

Invited Feature

Mangrove forests: Resilience, protection from tsunamis, and responses to global climate change

Daniel M. Alongi

Australian Institute of Marine Science, PMB No. 3, Townsville MC, Queensland 4810, Australia

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Abstract

This review assesses the degree of resilience of mangrove forests to large, infrequent disturbance (tsunamis) and their role in coastal protection, and to chronic disturbance events (climate change) and the future of mangroves in the face of global change. From a geological perspective, mangroves come and go at considerable speed with the current distribution of forests a legacy of the Holocene, having undergone almost chronic disturbance as a result of fluctuations in sea-level. Mangroves have demonstrated considerable resilience over timescales commensurate with shoreline evolution. This notion is supported by evidence that soil accretion rates in mangrove forests are currently keeping pace with mean sea-level rise. Further support for their resilience comes from patterns of recovery from natural disturbances (storms, hurricanes) which coupled with key life history traits, suggest pioneer-phase characteristics. Stand composition and forest structure are the result of a complex interplay of physiological tolerances and competitive interactions leading to a mosaic of interrupted or arrested succession sequences, in response to physical/chemical gradients and landform changes. The extent to which some or all of these factors come into play depends on the frequency, intensity, size, and duration of the disturbance. Mangroves may in certain circumstances offer limited protection from tsunamis; some models using realistic forest variables suggest significant reduction in tsunami wave flow pressure for forests at least 100 m in width. The magnitude of energy absorption strongly depends on tree density, stem and root diameter, shore slope, bathymetry, spectral characteristics of incident waves, and tidal stage upon entering the forest. The ultimate disturbance, climate change, may lead to a maximum global loss of 10–15% of mangrove forest, but must be considered of secondary importance compared with current average annual rates of 1–2% deforestation. A large reservoir of below-ground nutrients, rapid rates of nutrient flux and microbial decomposition, complex and highly efficient biotic controls, self-design and redundancy of keystone species, and numerous feedbacks, all contribute to mangrove resilience to various types of disturbance. © 2007 Elsevier Ltd. All rights reserved.

Keywords: climate change; disasters; disturbance; mangrove forest; resilience; tsunami

1. Introduction

Change is a natural attribute of Earth's ecosystems, with organisms responding and adapting to spatial and temporal patterns in climate and other physical characteristics, including tectonic events, atmospheric and oceanic circulation, and landform settings. Such biological and ecological changes are often the result of individual, population, or community attributes such as tolerance to physicochemical factors, the ability to compete for limiting resources, and functional processes (ingestion, growth, respiration rates). All of these changes occur within

a milieu of natural disturbance to the ecological equilibrium or 'steady-state'. All ecosystems are subject to a variety of disturbances both natural and anthropogenic that vary in their duration, frequency, size, and intensity, and play a crucial role in facilitating adaptive change (Odum and Barrett, 2004).

Mangrove forests, like other ecosystems, are subject to various disturbances that vary in their intrinsic nature (e.g., geological, physical, chemical, biological) in time and space. Inhabiting the interface between land and sea at low latitudes, mangroves occupy a harsh environment, being daily subject to tidal changes in temperature, water and salt exposure, and varying degrees of anoxia. Mangrove forests and their inhabitants are therefore fairly robust and highly adaptable (or

E-mail address: d.alongi@aims.gov.au

tolerant) to life in waterlogged saline soils within warm, sub-tropical and tropical seascapes.

Mangroves may therefore exhibit a high degree of ecological stability. The term stability has been variously used to refer to environmental constancy, community persistence, and community or ecosystem response to disturbance. Because the term stability conveys different meanings, I here use the terms persistence and resilience as defined by Boesch (1974) in reference to estuarine ecosystems. *Persistence* refers to constancy over time, regardless of environmental perturbation. *Resilience* means the ability to recover from disturbance to some more or less persistent state. This definition has more recently been termed *ecological resilience* (Gunderson et al., 2002) as opposed to *engineering resilience* which conceives of the speed of an ecosystem to return to a stable steady-state.

Mangrove forests currently occupy 14,650,000 ha of coastline globally (Wilkie and Fortuna, 2003), with an economic value on the order of 200,000–900,000 USD ha⁻¹ (UNEP-WCMC, 2006). Regardless of their monetary value, mangrove ecosystems are important habitats, especially in developing countries, and play a key role in human sustainability and livelihoods (Alongi, 2002), being heavily used traditionally for food, timber, fuel, and medicine (Saenger, 2002). These tidal forests are often important nursery grounds and breeding sites for birds, mammals, fish, crustaceans, shellfish, and reptiles; a renewable resource of wood; and sites for accumulation of sediment, nutrients, and contaminants (Twilley, 1995; Kathiresan and Bingham, 2001; Manson et al., 2005). As addressed in this review, it is believed that mangroves offer protection from waves, tidal bores, and tsunamis, and can dampen shoreline erosion (Mazda et al., 2007).

Little attention has been paid to the adaptive responses of mangrove biota to disturbance (Smith, 1992; Ellison and Farnsworth, 2000). The lack of attention to disturbance-induced impacts likely reflects the perception that mangrove forests are in steady-state (Lugo, 1980) and are of generally low diversity. Mangroves have a variety of key features that contribute to their resilience to disturbance, whether they are acute disasters such as a tsunami or millennial change in climate. These characteristics are: (1) a large reservoir of below-ground nutrients that serve to replenish nutrient losses; (2) rapid rates of nutrient flux and microbial decomposition that facilitate rapid biotic turnover; (3) complex and highly efficient biotic controls (e.g., high rates of water-use and nutrient-use efficiency) that allow predominantly internal reuse of resources to augment recovery; (4) self-design and simple architecture that lead to rapid reconstruction and rehabilitation post-disturbance, despite different species composition; (5) redundancy of keystone species, or species legacies, which can lead to restoration and recovery of key forest functions and structure; and (6) positive and negative feedback pathways that provide malleability to help dampen oscillations during recovery to a more stable, persistent state. These tidal forests can attain immense biomass and height, rivalling the size of tropical rainforests; their standing crop is ordinarily greater than other aquatic ecosystems as equatorial forests often reach an above-ground weight of 300–500 t DW ha⁻¹ (Alongi, 2002).

The objective of this review is to critically examine the resilience of mangrove forests to large-scale acute and chronic disturbance, especially climate change and, as illustrated by the events of 26 December 2004, to disasters such as tsunamis. Such disparate events are, of course, not causatively linked, but both are forms of disturbance that cause physical damage and may provide clues as to how mangroves will respond to disturbances in future. The review also addresses the related themes of the role of mangroves in protecting hinterland and future losses of forest in the face of these disparate disturbances.

2. Clues from the past: sea-level reconstruction and forest development

Most of today's mangroves rests upon the remains of their past—a reflection of the ebb and flow of Earth's history. The current position of the world's mangrove forests is a legacy of the Holocene (Woodruffe, 1992, 2002; Lessa and Masselink, 2006). When viewed across geological time scales, mangroves come and go at considerable speed. Ancestral mangroves can be traced back 65 million years (Duke, 1992), and vast tracts of forest have waxed and waned since then. Because of their location, mangrove forests are—like their environment—highly dynamic. They must not be viewed as static entities.

Over the last few thousand years, mangroves have undergone almost continual disturbance as a result of fluctuations in sea-level (Woodruffe, 1990, 1992; Yulianto et al., 2005). The general pattern for the last interglacial–glacial cycle is one of overall sea-level fall through a series of oscillations related to ice-sheet accumulation, reaching the last glacial maximum at $\approx 18,000$ yr B.P. Since then, the ice has melted and sea-level has risen rapidly, at average rates of 5–15 mm yr⁻¹ (Woodruffe, 1990).

Evidence for dynamic change in mangroves over geologic time is provided by the existence of fossils and mangrove peat deposits in various parts of the world (Ellison and Stoddart, 1991; Plaziat, 1995; Kim et al., 2005). For example, on the Great Barrier Reef, relict mangrove deposits are commonly found within palaeo-channels of river beds that traversed the shelf out to the edge of the continental margin when sea-level was lower 7000 years ago. Sediment cores taken within these ancient river beds support the notion that sea-level change was abrupt (Hull, 2005). Further, as discovered at other locations, the deposits contain intact pieces of wood, bark, leaves, and roots and preserved well enough to identify to what family the trees belonged (mostly Rhizophoraceae). The persistence of these deposits indicates remarkably slow microbial decay, but it also signifies that local extinction of these forests was sudden (Hull, 2005). This interpretation supports the chronological record from cores taken further north off Indonesia on the Sunda Shelf, which indicate a rapid rise of sea-level, as much as 16 m within 300 yr (Hanebuth et al., 2000). The pattern of late Quaternary sea-level change consisted of two phases: (1) an early-Holocene phase of rapid sea-level rise (the post-glacial transgression) and (2) a mid- to late-Holocene phase of comparative stability of sea-level (Woodruffe, 2002). The broad pattern is what is reflected

beneath the Great Barrier Reef and on other palaeo-shores in Australia, and in much of the Indo-Pacific (Hanebuth et al., 2000). This two-phase pattern of sea-level change, however, is not seen in the Americas where the scenario was one of continual sea-level rise, but at a decelerating rate up until the present (Ellison and Stoddart, 1991; Parkinson et al., 1994). Despite local and regional variations in mangrove response to sea-level change, the analysis of stratigraphic sequences in mangrove peat deposits indicate that mangroves gradually moved inland while the fringing seaward stands died back as sea-level rose during the Holocene (Woodruffe, 1990; Plaziat, 1995; Kim et al., 2005).

Mangroves can demonstrate persistence at timescales over which morphological evolution of shorelines occur. This statement does not exclude the fact that mangroves are often pioneers, colonizing newly formed mudflats, but shifts in intertidal position of existing mangroves do occur in the face of environmental change. While occurring in a variety of settings dominated by rivers, tides, waves, carbonate deposits, or a composite of dominant physical factors, mangrove development in relation to sea-level may take one of six patterns (Fig. 1a–f):

- With a sea-level rise and other physical conditions held constant, the mangrove surface accretes asymptotically until accumulation of sediment raises the forest floor above tidal range;
- With constant rise in sea-level, the floor of a maturing forest continues to accrete at a pace similar to sea-level rise;
- With an irregular rise in sea-level, the forest floor accretes at intervals of time above tidal range (these intervals are when peat accumulates);
- With a stable sea-level but with episodic subsidence, the forest floor accretes back to tidal range;
- With a rising sea-level and episodic subsidence, mangrove response is complex, but the pattern is still one of overall accretion; and
- With a rise in sea-level but no change in sedimentary volume, the forest floor is set back or abandoned.

While the concept of mangroves as ‘land builders’ (Davis, 1940) has been overstated, it is generally accepted that mangroves colonize intertidal areas where quiescent conditions permit sediments to accumulate (Woodruffe, 2002; Perry, 2007). Various geophysical studies have shown that mangroves efficiently trap fine sediment particles by slowing water movement to speeds conducive for settlement of fine clay and silt particles (Wolanski, 1995; Young and Harvey, 1996). Other factors are involved in slowing tidal water movements and subsequent sedimentation: by moving up tidal creeks and into a forest, the area of forest is ordinarily large in relation to the area of the waterway, thus slowing water movement as it spreads out. Also, tree trunks, roots, pneumatophores, and animals colonizing above-ground tree parts add to the friction created by the soil surface, forest floor slope, and the numerous burrows, cracks, and fissures that pockmark the forest floor. Furthermore, fine roots bind sediment as does mucus secreted by bacteria and other organisms living in or on the soil (Alongi, 2005).

Not all mangroves accumulate peat or mineral particles, but the ability to capture fine particles may mean that a forest can move inland. In Western Australia, where eroding coastlines are the rule rather than the exception, macrotides are naturally eroding cliffs and creek banks, and by sheet erosion, progressing at $1\text{--}3\text{ cm yr}^{-1}$ (Semeniuk, 1994). Erosion simulates the effect of rising sea-level, and mangroves in Western Australia respond by colonizing landwards, keeping pace with the rate of coastal erosion. Semeniuk (1994), however, pointed out not all mangrove stands accumulate sediment uninterruptedly. Survivability depends on the composition and structure of the mangrove communities in relation to the natural tidal range; in microtidal areas, even a small rise in sea-level would inundate existing mangroves, particularly in arid zones where mangrove grow slowly because of high salt concentrations, low humidity, high temperatures, and extreme light conditions (Cheeseman, 1994). A similar situation exists for mangroves living in carbonate environments, which reflect a lack of terrestrial sediment input. An analysis of peat accumulation in mangroves living in carbonate sediments in the Caribbean suggests

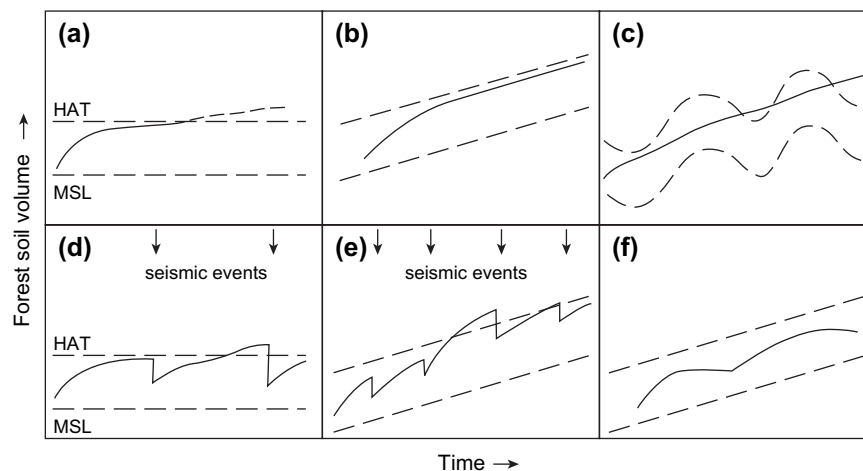


Fig. 1. Representation of six patterns of mangrove development in relation to changes in sea-level. See text for description of the patterns shown in windows (a)–(f). Modified from Woodruffe (2002).

accretion rates ranging from 1.0 to 3.7 mm yr⁻¹, which would allow mangroves to survive if sea-level rise is low (≈ 1.0 mm yr⁻¹), but not if sea-level rises at rates greater than predicted by some models (Parkinson et al., 1994).

Other historical trends are problematical. Based on mangroves in Bermuda, Ellison and Stoddart (1991) and Ellison (1993) have suggested that mangroves may face collapse if faced with sea-level rise on the order of 0.9–1.2 mm yr⁻¹. This prediction has been criticized (Pernetta, 1993; Snedaker et al., 1994; Snedaker, 1995) in view of the fact that mangroves in nearby Key West, Florida, have shifted inland by 1.5 km since the mid-1940s under a regime of sea-level rise of 2.3–2.7 mm yr⁻¹ (Ross et al., 2000). From all of the above evidence, we can conclude that mangroves will move inland if the pace of sea-level rise allows.

3. Zonation and succession: recovery from disturbance by opportunists?

Preoccupation with apparent patterns of mangrove zonation (Chapman, 1976) has led to the inference that these zones are replaced over time, either landward or seaward. In other forested ecosystems, species composition and productivity changes over time, from primary forests to climax and post-climax forests, showing peak structural complexity in middle age with a slow decline thereafter (Kimmins, 2004). The unifying concept of disturbance and recovery of terrestrial forests holds that when less rigorous species die, fast growing tree species that are poor competitors replace the dead trees, leading to a sequence of succession of superior competitors—species capable of monopolizing light—until a steady-state equilibrium is achieved in climax and post-climax sequences of forest development (Kimmins, 2004).

One question pertinent to the ability of mangroves to cope with environmental change bears asking: are trends in mangrove forest replacement in response to catastrophic disturbance the result of somewhat deterministic sequences as in terrestrial forests, or are they the result of a stochastic, ‘first come, first served’ opportunistic response, or neither? It is well established that temperature, salinity (as affected by rainfall and extent of freshwater runoff), frequency of tidal inundation, soil texture and degree of soil anoxia, pH, predation, and competition are the main factors that account for the apparent zonation of mangrove trees (Smith, 1992). In reality, a few of these factors operate synergistically and antagonistically over different spatial and temporal scales to control mangrove distribution. At the ecosystem scale, natural changes occur on the order of minutes to days for physiological functions, of months to years for tree growth and replacement, and of decades to at least a century for whole-forest changes (Twilley et al., 1996; Chen and Twilley, 1998).

Mangrove species and communities appear to have more pioneer-phase than mature-phase characteristics: numerous and continuous production of propagules, long propagule dormancy and viability, abiotic means of dispersal, wide dispersability, light-demanding seedlings, dependence on seed reserves, early reproductive age, uniform crown shape, competition for light,

non-specific pollinators, prolonged flowering period, tendency towards inbreeding, poor species richness, no or little canopy stratification, even-sized tree distribution, few climbers, and few epiphytes (Smith, 1992).

Mangroves vary in their recovery time from large-scale disturbances with rates of recovery (on a scale of years to decades) dependent on the scale of the disturbance (Ball, 1980; Putz and Chan, 1986; Jimenez et al., 1985; Fromard et al., 1998; Piou et al., 2006; Ross et al., 2006). In this regard, mangroves respond within timescales and in patterns similar to those observed in other tropical forests (Chazdon, 2003; Sheil and Burselem, 2003). In one of the best-studied examples of mangrove recovery from catastrophic disturbance (Ward et al., 2006), long-term trends in forest structure and turnover were examined following hurricane damage in south Florida in 1992. Over the ensuing decade, biomass of mangrove stands impacted by the hurricane converged with biomass of forests outside the path of the hurricane, to an asymptotic biomass after 4 years. Forest recovery conformed to size-structured organizing principles as described for upland forests—forests that have been recently disturbed should exhibit more negative scaling relationships which would then be expected to increase through time as the forest matured, becoming dominated by fewer, older, large individuals (Niklas et al., 2003). In south Florida, intraspecific competition was a key factor in structuring forests during recovery. As in other forests, stem density decreased as mean stem diameter increased, as predicted from self-thinning theory of mono-specific stands (the ‘self-thinning’ rule; Kimmins, 2004). Thus, the scaling relationships suggested by Enquist and Niklas (2001) and Niklas et al. (2003) in which forest biomass is represented by an average community size–frequency scaling relationship of negative two (Fig. 2), appears to be a reasonable model of mangrove forest structure as it progresses from a regenerating to a maturing stand.

Recovery of mangrove forests may follow classic large gap-phase dynamics, whereby enhanced recruitment rates are

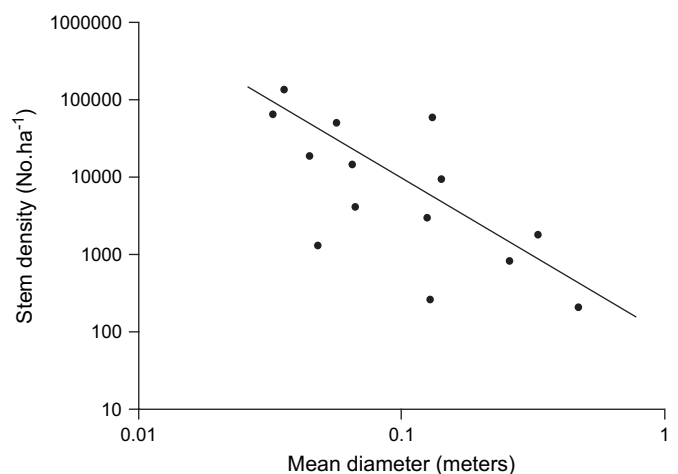


Fig. 2. Stem density as a function of mean stem diameter for terrestrial forests with the negative two scaling relationship as indicated by the solid line. Modified from Enquist and Niklas (2001).

matched by greater mortality following gap formation as the forest returns to the closed canopy state. The increase in stand biomass during recovery in south Florida did not correlate with changes in soil salinity, suggesting that the primary factor limiting recruitment within gaps was light availability. The primacy of light as a limiting factor has been confirmed for other mangrove forests (Ellison and Farnsworth, 1993; Sherman et al., 2000). The south Florida study supports the prediction of Twilley et al. (1996) that initial differences in stand structure and establishment rates of saplings would largely control recovery trends following disturbance. This does not mean that recovery is stochastic with no distinct succession stages, just that the early sequences of species replacement are greatly influenced by species present at initial recovery. Empirical data from other locations support this idea (Clarke and Kerrigan, 2000; Clarke et al., 2001; Ross et al., 2006; Sousa et al., 2007).

The recovery dynamics of mangrove forests as suggested by the south Florida study resembled trends observed for forests in other areas of south Florida (Ball, 1980) and in Malaysia (Putz and Chan, 1986), Puerto Rico (Jimenez et al., 1985), Vietnam (Clough et al., 1999), French Guiana (Fromard et al., 1998), and Belize (Piou et al., 2006). Due to widespread destruction during the Vietnam War and subsequent replanting of mangroves, examination of mono-specific stands of *Rhizophora apiculata* provided an opportunity to determine how the size-class frequency of mono-specific stands changes with forest age in the Mekong delta (Clough et al., 1999). An analysis of these plantation stands shows that tree densities decline with increased forest age, as forests become less dense, but individual trees become larger, due to self-thinning (Fig. 3). With fewer but larger trees, above-ground biomass increased with forest age. Long-term data from French Guiana similarly indicate that mangrove stands follow a series of succession stages from an initial dense burst of pioneering saplings to rapid early development, to maturity, senescence, and death (Fig. 4). Long-term changes in mangrove forest structure have rarely been studied (Alongi, 2002), but the few data sets available offer some important insights into gap and stand dynamics, especially in relation to recovery from disturbance. A number of studies that compared aerial photographs or data sets from two (or more) discrete time periods have similarly suggested species replacement over time (Ball, 1980; Johnstone, 1983; Putz and Chan, 1986; Flower and Imbert, 2006).

The long-term patterns indicate that mangrove forests are a mosaic of patches (these can be very large or small) of different succession stage, if there is a high frequency of gaps, and of transitory variations in an otherwise zonal or mono-specific forest, if gaps are rare. Assuming that mangroves are subject to more frequent disturbance than terrestrial forests, intermediate disturbances would be unlikely to culminate in a classic climax community (Lugo, 1980). Based on the available data, we can state that *for mangrove forests, stand composition and structure are the result of a complex interplay of physiological tolerances and competitive interactions leading to a mosaic of interrupted or arrested succession sequences in response to physical/chemical gradients and changes in geomorphology.*

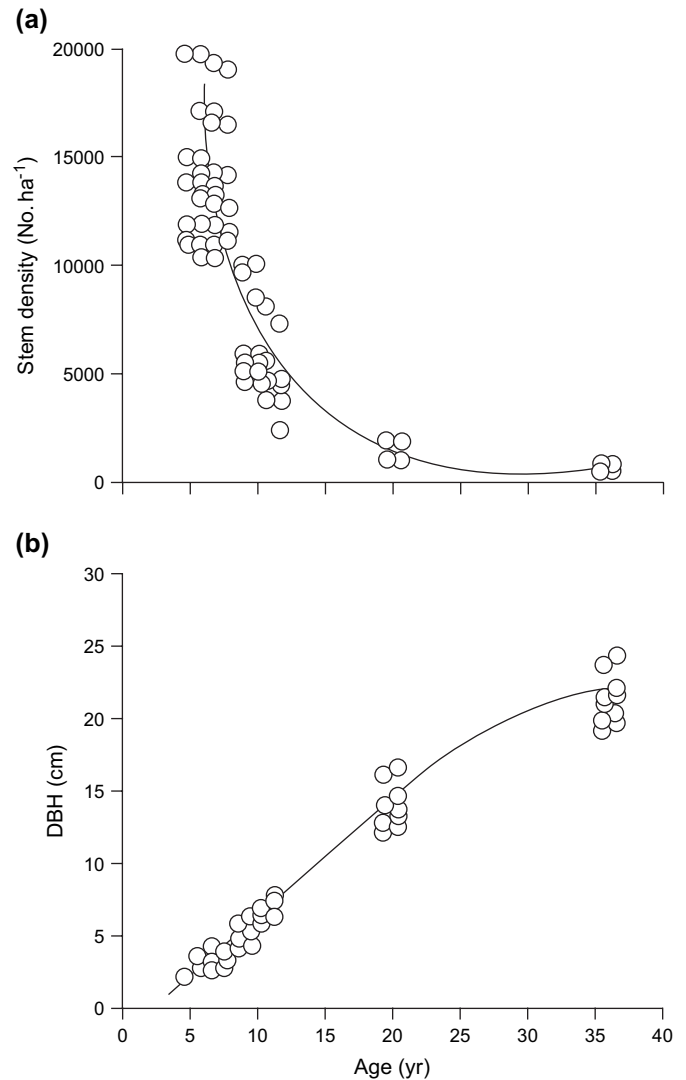


Fig. 3. Relationship of (a) stem density and (b) diameter at breast height (DBH) to age of *Rhizophora apiculata* forests in the Mekong delta, Vietnam. Modified from Clough et al. (1999) and Alongi (2002).

All, some, or perhaps only one, of these factors may play a role in a specific region depending upon the disturbance regime. That is, if a given forest remains relatively undisturbed for long periods of time relative to individual life span (e.g., in Papua New Guinea and Malaysia, Johnstone, 1983; Putz and Chan, 1986), or that a primary area is being colonized (e.g., newly formed mudbanks such as near the Amazon in French Guiana, Fromard et al., 1998), mangrove forests can undergo a series of successional stages reminiscent of those that are undergone by terrestrial forests. However, in most coastal environments intertidal areas are frequently disturbed, being inundated by tides that usually accrete or erode sediment deposits, transport propagules to and from stands, and subject forest biota to waterlogging and fluctuating physicochemical conditions. Because of this daily regime, mangrove forests are often a patchwork of interrupted succession sequences, as per the scenario predicted by Odum (1981) for ecosystems undergoing ecological succession under stress.

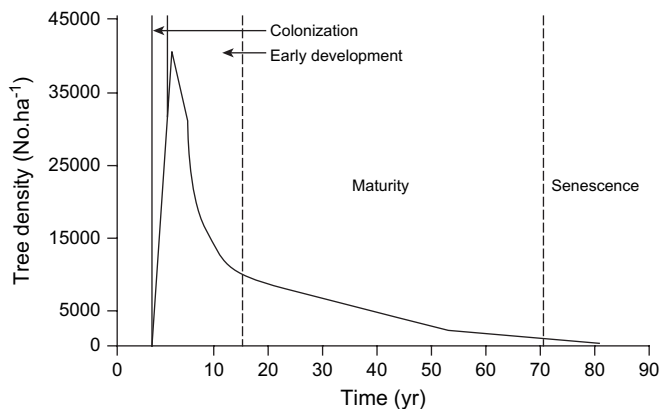


Fig. 4. Temporal pattern of development of mangrove forests over eight decades in French Guiana. Data from Fromard et al. (1998) and modified from Alongi (2002).

4. Do mangroves offer protection from catastrophic events?

The array of features that allow mangroves to sustain substantial environmental challenges such as sea-level rise and storm damage may also function to ameliorate the effects of catastrophes such as hurricanes, tidal bores, cyclones, and tsunamis. The notion that mangroves offer significant protection has become a dictum in tropical coastal ecology (Chapman, 1976; UNEP-WCMC, 2006), yet this ecosystem service has rarely been empirically tested or adequately assessed (Ewel et al., 1998; Valiela and Cole, 2002) — just presumed based on observational evidence.

The answer depends on the type of environmental setting and other relevant features and conditions. The factors determining the extent of protection from tsunamis, for example, offered by mangroves include: width of forest, slope of forest floor, tree density, tree diameter, proportion of above-ground biomass vested in roots, tree height, soil texture, forest location (open coast vs lagoon), type of adjacent lowland vegetation and cover, presence of foreshore habitats (seagrass meadows, coral reefs, dunes), size and speed of tsunami, distance from tectonic event, and angle of tsunami incursion relative to the coastline.

On 26 December 2004 the largest earthquake in 40 yr (seismic magnitude $M_W = 9.0$) produced the most devastating tsunami in recorded history, killing more than 283,000 people throughout the Indian Ocean region. The earthquake was so powerful it wobbled the Earth's rotation (Lay et al., 2005). The tsunami triggered by the seismic event swept across the Indian Ocean at speeds up to 800 km h^{-1} , with succeeding waves reaching heights of up to 30 m. Along with vast numbers of people, man-made and natural structures and habitats were destroyed or damaged, including coral reefs, mangroves, beaches, seagrass beds, and other coastal vegetation. The extent of mangrove damage or loss has been difficult to verify in some areas due to the level of devastation and the focus on restoring human lives and infrastructure. Table 1 gives a summary of mangrove damage and loss in some of the affected countries, and shows

Table 1
Summary of the impact of the 2004 Asian tsunami on mangrove forest. Data were from UNEP (2005), Chang et al. (2006) and Iverson and Prasad (2007)

Location	Pre-impact mangrove area (ha)	Damage/loss of mangroves (ha)
Aceh province, Sumatra	1000	300–750
Andaman coast, Thailand	181,374	306
Sri Lanka	10,000	Minimal
N. Andaman Island, India	83,850	Minimal
S. Andaman Island, India	12,750	3825–10,200

that only a modest percentage of forests were damaged or killed as a result of the tsunami. Most mangroves affected had broken stems or were uprooted due to massive soil erosion or died due to prolonged inundation (UNEP, 2005). The impact of the tsunami on the Andaman Islands is most illustrative, being typical of the patchy response to the tsunami due to differences in stand location and angle of impact (Dam Roy and Krishnan, 2005). In South Andaman, 30–80% of *Rhizophora* spp. trees died due to continuous inundation, but stands of *Avicennia marina* and *Sonneratia alba* inhabiting the intertidal zone behind the *Rhizophora* spp. were not affected. In Middle Andaman, mangroves were not affected. In North Andaman, however, the impact of the earthquake elevated the land mass to the extent that the *Rhizophora*-dominated stands are now not inundated by tides even at highest astronomical tide. These stands are dying and expected to be succeeded by terrestrial flora.

Mangrove forests impacted by the 2004 Indian Ocean tsunami were located in sheltered areas (bays, lagoons, estuaries) with very few located on open coast, making it initially difficult to assess whether the areas impacted by the tsunami suffered less because of the intrinsic protective capacity of the forests, or because they were sheltered from direct exposure to the open sea (Chatenoux and Peduzzi, 2007). However, several reports based on initial post-impact surveys in southeastern India, the Andaman Islands, and Sri Lanka (Danielsen et al., 2005; Dahdouh-Guebas et al., 2005; Kathiresan and Rajendran, 2005; Chang et al., 2006) indicated that mangroves offered a significant defense against the full impact of the tsunami. The conclusions of Kathiresan and Rajendran (2005) and Vermaat and Thanpanya (2006) that the presence of mangroves saved lives along the Tamil Nadu coast of southeast India are invalid however as inappropriate statistical tests were used (Vermaat and Thampanya, 2007). A more proper test of the same data indicated no significant effect of the presence or absence of mangroves on the human death toll (Kerr et al., 2006) and points to the need for caution to avoid overstating the role of mangroves in tsunami protection. Nevertheless, ground surveys and QuickBird pre-tsunami and IKONOS post-tsunami image analysis (Danielsen et al., 2005) and multivariate analysis of mangrove field data (Dahdouh-Guebas et al., 2005) covering the entire Tamil Nadu coast suggest less destruction of man-made structures located directly behind the most extensive mangroves.

Mangrove forests can attenuate wave energy, as shown by various modelling and mathematical studies (Brinkman

et al., 1997; Mazda et al., 1997, 2006; Massel et al., 1999; Quartel et al., 2007) which indicate that the magnitude of the energy absorbed strongly depends on forest density, diameter of stems and roots, forest floor slope, bathymetry, the spectral characteristics (height, period, etc.) of the incident waves, and the tidal stage at which the wave enters the forest. For instance, one model estimates that at high tide in a *Rhizophora*-dominated forest, there is a 50% decline in wave energy by 150 m into the forest (Brinkman et al., 1997). Mazda et al. (2006) similarly found that waves were reduced in energy by 50% within 100 m into *Sonneratia* forests. Mazda et al. (1997) and Tanaka et al. (2007) showed that another important factor is vegetation type, for example, the percentage of forest floor area covered by either prop roots or pneumatophores, as the drag coefficient of these structures is related to the Reynolds number (which differs for each species depending on diameter and above-ground root architecture).

The hydraulic characteristics of tsunamis are, however, likely to be very different from those of wind waves and tidal waves (Latief and Hadi, 2007). The period of a tsunami is usually between 10 min and 1 h as compared with periods of 12–24 h for normal waves (Mazda et al., 2007). A tsunami propagates like a tidal bore in that its momentum increases with movement upstream into shallower water. Model simulations using data from hydrological experiments to predict the attenuation of tsunami energy by mangroves were generated by Hiraishi and Harada (2003) based on the 1998 tsunami that destroyed parts of the north coast of Papua New Guinea. The model output (Fig. 5) suggests a 90% reduction in maximum tsunami flow pressure for a 100-m wide forest belt at a density of 3000 trees ha⁻¹. Model results obtained by Hamzah et al. (1999), Harada and Imamura (2005), Latief and Hadi (2007), and Tanaka et al. (2007) for various types of coastal vegetation, including mangroves, were very similar.

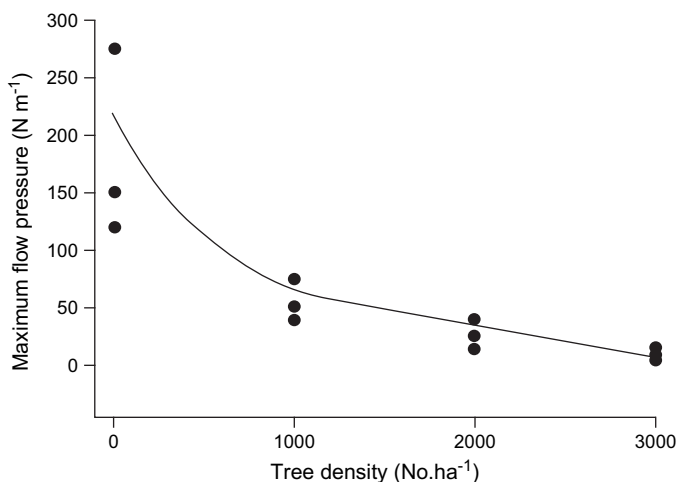


Fig. 5. Model simulation of the decline in maximum flow pressure of a tsunami with increasing mangrove tree density, based on data collected after the 1998 tsunami on the north coast of Papua New Guinea. Modified from Hiraishi and Harada (2003).

Tanaka et al. (2007) modelled the relationship of species-specific differences in drag coefficient and in vegetation thickness with tsunami height, and found that species differed in their drag force in relation to tsunami height, with the palm, *Pandanus odoratissimus*, and *Rhizophora apiculata*, being more effective than other common vegetation, including the mangrove *Avicennia alba* (Fig. 6). These data point to the importance of preserving or selecting appropriate species to act as wave barriers to offer sufficient shoreline protection.

Tsunamis (like hurricanes and tidal bores) can be categorized as another form of disturbance, albeit massive and infrequent. But should large, infrequent disturbances (LID) be considered qualitatively different from small, frequent disturbances (SFD) for mangroves? If we accept the heuristic model of Romme et al. (1998) which states that the disturbance impact must increase abruptly with increasing disturbance if a threshold (or thresholds) has been exceeded, then large disturbances are qualitatively different from small ones. In the case of balsam fir and white cedar forests, Romme et al. (1998) used the example of damage by fire, in that a threshold is exceeded in these temperate forests because these species are usually eliminated from a large burnt patch due to their susceptibility to fire and their inability to disperse seeds over an adequate distance to recolonize a large gap. Based on this model criterion of a threshold, then there are qualitative differences in mangrove ecosystems between LID and SFD if the answer to the question “Does mangrove species replacement differ with gap size?” is yes, assuming that the primary impact of an LID is large gap creation. As most of the evidence (see Section 3) points to an ability of mangroves to function as pioneers (i.e., lack of gap specialists) in replacing lost canopy members with seeds of members of the same species (e.g., Clarke and Kerrigan, 2000) or in demonstrating little or no change in species composition between gaps and adjacent canopies (e.g., Imai et al., 2006), then LID and SFD are unlikely to be qualitatively different in most mangrove forests.

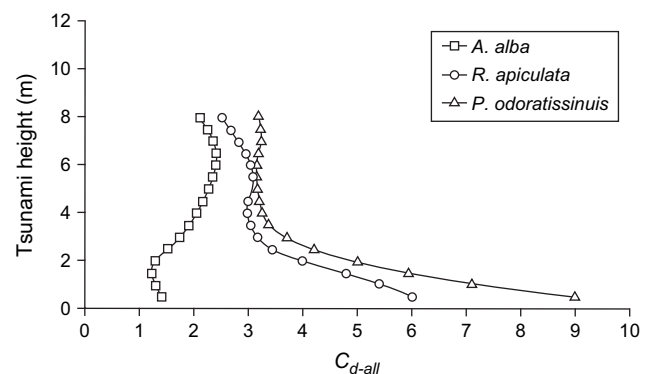


Fig. 6. Changes in the relative drag coefficient for vertical vegetation structure with increased height of a tsunami for the mangroves, *Avicennia alba* and *Rhizophora apiculata*, and the palm, *Pandanus odoratissimus*, estimated from modelling data from Sri Lanka and Thailand. Modified from Tanaka et al. (2007).

5. How will the world's mangrove forests respond to the ultimate disturbance—climate change?

A number of prognostications have been made regarding the future of the world's mangrove forests in the face of climate change with local, regional, and global forecasts ranging from extinction to no or little change in areal coverage (Woodruffe, 1990; Aksornkae and Paphavasit, 1993; Pernetta, 1993; UNEP, 1994; Semeniuk, 1994; Snedaker, 1995; Miyagi et al., 1999; Nicholls et al., 1999; Alongi, 2002; Schaeffer-Novelli et al., 2002; Gilman et al., 2006; McLeod and Salm, 2006). The vast majority of differences in assessments can be related to site differences in coastal position (open coast versus lagoon) and tidal (micro- versus macrotide) regime.

The 2007 IPCC assessment (Solomon et al., 2007) has predicted that during this century:

- Atmospheric CO₂ concentrations will increase by 1.6–1.9% yr⁻¹;
- Atmospheric CH₄ concentrations will increase by 27–175% to 2100;

- Atmospheric N₂O concentrations will increase by 0.3% yr⁻¹;
- Average rates of sea-level rise will be in the range of 3–4 mm yr⁻¹;
- Ocean temperatures will increase by 0.10° per decade;
- The incidence of flooding, drought, fire, insect pests, and disease will increase;
- Ocean acidification will continue, as pH has declined by 0.1 unit since industrialization;
- Up to 30% of coastal wetlands will be lost, with wetlands on small islands and on the mega-deltas of Asia and Africa most at risk; and
- Precipitation will decline in tropical regions of Central and South America and in West Africa, but increase in East Africa and in Southern Asia.

Table 2 summarizes predicted impacts of climate change on mangrove ecosystems, at least where there appears to be agreement among the various assessments. Using the latest IPCC predictions, we can briefly assess the various hazards separately with respect to confounding factors and regional risks, considering particularly the results from various experimental approaches.

Table 2

Predicted impacts of various aspects of climate change on mangrove ecosystems, with particular emphasis on areas of agreement among sources (Woodruffe, 1990; Aksornkae and Paphavasit, 1993; Pernetta, 1993; UNEP, 1994; Semeniuk, 1994; Snedaker, 1995; Miyagi et al., 1999; Nicholls et al., 1999; Hogarth, 2001; Alongi, 2002; Schaeffer-Novelli et al., 2002; Done and Jones, 2006; Gilman et al., 2006)

Hazard	Predicted response	Extenuating factors
Rise in sea-level	Landward progression. Erosion of seaward margin. Secondary productivity may increase due to greater nutrient availability from erosion.	Areal extent on impact will greatly depend on slope of intertidal area; may be constrained by topography and accretion rate; re-establishment rate of plants will depend on rate of sea-level rise; change in species composition as SL rise may favour faster growing spp in new areas. Depends on position in estuary/open coast. Depends on erosion rate; change in species diversity at increased rate of nutrient input.
Rise in atmospheric CO ₂	No or little increase in primary production and respiration. Enhanced water-use efficiency. Advance in flowering period	Depends on nutrient availability and species-specific responses. Change in water vapour concentration and pattern. Pollinators may be de-synchronized with plants.
Rise in air and water temperature	Decreased survival in areas of increased aridity Expansion of latitudinal range Increased net and gross primary production Increase in water vapour pressure deficit.	Depends of localized changes in temperature. Only species most temperature tolerant Growth patterns will vary and depend on local temperature regime. Depends on extent of change in atmospheric water vapour concentration.
	Increased secondary production (especially microbes) and shift in species dominance. Changes in phenological patterns of reproduction and growth. Increase in biodiversity.	Depends on local species composition and availability of new recruits.
Change in precipitation/storm patterns, frequency and intensity	Changes in mangrove species composition and growth due to change in soil water content, salinity. Increased primary production due to increase in precipitation/evaporation ratio. Changes on faunal biodiversity. Increase in gaps and gap recruitment.	Depends on species composition of initial stands. Depends on species composition of initial stands. Euryhaline species unaffected, but loss of stenohaline species. Depends on change in level of storm intensity, frequency, etc. and stand location relative to wind field.

5.1. Sea-level rise

Mangroves thrive in a tidal environment where adaptation to change in sea-level over long timescales is the rule rather than the exception. The ability of mangroves to successfully adapt to change in sea-level, as already noted, depends on accretion rate relative to rate of sea-level change. How do today's mangroves fare in this regard? The data are scanty, but a plot of a number of empirical measurements of accretion rate (most were based on nuclide radiochemistry) vs regional mean sea-level rise, indicate that mangroves are more than keeping pace with sea-level (Fig. 7). Twelve of the 15 points lie above the 1:1 line, indicating average sedimentation rates somewhat greater than the rate of mean sea-level rise. Although not all mangroves accrete (e.g., Semeniuk, 1994), these data support the earlier suppositions and evidence that mangroves generally facilitate deposition of fine organic and inorganic sediment particles (but there are exceptions and complications, cf. Whelen et al., 2005).

Only a handful of experimental studies (e.g., Ellison and Farnsworth, 1997; He et al., 2007) have examined potential effects of sea-level change on mangroves. In their study, Ellison and Farnsworth (1997) subjected seedlings of *Rhizophora mangle* to a 16 cm increase in sea-level, a 16 cm decrease in sea-level, and to current sea-level conditions as a control. They found that seedlings in the tanks simulating sea-level rise initially grew faster than plants in the other treatments, but growth slowed rapidly by sapling stage. Control plants by the end of the 2.5 yr experiment were 10–20% larger than those in the experimental tanks, although there were no clear anatomical differences in plants among the three treatments. As a further complication, mangrove species appear

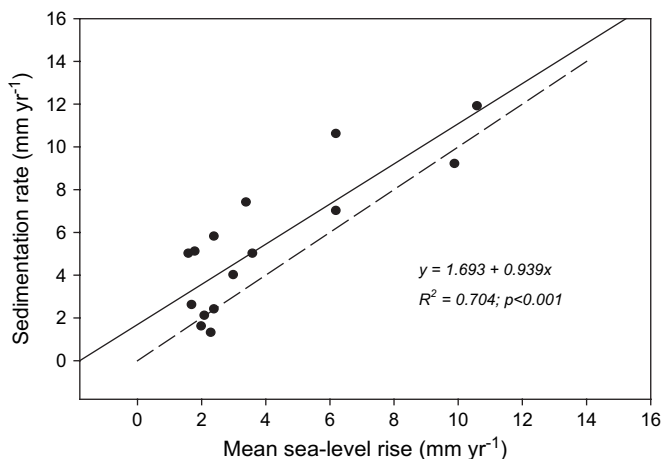


Fig. 7. Relationship between sediment accretion rates in various mangrove forests and mean sea-level rise. The sea-level rise data are from altimetry data available from the website: http://www.jason.oceanobs.com/html/actualites/indic/msl/selection_uk.html. Mangrove sedimentation rates are from Lynch et al. (1989), Parkinson et al. (1994), Ellison and Farnsworth (1996), Young and Harvey (1996), Saad et al. (1999), Smoak and Patchineelam (1999), Krauss et al. (2003), Brunskill et al. (2004), Alongi et al. (1999, 2001, 2004, 2005a,b), Van Santen et al. (2007), Alongi (unpublished data, Timor Leste). Solid line is the linear regression for the untransformed data; the dashed line delimits a 1:1 relationship.

to differ in their tolerance to flooding (He et al., 2007). In mesocosm experiments simulating changes in sea-level, He et al. (2007) found that tolerance to flooding differed among five species as follows (from most to least tolerant): *Avicennia marina* > *Aegiceras corniculatum* > *Rhizophora stylosa* > *Bruguiera gymnorrhiza*. These studies suggest possible whole-forest changes in community composition in relation to sea-level rise.

5.2. Rise in atmospheric CO₂

Experimental studies point to mangrove species-specific responses to increases in atmospheric CO₂ concentration, with predicted responses confounded by demonstratively wide variations in mangrove photosynthesis with salinity, nutrient availability, and water-use efficiency (Ball and Munns, 1992; Farnsworth et al., 1996; Ball et al., 1997; Snedaker and Araújo, 1998). The studies by Ball and her co-workers (Ball and Munns, 1992; Ball et al., 1997) showed that over 14 wk, increased CO₂ did not affect growth rates of *Rhizophora apiculata* or *Rhizophora stylosa* limited by high salinity, but did enhance growth when the plants were limited by humidity. Both species, but especially *R. apiculata*, showed faster growth with enhanced CO₂ under low salinity conditions (i.e., when they were not limited by freshwater). Over longer experimental periods (1 yr) the congener, *Rhizophora mangle*, exhibited increased growth and biomass, and increased branching activity, under higher CO₂ conditions (Farnsworth et al., 1996). Moreover, the plants under these conditions showed earlier maturation than ambient controls. In similar experiments, Snedaker and Araújo (1998) found species-specific responses to elevated CO₂ with no significant change in net primary productivity in *Rhizophora mangle*, *Avicennia germinans*, and *Conocarpus erectus*, but a decrease in productivity in *Laguncularia racemosa*; all four species exhibited decreases in stomatal conductance and transpiration, and increases in transpiration efficiency, with increased CO₂. Based on these studies alone, there is likely to be no or little change in canopy production with increasing CO₂ levels, but species patterns within estuaries are likely to change based on species-specific responses to the interactive effects of rising CO₂, sea-level, temperature, and changes in weather patterns.

5.3. Rise in atmospheric temperature and changes in weather patterns

Functional processes from the scale of individuals to ecosystems tend to increase in rate as temperatures increase (Odum and Barrett, 2004), so it is unreasonable to expect mangrove plants and associated biota to behave any differently. It is uncertain, however, what the effect of rising temperatures will be on mangrove forests when the interactive effects of changes in precipitation and other weather-related factors are considered (Table 2). Temperature changes in the tropics may not be as great as in boreal and temperate regions (Solomon et al., 2007), and changes are likely to vary greatly on local and regional scales. Increased frequencies of severe storms

and hurricanes are predicted for some regions (the Caribbean), but not in others (southeast Asia).

Temperature changes alone would likely increase rates of photosynthesis, respiration, growth, and reproduction as well as lead to alteration in community composition, floral and faunal diversity, and an expansion in latitudinal limits, at least at local temperatures $<30\text{--}33\text{ }^{\circ}\text{C}$. Most mangrove species that have been tested show a levelling-off of photosynthetic rate within this temperature range, with a clear decline at temperatures $>33\text{ }^{\circ}\text{C}$ (Cheeseman, 1994). The empirical data therefore suggest a decline in mangrove photosynthesis in arid regions, such as in the Red Sea and parts of northern Australia, and a marginal increase in photosynthetic rates in areas of high rainfall and river input (e.g., southeast Asia).

6. What mangrove ecosystems will be most affected by climate change?

Clearly, some mangroves will survive and perhaps even thrive with the predicted changes in climate. But it is just as clear that some won't survive. Given all of the confounding responses by mangroves to increases in humidity, CO_2 , and sea-level, the most realistic scenario is to delimit the least and most vulnerable forests, an exercise that has been done for tropical rainforests (Cramer et al., 2004).

Accepting the notion that mangroves along macro-tidal ($>4\text{ m}$) coastlines, along wet tropical coasts and/or in areas adjacent to significant river input, are the least vulnerable to the impact of sea-level rise (Woodruffe, 1995; Schaeffer-Novelli et al., 2002; McLeod and Salm, 2006), and overlaying the distribution of mangrove forests with these criteria, then the resultant diagram (Fig. 8) shows that a moderate proportion of the world's mangrove forests are likely to be greatly affected. The delineation of these areas was set by also considering current rates of deforestation and whether or not

a given area of mangrove forest is protected in a marine reserve.

Mangroves occupying low-relief islands and/or carbonate settings, where rates of sediment supply and available up-land space are ordinarily low, such as on small islands in the Pacific, are most vulnerable. Also most vulnerable are forests where rivers are lacking and/or where the landform is subsiding. The least vulnerable, aside from those occupying macro-tidal estuaries, wet tropical areas and shores adjacent to rivers, are those stands occupying high-relief islands and remote areas where humans are unlikely to block landward migration.

The IPCC (Solomon et al., 2007) prediction of a global loss of $\approx 30\%$ of coastal wetlands, including mangroves, may therefore be at the high end of the range of forecasts, accepting the above-mentioned criteria. A detailed analysis by Gilman et al. (2006) predicts a 13% decline in Pacific island mangroves from the current situation to the year 2100, assuming that the upper limit of IPCC sea-level rise predictions applies. Other regional analyses predict similar losses (e.g., Snedaker, 1995), so a 10–15% decline in global mangrove area by 2100 seems a realistic projection.

The potential impact of climate change, regardless of whether or not it is in the range of 10–15% loss, must be kept in perspective as mangroves currently face a more predictable and insidious threat —deforestation (Valiela et al., 2001). At an average rate of loss of between 1% and 2% total area yr^{-1} (Alongi, 2002; Duke et al., 2007), most of the world's mangrove forests may be lost before the peak impacts from climate change will be felt. Regardless of the magnitude of the predictions available, management agencies must invoke the precautionary principle in facilitating resilience in natural and in restored mangrove forests (Duke et al., 2007). Living in a comparatively harsh environment has poised most mangrove forests to survive into the future, assuming that current rates of deforestation can be reduced.

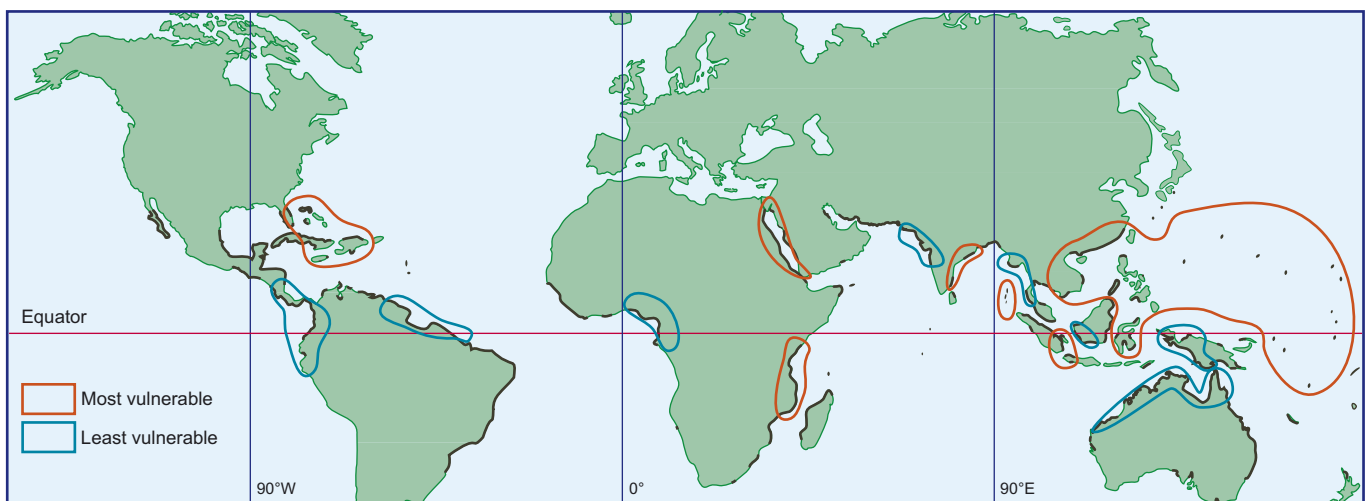


Fig. 8. Identification of least and most vulnerable regions to climate change of the world's mangrove forests, based on assumptions in text (Section 6). Based on information in Wilkie and Fortuna (2003), Gilman et al. (2006), UNEP-WCMC (2006), and Solomon et al. (2007).

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