Caribbean Mangrove Swamps

Despite their ubiquity and prominent position between land and sea, these tropical ecosystems still hold countless surprises for researchers

by Klaus Rützler and Ilka C. Feller

One perceives a forest of jagged, gnarled trees protruding from the surface of the sea, roots anchored in deep, black, foul-smelling mud, verdant crowns arching toward a blazing sun, the whole mass buzzing with insects. These are the first impressions a visitor develops when approaching one of the most common sights on tropical shores—a mangrove swamp. Here is where land and sea intertwine, where the line dividing ocean and continent blurs. In this setting the marine biologist and forest ecologist both must work at the extreme reaches of their disciplines.

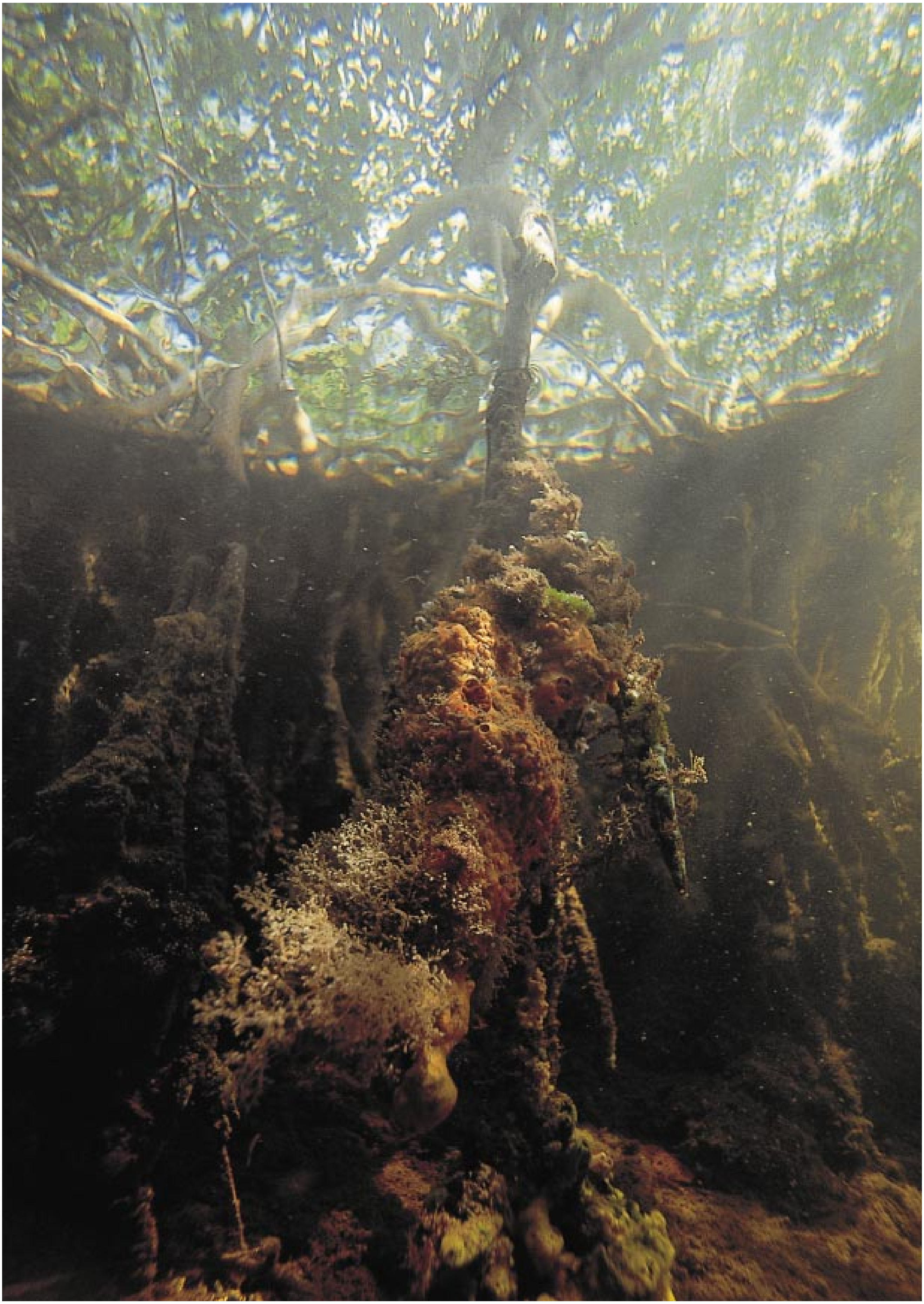
Naturalists have long struggled to define, in proper ecological terms, the environment of a mangrove swamp. Is it an extreme form of coral reef or a flooded coastal forest? Compared with the tropical timberlands of some continental interiors (which can house as many as 100 species of tree on a single hectare), a mangrove forest appears puny, monotonous and depauperate. Even the relatively rich Indo-Pacific coasts boast only some 40 mangrove species along their entire length. In the Western Hemisphere only eight or so mangrove species can be found. And of this small set just three kinds of mangrove tree are truly common.

The word "mangrove" itself is somewhat misleading. It is not a formal taxonomic term; rather, it applies to those vascular plants that share a set of physiological mechanisms for living in shallow seawater. For example, mangrove trees are able either to exclude or to excrete salt from their tissues. These plants can also sprout aerial roots that permit the exchange of gas for aerobic respiration. This adaptation allows the trees to survive despite being firmly rooted in oxygen-deprived intertidal soils. Although a salty habitat is not strictly required for growth, mangrove communities develop only near the sea because they cannot compete successfully with freshwater flora.

Mangroves are also limited by a need for rather balmy conditions. As is the case with corals, these trees cannot survive in places where the average water temperature falls below about 23 degrees Celsius (73 degrees Fahrenheit). This requirement causes bands of mangrove and coral to grow largely in parallel swaths along the world's tropical coastlines. But deviations from this simple pattern occur commonly. For instance, coasts that are continuously subjected to large influxes of sediment (such as the shores of western Africa) or areas where deep, cold water rises to the surface (such as the coastal waters off eastern Venezuela) lack coral reefs but can support extensive mangrove swamps. Conversely, some coral islands in the central Pacific lack an accompanying fringe of mangroves, apparently because the floating propagules that serve as seeds for these trees cannot reach such remote isles.

Mangrove swamps typically fall within one of two broad categories of classification: mainland or oceanic island. The former group includes those communities that border continental coasts and are thus permanently sandwiched between salty ocean water and freshwater carried by streams from the interior. Hence, mainland mangroves must usually cope with a pronounced variation in salinity across their width. This situation is quite distinct from that of ocean-

TROPICAL SHORES around the world are commonly lined with mangrove swamps (*above*). Salt-tolerant mangrove trees thrive along coasts where the average temperature remains sufficiently warm. Mangroves on the barrier reef bordering Belize (*inset*) are central to the authors' long-term research. These swamps (*opposite page*) host rich communities of plants and animals within the shady tree canopy and around the permanently submerged mangrove roots. The swamps also support a distinctive group of creatures that have adapted to life in the thin zone between high and low tide levels.



CHIP CLARK *Smithsonian Institution*

JIMMY SMITH *Islands from the Sky*

CARRIE BOW ISLAND (*foreground*) and Twin Cays (*center*) have served the authors as a permanent base and natural laboratory. Straight, dashed lines on the bottom of the lagoon mark scars in the sea-grass bed where oil-exploration crews used explosives to make seismic surveys during the 1960s.

ic-island mangroves, which form on shallow banks or in lagoonal areas well separated from the mainland. They are normally less affected by freshwater carried laterally than by the intermittent shifts in salinity that result from intense evaporation or from frequent tropical downpours.

Although interest in mangrove biology reaches back in history at least as far as Alexander the Great's expeditions to the Arabian Sea, scientific knowledge of this intriguing ecosystem is still rudimentary, and key questions remain largely unanswered. Are mangrove communities as rich and productive as other tropical environments? Is their role in protecting juvenile fish indeed as important to commercial fisheries as many people have speculated? Do mangrove swamps serve to protect coastlines from erosion? Although researchers have made detailed observations of many different mangrove swamps around the world, a huge gap exists in the understanding of how the different components of such intricate natural systems work together.

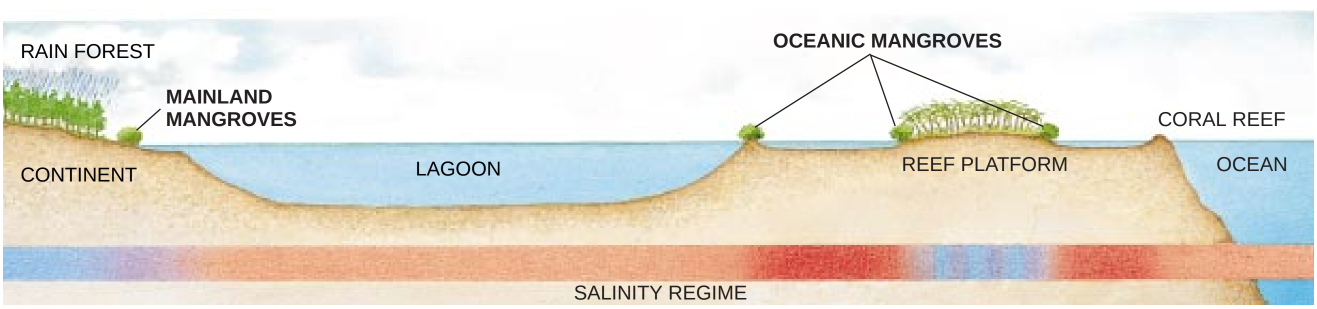
A Cay is Key

Concerns about the limited understanding gleaned from isolated studies of mangrove swamps motivated us to mount a long-term research campaign at one place. We chose to examine the biodiversity and ecology of a locale that was relatively accessible—the spectacular barrier reef off the coast of Belize. We are fortunate to have been able to conduct our fieldwork there from a permanent station situated on a tiny coral island about 10 miles offshore. One of us (Rützler) discovered this site on a memorable morning in February 1972. It was something of a serendipitous find during an excursion with a colleague, Arnfried Antonius.

We had chartered a small boat out of Belize City, some 50 miles to the north, and were looking for a passage through the shoals—one through which we had traveled several times before. But our boat's crew was unfamiliar with the local waters and misguided us in our search for the break in the reef. As we motored seaward, we could hear the splash of waves breaking on the shallow coral, but neither of the two islands in front of us matched what we remembered from our previous visits. To our astonishment we noticed several buildings on the smaller island ahead and decided to make a closer examination of this curious display of civilization within a rather remote wilderness. A few moments later we tied up our vessel on the island's concrete dock and walked toward the largest house. No inhabitants greeted us (other than a few mildly disturbed pelicans), but hanging above the main gate was a sign: "Welcome to Carrie Bow Island."

Little did we know then that this speck of sand containing three cottages and two outhouses was the property of Henry T. A. Bowman, a citrus planter with a passion for the sea who had acquired the island in 1943 in order to build a summer home for his wife, Carrie. Nor could we then imagine that within eight years the Bowman family's appreciation and support for the natural sciences would transform this remote vacation retreat into a permanent laboratory—one that has since hosted more than 70 scientists from 40 institutions, enabling hundreds of scholarly studies of the surrounding reefs to be conducted.

Having Carrie Bow Island available as a convenient base, we decided to center our examination of mangroves on the nearby Twin Cays, a largely untouched mangrove range covering more than a square kilometer of a shallow lagoon. More than 20 other researchers from the Smithsonian Institution's National Museum of Natural History (and at least as many colleagues from collaborating



ROBERTO OSTI

BELIZE'S BARRIER REEF is separated from the coast by a wide, shallow lagoon. Mainland mangrove communities (*left*) endure a permanent lateral gradient in the saltiness of ambient waters, where freshwater (*blue in band*) gives way to salty conditions (*red*). Mangroves situated offshore (*right*) more often cope with erratic fluctuations in salinity.

institutions in the Americas, Europe and Australia) also conduct regular research on the mangrove communities there.

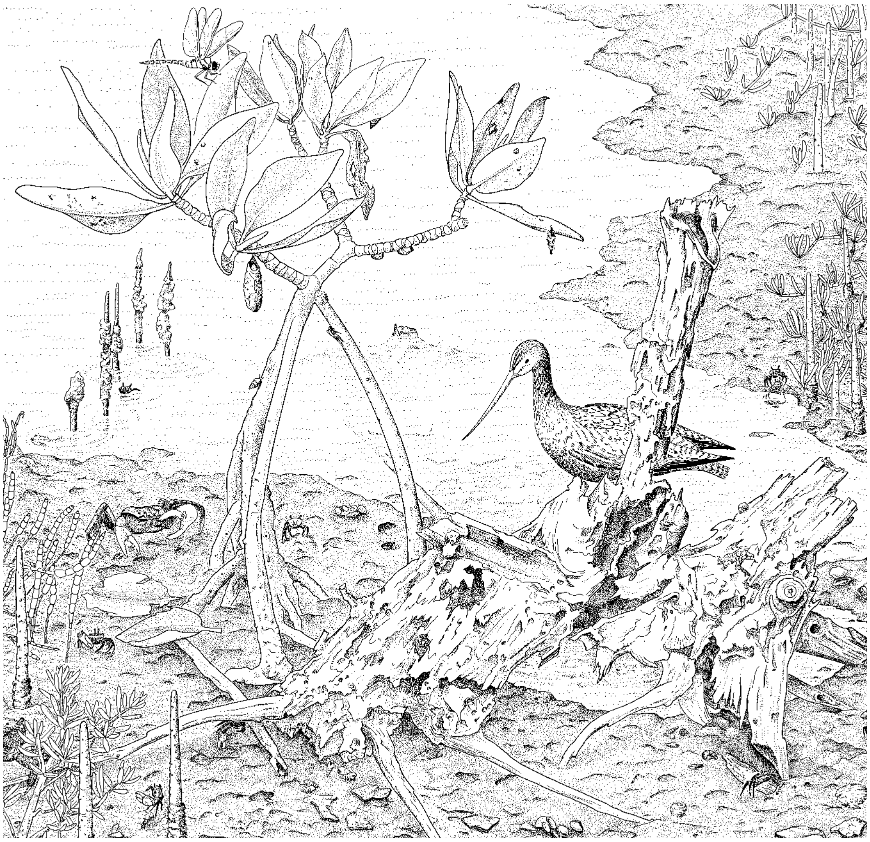
A Natural Landscaping

The mangroves of Twin Cays belong to the oceanic-island type. The distribution of such scattered mangrove islands among the patches of reef within the wide lagoon suggested to us that the first trees at Twin Cays may have settled on isolated coral clusters. But work by our geologist colleague Ian G. Macintyre disproved this surmise. Several "vibracores" (geological samples obtained by pushing a vibrating pipe into the unconsolidated sediment bottom) indicated that the mangroves at Twin Cays did not begin growing on coral. Rather the community established itself some 7,000 years ago on what was then just elevated ground. This mangrove swamp has since built a foundation of seven meters of peaty soil as it reacted to rising sea level.

The topography of Twin Cays reflects several thousand years of natural history and provides a testament to the power of the countless storms and hurricanes that have buffeted this tiny forest. For instance, clear evidence of at least one dramatic event in the past remains in the shallow channel that bisects the island and then splits, with one branch that has no outlet. At the bends in the dead-end extension lie deep cuts that have not yet filled with peat or sediment. These submerged excavations indicate that strong currents must have flowed freely through the passage before an unrecorded tempest deposited enough sediment to dam one end of the channel.

The periphery of Twin Cays and its canals is bordered by tall red mangroves (*Rhizophora mangle*) that extend stilt-like roots into the deeper water, beyond the peat bank that supports the trees. Toward the interior, first black mangrove (*Avicennia germinans*) and then white mangrove (*Laguncularia racemosa*) mark zones of shallow floodwater and extended mudflats that develop as the tide moves in and out. Because evaporation under the intense sun can rapidly remove much of the standing water, the brine that remains in pools often contains a high concentration of salt. Karen L. McKee of Louisiana State University has found that hypersaline conditions in the upper reaches of the intertidal zone favor black mangrove seedlings because that species has the greatest tolerance for salt. White mangrove seedlings cannot survive the salinity and the periodic flooding that sweeps this region, and hence these trees are restricted to higher ground. Red mangrove dominates the lower reaches of the intertidal zone not only because it stands on stilt roots but also because its seedlings can better survive the rigors of the fringing environment (hardships that include a dearth of nutrients and an abundance of possible predators).

The interior of Twin Cays is lined with numerous shallow ponds and mudflats. Some of these areas are now without growing trees; some places contain eroded stumps of large trees that must have towered there in the past. Other flats are covered by dwarf forms of red mangrove. These tiny trees are barely one meter tall, yet our studies indicate that they may be several decades old. Initially we assumed that the physiological stresses associated with the increased salinity and high temperature of the mudflats accounted for the slow growth of these bonsai-like mangrove trees. But



MOLLY KELLY RYAN *Smithsonian Institution*

SANDY CANUPP

SUPRATIDAL RESIDENTS of a mangrove swamp include a variety of plants, arthropods, snails and insects, and it is no surprise that the marbled godwit (*bird shown in drawing*) has little trouble finding food.

ILKA C. FELLER *Smithsonian Institution*

CHIP CLARK *Smithsonian Institution*

INTERTIDAL MANGROVE stilt roots are ubiquitously coated by a mixture of algal species called bostrychietum. Such surfaces also host many invertebrates such as the mangrove oyster (*Isognomon*) and mangrove-tree crab (*Aratus*).

by direct experimentation, one of us (Feller) proved that this stunted growth on Twin Cays and similar Belizean mangrove islands resulted from the lack of a single critical nutrient, phosphorus.

Life from Top to Bottom

Naturalists have traditionally placed a great deal of emphasis on the lateral transition of mainland mangrove forests, from the near-oceanic realm of the coast, through the estuarine environment of river mouths, and upstream into regions of freshwater—the domain of the rain forest. Such horizontal variation is not particularly pronounced on Twin Cays. But there is on the island a well-developed vertical stratification that encompasses the forest canopy, the intertidal region and a reeflike zone below even the slackest water. A substantial part of our research has sought to examine the flora and fauna of these three distinctive environments.

Living within the upper forest levels at Twin Cays are countless insects, lizards, snakes and birds. Although the insects are the most abundant group, the ferocity of the sun and lack of freshwater create a harsh environment for them. Only a few types are active during the day. Most insect species avoid the sun's rays by feeding at night or by living entirely within plants. Consequently, the traditional methods for collecting insects—trapping, baiting, or fogging vegetation with pesticides—yield few specimens. But by dissecting plant parts and by collecting larvae and rearing them, we have found that the mangrove insect fauna is much more diverse and ecologically important than previously suspected.

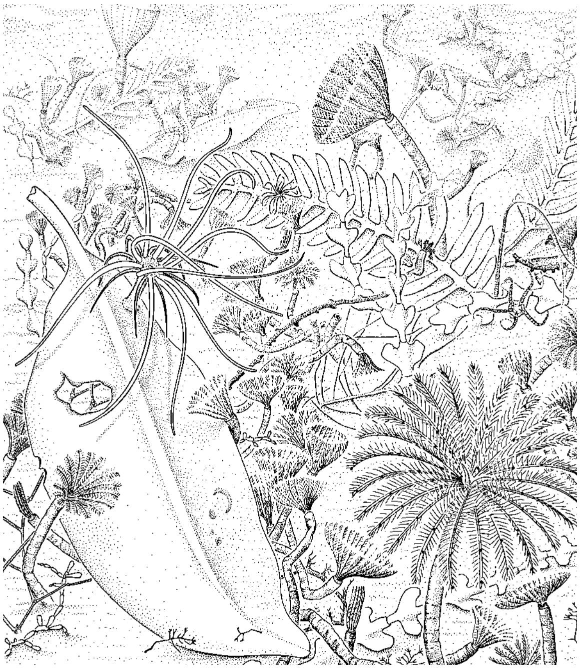
For example, the live branches of red mangrove host several species of specialized wood-boring moths and beetles. Larval stages of these insects feed internally within twigs, creating hollow cylinders of deadwood. After these primary excavators emerge, some 70 other species of ants, spiders, mites, moths, roaches, termites and scorpions use the hollowed twigs for food and as sites in which to hunt, nest and take refuge from the burning sun.

As diverse and interesting as they are, the animal communities suspended above the high watermark are in many ways similar to those found in other tropical woodlands. But the deeper forest environments of tangled red mangrove stilt roots, black mangrove pneumatophores, peat banks and mudflats host inhabitants that are unique to mangrove swamps.

Although the normal tidal range at Twin Cays is only about 20 centimeters, these mangrove forests have distinctive intertidal communities occupying the dank stratum between the high and low tide levels. Aerial roots are typically covered with a combination of red algae that is especially adapted to retaining water when the tide withdraws. Such hard surfaces also support barnacles, oysters and crabs. A rather unusual inhabitant of the intertidal zone is a small fish called the mangrove rivulus (*Rivulus marmoratus*). William P. Davis of the Environmental Research Laboratory of the Environmental Protection Agency and D. Scott Taylor of the Mosquito Control District in Brevard County, Florida, along with several of their colleagues, found that Twin Cays harbors this hermaphroditic species—one of nature's rare examples of a vertebrate that can clone itself.

By far the richest and most densely populated habitat in the mangrove swamp surrounds the subtidal area of the red mangrove stilt roots. Successful colonizers of this space include various species of algae, sponges and anemones. These organisms form biological coatings that cover the stilt roots and offer food and refuge to a variety of fauna, such as mangrove oysters and crabs. Interestingly, our experiments have demonstrated that the roots do not especially attract the "fouling" organisms. After a week of exposure to these waters, any nontoxic material—different woods, plastic or glass—becomes similarly covered, first with a mucous, microbial coating and then by a variety of algae and invertebrates. Mangrove roots seem to benefit from this process: Aaron M. Ellison of Mount Holyoke College and Elizabeth J. Farnsworth of Harvard University have shown that the fouling community protects the trees, at least partially, from the attack of root-boring animals.

The sedimentary bottom of the subtidal swamp is covered with thick stands of sea grass, particularly in well-sunlit channels. In some places on the bottom, algae and jellyfish thrive. The sediment consists of a mixture of sand, mud and detritus that is constantly stirred by the moving water and by the actions of various organisms. Such large bottom feeders as manatees often plow the channel, as do speeding motorboats. Less obvious but much more important, the sediment is continuously being turned over by burrowing animals such as polychaete worms and crustaceans. These creatures act much as earthworms and moles do on land. Peter Dworschak and Jörg Ott of the University of Vienna have shown that some crustaceans can dig and maintain complex burrows of branching tunnels that extend near-



SUBTIDAL COMMUNITIES include sabellid worms living among the great quantities of decaying leaf litter (*left*) and the Caribbean fire-sponge (*Tedania ignis*), a beautiful but toxic species (*above*) that can cause severe skin inflammation.

ly two meters into the muddy bottom.

Examinations of algae, aquatic invertebrates and insects on Twin Cays have revealed an astonishing number of new species. Even for relatively well studied groups, such as crustaceans, some 10 percent of the species found there have proved to be novel. We estimate that perhaps as many as 20 to 30 percent of the microbes, algae, sponges and worms living on Twin Cays may also be among as yet undiscovered species.

Biodiversity at Risk

The richness of life contained within the mangrove forest at Twin Cays raises immediate concern for the risk to biodiversity that develops as such delicate environments are lost to human hands. After mangrove forests are cut, it may be difficult or even impossible for them to recover because irreversible changes in the fundamental structure of the ecosystem ensue once the trees are destroyed.

We were able to observe such unfortunate consequences on a black mangrove plot that was illegally clear-cut by fishermen on the western side of Twin Cays. The remaining barren tidal flat was rapidly overrun by saltwort (a small shrub that can tolerate high salinity), reducing the space available for new black mangrove trees, which reproduce more slowly. Where the natural red mangrove fringe was disturbed, currents driven by wind and tides rapidly eroded the peat-rich soil and left a bottom surface on which the seedling propagules had difficulty anchoring.

Some of our field experiments show another impediment that prevents new mangrove trees from establishing themselves after a forest is downed. We found that mangrove seedlings take hold and grow much better in the shade than in the open, indicating that the natural repair of damaged swamps may prove too slow to keep up with the erosion of denuded land.

Such observations demonstrate that mangrove forests indeed constitute extremely delicate natural systems. Although the government of Belize has enacted laws protecting its mangrove species, these trees have nonetheless proved vulnerable because they are situated so directly in the path of commercial development. As on other coasts around the world, people often cut trees and fill low-lying areas to construct housing and industrial facilities.

Because mangrove swamps destroyed in this way would have otherwise supported countless varieties of animals, including juvenile deepwater fish, it seems clear that these losses will increasingly threaten the natural wealth of the ocean, both near and far from shore. But mounting concern about environmental degradation within the world's developing nations has brought renewed scientific attention to mangrove forests. Although much work remains to be done, the research conducted at Twin Cays is slowly but steadily building a body of critical long-term observations. This knowledge should aid future attempts to predict the fate of the earth's fragile tropical shorelines and to foster legislation that might ultimately serve to protect the fascinating mangrove communities found there.

The Authors

KLAUS RÜTZLER and ILKA C. FELLER study mangroves together, but from complementary points of view. Rützler is a marine biologist, Feller a forest ecologist. Rützler began his research in submarine caves of the Croatian Adriatic. In 1963 he earned a Ph.D. at the University of Vienna and in 1965 moved to the Smithsonian Institution's National Museum of Natural History, where he now directs the museum's research program on Caribbean coral reef ecosystems. Feller earned a B.A. as a botanist and scientific illustrator. In the 1980s she worked at the Smithsonian's natural history museum. In 1993, after completing a Ph.D. at Georgetown University, she shifted to the Smithsonian Environmental Research Center in Edgewater, Md., where she is currently a postdoctoral fellow.

Further Reading

THE ECOLOGY OF MANGROVES. A. E. Lugo and S. C. Snedaker in *Annual Review of Ecology and Systematics,* Vol. 5, pages 39–64; 1974.

MANGROVE SWAMP COMMUNITIES. K. Rützler and I. C. Feller in *Oceanus* (Woods Hole Oceanographic Institution), Vol. 30, No. 4, pages 16–24; Winter 1987/1988.

THE BOTANY OF MANGROVES. P. B. Tomlinson. Cambridge University Press, 1995.