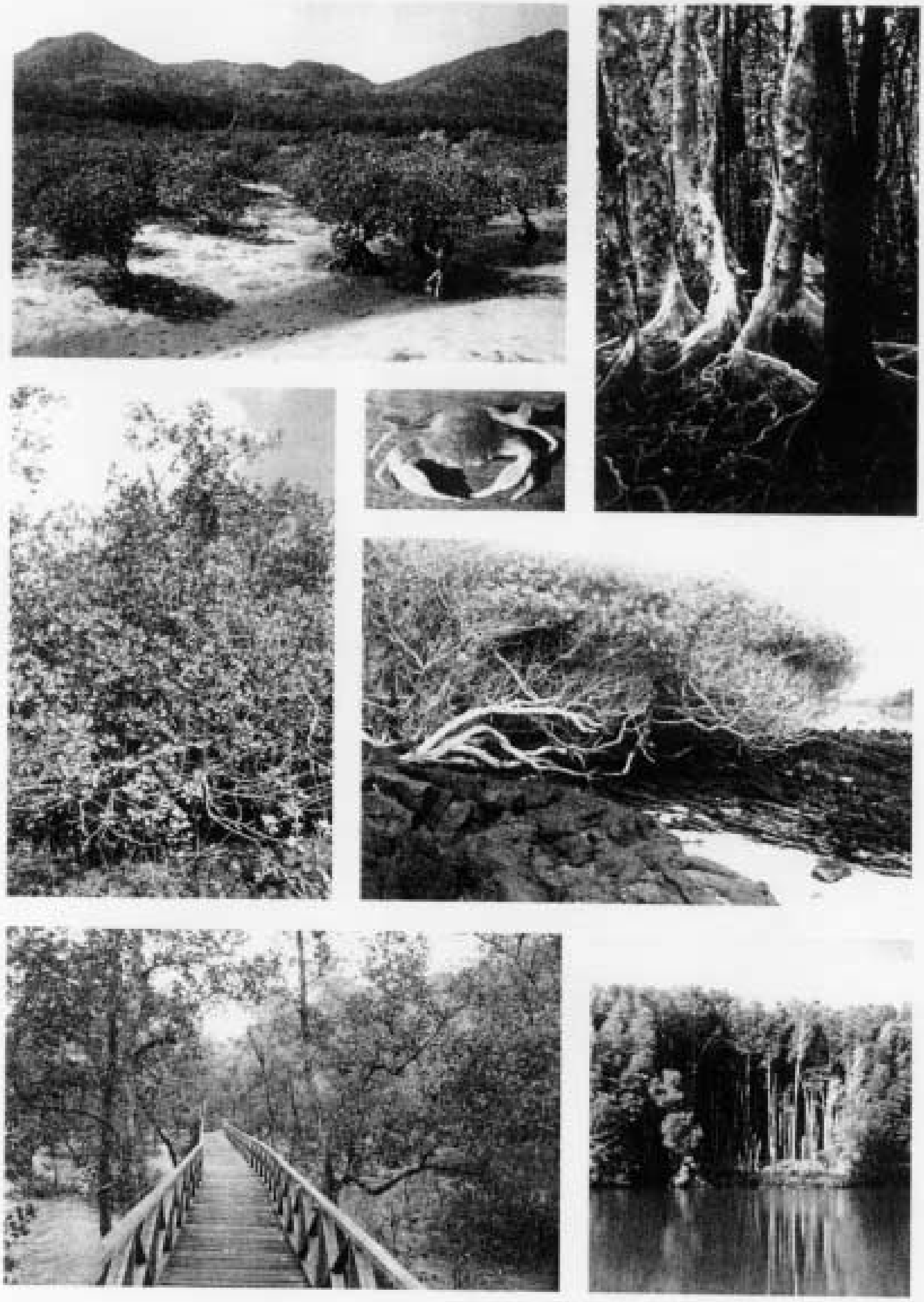


Figure 16.2 Mangrove communities throughout the world. Clockwise from top left: *Ceriops* mangal in a semi-arid environment (Australian Institute of Marine Sciences, Townsville, Australia); *Xylocarpus* stand in the very wet forests of Kosrae, Federated States of Micronesia; *Rhizophora* thicket on bare lava (Galápagos Islands, Ecuador); Managed stand of *Rhizophora apiculata* (Matang, Malasyia); Boardwalk through the *Sonneratia* fringe of Bako National Park (Sarawak); *Rhizophora* fringe with the endemic *Heritiera fomes* emerging from the canopy (Sundarbans Biosphere Reserve, India). The crab in the center is *Scylla serrata*. All photographs by the authors.

tioning among mangrove species (Murphy 1990; Farnsworth and Ellison 1991; Veenakumari et al. 1997).

PHOTOSYNTHESIS AND WATER-USE EFFICIENCY. Studies across six genera (*Aegiceras, Avicennia, Bruguiera, Ceriops, Rhizophora,* and *Sonneratia*) illustrate that mangroves also tend to exhibit high water-use efficiency, as stomatal conductance remains low even as moderate photosynthetic rates are achieved (Ball 1988; Clough and Sim 1989; Cheeseman 1994). High water-use efficiency enables mangroves to transpire, to withdraw water very slowly from the soil, and hence to slow a buildup of salt around the roots (Ball and Passioura 1993). Mangroves also can flexibly increase water-use efficiency when exposed to increased soil salinities (Ball 1996) and elevated atmospheric carbon dioxide (Ball et al. 1997; Farnsworth et al. 1996). The conservative photosynthetic rates exhibited by mangroves tend to saturate at relatively low light levels (< 1000 μmol m^{-2} s^{-1}), given the high irradiance characteristic of exposed, tropical coasts (> 2000 μmol m^{-2} s^{-1}). Mangrove leaves must therefore accommodate an excessive light load whose excitation energy can readily damage photosystems. Mangroves may dissipate this energy and avoid photoinhibition by producing protective xanthophyll pigments in sun leaves (Lovelock and Clough 1992) and UV-absorbing phenolics (Lovelock et al. 1992) at the cost of reduced efficiency of quantum yield at low irradiance (Björkmann et al. 1988; Farnsworth and Ellison 1996b). Allocation to pigments and other secondary compounds may entail a nitrogen cost and alter the palatability of leaves to consumers and detritivores—an idea that has not yet been explored.

Mangroves can also adjust leaf display angle, leaf size, specific leaf area, leaf turnover rates, and whole-plant deployment of leaves to evade high light and elevated leaf temperatures (Ball 1996; Farnsworth and Ellison 1996b). Thus, light, salinity, and high temperatures act synergistically on foliar architecture, chemistry, and physiology—characters that themselves change as both leaves and whole mangrove plants age (Farnsworth and Ellison 1996b). Although mangrove leaves may look superficially homogeneous, there is considerable heterogeneity within and among individuals and species that have implications for carbon gain, evapotranspiration, and leaf processing by consumers at the system level.

PHYTOHORMONES AND VIVIPARY. Although some aspects of mangrove physiology have been well studied, little is yet known about how plant hormones regulate mangrove responses to stresses such as salinity. Changes in phytohormone action may figure importantly in the evolution of mangrove traits such as viviparous reproduction (Farnsworth and Farrant 1998) and prolonged floating of propagules during dispersal (Smith et al. 1996). Precocious seed germination (in which the embryo never enters physiological dormancy) and its extreme variant, viviparous reproduction (in which there is translocation of maternal resources to a constantly growing embryo) are unusual traits among angiosperms in general, but have arisen in nine genera of six families of mangroves. Comparisons with other nondormant wetland plants and with viviparous mutants suggests a common physiological basis for this phenomenon, namely reduced production of abscisic acid and stress proteins that are involved both in the enforcement of dormancy in the developing embryo and the adjustment of the maternal plant to osmotic stress (Farrant et al. 1996; Farnsworth and Farrant 1998). The physiology of vivipary remains a fruitful area for further study, and mangroves constitute an excellent model system for comparative study of seed ontogeny in general. The fitness advantages of this apparent convergence have been articulated in the literature since the early 1900s (reviewed by Farnsworth 1997), but there are attendant maternal costs with investing energy in producing numerous propagules that are highly apparent to herbivores and that can remain on the parent tree for up to a year (Pannier 1962; Farnsworth and Ellison 1997a).

ROOTS. In the underlying peats and mucks, mangrove roots encounter saturated, anoxic, and saline soils, making nutrient and water extraction difficult for the plant. Many mangroves possess wildly elaborated root systems, including knees, pneumatophores, stilt roots and plank roots that are studded with lenticels (air pores) and consist largely of aerenchyma. These systems permit passive diffusion of oxygen from the atmosphere and boundary layer into root tissues during low tides (Curran 1985). Simultaneously, however, roots leaking oxygen oxidize the soil surrounding them (Thibodeau and Nickerson 1986). The impact of localized soil oxidation on microbial ecology and nutrient availability for different mangrove species deserves further study (Sherman et al. 1998). Mangrove roots also afford habitat for burrowing intertidal organisms, especially crabs, which in turn oxygenate and nutrify soils (Smith et al. 1991), and for fouling epibenthic species that may have important impacts on the host plants (Farnsworth and Ellison 1996b; see "Animal-Plant Interactions in Mangal," following).

Architectural and Physiognomic Convergence

The virtually impenetrable thicket of aerial roots may be one of the most distinctive features of mangroves, but they share other architectural attributes as well. Tomlinson (1986) observed that many mangrove species seem to converge on Attim's or Petit's architectural models of plant form (sensu Hallé et al. 1995), in which a single monopodial trunk gives rise to equivalent branches initiated at fixed angles. Many mangroves loosely resemble a candelabra, in which clusters of leaves are held far from each other at the tips of twigs. Hence, even in dense forest stands some dappled light reaches the understory (by our measurements ~10% of full sun on average), and a mangrove forest is rarely "dark" compared to other tropical forests (cf. Chazdon and Fetcher 1984). The mangrove light environment is made more complex by water reflectivity and diffraction, which complicate unidimensional models of light capture.

Despite their adherence to a few, relatively simple baüplans, mangroves can be quite plastic in form. Hypersaline or drought-stressed areas tend to support sparse assemblages of scrubby trees that are short, brittle, and exceedingly slow-growing relative to trees growing in riverine or basin mangals (Figure 16.2). Lugo and Snedaker (1974) recognized no less than six mangal typologies in the Neotropics alone, which arise at least in part from the geomorphological milieu in which the trees occur and from differential limitation of nutrients, especially phosphorus (Feller 1995). Primary productivity, hydrology, litter turnover, responses to stress, and the species composition of faunal associates all vary among these contrasting physiognomic types (Lugo and Snedaker 1974; Lin and Sternberg 1992; Twilley 1995), factors that must be accounted for when modeling ecosystem properties at a landscape scale. Geomorphological processes such as erosion and sedimentation regimes can significantly influence growth rates and productivity of mangroves, even where species composition and physiognomy appear superficially similar (Ellison and Farnsworth 1996b).

Community-Level Similarities among Mangals

THE MANGROVE UNDERSTORY. The apparent lack of a layer of understory plants in mangal has stimulated considerable discussion (Janzen 1985; Corlett 1986; Lugo 1986; Snedaker and Lahmann 1988). With the exception of transient carpets of mangrove seedlings produced in seasonal reproductive flushes (Ellison and Farnsworth 1993), the understory generally lacks the shrubs, vines, and other mid-size plants that typically stratify more diverse upland tropical forests. Janzen (1985), working in the Neotropics, suggested that the filtered light of the understory is insufficient to support growth of many non-mangrove species that are simultaneously contending with edaphic stress—a hypothesis elaborated on by Lugo (1986) and Snedaker and Lahmann (1988) that remains largely untested in the field. Observations of paleotropical mangal, however, reveal a richer collection of understory species (Corlett 1986), although Snedaker and Lahmann (1988) considered these data to reflect high levels of disturbance within the studied mangal. Additionally, the pantropical fern *Achrostichum aureum* can monopolize the ground level in mangal, dramatically altering patterns of mangrove seedling recruitment (Srivastava et al. 1987). Finally, in many parts of the world, grapsid crabs rapidly consume seeds and fallen propagules of mangroves (Smith et al. 1989), and these crabs likely would consume the occasional non-mangrove recruit as well (Snedaker and Lahmann 1988). Crabs, disturbance regimes, light environments, and other factors differ significantly around the world, and no single explanation for the lack of a mangrove understory is likely to have universal applicability. These observations highlight the importance of comparing mangrove structure and function across a broad array of sites. Of current concern is the potential for invasive plant species to colonize this underused spatial resource, especially where human or natural disturbances have altered canopy density and ecotone boundaries (Smith et al. 1994). Lugo (1998) hypothesizes that most invasive species will have difficulty penetrating mangroves unless given the opportunity by large disturbance events.

ECOSYSTEM DYNAMICS. For many years, mangrove forests worldwide were viewed as identical, essentially detritus-based ecosystems that exported significant amounts of carbon and nutrients to adjacent seagrass meadows, coral reefs, and the open ocean (Odum and Heald 1975). Although research in the intervening two decades has shown this model to be overly simplistic (reviewed by Alongi el al. 1992; Robertson et al. 1992; Alongi 1998), ecosystem-level processes in mangals throughout the world do share many characteristics. In most mangrove forests, 30–80% of fallen leaves, branches, flowers, and fruits are consumed rapidly and directly by sesarmid crabs (Robertson et al. 1992), whereas < 50% of the litter is decomposed microbially. Carbon export to adjacent systems varies among mangals by as much as two orders of magnitude (Twilley et al. 1992) and is controlled principally by local hydrodynamics (Wolanski et al. 1992). Most adjacent pelagic food webs are based on epiphytic algae and phytoplankton, rather than on mangrove detritus itself (Newell et al. 1995). Nutrient retention in mangal is surprisingly high (Alongi et al. 1992; Alongi 1998), and fewer nutrients appear to be exported to adjacent ecosystems than thought previously. Complete ecosystem models are available only for two mangals—Hitchinbrook Island, Australia (Alongi et al. 1992; Roberston et al. 1992), and Rookery Bay, Florida (Twilley 1985; Twilley and Chen 1998)—so global generalizations regarding ecosystem functioning in mangal will require additional research in other geomorphological and climatic settings. Given the paucity of data, it is probably premature to assign ecosystem "functions" to the many taxonomically diverse components of the mangal ecosystem.

COMMUNITY ECOLOGY OF MANGROVES

Plant-Plant Interactions in Mangal

INTERACTIONS AMONG MANGROVES. Because mangals are relatively simple systems in terms of tree species composition, the probability that conspecifics will co-occur, and presumably interact in ecologically meaningful ways, is high. Thus, it is somewhat surprising that intraspecific interactions—and in fact, interspecific interactions—among mangroves have received very little attention in the literature to date. The few studies that have addressed this issue have examined how seedlings are influenced by adult trees. McKee (1995) and Clarke (1993) provided evidence from field surveys that seedling densities of *Rhizophora mangle* and *Avicennia marina* (in Belize and Australia, respectively) are correlated with proximity to reproductive conspecifics; by contrast, establishment rates of *Rhizophora racemosa* and *Avicennia bicolor* seedlings in western Costa Rica show no such correlations (Jiménez and Sauter 1991). These differences may reflect differential consumption of propagules by grapsid crags in different parts of the world (Smith et al. 1989). All of these processes are mediated by dispersal dynamics and subsequent establishment of mangrove propagules, of which little is known (Steinke 1986; McGuinness 1997). Reflecting this uncertainty, the numerous hypotheses that purport to explain how viviparous reproduction and differential dispersability confer selective advantages on buoyant mangrove propagules (Elmqvist and Cox 1996) remain to be tested.

In any case, both pre- and post-dispersal seed and seedling herbivores can seriously alter the availability of viable propagules establishing in an area (Rabinowitz 1977; Smith et al. 1989; Robertson et al. 1990; Dadouh-Guebas et al. 1997; Farnsworth and Ellison 1997a). Mature plants also can act as local sources for other types of herbivores on seedlings (Onuf et al. 1977). Ellison and Farnsworth (1993), for example, observed that rates of folivory were significantly lower on *Rhizophora mangle* seedlings growing in an area where the canopy of adult conspecifics had been removed. The canopy removal experiment described in Ellison and Farnsworth (1993) also demonstrated that seedlings in gaps grew significantly faster than those suppressed under a canopy, a result that was later supported with observations comparing naturally occurring sun and shade populations (Farnsworth and Ellison 1996). Other studies of mangrove gap dynamics following storms or other disturbances are beginning to yield data on the successional regeneration of mangal (Roth 1992; Smith et al. 1994). However, almost nothing is known about potential below-ground interactions among mangroves or about the roles of plant competition and facilitation in shaping mangal. Ball (1988) speculated that mechanisms of competitive exclusion may contribute to species richness patterns along salinity gradients; the experiments have yet to be done to test this interesting hypothesis. In addition to transplant studies (Smith 1987; Ellison and Farnsworth 1993; McKee 1995; Osunkoya and Creese 1997), well-controlled, experimental field manipulations of plant densities, canopy structure, and edaphic factors are needed in order to make strong inferences about the importance of plant-plant interactions in mangrove community ecology. We also need to understand regeneration following canopy removal in large stands managed for forestry (see "Management, Restoration and Conservation of Mangal," following).

MANGROVES AND THEIR EPIPHYTES. Although understory plants are uncommon in mangal, vascular plants do inhabit the mangrove canopy, which itself does not suffer from the same edaphic constraints of the peat surface. Epiphytes are still subject to salinity stress from salt spray, and the species diversity of ephiphytic orchids, bromeliads, mistletoes, and ferns in mangal (Rico-Gray et al. 1989; Goldstein et al. 1990; Gomez and Winkler 1991; Murren and Ellison 1996) is substantially lower than that found in upland tropical forests. Although most of these epiphytes exhibit few direct interactions with mangroves, mistletoes do affect water, carbon, and nitrogen balances of their mangrove hosts (Orozco et al. 1990). One of the common orchids in Neotropical mangal, *Schomburgkia tibicinis*, hosts ants in its enlarged pseudobulbs (Rico-Gray et al. 1989), but the mealy-bugs tended by the ants reduce the fitness of the orchid (Rico-Gray and Thien 1989).

Algae and cyanobacteria grow epiphytically on roots, stems, and leaves of mangrove trees (Lambert et al. 1987; Littler et al. 1989; Steinke and Naidoo 1990; Sheridan 1991; King and Puttock 1994; Farnsworth and Ellison 1995; Pedroche et al. 1995; Saifullah et al. 1997). Because their growth is usually limited by both light and nutrients, these epiphytes account for a variable but generally small fraction of the total primary productivity in mangal (Lapointe et al. 1987; Alongi 1994, 1998; Dawes 1996). In some mangrove forests, however, nitrogen fixation by epiphytic cyanobacteria may contribute substantially to the total nitrogen budget of the ecosystem (Alongi et al. 1992; Sheridan 1992). Algal and bacterial epiphytes on fallen leaves also are the dominant contribution of mangroves to offshore food webs (Newell et al. 1995).

Animal-Plant Interactions in Mangal

REPRODUCTION AND POLLINATION. The flowers of some mangrove species support a diverse—and in some areas economically important—fauna of native pollinators. The honey derived from *Avicennia* flowers and the nectar from *Nypa fruticans*, for example, are important food sources for humans and other consumers in both Caribbean (Padrón et al. 1993) and Indo-Pacific (Tomlinson 1986) mangal. The exuberant, pollen-rich flowers of *Sonneratia* support the same populations of bats that fertilize the coveted *Durio* fruit trees of Southeast Asia (Marshall 1983). Other mangrove species appear to be wind-pollinated (Tomlinson 1986) or cleistogamous (Klekowski et al. 1994), but the breeding systems and plant-pollinator interactions of mangroves worldwide have not been documented systematically. Rates of outcrossing will influence the heterozygosity, genetic diversification, and fitness of mangroves. Conservation of mangroves and their pollinators should be informed by a more comprehensive understanding of their population genetics, mutation loads, and viability (Klekowski and Godfrey 1989; Lowenfeld and Klekowski 1992), as well as morphometric (Dominguez et al. 1998) and biochemical variability (Dodd et al. 1998).

HERBIVORY. In addition to their roles in establishment described above, herbivores can clearly influence whole-plant growth of mangroves throughout the world. Neotropical mangals host a diverse insect fauna, including generalist, species-specific, and organ-specific herbivores (Onuf et al. 1977; Farnsworth and Ellison 1991, 1993; Feller 1995; Feller and Mathis 1997). These insects can remove 10–25% of primary production (Farnsworth and Ellison 1991), potentially slow growth rates of understory seedlings (Ellison and Farnsworth 1993), influence leaf form and secondary chemistry (Lacerda et al. 1986; Schoener 1987), and alter the branch architecture of mature trees (Feller and Mathis 1997), and forests (Feller and McKee 1999). The insect fauna of paleotropical mangal is at least an order of magnitude more diverse than that of the Neotropics (Murphy 1990), paralleling the global pattern of mangrove species richness. Although insect herbivory in paleotropical mangal has not been studied extensively (Murphy 1990; Lee 1991), there are several reports of insects defoliating entire stands of trees (Newberry 1980; Piyakarnchana 1981; Whitten and Damanik 1986; Anderson and Lee 1995; McKillup and McKillup 1997).

Marine invertebrates consume mangrove leaves and roots as well. Grapsid crabs not only consume fallen leaf litter and propagules, but also eat leaves, flower buds, flowers, and fruits directly off the tree (Warner 1967; Beever et al. 1979; Farnsworth and Ellison 1991). Isopod crustaceans burrow into developing mangrove roots, reducing root growth rate by up to 50% (Rehm and Humm 1973; Perry 1988; Ellison and Farnsworth 1990). Major mammalian herbivores occur in paleotropical mangal. Proboscis monkeys eat mangrove leaves in Borneo, deer forage on shoots in the mangals of the Indian Sundarbans and the Andaman Islands, and hippopotami frequent the mangals of South Africa. Interactions between these large mammals and mangrove plants or forests have not been studied. These interactions may become increasingly important as mangals provide refugia for mammals driven out of their primary, upland habitats because of large-scale anthropogenic disturbance (Ellison, in press).

INTERACTIONS WITH NON-CONSUMER MARINE INVERTEBRATES. Mangrove forests share characteristics of both hard-substrate and soft-sediment benthic communities. The peaty mucks in which mangroves grow have a high silt content and are inhospitable to most suspension- and filter-feeding invertebrates. In contrast, mangrove roots and trunks represent islands of hard substrate surrounded by soft sediments. Depending on local tidal amplitude and geomorphological setting, roots and trunks can constitute either subtidal or intertidal habitats. All community-level studies to date have focused on one or the other of these two habitats within mangal. However, this dual physical setting presents unique opportunities for comparative studies of the relative importance of ecological processes shared by soft-sediment and hard-substrate communities.

Mud-dwelling sesarmid, portunid, and ocypodid crabs, predominantly in the genera *Cardisoma, Scylla, Sesarma, Uca,* and *Ucides,* are ubiquitous in mangal (Jones 1984; Tan and Ng 1994; Keenan et al. 1998; Figure 16.2). As described earlier in this chapter, these crabs may directly process the bulk of the leaf litter produced in a given season and can directly alter plant reproductive effort and success. Further, the burrowing activity of these crabs oxygenates the peat substrate, alters the distribution of toxins within the peat, and changes local microtopography (Smith et al. 1991; reviewed by Lee 1998). These activities also significantly affect distribution and abundance patterns of sediment epifauna and meiofauna (Dye and Lasiak 1986; Olafsson 1996). These results are directly analogous to those derived from similar studies conducted in temperate salt-marshes (Hoffman et al. 1984; Bertness 1985). Because mangrove crabs are a prized food source, they are harvested in large quantities in many parts of the world (Hudson and Lester 1994; Fouda and Almuharrami 1995; Blakensteyn et al. 1997). Although this practical interest in mangrove crabs has led to much research on the autecology of these species, the impact of harvesting crabs on community and ecosystem dynamics within mangal has been considered only rarely (Fouda and Almuharrami 1995).

As one moves out of the soft sediment and onto the hard mangrove roots, the species composition of the invertebrate communities changes dramatically. Where tidal amplitude is relatively low (generally < 1 m) and peat banks are undercut by tidal action, roots are continuously submerged and host a luxuriant community of sessile filter- and suspension-feeders dominated by ascidians and sponges (Rützler 1969; Ellison and Farnsworth 1992; Goodbody 1993, 1994; Farnsworth and Ellison 1996a; Bingham and Young 1996). As with many other subtidal fouling communities, the patterns of distribution and abundance of mangrove-root epibionts is controlled at local scales by larval recruitment dynamics and at larger scales by physical factors, current regimes, and stochastic events (Farnsworth and Ellison 1996a; Bingham and Young 1996).

Whereas most of these epibionts do not interact directly with the plants, the dominant group within this fouling community, massive sponges, have both direct and indirect effects on plant growth. The presence of sponges precludes colonization of, and subsequent damage to, roots by isopod crustaceans (Ellison and Farnsworth 1990); this indirect positive effect of sponges on root growth appears to be mediated principally by the physical structure of the sponges themselves. Massive sponges also are a significant nitrogen source for mangroves (Ellison et al. 1996). When present on roots, massive sponges can induce fine rootlet formation by mangroves. These rootlets absorb nitrogenous wastes (principally ammonium) produced by the sponges and also leak significant amounts of carbon compounds that are incorporated into the sponge tissue (Ellison et al. 1996). Based on these data, we estimate that in fringing mangroves in Belize, Central America, 5–10% of the plant's nitrogen uptake may be derived from massive sponges. Sponge-dominated assemblages on mangrove roots are found most commonly and have been studied only in the Caribbean basin. We also have encountered them on mangrove roots on the Pacific Islands of Hawai'i, Pohnpei, and Palau, in the Indian Ocean on the Andaman and Nicobar Islands, and the Kenyan coast, but the relationships between root fauna and their host plants in these areas are as yet unknown.

Intertidal mangrove-root communities are dominated by barnacles and oysters (Mattox 1949; Bacon 1971; Pinto and Wignarajah 1980; Ross and Underwood 1997). Barnacle cover can reduce root growth rates significantly (Perry 1988), but consumption of barnacles by predatory snails ameliorates this negative effect (Ellison and Farnsworth 1992). Casual observations suggest that heavy colonization by oysters on roots could lead to their mechanical damage or breakage, but this has not been studied. Like mangrove crabs, mangrove oysters, especially those in the genus *Crassostrea*, are consumed worldwide by humans and other primates (Mattox 1949; Pinto and Wignarajah 1980; Fernandes 1991). In contrast with crabs, however, most mangrove oysters destined for human use are cultivated (e.g., Quesada et al. 1985; Vélez 1991), and there may be little direct impact to mangal resulting from oyster harvests.

Fungi and Pathogens

There is a very high diversity of fungal species in mangal, and dozens of new species are described annually (see reviews by Kohlmeyer 1969; Hyde and Jones 1988; Steinke and Gareth-Jones 1993; Hyde et al. 1998). These marine fungi are the dominant agents of decomposition of mangrove wood and leaves (Swift and Cragg 1982; Newell 1992; Tan and Leong 1992; Kohlmeyer et al. 1995; Hyde et al. 1998) and are hypothesized to play a significant role in nutrient cycling within mangal (Hyde and Lee 1995). Fungi that grow on living leaves are the primary food source for the mangrove periwinkle *Littoraria angulifera* (Kohlmeyer and Bebout 1986), whereas others decompose fallen leaf litter (Newell 1992; Hyde and Lee 1995; Hyde et al. 1998). In a recent review, Hyde et al. (1998) hypothesized that the high diversity of mangrove fungi likely includes many "redundant" species, in terms of their functional roles in mangrove ecosystem dynamics. This hypothesis merits additional research, given the apparent importance of fungi in mangal.

Pathogens, by contrast, have been poorly studied in mangal. Recently, Weir et al. (2000) identified the fungal pathogen *Cytospora rhizophorae* as the causative agent of mass die-back of *Rhizophora mangle* in Puerto Rico (see also Tattar et al. 1994). These pathogens may become more frequent in mangals that are heavily impacted by pollution (Ellison and Farnsworth 1996a).

DISTURBANCE AND MANGROVE COMMUNITY DYNAMICS

The importance of disturbance in population and community dynamics is widely recognized and extensively studied. Curiously, although major syntheses of the role of disturbance in ecological communities have emerged from studies in the marine intertidal (e.g., Paine and Levin 1981) and in upland tropical forests (e.g., Denslow 1987), there has been little application of these theories to either the animal or plant communities in mangal (also see Ellison and Farnsworth 1993; Smith et al. 1994). We suspect that the lack of attention paid to disturbance in mangal reflects the perception that the comparatively low (plant) species composition and diversity of mangal will be unaffected by disturbance and the currently dominant paradigm that these systems are in "steady-state" (Lugo 1980).

We classify disturbances to mangrove ecosystems along three axes defined by the duration, intensity, and frequency of occurrence (Figure 16.3). Although "natural" disturbances such as tree falls, lightning strikes, and cyclonic storms are relatively infrequent, anthropogenic disturbances such as selective extraction, forest clear-cuts, and pollution events (oil spills, garbage disposal, etc.) occur more frequently in mangal. Anthropogenic disturbances also tend to have both large intensities and durations, whereas natural disturbance processes are either large in intensity or of long duration, but rarely both. Geomorphological processes and changes in local sea level can also be placed in the disturbance "space" illustrated in Figure 16.3; they are uniquely of large intensity, duration, and return time. Anthropogenic impacts on climate, however, may substantially decrease the return time of these two large-scale types of disturbance.

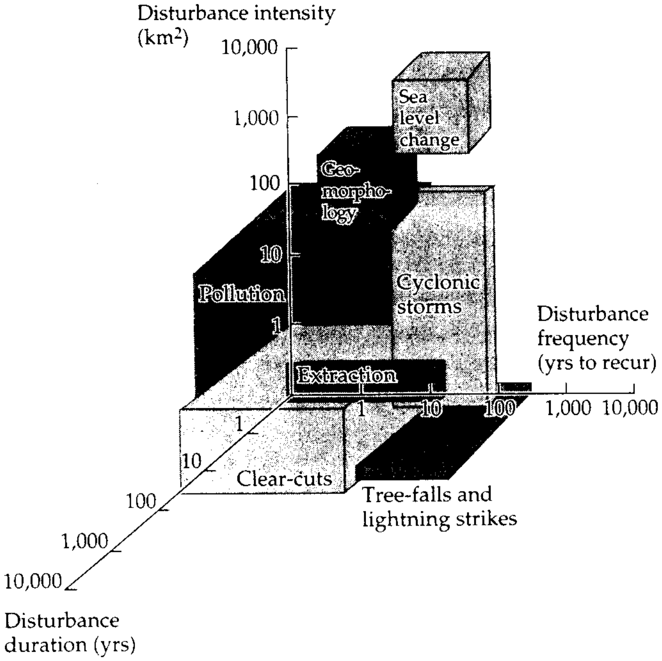


Figure 16.3 Typology of disturbances to mangal.

Tree-Falls, Lightning Strikes, and Cyclones

Compared to the attention they have received in upland tropical forests, tree-fall gaps have been little studied in mangal. Lightning strikes are a regular source of canopy disturbance in mangals of Australia, Florida, the Dominican Republic, and Panama (Smith et al. 1994). We found that suppressed seedlings growing in the understory responded rapidly to experimental removal of the mangrove canopy (Ellison and Farnsworth 1993). Soil characteristics and infaunal composition are likely to change following gap creation; the former has been studied only correlatively (Ewel et al. 1998; Feller and McKee 1999), and the latter not at all.

The effects of tropical cyclonic storms (hurricanes, typhoons, and cyclones) on mangals have been widely documented (e.g., Wadsworth and Englerth 1959; Steinke and Ward 1989; Roth 1992; Smith et al. 1994; Imbert et al. 1996; Swiadek 1997; Alleng 1998). Although mangals afford significant protection from cyclonic storms to upland habitats (UNESCO 1979), mangroves themselves can be killed by wind damage, lightning strikes, and surges accompanying severe storms (Roth 1992; Doyle et al. 1995; McCoy et al. 1996; Imbert et al. 1996; Swiadek 1997). Only a handful of mangrove species resprout following damage to the main trunk (Tomlinson 1986; Roth 1992), and regeneration of mangrove forests following hurricanes results almost entirely from seedlings. This regeneration can lead to a rearrangement of species sequences along intertidal gradients. For example, in Florida, the normally high-intertidal species *Laguncularia racemosa* now dominates the lower intertidal in regenerating stands in mangal of southern Florida destroyed by Hurricane Andrew in 1995 (Baldwin et al. 1995; A. M. Ellison, pers. obs.). The aforementioned studies on mangals' responses to cyclonic storms illustrate that these communities have recovery times on the order of decades, but that the trajectories of recovery are system specific and rarely predictable. The 50–100 year return time of cyclonic storms also necessitates a reevaluation of the concept of old-growth forests as applied to mangal (Lugo 1997). Much additional research is needed to integrate mangal into current syntheses concerning community- and ecosystem-level responses to "natural" disturbance regimes.

Anthropogenic Disturbances to Mangal

Because of their occurrence on coastlines where the majority of the world's population lives, there is much more information on the responses of mangal to anthropogenic disturbances (reviewed recently by Saenger et al. 1983; JIAM/ISME 1993; Ellison and Farnsworth 1996a; Farnsworth and Ellison 1997b; Farnsworth 1998). Mangrove forests once occupied ~75% of sheltered tropical coasts worldwide, but people are displacing mangroves at alarming rates throughout the world. A recent global survey identified reclamation for village expansion, agriculture, tourism, and aquacultural impoundments as the primary global threats to mangal (Farnsworth and Ellison 1997b). Oil spills have impacted mangal dramatically in the Caribbean (Ellison and Farnsworth 1996a), but because of less tanker traffic are less of a threat elsewhere in the world. Activities that occur outside mangal boundaries *sensu stricto,* such as upland farming and road construction, can also exert indirect pressures on these systems by diverting freshwater or releasing pollutants (e.g., Twilley et al. 1998). Ecologists must team with economists and sociologists to examine the factors that promote mangrove exploitation in certain areas, to model the reciprocal effects that human economic pressures and mangrove decline exert on one another, and to develop biologically tenable measures of success for a range of conservation strategies (see Ruitenbeek 1994; Gilbert and Janssen 1998; Twilley et al. 1998 for useful examples).

Although it is becoming easier to detect and quantify losses of mangal using remote-sensing technology (where military or political impediments to such data gathering do not exist), less is understood about how the loss of mangrove tree species affects the diversity and ecology of other members of mangal and adjacent communities such as seagrass beds and coral reefs. It is also imperative to assess the ecological impacts of potential "solutions" for mangrove conservation "problems." For example, ecotourism has long been regarded as a means of encouraging public appreciation for, and hence conservation of, mangrove systems (e.g., Barzetti 1993). However, accommodating tourists often entails conversion of these same habitats for visitors' facilities (e.g., Hudson 1983), installation of boardwalks that themselves alter benthic community structure (Figure 16.2; Kelaher et al. 1998a,b), and increased boat traffic with attendant wakes and noise (the ecological ramifications of which have received little attention). Ecological studies can greatly augment the reliability of cost-benefit analyses of these projects. Much of the scientific information is in place to comprehend the functional consequences of our actions on mangroves and to predict the outcome of various conservation scenarios (e.g., Ruitenbeek 1994; Gilbert and Janssen 1998). However, education of local users and policy makers is essential to ensure that mangroves are protected and restored properly, and ecologists are in arguably the best position to disseminate accurately data on mangrove ecology and their values to ecosystem function.

Mangal Responses to Sea Level Rise

It is now widely accepted that global climate has been and is likely to continue changing due to accelerating anthropogenic releases of carbon (IPCC 1997). A measurable rise in sea level on many coasts is a probable outcome of the oceanic thermal expansion and subsidence of ice sheets that will accompany such "global warming," and mangal, like other coastal systems, will be among the first ecosystems to experience this change. How will mangrove communities respond to increased sea level and possible changes in tidal amplitude? We can glean predictions from three sources of information: (1) paleoecological studies that reconstruct mangal's responses to sea level increases in the past; (2) long-term field studies characterizing how the shape and structure of mangal is changing in response to contemporary changes in tidal regime; and (3) laboratory and field experiments that elucidate individual responses to manipulated tidal conditions.

Analyses of stratigraphic sequences from peat cores indicate that mangals gradually moved upland and their seaward fringes died back as sea level rose during periods of Holocene transgression (Woodroffe 1982; Ellison and Stoddart 1991; Ellison 1993; but see Alleng 1998). Today, such inland migration can occur only where mangal can colonize amenable wetland habitat along an elevational gradient, and where such habitats are not constrained or fragmented by road development, urbanization, or water diversion.

Local sedimentation regimes can offset (Pernetta 1993) or exacerbate (Ellison and Farnsworth 1996b) negative effects of sea level rise on mangrove growth. Mangals on shallow, flat, carbonate platforms throughout tropical reef areas may eventually be submerged altogether if sediment accretion cannot keep pace with erosion and inundation (Parkinson et al. 1994).

Bacon (1994) reviewed methods for evaluating the risks of sea level rise to different types of mangal in the Caribbean.

This type of assessment must be applied to other regions, and restoration and mitigation measures developed, particularly in areas where the consequences of sea level rise and inappropriate coastal zone management measures are already being felt (Mimura and Nunn 1998). Mangals themselves are potentially excellent tools for monitoring the changes currently underway (Blasco et al. 1996; Ellison and Farnsworth 1996a; Michener et al. 1997). Species responses will reflect differential tolerances to salinity and flooding and the influence of these features on interspecific interactions. Several mangrove species exhibit depressed growth when grown under flooded treatments that mimic field conditions (Naidoo 1985; Hovendon et al. 1995; McKee 1996; Ellison and Farnsworth 1997), yielding pessimistic prognoses for mangals that are restricted in area. Multi-species trials are required to determine how rising sea level will influence mangrove species richness, composition of floral and faunal components of the community, and indicators of ecosystem function.

Mangrove Community Responses to Other Facets of Climate Change

As the climate changes, rising sea level will be accompanied by increases in atmospheric concentrations of carbon dioxide and probable increases in mean annual temperatures of both air and ocean surface waters. Studies to date of mangrove responses to climate change have not yet considered all these factors together, and multi-species factorial experiments must be performed before issuing prognoses of mangrove performance (Field 1995). Reports of mangrove responses to elevated CO_2 alone suggest that water use efficiency and growth of individual trees will be enhanced, but that the magnitude of these effects will differ among species and photosynthetic acclimation may inhibit long-term responsiveness (Ball and Munns 1992; Farnsworth et al. 1996; Ball et al. 1997; Snedaker and Araújo 1998). Age at first reproduction, as well as patterns of reproductive phenology, may be altered in some species (Farnsworth et al. 1996), with implications for plant-pollinator syndromes, seed predation, and seedling establishment. As soil, air, and water temperatures increase, species composition and activities of microbial and benthic associates of mangroves will likely change. At larger scales, it is necessary to predict whether mangroves will shift their ranges as some regions grow arid and others grow lush under modified rainfall regimes. Currently limited at their northern (Florida/Bermuda) and southern (New Zealand) boundaries by their sensitivity to cold (MacMillan 1975), mangroves could expand their foothold as temperatures moderate.

MANAGEMENT, RESTORATION, AND CONSERVATION OF MANGAL

For centuries, mangrove forests have provided a wide range of products that people use, including (but not limited to) timber and fuelwood, finfish and edible crustaceans, and bioactive compounds for tanning and medicine (reviewed by Walsh 1977; Bandaranayake 1998). Only in the last hundred years or so, however, have these forests been managed actively, first for timber, fuelwood, and pulpwood production (reviews in Hamilton and Snedaker 1984; JIAM/ISME 1993; Chowdhury and Ahmed 1994; FAO 1994), and more recently for cultivation of fish, shrimp, and especially the tiger prawn, *Penaeus monodon* (e.g., Hamilton and Snedaker 1984; Hong and San 1993; Chaudhuri and Choudhury 1994; Primavera 1995; de Graaf and Xuan 1998; Semesi 1998; Twilley et al. 1998) or eco-tourism (Bacon 1987; Barzetti 1993; Government of West Bangal, n.d.). Despite repeated claims that mangrove forests can be managed sustainably (e.g., Hamilton and Snedaker 1984; FAO 1994; Chowdhury and Ahmed 1994), managed (and unmanaged) mangals continue to degrade (e.g., Gong and Ong 1995; Farnsworth and Ellison 1997b). As a result, much current attention is focused on restoration of degraded mangal (Field 1996, 1998; Kalay and Jones 1998) and conservation of the remaining less-impacted mangal throughout the world (e.g., Clough 1993; Diop 1993; Lacerda 1993; Suman 1994).

Mangrove Forestry

Many mangrove species, especially in Southeast Asia, India and Bangladesh, and East Africa, grow large enough to be used extensively as construction and boat-building timbers (JIAM/ISME 1993; FAO 1994). The ± 10,000 km^2 of mangrove forests that cover the Sundarbans region of India and Bangladesh have the longest history of management for timber and provide an illustrative example of how even deliberate, well-intentioned management has resulted in the decline and degradation of the world's largest mangal. The earliest forest inventory for this mangal dates to 1769, and the first detailed working (harvest) plan was prepared in 1893–1894 (Chowdhury and Ahmed 1994). The focus of this and subsequent working plans was on two species, the Sundarbans endemic *Heritiera fomes* and *Excoecaria agallocha*. Other harvested species included *Avicennia officinalis*, *Xylocarpus granatum*, *Sonneratia apetala*, *Bruguiera gymnorhiza*, and *Amoora cucullata*.

Prior to 1930, the management plans set the minimum harvestable size of *H. fomes* at 90–100 cm diameter at breast height (dbh), and the other species at ~ 60 cm dbh (Chaffey et al. 1985; Chowdhury and Ahmed 1994). Prompted by increasing demand and a perception that "overmature" trees were not being exploited, Curtis (1933) developed a new 20-year working plan for these forests that reduced the minimum harvestable diameter of *H. fomes* to 7–30 cm dbh (depending on quality), and that of *E. agallocha* to 10–30 cm dbh. Other species were similarly reduced. These diameters corresponded to tress ranging in age from 100–125 years old. A subsequent inventory and management plan further reduced the minimum cuttable diameter to 16–26 cm for *H. fomes*, 11–15 cm for *E. agallocha*, and comparable reductions for the other species (Choudhury 1968). By 1983, the total saleable volume of timber of these two species had been reduced by 40–50%, and the forest was considered seriously over-exploited (Hussain and Ahmed 1994). Commercial harvesting of *H. fomes* has been banned in Bangladesh since 1994.

This last period of intensive harvesting of mangroves coincided with dramatic increases in the numbers of human inhabitants in the Sundarbans of Bangladesh (approximately 10 million in 1995) and concomitant increases in human mortality during annual cyclones. Recognition of the relationship between deforestation of mangroves and increased damage and mortality from cyclones led to the initiation of mangrove reforestation projects beginning in the mid-1960s (Siddiqi and Khan 1996). Through 1995, nearly 140,000 ha had been replanted, primarily with *Sonneratia apetala* and *Avicennia officinalis*, both of which grow rapidly and are transplanted more easily and successfully than the other native species (Siddiqi and Khan 1996). Overall, reforestation success has varied dramatically among sites, although causes of local failure are hard to pinpoint (Siddiqi and Khan 1996).

A parallel example is provided by the ~ 40,000 ha mangrove forest of Matang, Malaysia. Most (~85 %, or 35,000 ha) of this forest has been managed for fuelwood production since 1902. The managed forest is now a virtual monoculture of *Rhizophora apiculata*, which provides charcoal that has very high caloric value, burns very slowly, and produces virtually no smoke (Bandaranayake 1998). Clear-cutting of stands occurs on a 30-year rotation. Despite assertions that the managed mangrove forest of Matang is "one of the best managed [mangrove forests] in the world" (Chan 1996: 75), yields have declined dramatically: from 296 t/ha in the virgin stands of the early 1900s, to 158 t/ha in the late 1960s and 136 t/ha in the 1970s (Gong and Ong 1995; Chan 1996). Continued exploitation of this forest requires intensive use of herbicides to remove the mangrove ferns *Acrostichum aureum* and *A. speciosum* (which inhibit *Rhizophora* seedling growth) and direct planting of seedlings and saplings (Chan 1996). Economic costs of these activities can exceed $800/ha, while the realized income from the forest rarely tops $1,000/ha (Chan 1996).

Elsewhere in the world, existing regulations concerning the extraction of wood products from mangroves are generally unenforced (Ellison and Farnsworth 1996a; Farnsworth and Ellison 1997b), and reforestation efforts are sporadically applied and only now being assessed for their long-term efficacy (Field 1996; Kaly and Jones 1998). Despite the known relationships between mangrove plant productivity and animal (especially finfish and edible crustacean) productivity, management and reforestation plans focus almost exclusively on the trees (Kaly and Jones 1998). This results in the creation of forests that may be biological deserts: for example, mangrove crabs are uncommon in managed stands of *Rhizophora apiculata* in Matang (A. M. Ellison and E. J. Farnsworth, pers. obs.)

Fisheries, Aquaculture, and Mariculture

The relationship between mangrove forest cover and yields of finfish and crustaceans is well known and well documented (e.g., D'Croz and Kwiecinski 1980; Jeyaseelan and Krishnamurthy 1980; Ong 1982; Krishnamurthy et al. 1984; Mepham and Petr. 1986; Richards and Bohnsack 1990; Twilley et al. 1991, 1998; Ruitenbeek 1994; Fouda and Almuharrami 1995; Vance et al. 1996; de Graaf and Xuan 1998; Primavera 1998). It is routine to hear that fish and prawn catches decline where mangroves are removed, following selective extraction of high-grade trees or clear-cuts for fuelwood or pulpwood destined for rayon mills. Similar losses are asserted where mangroves are cleared for aquaculture (finfish) or mariculture (shrimp and prawn) ponds, but quantification of these losses is scarce.

In the Philippines and Ecuador, > 50% of the mangrove forests have been converted to shrimp ponds in the last 30 years (Twilley et al. 1993; Primavera 1995), and shrimp pond production increased 30-fold (from 3,000 ha to 100,000 ha) in Vietnam from 1980–1992 (de Graaf and Xuan 1998). In their initial phases, these mariculture operations rely on locally caught wild larvae to seed the shrimp ponds. Rapid depletion of wild larval supplies (which rely on mangal for food and protection from predators) leads to an increasing emphasis on lab-reared larvae (e.g., de Graaf and Xuan 1998). In the early 1990s, viral infections decimated shrimp ponds worldwide, and they remain persistent in coastal waters around the world (Primavera 1995; Corea et al. 1998; de Graaf and Xuan 1998). At the same time, coastal fisheries have shown parallel declines (Richards and Bohnsack 1990; Ellison and Farnsworth 1996a). Data from Vietnam illustrate that the catch per unit effort peaked in 1982, but declined precipitously with the construction of shrimp ponds and is now at its lowest recorded level ever (de Graaf and Xuan 1998). Because construction of shrimp ponds results in the exposure of strongly reducing, acid-sulphate soils, replanting of mangroves in abandoned ponds is difficult to impossible (Corea et al. 1998; de Graaf and Xuan 1998).

More integrated management of mangrove forestry and fisheries is clearly required. A recent simulation study by Twilley et al. (1998) suggested that maintenance of mangrove forest stands in and around shrimp ponds in Ecuador could ameliorate the increased eutrophication and decreased water quality in estuaries cleared of mangroves for shrimp pond construction. Binh et al. (1997) demonstrated 30–50% higher economic returns from management schemes in Vietnam that integrated mangrove forestry with shrimp farming relative to either one by itself. In areas where aquaculture and mariculture operations in mangroves are just beginning (notably, East Africa [Semesi 1998]), there are real opportunities to develop joint aquaculture-forestry operations within mangal that may be truly sustainable.

Conservation and Ecotourism

Most elements of the mangrove flora and fauna are unique to this ecosystem, and this observation has led to a marked increase in attempts to inventory, protect, and conserve the remaining, relatively undisturbed, mangals throughout the world. Most countries in Latin America, Southeast Asia, and the Indian subcontinent have developed conservation plans for, broad educational programs about, and strict legislation concerning uses of mangal (reviews in Clough 1993; Lacerda

1993; Suman 1994), while development of similar national strategies in Africa lags by several decades (compare reviews in Diop 1993). Ecotourism is being developed increasingly as an opportunity for apparently low-impact use of mangal (but see our previous discussion of disturbance) that simultaneously can provide high economic returns and has the potential to educate visitors about the social, economic, and intrinsic values of mangal (Bacon 1987; Barzetti 1993). For example, because of the concentration of waterbirds in mangal, these ecosystems are high on the list of places for bird-watchers to visit (e.g., Bacon 1987; Klein et al. 1995; Ellison and Farnsworth 1996a). We note, however, that even ecotourism can have significant negative impacts on mangal. These impacts include: habitat destruction attendant to hotel construction (Hudson 1983; Bildstein 1990; Conde and Alarcón 1993); coastal pollution that leads to eutrophication and species loss (Aguilera et al. 1992; Tattar et al. 1994; Klekoswki et al. 1999); changes in substrate structure, seedling distribution, faunal diversity, and species composition following boardwalk construction (Skilleter 1996; Kelaher et al. 1998a, 1998b; Skilleter and Warren 2000); and erosion of peat banks when high-speed motorboats cruise through mangrove-lined channels (Farnsworth and Ellison 1997b).

In virtually all countries where mangal occurs, governments, corporations, and individuals recognize the economic, social, and intrinsic values provided by these ecosystems. Increased understanding of the ecology of mangal makes it truly feasible to develop strategies for the long-term sustainable use and conservation of these systems (reviewed by Farnsworth 1998). Site management and conservation plans can be developed that incorporate forestry, aquaculture, tourism, and areas with restricted access (Figure 16.4). Development of these plans requires a fundamental appreciation for the intrinsic value of mangal and a comprehensive understanding of the links between mangal, adjacent ecosystems, and human inhabitants. In this chapter, we have documented the existence of the basic information necessary for a better understanding of mangal in the service of such a plan. Although many open questions remain regarding the ecology of mangal, we are optimistic that this unique ecosystem will be protected and maintained far into the future if existing (and future) data are widely shared and disseminated, if mangal is recognized as a genuine conservation and management priority, and if all parties affected by land-use decisions are involved in the development of site conservation and management plans.

RECOMMENDATIONS FOR FUTURE RESEARCH

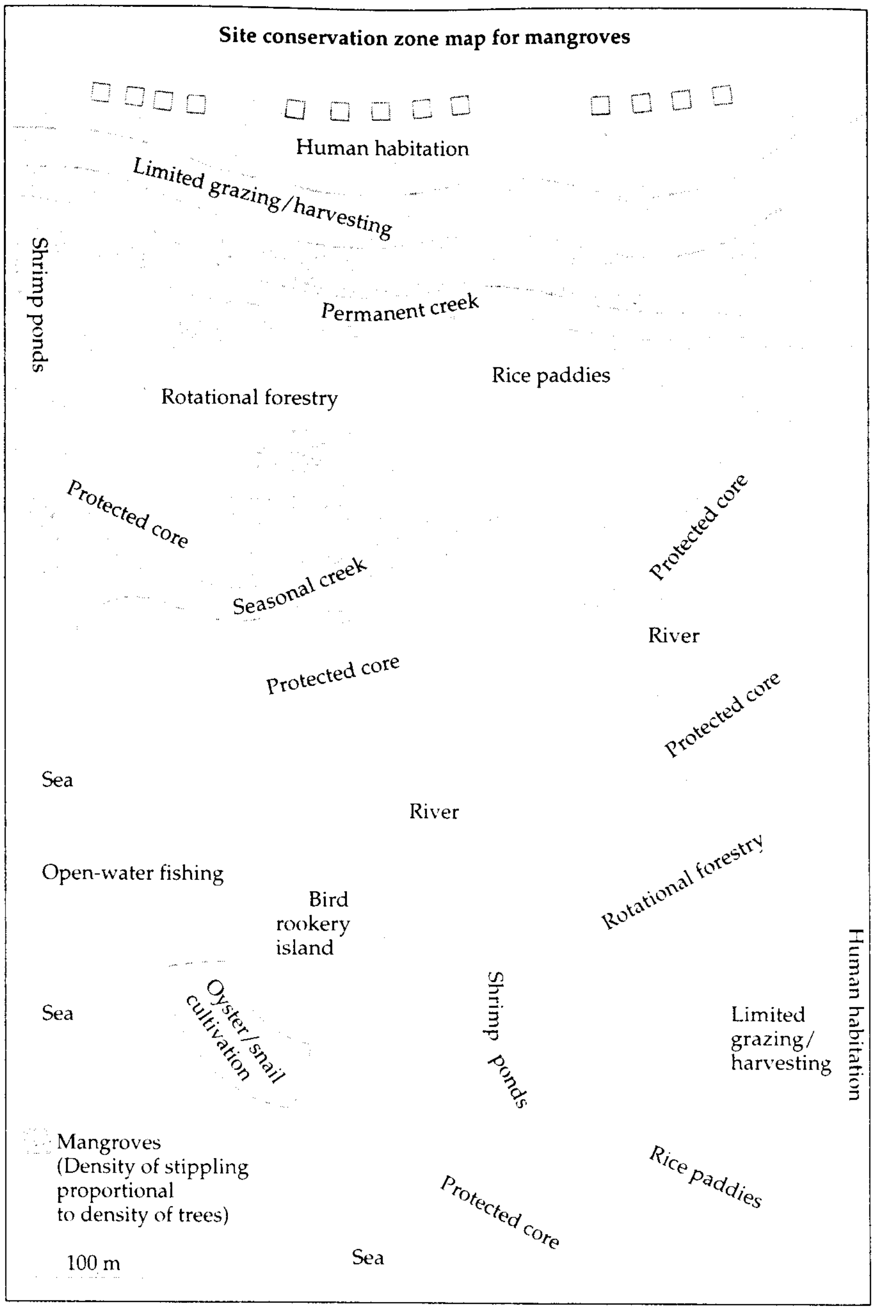
Our review has illustrated that substantial data are available to address the ecology of mangroves and mangal, but there are also ample lacunae in our understanding of these plants and the communities that they define. Biogeographic patterns are clearly documented, but the roles of propagule dispersal and seedling establishment in determining these patterns at local, regional, continental, and global scales remains poorly understood. Species-specific ecophysiological processes—including regulation of salt uptake, oxygen levels, and microbial activity at the soil-root interface; water transport; tolerance of salinity during growth and reproduction; and nutrient-use efficiency—have been studied in only a few mangrove species, but are major drivers of population-, community-, and ecosystem-level dynamics. Similarly, investigations of trade-offs between osmotic physiology, carbon balance, nutrient-use efficiency, nutrient limitation, and production of plant secondary compounds are needed to develop a better understanding of specialization of herbivores and pathogens and the patterns of insect and fungal outbreaks in mangal.

Ecosystem models are well developed for only two mangals, and there is a real need for expanding the scope of these models to incorporate mangrove forests that grow in different geomorphological situations (from estuaries to carbonate platforms); that occur in a wide range of tidal amplitudes; and that fully account for past land-use history and cross the spectrum from "pristine" sites to degraded and restored sites. These models need to fully incorporate physiological-, population- and community-level interactions that mediate and control system-wide nutrient and energy fluxes.

The impacts of human activities on mangal increase daily, and data are sorely needed that can be applied directly to conservation, management, and restoration of these communities. Fragmentation of these communities worldwide could disrupt plant-pollinator interactions and lead to isolation of small populations. A more detailed understanding of mangrove population genetics is needed to assess the importance of inbreeding depression in isolated stands. Dispersal and establishment properties of mangrove propagules can limit or enhance such isolation. A better understanding of establishment dynamics is also needed to aid in management of mangal. Because population-level studies of mangroves have emphasized controls by edaphic factors on plant population dynamics and mutualisms between mangroves and faunal associates, we know little about how intra- and interspecific interactions could change in fragmented or managed stands. Such data could also be used to devise sound strategies for sustainable forestry, afforestation programs, and restoration of degraded mangal. These data would allow for the assessment of the effects, both positive and negative, of conservation "solutions" on mangrove populations and communities. Because mangals are coastal communities, there is a pressing need to develop experimentally testable, quantitative models for the responses of these communities and their constituent species to changes in sea level. Additional studies on the responses of individual species and whole communities to other facets of global change, including carbon and nitrogen enrichment, are also needed to more reliably predict the effects of such global-scale anthropogenic disturbances on mangal.

It appears to us to be especially important to view these research topics through four broad, conceptual lenses. First, general ecological theories deriving from decades of research in physiology and physiological ecology, marine biology,

Figure 16.4 Hypothetical site conservation plan for sustained use and conservation of a mangal ecosystem. Modified from Farnsworth (1998).



community ecology, and evolutionary biology should be applied to studies of mangrove ecology; in the past such theories have been applied only rarely. Second, these studies should take advantage of the fact that mangal is simultaneously a hard-substrate and a soft-sediment system. This fact can be used to develop new general theories that unite data from studies in other benthic communities that occur in only one of these habitat types. Third, such studies should cross levels of biological organization, from individual physiology through ecosystems. The comparatively small number of species in mangal (relative to other tropical communities) should make it possible to clearly link physiological processes to population dynamics and population processes to community and ecosystem-level phenomena. Lastly, the existence of global, taxonomically-independent convergences in structure and function of individual mangrove species and whole mangrove communities make it feasible to undertake experimentally-based comparative studies of ecological processes. Mangrove ecology remains a rich area for intellectual exploration, and mangrove forests themselves are compelling places in which to work.

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