# Biocomplexity in Mangrove Ecosystems

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## Key Words

emergent properties, collective properties, trait plasticity, habitat stability, nutrient cycling, individual-based models

## Abstract

Mangroves are an ecological assemblage of trees and shrubs adapted to grow in intertidal environments along tropical coasts. Despite repeated demonstration of their economic and societal value, more than 50% of the world's mangroves have been destroyed, 35% in the past two decades to aquaculture and coastal development, altered hydrology, sea-level rise, and nutrient overenrichment. Variations in the structure and function of mangrove ecosystems have generally been described solely on the basis of a hierarchical classification of the physical characteristics of the intertidal environment, including climate, geomorphology, topography, and hydrology. Here, we use the concept of emergent properties at multiple levels within a hierarchical framework to review how the interplay between specialized adaptations and extreme trait plasticity that characterizes mangroves and intertidal environments gives rise to the biocomplexity that distinguishes mangrove ecosystems. The traits that allow mangroves to tolerate variable salinity, flooding, and nutrient availability influence ecosystem processes and ultimately the services they provide. We conclude that an integrated research strategy using emergent properties in empirical and theoretical studies provides a holistic approach for understanding and managing mangrove ecosystems.

## INTRODUCTION

Mangrove ecosystems are coastal wetlands dominated by woody plants that span gradients in latitude (30°N to 37°S), tidal height (<1 m to >4 m), geomorphology (oceanic islands to riverine systems), sedimentary environment (peat to alluvial), climate (warm temperate to both arid and wet tropics), and nutrient availability (oligotrophic to eutrophic). Across this spectrum, mangrove ecosystems are critical not only for sustaining biodiversity but also because of their direct and indirect benefits to human activities (Walters et al. 2008, Koch et al. 2009). Yet, at least 35% of the world's mangrove forests have been lost in the past two decades (Valiela et al. 2001, Alongi 2002), which directly affects ecosystem services such as habitat for fish, prawns, and crabs (Aburto-Oropeza et al. 2008). Additionally, degradation of the remaining mangrove habitats results in loss of ecological functionality, putting millions of coastal people in jeopardy. Understanding the immense complexity of the interacting processes that determine and maintain biodiversity and productivity of mangrove ecosystems is a major challenge.

## HIERARCHICAL APPROACHES TO MANGROVE ECOLOGY

Mangroves have been the subject of some of the earliest attempts to model the function of coastal ecosystems via energy and material flux (Odum & Heald 1975). From these inspiring early models, work on the function of mangroves has expanded to other sites and has revealed a high level of variability in many aspects of these ecosystems (Robertson & Alongi 1992). As researchers have tried to evaluate variation in these ecosystems, hierarchical schemes have been developed. Some of the most successful are based on the geomorphological models by Thom (1982), which were improved by Semeniuk (1985) and Woodroffe (1992). More recently, ecohydrology models (Twilley & Rivera-Monroy 2005) are based on an overarching influence of climatic and geomorphological features on mangrove forests, which are then modified by factors lower in the hierarchy and at smaller spatial scales of topography and hydrology, giving rise to characteristic mangrove and associated vegetation.

A hierarchical scheme based on physical characteristics (geomorphology, topography, hydrology) has been recommended for use in restoring mangrove forests (Rivera-Monroy et al. 2004, Krauss et al. 2008), approximating the value of ecosystem services (Ewel et al. 1998) and assessing the vulnerability to climate change, particularly sea-level rise (Lovelock & Ellison 2007, Gilman et al. 2008). Although climatic, geomorphological, topographic, and hydrological classifications are attractive for their simplicity, it is unclear whether these models are sufficient to describe ecological function within mangroves. For example, the trees that form mangrove ecosystems are doubtless the foundation species (Ellison et al. 2005), but hydroperiod and competition for limited resources have profound effects on their growth and community structure (Rivera-Monroy et al. 2004). Such tree-level interactions cause a cascade of spatiotemporal patterns (e.g., species zonation), which emerge at higher hierarchical levels of the ecosystem but, in turn, affect the interactions and traits of the abiotic components and organisms at lower levels.

Individual-based models (IBMs), which explicitly address the traits and interactions of organisms and their environment, have been less well explored than higher-level geomorphological models. However, IBMs provide new opportunities for understanding the biocomplexity of mangroves (Berger et al. 2008) (see sidebar, Biocomplexity, below). In this review, our aim is to evaluate the interplay between processes occurring at different levels in the hierarchy. We use the concept of emergent properties to explore and highlight characteristics of mangrove ecosystems that arise from interactions among ecosystem components at different levels/scales and are manifested in different spatiotemporal patterns. Such traits are frequently described in empirical studies but are

## BIOCOMPLEXITY

The term biocomplexity, a fusion of biological and complexity, was coined by Colwell (1998) in a research initiative at the National Science Foundation. Biocomplexity is concerned with the complex interrelationships among all ecosystem components, including human societies. Moreover, these interrelationships may span multiple scales in space and time and include nonlinear behavior (Ascher 2001). A unique aspect of biocomplexity research is its emphasis on emergent properties—those properties that arise from a system's components acting in concert and may not be readily identified or understood by the study of those components in isolation. The study of biocomplexity may lead to improved understanding of global phenomena and to better ways for humans to interact with the environment. Biocomplexity research takes a holistic approach, requires multidisciplinary teams working at different scales of inquiry, and produces data that are robust when applied to real-world situations. As a case study, the Mangrove Biocomplexity project, funded by the National Science Foundation's Biocomplexity in the Environment program, brought together a multidisciplinary team of scientists to study microbial and nutrient controls on mangrove ecosystems (Feller & Venable 2005). The study's focal site was located in a mangrove archipelago (Twin Cays) in the Mesoamerican Barrier Reef Complex off the coast of Belize.

seldom used for decoding the underlying ecological processes. Scientists working on complexity theory and complex adaptive systems still debate the exact meaning of emergence and emergent properties, but for our purpose, only a general definition is needed. Emergent properties (see sidebar, Emergent Properties and Complex Systems, below) (**Figure 1**) are patterns or processes that occur at multiple hierarchical levels within ecosystems. They emerge from traits of system components and their interactions (Breckling et al. 2006). This approach allows us to expand our understanding beyond ecogeomorphologic models, which reduce interactions to the exchange of energy and matter, and IBMs, which usually address the level of organisms but frequently ignore their embedding within lower and higher hierarchical levels. Additionally, the emergent-property framework has potential use in the management of ecosystems (Nielsen & Müller 2000) and in understanding coupled human-natural systems (Liu et al. 2007).

## EMERGENT PROPERTIES AND COMPLEX SYSTEMS

The term emergence is central to theories of complex systems. Whereas the concept that "the whole is greater than the sum of its parts" has been in use since Aristotle, interest in analyzing emergent structures and properties has flourished during the past decades and is tied to the research on complexity, complex adaptive systems, and self-organization. Three criteria define emergent properties (Nielsen & Müller 2000, Grimm & Railsback 2005) as we use this term (**Figure 1**):

1. Emergent properties are not simply the sum of the properties of the components; rather, they represent a new quality that derives from the properties and interactions of the components.
2. Emergent properties are of a type different from the properties of the components.
3. Emergent properties cannot be easily predicted from individual components.

The latter does not mean that the emergent behavior of a system is always nebulous, impossible to understand, and uncertain. In fact, one of the major goals of complexity research and individual-based ecology (Grimm & Railsback 2005) is to understand how properties of ecological systems emerge from the traits and interactions of individuals and their environment.

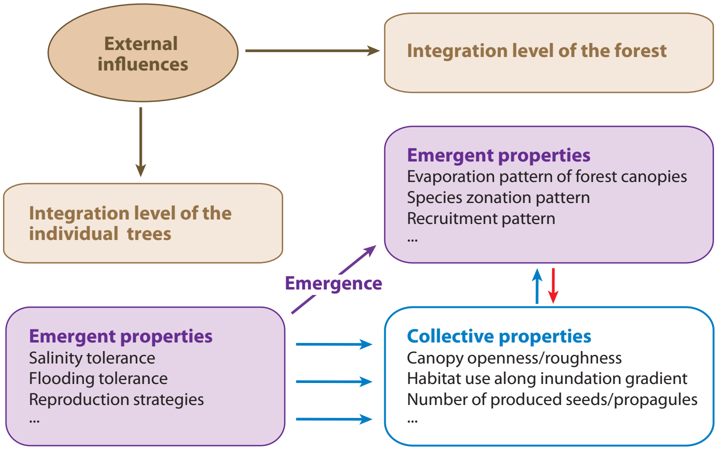

**Figure 1**

Characteristic patterns and structures appear as emergent properties at higher hierarchical levels that include basic physiological processes, interactions among organisms, as well as external influences. The emergent properties of the forest coexist with collective properties that result directly as a consequence of the properties of related components at lower hierarchical levels.

## HIERARCHIES/SCALES OF EMERGENT PROPERTIES

### Specializations for Variable Salinity, Flooding, and Nutrient Availability

In the 57 or so species from 21 families that have made the evolutionary leap into mangrove habitats (Duke 1992, Ricklefs et al. 2006), salinity and flooding tolerances and the ability to persist in variable habitats emerge as a result of the interactions among biochemical and morphological traits with environmental factors. Environmental factors that are important to development of individual trees are those that influence fundamental physiological processes, e.g., temperature, light, humidity, nutrient availability, $CO_2$ concentration, oxygen, ion and toxin concentrations in the root zone, wind and wave velocity, and herbivory (Krauss et al. 2008). Many of these factors, which are strongly affected by human activities in the coastal zone and by climate change, influence the properties of tissues, individuals, and ecosystem characteristics at higher hierarchical levels (Chapin 2003, Liu et al. 2007).

**Salinity tolerance.** Soil salinity is variable in mangrove habitats, depending on the balance between evaporation, which concentrates salt, and freshwater flushing, which dilutes salt. Although most mangroves are halophytes that tolerate saline conditions, some species need salt to grow and complete their life cycle (Ball 2002). Nevertheless, high salinity has negative consequences for metabolic processes and growth rates (Ball 1988), and it limits the height and productivity of trees (Cintrón et al. 1978).

Salinity tolerance requires that halophytes, including mangroves, maintain sufficient freshwater inside their cells and tissues to maintain metabolic function against a higher osmotic pressure in the exterior root environment, which can vary between freshwater and three-times seawater salt concentration. The mechanism by which salinity tolerance is achieved is complex and controlled by a plethora of genes (Flowers & Colmer 2008, Munns & Tester 2008). In halophytes, some of the most commonly identified metabolic traits leading to salinity tolerance include the capacity to (*a*) control the uptake of $Na^+$ and $Cl^-$ ions; (*b*) isolate salt from sensitive organelles, store $Na^+$ and

$Cl^-$ ions, and excrete the salt in some species (salt glands); and (*c*) produce high concentrations of osmotically compatible solutes (Lovelock & Ball 2002, Flowers & Colmer 2008).

In addition to adaptations for ion management in tissues, salinity tolerance also encompasses physiological and morphological traits that strongly influence ecosystem processes (Ball 1988, Lovelock & Ball 2002). The ability of halophytes to achieve and maintain high rates of photosynthesis under saline soil conditions is linked to higher water-use efficiency than that found in nonhalophytes (Ball & Farquhar 1984, Clough & Sim 1989). High water-use efficiency is achieved and safely sustained by a range of traits, which vary among species and influence ecosystem function at higher scales. These traits include the following:

1. a specialized stomatal anatomy that limits water loss (Tomlinson 1986);
2. high levels of protection from photooxidative damage (Lovelock et al. 1992, Cheeseman 1997);
3. modifications and arrangement of leaves to improve leaf energy balance, in which leaves are often smaller and thicker and have upright orientations that avoid direct sun exposure, thus minimizing transpiration per unit of carbon uptake and maximizing heat loss (Ball et al. 1988, Lovelock et al. 1992);
4. hydraulic architecture that minimizes the risks of embolism under water-limited conditions (Lovelock et al. 2006a, Stuart et al. 2007), which is associated with small vessels and dense wood (Verheyden et al. 2005, Schmitz et al. 2006); and
5. greater carbon investment in roots than leaves (Ball 1988, López-Hoffman et al. 2007) and deployment of roots into soil-water resources that are more favorable for physiological function (Greaver & Sternberg 2006, Lambs et al. 2008).

The traits associated with salinity tolerance give rise to mangrove forest canopies that have distinctive energy signatures (Souza-Filho et al. 2006). For example, thick, tough, low-nutrient tissues and hard wood lead to lower rates of decomposition (Middleton & McKee 2001), herbivory, and nutrient cycling (Feller et al. 2009).

Salinity tolerance incurs costs that influence ecological processes. High respiratory costs involved in salt uptake and storage (Burchett et al. 1989) influence recruitment and understory development (López-Hoffman et al. 2007). Despite high concentrations of salt and ammonium (and other ions) in mangrove soils, root respiration is low compared with that of terrestrial trees (Burchett et al. 1989) and is highly efficient with respect to nitrogen and phosphorus investment (Lovelock et al. 2006b). Low nutrient-use-efficient respiratory rates compared with those of many plant species are likely due to adaptations in root ion-uptake processes that are not understood (Malagoli et al. 2008) but have flow-on effects on carbon and nutrient cycling at the ecosystem level.

**Flooding tolerance.** Emerging from a collection of morphological and physiological traits, flooding tolerance is the basis of some of the most valued ecosystem services provided by mangrove forests. Flooding usually decreases plant growth as it reduces $O_2$ concentrations at the root surface, inhibiting water uptake and other primary physiological functions (Gibbs & Greenway 2003). Flooding tolerance influences processes ranging from individual growth to community and landscape development. Traits that contribute to flooding tolerance include aerial root systems and aerenchyma (Scholander et al. 1962). Differential flooding tolerance among mangrove species is linked to variations in root morphologies and physiology (Naidoo 1985, He et al. 2007), which in turn strongly influence growth and recruitment (Youssef & Saenger 1998) and vegetation patterns along hydrologic gradients (Smith 1992).

Aerial roots strongly influence the emergent properties of mangrove ecosystems, their function, and the services they provide. Aboveground roots and stems influence flow rates of tidal waters, determining particle-settling rates and sediment retention in mangroves (Wolanski et al. 1992). Sedimentation is an extremely important process in coastal wetlands, determining nutrient inputs, productivity, and surface accretion, which in turn influence mangrove forest interactions with nearshore habitats as well as mangrove responses to sea-level rises and intense storms (Krauss et al. 2003, Day et al. 2008).

**Reproductive traits and regeneration.** Many mangroves have evolved a specialized reproductive strategy in which seeds lack dormancy and are viviparous, germinating precociously while still attached to the parent plant. These seedlings are buoyant, photosynthetically competent, and transported in tidal (Rabinowitz 1978, Stieglitz & Ridd 2001) and ocean currents, often over long distances (Nettel & Dodd 2007). Vivipary is found in many of the most salt- and flood-tolerant mangrove families (i.e., Rhizophoraceae, Avicenniaceae, Myrsinaceae, Plumbaginaceae, Pelliceriaceae, Aracaceae) and is associated with low levels of abscisic acid within the embryonic tissues (Farnsworth & Farrant 1998).

Vivipary and the buoyancy of seeds and propagules influence processes that are observed at a range of scales. Patterns in mangrove vegetation (zonation) were long thought to be due to the differential movement of propagules of various sizes with tidal movements (Rabinowitz 1978). Although little experimental support has been found for the propagule-sorting hypothesis (Sousa et al. 2007), seasonality in reproductive output (Duke 1990) and tidal movement of propagules upstream has been observed at a rate of 3.2 km/day. This movement is driven by seasonal salinity gradients and turbulence in creeks (Stiegliz & Ridd 2001), indicating that patterns in recruitment and vegetation may emerge from complex interactions among propagule characteristics, phenology, and climatic factors.

The production of viviparous propagules is a risky strategy, potentially sustaining high costs that may have influenced the evolution of other traits. Because of a lack of seed dormancy, forests affected by large-scale disturbances (hurricanes, tsunamis) may not have local seed reserves, necessitating reseeding from other sites less impacted by disturbance and requiring long-distance dispersal in water and longevity of propagules (Nettel & Dodd 2007). Other costs of vivipary may include a large investment in propagules versus investment in seeds in nonmangrove species. For example, Bunt (1995) reported the proportion of litterfall that is reproductive material varies between 4% and 50% of annual litterfall for mangroves at a range of sites around Australia, whereas for terrestrial tropical forests, the proportional contribution of reproductive material in litter ranges from 0.4% to 13.1% (Green 1998).

Regeneration of forests after small-scale (gap formation; Duke 2001) or large-scale (hurricanes; Cahoon et al. 2003) disturbances is dependent not only on seedling recruitment but also on resprouting of damaged trees (Baldwin et al. 2001). The capacity to resprout or coppice after disturbances varies among mangrove species. Species in the Avicenniaceae resprout from epicormic buds, but this does not occur in species in the Rhizophoraceae, making Rhizophoraeae forests particularly vulnerable to hurricanes (Baldwin et al. 2001, Cahoon et al. 2003), cyclones, frosts (Lugo & Patterson-Zucca 1977, Smith et al. 1994), and sediment deposition from storms or human activities (Ellison 1998). Both the impacts of disturbance on mangrove forests and their recovery from disturbances can depend on the dominant species, phenology, and the distribution and longevity of reproductive individuals.

**Nutrient availability.** Soil nutrient availability is variable within and among mangrove ecosystems, ranging from extremely low in oceanic settings to very high in accreting muddy systems and those receiving effluent from rookeries, aquaculture, and human developments (Alongi 2009). It can vary spatially along tidal gradients and temporally with seasonal and interannual variation in nutrient delivery and cycling. From fertilization experiments over a range of sites, it has been established that tree growth is nutrient limited in many mangrove forests (Lovelock et al. 2007, Naidoo 2009).

Many mangrove species have traits that give rise to efficient nutrient use and conservation when challenged by nutrient limitations (Feller et al. 2009). High nutrient-use efficiency (NUE) and variation in NUE in mangrove species emerge from a range of physiological and morphological traits, including enhanced investment in roots relative to shoots (Naidoo 2009); long leaf life spans (Duke 1990, Suárez 2003); high resorption efficiencies in tissues prior to senescence (Feller et al. 2009); thick, sclerophyllous leaves (Feller & Chamberlain 2007); low leaching losses (Wanek et al. 2007); high photosynthetic NUE (Lovelock & Feller 2003, Martin 2007); and NUE of root and other metabolic processes (Lovelock et al. 2006c).

Plant traits that confer tolerance of low nutrient availability have strong effects on ecosystem processes (Chapin 2003) and contribute to the emergent properties of mangrove ecosystems at greater spatial and temporal scales (Feller et al. 2009). Two neotropical species observed to be highly adapted to low nutrient availability are *Rhizophora mangle* and *Laguncularia racemosa*. Respiration and photosynthesis per unit tissue nutrient are high in these species compared with their competitor *Avicennia germinans* (Lovelock et al. 2006a, 2006b). Additionally, investment in roots, tissue nutrient concentrations, and sclerophylly and chemical defenses are also enhanced in *R. mangle* and *L. racemosa* relative to *A. germinans* (McKee 1995). These species differences in traits related to nutrient conservation influence resistance to herbivores and pathogens (Feller 1995, Feller & Chamberlain 2007), decomposition of tissues (Middleton & McKee 2001), and surface elevation gains (Krauss et al. 2003). Differences in NUEs may also contribute to patterns of species distribution over salinity, hydrologic, and nutrient gradients (Berger et al. 2006), which in turn alter productivity (Saenger & Snedaker 1993), responses to disturbance, and patterns of succession (Sherman et al. 1998, Piou et al. 2006).

## Trait Plasticity

High levels of plasticity in plant traits arise and are maintained in populations when environments are variable, environmental cues are reliable, and specialization has costs (Callaway et al. 2003). Mangroves display a high level of trait plasticity in response to salinity, flooding, and nutrient availability. For example, growth and metabolism of many mangrove species decline when salt is withheld (Ball 2002), suggesting a loss of competitive ability under "terrestrial" conditions. Growth of mangroves is also slowed under hypersaline conditions, but many species can maintain some level of growth (e.g., dwarf or scrub forms), albeit at a very slow rate, under extremely adverse conditions (Feller 1995, Lovelock et al. 2005). Species that form dwarf or scrub forest stands are often capable of attaining very high growth rates that match those of terrestrial forests (Dadhouh-Guebas et al. 2004, Feller et al. 2009). Mature tree size for the neotropical species *R. mangle* varies between 0.5 and 40 m (Lugo 1997, Golley et al. 1975). The coefficient of variation of hydraulic conductivity (which can be used as a measure of trait plasticity) of *R. mangle* stems is 0.2 greater than the variation in nutrient availability. By way of contrast, the mean coefficient of variation of hydraulic conductivity among 17 different species of oaks is 0.12 (Cavender-Bares et al. 2004). These and other examples of trait plasticity (McKee et al. 2007b, Feller & Chamberlain 2007) suggest that mangrove species are highly plastic in comparison to many terrestrial species.

On an ecosystem level, high levels of trait plasticity yield forests that can vary widely in structure and age but are comprised of one species (Dadhouh-Guebas et al. 2004, Lovelock et al. 2005). Even though studies of competition and facilitation among mangrove tree species are rare, the range in plasticity among mangrove tree species in response to salinity (Ball 1996), nutrient availability

(Lovelock & Feller 2003), flooding, and climate (Cardona-Olarte et al. 2006, He et al. 2007) may influence community composition and, ultimately, carbon and nutrient cycling in forests.

## EMERGENT AND COLLECTIVE PROPERTIES OF FORESTS

### Zonation

Landscape-level patterns that emerge in mangrove forests have long captivated scientists, giving rise to a rich observational and experimental tradition (Krauss et al. 2008). Mangrove forests are described as having "zones" of vegetation, typically arranged along tidal gradients that are dominated by one or two species. Although species zones have been represented graphically (Smith 1992), they have defied statistical detection in species-rich regions, leading Smith (1992), Bunt & Stiegliz (1999), and Ellison et al. (2000) to conclude either that environmental gradients and their effects on species performances are very complex or that dispersal and recruitment are random.

Ecophysiological studies have revealed that many species may co-occur because of similar physiological requirements (Ball 1996) and that strong patterning in vegetation emerges on the extreme ends of environmental gradients (e.g., salinity, flooding, nutrient availability) (Ball 1998). Thus, abiotic factors are likely to be most important in driving vegetation patterns through their differential effects on seedling growth and mortality in unfavorable environments (Ball 1996). In more favorable settings, competition or facilitation among species may also be important in determining zonation. Different species may modify environments sufficiently to affect competitors either above- or belowground (Passioura et al. 1992). Variations in species salinity tolerance (Ball 1996), shade tolerance (Lovelock et al. 1992, López-Hoffman et al. 2007), flood tolerance (Cardona-Olarte et al. 2006, He et al. 2007), and nutrient requirements (Lovelock & Feller 2003) may all have a role, although there are few experimental tests of direct competition (Smith 1992). Experimental studies have also indicated an important role for biological agents, with particular emphasis on seedling predators (crabs and beetles) (Smith 1987, Sousa et al. 2007).

Tree species zonation, or at least differential tree species distributions, within the intertidal zone have wide-ranging effects on the properties of mangrove ecosystems that depend on the traits of species and their interactions with the environment (Chapin 2003). Differences among species in root structure, stem densities, and canopy characteristics influence material exchange during tidal flow, atmospheric exchange, as well as ecosystem responses to disturbances (Cahoon et al. 2003, Koch et al. 2009) and sea-level rise (McKee et al. 2007a). The variable effects of human exploitation and activities on mangrove forests are also heavily dependent on species distributions (Dahdouh-Guebas et al. 2005, Alongi 2009).

### Productivity

The productivity of mangrove forests is important for supporting mangrove and adjacent coastal food webs and for the stability of mangrove-fringed coasts. The productivity of mangrove forests can be equivalent to the most productive terrestrial forests, although it is highly variable over both large (latitudinal) and smaller (hydrological) scales (Bouillon et al. 2008, Alongi 2009). For example, in nutrient-rich riverine systems or the bird rookeries of the Neotropics, *Rhizophora* trees grow to more than 40 m tall and are highly productive (Golley et al. 1975). However, behind tall fringing forests or in nutrient-poor areas on offshore islands, old-growth forests at many sites are dominated by stunted stands with low productivity, $\leq$1.5 m tall (Lugo 1997). Variation in the primary productivity of mangrove forests emerges from a wide range of biotic and abiotic factors and results in highly variable environments for seedlings and other plants and fauna. Interactions among productivity, geomorphology, and hydrology influence material exchange with tidal waters via outwelling and inwelling, thus also impacting the services provided by mangrove ecosystems within larger and connected coastal ecosystems (Alongi 2009).

Net primary productivity (NPP) of forests is determined by the balance of the total $CO_2$ fixed by the forest (gross primary productivity) and total plant respiration, suggesting NPP can be considered a collective property of ecosystems. Gross primary productivity in mangrove forests, like that of terrestrial forests, is often estimated with simple algorithms using leaf area index (leaf area per unit ground area), light attenuation, or photosynthetic rates (Alongi 2009). The respiratory components of mangrove forests are poorly parameterized, though rates of $CO_2$ release from trees are substantial and dominated by the woody parts and roots (Lovelock 2008, Alongi 2009). The contribution of soil microbial processes in current carbon budgets of mangrove ecosystems is likely to be underestimated. Mineralization of sediments (imported), organic matter (particularly fine roots), and microbially derived organic matter may also be important in some areas, with these processes possibly leading to substantial carbon exports from porewater to coastal waters (Alongi 2009, Bouillon et al. 2008). Additional research is needed to better constrain the rates of and controls on soil respiration so that the fates of mangrove-derived and other organic matter within mangrove forests can be determined.

In mangrove forests, as in other forests, NPP has usually been estimated by leaf litterfall, but litterfall may represent only ~25–30% of mangrove forest NPP. Thus, NPP has been generally underestimated (Bouillon et al. 2008, Alongi 2009). Increments in accumulated wood and roots and losses of roots and other tissues as well as root exudates have been measured less frequently but may account for up to 70% of NPP. Variations among the components that comprise NPP among forests over environmental gradients are likely to influence ecosystem function, particularly affecting processes that link mangroves to adjacent ecosystems.

Other primary producers in mangrove ecosystems that are not usually considered in NPP include phytoplankton in tidal waters, benthic cyanobacterial and microalgal mats, algal turfs, and the distinctive root epiphytic algal community (the Bostrychietum) that adheres to aboveground roots and stems. These components may be more important than their absolute contribution to NPP because they may be preferentially decomposed and consumed (Bouillon et al. 2008). Benthic cyanobacterial and microalgal mats are common in scrub forests where high light levels reach the benthos. In these habitats, the mats may be as or more productive than the trees. These mats also play key roles in nutrient cycling (Lee & Joye 2006). The epiphytic algal community is also highly productive, contributing up to 15% of forest gross primary productivity (Dawes et al. 1999). In addition to providing tissue that is more palatable to consumers than mangrove leaves, the epiphytic algal community increases frictional resistance, which affects flow rates of the water and deposition of sediment, nutrients, and organic matter within the mangroves (Wolanski et al. 1992).

## Nutrient and Carbon Cycling

The biogeochemical signature of mangroves and other coastal wetlands is a collective property stemming from the biological, physical, and chemical interactions among flood- and salt-tolerant plants and microbial processes in soils. Mangrove forests are intensely affected by a tidally mediated exchange of materials. Tides connect the mangrove fringe and the nearshore waters, whereas interior forests are more isolated in the landscape. The fringe is an open system, often accumulating subsidies of sediments as well as wrack (Wolanski et al. 1992) and nekton (Sheaves 2005), while exporting particulate and dissolved organic matter via tidal exchange (Jennerjahn & Ittekkot

2002). Interior habitats, which are often dominated by scrub forests, are closed systems with a more pulsed materials exchange. Differing degrees of "openness" between fringe and interior habitats impact their nutrient stoichiometry (Kristensen et al. 2008).

Allocthonous subsidies (e.g., seagrass wrack, polysaccharide-bound particulates, nekton waste products) to mangrove fringes have low C:P and C:N values (Ayukai & Wolanski 1997), compared with outwelled materials of mangrove origin, which have higher C:N:P ratios (Bouillon et al. 2008). Scrub forests, ponds, and microbial mats export substantial amounts of dissolved organic nitrogen and carbon to tidal creeks (Joye et al. 2005). Nitrogen fixation in microbial mats provides a nutrient subsidy for scrub mangrove trees, adjacent forests, and benthic and planktonic communities (Joye & Lee 2004, Lee & Joye 2006).

Nutrient cycling in mangrove habitats reflects a balance between nutrient inputs, availability, and internal cycling (Lee et al. 2008). Microbial processes alter soil nutrient concentrations and nutrient cycling. Denitrification reduces inorganic nitrogen concentrations and could drive nitrogen limitation of plant production (Joye 2002). In contrast, microbial nitrogen fixation increases nitrogen inventories and ameliorates nitrogen limitation of plant production (Joye & Lee 2004). Microbial processes affect phosphorus availability indirectly. In addition to mediating nutrient cycling, anaerobic microbial processes oxidize particulate and dissolved organic matter in soils (Lee et al. 2008). Thus, nutrient availability and cycling are intimately linked to microbially mediated carbon turnover in mangrove soils.

Inputs of excess nutrients to mangroves can alter patterns of nutrient limitation over time, but not all ecological processes or ecosystem components exhibit the same pattern of nutrient limitation (Feller et al. 2009). However, nutrient controls on ecosystem components, such as benthic microalgae, are poorly described or unknown (Joye & Lee 2004). Nitrogen enrichment may increase release of dissolved organic matter from mangrove soils occupied by microbial mats, as documented in benthic microalgae-dominated salt marsh sediments (Porubsky et al. 2008).

Despite their small areal extent, mangrove forests play an important role in global carbon cycling. They are responsible for substantial fluxes of dissolved organic carbon (DOC) to the ocean (Dittmar et al. 2006, Bouillon et al. 2008), accounting for 15% of the carbon stored in marine sediments and sequestering a global average of 10.7 mol carbon m-2yr-1 of atmospheric $CO_2$ in peat (Jennerjahn & Ittekkot 2002). Dittmar et al. (2006) found that 10% of the terrestrially derived DOC in the oceans is derived from mangroves. Similarly, high fluxes of dissolved organic nitrogen and DOC from mangrove soils to the overlying waters were documented in Belize and Panama (Joye et al. 2005). These fluxes of nutrients and organic material to the ocean are expected to increase further as a result of mangrove clearing and nutrient enrichment (Bouillon et al. 2008).

Microbial biomass and activity estimates in mangrove soils suggest that most bacteria remain unconsumed, eventually lysing to support continued bacterial production and release of dissolved nutrients (Kristensen et al. 2008). Microbial activity in soils and sediments are ultimately controlled by inputs of dissolved and particulate organic matter and may also be limited by nutrient availability (Sundareshwar et al. 2003). Variation in nutrient versus carbon limitation of microbial decomposition in mangroves may contribute to differences in carbon-recycling efficiencies. Although the flux of DOC from mangroves to the ocean is an important part of the carbon cycle, it remains poorly understood (Kristensen et al. 2008).

In addition to DOC fluxes via water, carbon accumulations in soils and flux to the atmosphere via root respiration are also important parts of the carbon cycle (Alongi 2008). In mangrove forests, fine root production, forest stature, and variations in nutrient availability are likely to be important factors determining carbon flux (Lovelock et al. 2006c), but soil respiration is similar to terrestrial systems and is correlated with aboveground production (Lovelock 2008).

## Habitats and Food Webs

A complex community structure distributed vertically through supratidal, intertidal, and subtidal zones and horizontally across the land-sea ecotone is an emergent property of mangrove forests that has arisen out of specializations of individual species to the intertidal zone. The structure provided by these species essentially defines mangrove communities and ecosystems by creating habitats and stable conditions, modifying abiotic environments, and modulating ecosystem processes. Similar to terrestrial trees, mangroves are composed of a woody bole and a leafy canopy inhabited by ecological communities not unlike those found in other tropical forests. But, unlike terrestrial species, the aerial root systems of mangroves also form an extensive aboveground structural framework, which dramatically increases the architectural complexity of these forests. These structures not only provide habitat for supratidal and intertidal communities, but they also often suspend into the adjacent water column where they are colonized by rich assemblages of organisms and provide food and shelter for fish, shrimp, and other nektonic organisms (Nagelkerken et al. 2008). Because mangroves are typically mud- or peat-based systems, prop roots provide the hard substrate essential for settlement by many sessile marine organisms.

Species diversity, as a collective property of mangrove ecosystems, stems directly from the spectrum of habitats created and modified by these trees. Despite low species richness of mangrove vegetation, recent reviews (Cannicci et al. 2008, Krauss et al. 2008, Nagelkerken et al. 2008) have summarized an extensive body of literature documenting the habitat function of mangroves and the impacts of the fauna on forest development, productivity, and structural complexity. In the supratidal, the mangrove canopy supports a terrestrial fauna that, like other forests, is dominated by insects but also includes birds, mammals, lizards, snakes, snails, crabs, and spiders. In the Neotropics, the diversity of vertebrates associated with mangroves is low with few endemic species. That situation is different in Australian mangrove communities, where there are many endemic species, especially birds (Luther & Greenberg 2009). Biogeographic studies indicate that most species are a subset of the terrestrial fauna and disperse into the mangrove by swimming, flying, or rafting inside or on pieces of wood or other floating debris (Rützler & Feller 1996, Brooks & Bell 2001).

Mangrove forests have been described as detritus-based ecosystems where primary consumers play a minor role (Tomlinson 1986). However, recent studies have shown that herbivory in mangroves is comparable to that of other temperate and tropical forests (Cannicci et al. 2008). Similar to their role in other ecosystems, mangrove herbivores play important ecological roles that include decreasing primary production, increasing habitat and community complexity, creating light gaps, interfering with internal nutrient cycling, and increasing nutrient losses (Feller 2002). This fauna is characterized by specialized, cryptic, endophytic species, that are comprised of miners, gallers, and borers (Feller & Chamberlain, 2007, Feller et al. 2007). In the intertidal, typical substrates for benthic organisms include tree trunks, aerial roots, peat banks, and mud- and saltflats. Here, alternating submergence and exposure and fluctuating salinity create stressful environmental conditions. Whereas the mangrove understory is noted for its lack of diversity of vascular flora, the intertidal portions of aerial roots support a diverse intertidal assemblage of algal epiphytes, which in turn host a variety of invertebrates (Kieckbusch et al. 2004, Lee 2008). Algal mats on the soil surface are also home to numerous taxa of marine invertebrates (Kathiresan & Bingham 2001). Mangrove mud- and saltflats are often covered in thick, laminated cyanobacterial mats that provide habitat and food resources for many benthic organisms, including invertebrates, amphibious fish, and sea snakes (Cannicci et al. 2008). The biocomplexity of mangrove communities is further enhanced by organisms (crabs, fish, birds, and mammals) that migrate across tidal zones and thereby link supratidal, intertidal, and subtidal food webs (Vannini et al. 2008).

Although mangrove productivity is highest in coastal and riverine forests, most species are found in the associated subtidal habitats. The subtidal communities of coastal mangroves are less diverse than in offshore mangrove islands where the water is clear and more reef-like (Rützler & Feller 1996). In those areas, aerial roots provide structure for a dense assemblage and colorful array of sessile epibionts, including algae, sponges, tunicates, and anemones, and support diverse ecological interactions between mangroves and these subtidal epibionts, ranging from mutualistic to parasitic.

# EMERGENT PROPERTIES OF ECOSYSTEMS AND LANDSCAPES

## Habitat Stability

Even though coastal systems are subject to changing sea levels, hurricanes, and tsunamis (Alongi 2008), many mangrove habitats sustain themselves for millennia (Gilman et al. 2008). For example, mangrove islands in the Mesoamerican Barrier Reef system of Belize have existed for ~8000 years and have accumulated more than 10 m of peat as sea level has risen (Macintyre et al. 2004). Vertical building of these islands has allowed them to maintain surface elevations within the intertidal (**Figure 2**), where mangroves have dominated for their entire history (McKee & Faulkner 2000, McKee et al. 2007a). Thus, an emergent property of these biogenic mangrove systems is habitat stability, which is defined here as persistence of the mangrove habitat, relatively unchanged, through time.

Stability of mangrove habitats arises from the interaction of physical, chemical, and biological components operating at different spatial, temporal, and organizational scales. Processes occurring at the cellular, organism, population, ecosystem, and landscape scales contribute to habitat stability. Any disturbance that alters these processes may cause the system to collapse or to convert to some other habitat, for example, where mangroves have invaded and converted a saltmarsh (Rogers et al. 2006). If sea-level rise exceeds the capacity of a mangrove system to build vertically, it will become a subtidal system, as is predicted for low-lying oceanic islands. Conversely, if elevation gain raises the mangrove surface above the intertidal, the system may be invaded by upland vegetation. However, the latter is unlikely to occur without exogenous input of sediments. As elevation changes, flooding depth and duration influence plant production and decomposition. This feedback process allows the mangrove system to adjust to prevailing water levels and persist through time (**Figure 2**).

For a group of mangrove islands in the Caribbean, McKee et al. (2007a) showed that peat is primarily composed of mangrove roots and that fossil roots, >7000 years old, are indistinguishable from modern roots. The buildup of peat caused upward expansion of the soil surface at rates sufficient to keep pace with sea-level rise over the Holocene. As sea-level rise in the Caribbean slowed ~2000 to 3000 years BP (before the present) (Toscano & Macintyre 2003), peat formation slowed. Elevation change on Belizean islands, measured with surface elevation tables from 2000 to 2008, average ~3.5 mm year$^{-1}$ (K.L. McKee, unpublished data), which is similar to global sea-level rise rates (3.4 mm year$^{-1}$; Nerem & Choe 2009). These data support the existence of a feedback mechanism that allows mangrove systems to adjust to prevailing sea-level conditions. This feedback likely occurs through the change in flooding conditions and its effect on sedimentation and production-decomposition processes as elevations fluctuate during soil formation. In peat soils with moderate flooding, root production is high and decomposition is slow, leading to peat formation. As peat accumulates and the soil surface expands upward, there is a decrease in flooding depth and duration. As flooding decreases, peat formation and sedimentation slows—leading to a feedback control on vertical land-building.

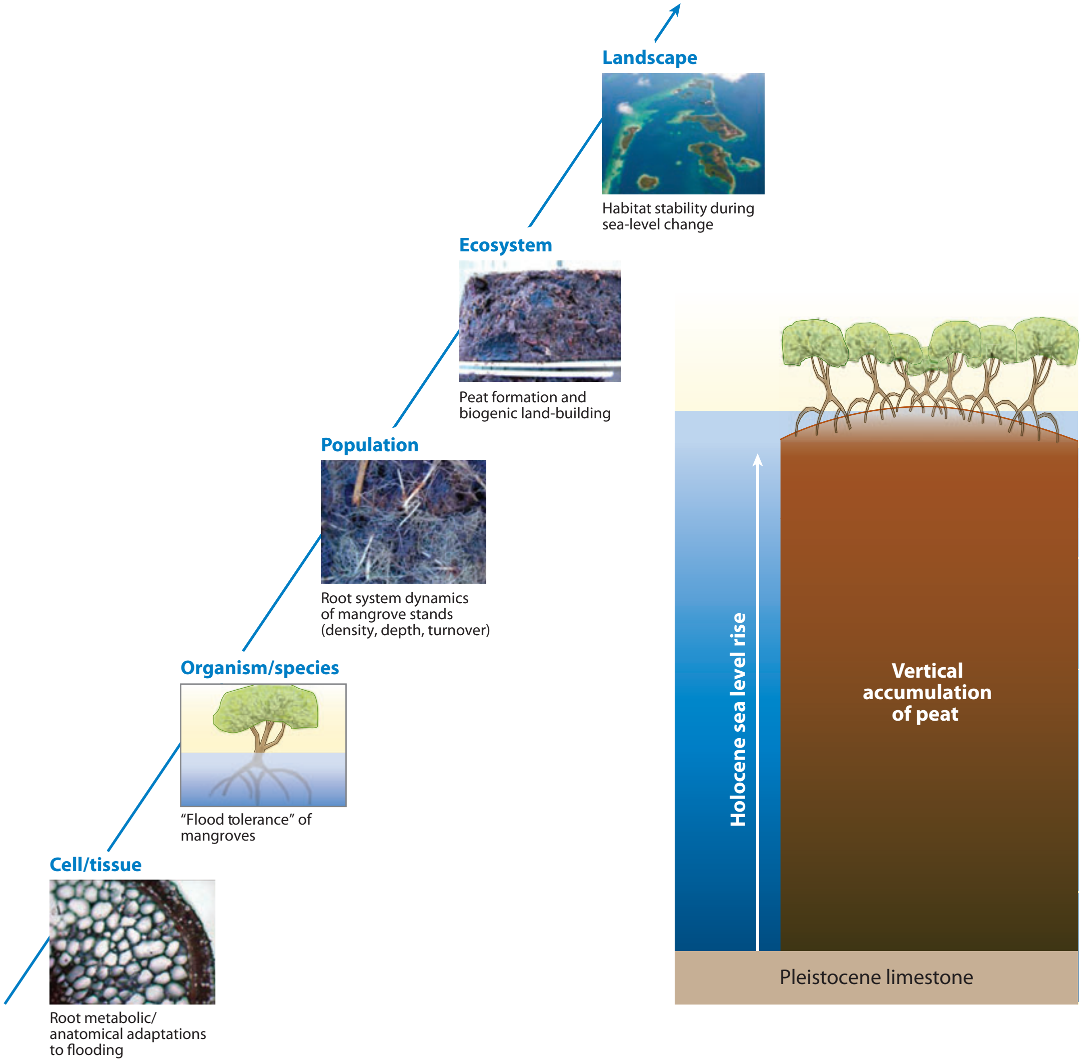

**Figure 2**

Biocomplexity of biogenic mangrove forests results in the emergent property of habitat stability, i.e., persistence during sea-level change via peat formation and vertical land-building. Characteristics of mangroves at different organizational scales generate a capacity to self-adjust to the prevailing flooding regime. Stress adaptations (metabolic and anatomical) to flooding at the cell or tissue scale lead to the emergent property of flood tolerance at the organism or species scale. The tolerance of anaerobic conditions allows prolific production of mangrove roots in flooded soils, but physical limits to root aeration promote root growth at or near the soil surface. As roots die, their decomposition is retarded owing to lack of oxygen, which promotes peat formation. The buildup of peat causes upward expansion of the soil surface and a consequent decrease in flooding depth and duration. As flooding stress decreases, peat formation slows—leading to a feedback control on vertical land-building. The net result of these feedback processes at the landscape scale is the emergent property of habitat stability. In some cases, mangrove forests may persist for millennia unless disturbed in such a way as to alter the feedback controls on land elevations.

Persistence of biogenic mangroves over geological time depends on processes occurring over shorter intervals, e.g., annual production of plant roots. Spatial variation in mangrove productivity, tidal fluctuation, nutrient availability, and other factors causes landscape-level variation in habitat stability. For example, spatial variation in elevation change is associated with different rates of belowground production (McKee et al. 2007a). Thus, habitat stability arises from interrelationships across spatial, temporal, and organizational dimensions.

When a disturbance causes widespread mortality of biogenic mangroves, the sudden death of the root system and lack of root production may lead to peat collapse and alter habitat stability, as occurred in the Bay Islands, Honduras, in 1998 following Hurricane Mitch (Cahoon et al. 2003). Forests with little damage showed elevation gains (5 mm $\text{year}^{-1}$) in concert with high rates of root production in the years following the hurricane. However, forest stands that suffered near-total mortality experienced peat collapse ($-11$ mm $\text{year}^{-1}$). Model simulations predicted that peat collapse would continue for at least eight more years at a rate of 7 mm $\text{year}^{-1}$ in the absence of mangrove recovery. Anthropogenic disturbances caused by sediment burial may also lead to the collapse of mangroves (Ellison 1998). Another growing threat results as mangroves are being cleared and filled to support resort development and vegetation typical of the beach habitat. In the Caribbean, developers are converting offshore mangrove islands into tourist resorts (Macintyre et al. 2009, McKee & Vervaeke 2009). Here, removal of mangroves and burial of the underlying peat with sediments dredged from the surrounding seafloor have altered soil characteristics, increased erosion, and reduced the capacity of these islands to keep pace with sea level. Thus, subsidence of the peat and sea-level rise will submerge such areas, despite temporary increases in elevation by filling.

## Connectivity

Mangroves are connected to both subtidal and terrestrial environments through movement of water across ecosystem boundaries and through movement of fauna. Mangroves serve not only as sources of subsidies (carbon and nutrients; Kristensen et al. 2008) and fauna for adjacent environments (Nagelkerken et al. 2008), but also as sinks in the land-seascape (Bouillon et al. 2008). The connectivity between mangroves and adjacent ecosystems and food webs (Aburto-Oropeza et al. 2008) is an emergent property that arises out of the interactions among the landscape, geomorphology, hydrology, climatic and tidal regimes, structural characteristics, accessibility to fauna, and the proportion of edge to area of mangrove forests, which enhances the potential for exchange across boundaries (Nagelkerken et al. 2008). This connectivity not only contributes to the economic value placed on mangroves, but also increases their vulnerability to human and natural disturbances (Alongi 2008).

Exchange of material and fauna in tidal waters has been extensively examined because of the vital role mangroves play in supporting fisheries (Nagelkerken et al. 2008), their role as filters where sediments and nutrients are trapped (Alongi 2009), and the recent discovery of the importance of mangrove-derived carbon to oceanic production through microbial processing (Dittmar et al. 2006). Although we have a general understanding of the scope of the ecosystem services provided through tidal connectivity of mangroves and near-shore waters, the factors that determine variability in the provision of these services are complex and likely nonlinear (Koch et al. 2009). The fisheries value of mangroves depends on a range of factors that include the species being considered (habitat, ontogenetic stage, feeding preferences); site characteristics (currents, tidal flow, turbidity, area and arrangement of habitats); climatic variability (diurnal, seasonal, annual, decadal); and presence, abundance, and movements of competitors and predators (Faunce & Serafy 2006, Aburto-Oropeza et al. 2008). Although mangroves may function as nurseries for many species, direct evidence for fish migrations between mangrove and offshore habitats is scarce (Nagelkerken et al. 2008). For successful integrated management of mangroves, an understanding of the complexity of factors that give rise to productive and diverse fisheries is vital. Marine protected areas that embrace multiple habitat types and include the terrestrial catchments have the greatest potential for success (Heyman & Kjerfve 1999).

Less well studied is the connectivity among terrestrial species and mangrove habitats and fauna. At the landscape scale, mangroves are ecotones where marine and terrestrial food webs often overlap, where marine organisms gain access to terrestrial prey, and where terrestrial fauna have access to marine prey or to other terrestrial fauna that visit mangroves for refuge or feeding (Nagelkerken et al. 2008). The interruption of mangrove-terrestrial ecotones is a common result of coastal developments, which alter tidal incursions and disrupt exchange across the ecotone with largely undocumented consequences (Walters et al. 2008).

Connectivity to rivers and tidal water underlies the biofiltration services mangroves provide. Variation in the level of sediment retention, which is important for adjacent coral reef and seagrass ecosystems requiring high light levels at the benthos, has been attributed to interacting factors, which include the following: (*a*) the friction to tidal fluxes offered by roots and burrows; (*b*) the position in the forest (forest edges trap more sediment and particles than do forest interiors); (*c*) seasonal variation in the heights and strengths of tidal flows; (*d*) variation in sediment loads; and (*e*) the geomorphology and hydrology that control riverine flows, currents, and tidal amplitudes (Wolanski et al. 1992). Nutrient exchange, which facilitates capture and liberation of nutrients that enhance coastal production, is influenced by spatial and temporal factors as well as factors that control primary production of trees, macroalgae, microphytobenthos, and microbial communities.

Disruption of connectivity between mangroves and other components of the landscape can have negative consequences. Loss of mangroves in the Philippines, for example, has resulted in a 90% drop of fisheries production over the 20 years of mangrove removal for shrimp aquaculture, which was ironically aimed at increasing total fisheries production (Primavera 1997). The devastating effects of the 2004 Indian Ocean tsunami on many tropical coastal communities underscored the economic value of mangroves in protection from waves (Koch et al. 2009).

## Modeling Biocomplexity and Emergent Properties

Biocomplexity is a synonym for intricacy, but there are differences between complex and complicated systems. For complicated systems, analyses of all subunits are required. For complex systems, interactions among environmental drivers, transient and nonequilibrium dynamics, as well as biotic and abiotic interactions and feedback loops must be addressed. Because of the constitutive hierarchy of ecological systems (Hölker & Breckling 2005), it is difficult to separate the consequences of single factors, processes, and data taken at multiple scales. In such hierarchies, interactions are nested, which complicates application of the concept of emergence in empirical studies. IBMs, which are mechanistic models at the level of individuals, have proven suitable for explaining complex patterns at population levels and for predicting responses to environmental changes and habitat alterations, which are obscure in population models. In simulation experiments using the gap model FORMAN, trajectories of mangrove attributes were forecast according to different restoration criteria at Cienega Grande (Colombia) at decadal timescales (Twilley et al. 1998). This study verified mechanisms controlling the rehabilitation of mangroves and contributed to the design and implementation of restoration projects. Simulation experiments with the IBM KiWi model (Berger & Hildenbrandt 2000) were used to understand secondary succession of mangroves in abandoned rice fields in northern Brazil (Berger et al. 2006). This study revealed that canopy structure was not explained by shade tolerance as originally hypothesized. To match the observed data, growth of the initial dominant species (*L. racemosa*) had to slow down relative to the subsequent dominant species (*A. germinans*). Differences in species-specific NUE (Lovelock & Feller 2003) may underlie this pattern.

Despite the increasing number of applications of IBMs for understanding mangrove forests and their responses to disturbances, limitations persist in empirical knowledge and model resources that restrict the use of these as management tools. None of the mangrove forest models available explicitly include recruitment processes (Berger et al. 2008), which can be important for regulating forest trajectories over time (Berger et al. 2006). Recruitment limitations linked to resource availability must be studied to understand how species richness and spatial distribution are maintained. Small gaps might, for example, restrict regrowth of pioneer species (Baldwin et al. 2001). Simulation studies addressing such issues must be linked across scales to field experiments focusing on the relationship between gap geometry and species distributions. Multifactorial experiments are needed to examine how hydroperiod and soil nutrient concentration limit growth of both seedlings and adult trees (Cardona-Olarte et al. 2006). There is also a need for mechanistic submodels and hybrid models to support the analyses of field experiments and to serve as input modules for environmental conditions in IBMs. Currently, only one model (NUMAN) simulates soil nutrients for mangrove systems (Chen & Twilley 1998). To address these problems, we need to combine and test advanced statistical models and mechanistic models, including linkage to large-scale data sets that allow validation with empirical data.

Most existing IBMs for mangrove forests consider only trees. Similarly for the fauna, only one IBM describes local movement of crabs (Piou et al. 2007). Developing models that include food webs and nutrient cycling is a challenge for ecologists and modelers (Cannicci et al. 2008). Comprehensive analyses of a complex system like mangroves require IBMs that cross trophic levels and hierarchies.

The description of trees in such models also needs to be improved and to include plant-plant interactions (Berger & Hildenbrandt 2000), which will provide insights into vegetation dynamics. Although empirical studies have shown that the relative importance of competition and facilitation may vary (McKee et al. 2007b), this is not considered in mangrove IBMs.

There is also limitation in the flexibility of plant models (Berger et al. 2008) to represent plasticity in tree architecture. They are not suitable for analysis of the influence of resprouting or deviations from circular crown shapes on forest dynamics. Although all mangrove forest models consider trees, scrub mangroves, such as the low-stature trees frequently occurring on the coastline or in the hinterlands, are not represented. A model capturing these features would be useful for analyzing forest dynamics. Inclusion of these will increase technical and scientific requirements of both empirical and theoretical studies and will also require a multidisciplinary approach.

## SUMMARY

Although the concept of emergent properties has been around for a long time, it continues to provide a framework for identifying and studying key features of an ecosystem that determine its uniqueness and importance both to science and society. Progress toward identifying key features and the underlying component processes that are important for improving our understanding of mangrove responses to climate change, land-use changes, and societal needs requires a more holistic approach than has been pursued in the past. We need an integrated research strategy for the future, where empirical and theoretical ecologists as well as computer scientists work together on formulating, implementing, parameterizing, testing, comparing, and selecting the new approaches that identify interconnectedness leading to emergent properties. Multidisciplinary studies are needed that provide the data at different trophic levels and a range of scales, including large-scale geographic comparisons, to identify and understand how processes lead to emergent properties. The development of international networks or observatories that provide large data sets needed to study variation in emergent properties is essential for moving forward beyond site-specific studies. Finally, enhanced effectiveness of conservation, restoration, and rehabilitation of mangrove ecosystems requires an understanding of what leads to desirable emergent properties that are the most important targets for conservation and restoration. We need to conduct research to provide the necessary information to design successful projects that will achieve one or more of these targets.

## DISCLOSURE STATEMENT

The authors are not aware of any potential biases that might be perceived as affecting the objectivity of this review.

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## Errata

An online log of corrections to *Annual Review of Marine Science* articles may be found at http://marine.annualreviews.org/errata.shtml