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PAPER

Ecological role and services of tropical mangrove ecosystems: a reassessment

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ABSTRACT

Aim To reassess the capacity of mangroves for ecosystem services in the light of recent data.

Location Global mangrove ecosystems.

Methods We review four long-standing roles of mangroves: (1) carbon dynamics – export or sink; (2) nursery role; (3) shoreline protection; (4) land-building capacity. The origins of pertinent hypotheses, current understanding and gaps in our knowledge are highlighted with reference to biogeographic, geographic and socio-economic influences.

Results The role of mangroves as C sinks needs to be evaluated for a wide range of biogeographic regions and forest conditions. Mangrove C assimilation may be under-estimated because of flawed methodology and scanty data on key components of C dynamics. Peri-urban mangroves may be manipulated to provide local offsets for C emission. The nursery function of mangroves is not ubiquitous but varies with spatio-temporal accessibility. Connectivity and complementarity of mangroves and adjacent habitats enhance their nursery function through trophic relay and ontogenetic migrations. The effectiveness of mangroves for coastal protection depends on factors at landscape/geomorphic to community scales and local/species scales. Shifts in species due to climate change, forest degradation and loss of habitat connectivity may reduce the protective capacity of mangroves. Early views of mangroves as land builders (especially lateral expansion) were questionable. Evidence now indicates that mangroves, once established, directly influence vertical land development by enhancing sedimentation and/or by direct organic contributions to soil volume (peat formation) in some settings.

Main conclusions Knowledge of thresholds, spatio-temporal scaling and variability due to geographic, biogeographic and socio-economic settings will improve the management of mangrove ecosystem services. Many drivers respond to global trends in climate change and local changes such as urbanization. While mangroves have traditionally been managed for subsistence, future governance models must involve partnerships between local custodians of mangroves and offsite beneficiaries of the services.

Keywords

Carbon dynamics, ecosystem services, land building, management, mangroves, nursery function, shoreline protection.

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INTRODUCTION

Mangrove research has increased exponentially in the last 50 years. The total number of publications on mangroves indexed by the Web of Science exceeded 8000 in 2010, and since 2006 has consistently surpassed those on salt marshes, with a widening gap. Early mangrove research focused on basic issues such as floristics and faunistics but these are increasingly replaced by ecological assessment of function and evaluation of the capacity of mangroves for ecosystem services such as fisheries, shoreline protection, carbon export/sequestration and bioremediation of wastes. Parallel to this shift in research focus is the progressive widening of the spatial scale of research, from earlier dominance of localized, small-scale (e.g. forest or tree level) matters to regional and global perspectives (e.g. Feller *et al.*, 2010; Spalding *et al.*, 2010; Donato *et al.*, 2011; Giri *et al.*, 2011; Alongi, 2012; Record *et al.*, 2013).

Over the past five decades, discussion of mangrove ecosystems and management has focused on: (1) the dynamics of carbon fixation, storage and mineralization; (2) their nursery function; (3) shoreline protection, and (4) their land-building capacity. Mangrove management world-wide has been guided by the scientific paradigms in these areas. In this analysis, we critically evaluate these claims on the roles of mangroves through an appraisal of recent data, and highlight issues and implications pertinent to their management at the global scale.

MANGROVE CARBON DYNAMICS – HAS THE TIDE TURNED?

Origin

Marine macrophytes generally produce more organic matter than required for maintenance, with high potential for export or storage (Duarte & Cebrian, 1996). The 'Caribbean model' of mangrove C dynamics, portraying mangroves as net exporters of C ('outwelling'), has dominated mangrove ecology and management for the past four decades. Lee (1995) concluded that while most mangroves seem to be net exporters, the spatial extent and amount of mangrove C exported are far less than hypothesized in early salt marsh work. However, the complex ground structure of mangrove forests may dampen water current, and promote the trapping of sediment and allochthonous organic matter (Furukawa *et al.*, 1997), thus potentially resulting in 'inwelling' (Bouillon *et al.*, 2002). Direct measurements of mangrove C budget and mangrove–nearshore C fluxes, however, remain scarce to date.

The different biogeographic settings of global mangroves may have strong implications for their C dynamics. The Atlantic-east Pacific (AEP) and Indo-west Pacific (IWP) have significantly different mangrove (Tomlinson, 1986) and key faunal species richnesses (Lee, 2008) that may result in differences in ecosystem performance, for example productivity and standing biomass. Threats to mangroves also occur in different forms in different geographic regions (e.g. aquaculture ponds in the IWP versus urban development in the AEP) (FAO, 2007). The loss of

ecosystem services due to mangrove destruction/conversion is likely to be different between biogeographic, geographic regions and forest types.

Remarkably, the recent renewed interest in tropical mangrove C dynamics relates to the direct opposite of the outwelling paradigm. Productive tropical, especially estuarine, mangroves in the IWP offer excellent prospects as C sinks if they retain autochthonous C and trap allochthonous C (Donato *et al.*, 2011). On some Pacific islands, mangrove forests offer the largest sink in the overall C stock (Donato *et al.*, 2012).

Current understanding

The fate of mangrove productivity

In contrast to their relatively simple forest structure and low diversity, tropical mangroves are ranked amongst the most productive natural ecosystems globally, notwithstanding the variable methodologies applied (Alongi, 2009). Loss of mangrove C production to herbivory is variable (Sousa & Dangremond, 2011), but generally only amounts to *c.* 2–3% of the overall C budget. The bulk of mangrove C is therefore processed through the detritus food chain. The contribution of mangrove detritus to faunal biomass is not ubiquitously significant (Bouillon *et al.*, 2000, 2002, 2004) and may deviate from simple availability (Bouillon *et al.*, 2002). Also, rapid mineralization can occur in the water column of the tidal channel (Kristensen *et al.*, 2008). Most attention has focused on the fate of above-ground production, as data on below-ground productivity or biomass are too limited to allow a reliable global assessment of this component.

The recent emphasis on the carbon storage role of mangroves can be attributed to: (1) questions on the utilization of mangrove detritus by consumers; (2) variability in the tidal export of mangrove organic matter (particulate and dissolved) in response to local geomorphological and tidal conditions; and (3) interest in the potential of global forests including mangroves as sinks for offsetting C emissions.

Utilization of mangrove particulate C, mainly in the form of leaf litter, was hypothesized in the 'Caribbean model' as a gradual process involving microbial enrichment before assimilation by macroconsumers (Odum & Heald, 1975). Assimilation of mangrove C has, however, been questioned recently because of (1) the low nutritive content (high C/N ratio, < 1% N) and refractory nature of mangrove litter and (2) the lack of apparent support from tracer, particularly stable isotope, data. While litter consumption is indisputable (e.g. Kwok & Lee, 1995), the paradox of how detritivores such as crabs can assimilate and survive on this low-quality C-rich food remains (Skov & Hartnoll, 2002). The N deficit would also need to be met from other sources, for example the sediment or predation of animal tissue (Thongtham & Kristensen, 2005; Lee, 2008). Work on terrestrial detritivorous and herbivorous crabs has revealed cellulase enzymes that aid the digestion of structural C (Linton & Greenaway, 2004, 2007); these have recently also been demonstrated in many estuarine animals, particularly detritivorous grassid crabs (Adachi *et al.*, 2012).

Stable isotope data seem to suggest a minor role for mangrove C in sustaining coastal secondary production, as the differences between the consumer and mangrove signatures are often *c.* +5‰ (Lee, 2005), which is much larger than the average trophic fractionation (+1‰ for $\delta^{13}\text{C}$) used to interpret stable isotope data. This anomaly has prompted the notion that even direct consumers of mangrove C, such as grapsid crabs, may not rely on mangrove C (e.g. Mazumder & Saintilan, 2010). Large trophic discrimination values have been reported for some detritivores (e.g. Fry & Ewel, 2003). The +1‰ used in previous mixing model calculations is the average from numerous consumer–food combinations (e.g. Layman *et al.*, 2012), and would be unlikely to apply to any specific feeding mode or consumer organism. However, this link is probably weaker in the AEP where detritivorous crab diversity and abundance are significantly lower.

Storage or export?

Direct consumption by macroconsumers such as grapsid crabs and gastropods may significantly reduce the detrital C stock in tropical mangroves (Kristensen *et al.*, 2008; Lee, 2008), but not all tropical mangroves support dense assemblages of these consumers. The size of the detrital C stock is strongly influenced by the magnitude of export, which is driven by the vector of transport (tides and river flows) and geomorphology. Microtidal conditions promote C storage, whereas macrotidal regimes facilitate C export. Concentrated rainfall events also drive the export of organic matter from estuarine storage (e.g. Alongi & McKinnon, 2005). With climate change and associated increases in the frequency and severity of tropical storms, the export pattern of mangrove C may be significantly modified, especially in macrotidal environments where storm surges may be maximum.

Mangroves in different environmental and biogeographic settings may produce and store C in different ways: significantly more C may be stored underground in IWP mangroves if the same above-ground to below-ground biomass ratio, particularly investment in fine roots (Alongi *et al.*, 2003), is maintained across the biogeographic regions (Lee, 2008; Donato *et al.*, 2011). This ratio is also affected by factors such as global as well as local growth conditions (Lovelock, 2008; McKee, 2011). Despite the significantly lower diversity of leaf-eating crabs in the AEP compared with the IWP, overall rates of leaf litter consumption are similar (Nordhaus *et al.*, 2006).

Data gaps and future research

The significant components and processes of mangrove C dynamics are poorly understood. Little is known about dissolved C, especially dissolved inorganic carbon (DIC), in the mangrove C budget. Although occupying only 0.1% of global land surface, mangroves can contribute up to 10% of the terrestrially derived dissolved organic carbon (DOC) pool in the nearshore tropical ocean (Dittmar *et al.*, 2001, 2006). The nature, diagenesis and flux of this DOC are complex (Marchand

et al., 2004, 2006; Kristensen *et al.*, 2008). Up to one-third of the mangrove DOC is rapidly lost due to photodegradation (Dittmar *et al.*, 2006) but utilization by consumers and producers is not quantified.

How DIC may help constrain the mangrove C budget is even less studied. Bouillon *et al.* (2008) suggest that the fate of *c.* 50% of the mangrove C produced is uncertain, with DIC export via either surface or porewater flow being a probable pathway, as recently demonstrated by Maher *et al.* (2013). To what extent this DIC export may sustain phytoplankton production in tropical estuaries is still unknown.

There is no strong evidence to dismiss the role of mangroves in sustaining coastal fisheries. Mangrove forests seem to function synergistically with adjoining habitats such as intertidal flats to deliver this important ecosystem service (Lee, 2004; Sheaves *et al.*, 2012), with hydrological and trophic connectivity being key drivers in the relationship (e.g. Meynecke *et al.*, 2008). Aquatic first-order consumers seem to turn over organic C about 10 times faster than their terrestrial counterparts, thus promoting C mineralization rather than storage (Cebrian, 2004). However, limited data on detritivore, especially meiofaunal, assemblages in mangrove forests prevent generic testing of this hypothesis. The balance between C mineralization and storage needs to be further clarified with local and biogeographic differences in mind.

Recent assessments of the C stock in tropical mangroves suggest a significantly higher C density than in terrestrial forests (Donato *et al.*, 2011) but estimates need to be refined with increased sample coverage encompassing different biogeographic regions, adjacent land uses (e.g. degree of urbanization), forest history and condition and a simple increase in sampling effort. Most C density data on mangrove soils are derived from small numbers of short, narrow cores (diameter at the centimetre scale) extrapolated to landscape-scale estimates. Rates of carbon accumulation are expectedly variable depending on factors such as forest productivity, export rate and *in situ* consumption, all highly responsive to variations in factors such as the hydrological regime, faunal activity and temperature. Alongi (2012) reported an average C burial rate of 174 gC m⁻² year⁻¹, but widely variable rates are evident. For example, burial rate was only 2% of total C input at the Matang Forest, Malaysia (Alongi *et al.*, 2004) but > 40% at a sheltered site in Hinchinbrook Channel, north-east Australia (Alongi *et al.*, 1999). Higher replication of carbon density/accretion data across larger spatial scales along with abundance of vegetation types and important covariates (e.g. stand structure, microtidal conditions) and the incorporation of this biological detail into future models would enhance estimates of carbon sequestration to better inform management decisions.

Many of the world's most populous and fast-developing cities are located in tropical estuaries. The discharge of domestic sewage and agricultural/aquacultural wastes provides relatively labile C and nutrients (N, P) to rapidly urbanizing tropical estuaries, modifying mangrove production (Lovelock *et al.*, 2007, 2009) and its trophic significance. These anthropogenic sources also indirectly alter the diversity of organic detritus

available to consumers and decomposers, for example a dominance of algal and anthropogenic over vascular plant organic matter (e.g. [Lee \(2000\)](#)). Complex interactions may result from these new mixes of detrital sources ([Taylor *et al.*, 2010](#); [Bishop & Kelaher, 2013](#)). Global data at the estuary scale are insufficient, however, to allow an assessment of such impacts.

MANGROVES AS NURSERIES

Origin

Empirical observations that mangroves and other shallow-water habitats support densities of juvenile fishes and invertebrates that are higher than those in nearby unvegetated areas gave rise to the hypothesis that mangroves act as nurseries for species utilizing different habitats as adults. Studies on crustaceans and fish in the US Atlantic Coast and Gulf of Mexico that supported this hypothesis led [Beck *et al.* \(2001\)](#) to define a nursery as a 'habitat for a particular species that contributes a greater than average number of individuals to the adult population on a per-unit-area basis in comparison to other habitats used by juveniles'. To identify the habitats that are most important in maintaining overall ecosystem function, [Dahlgren *et al.* \(2006\)](#) redefined marine nurseries in terms of their overall contribution to marine populations. In both definitions, a key factor is the connectivity between mangroves and the nearby habitats where adult populations live.

Current understanding

Mangroves as habitats for juveniles

[Beck *et al.* \(2001\)](#) hypothesized three main causes for the high number of juvenile fish and shrimps often found in mangroves: (1) the high abundance of food, (2) lower predation pressure due to shallow-water microhabitats, higher turbidity and reduced visibility compared with unvegetated nearby habitats, and (3) their complex physical structure, for example prop and aerial roots ([Lee, 2008](#); [Nagelkerken, 2009](#)). These factors can act in synergy to constitute directly and/or indirectly the nursery role of mangroves, enhancing density, growth and survival of juvenile fish and invertebrates. The structural complexity of mangroves provides shade from the canopy, high turbidity and fine sediments that reduce the rate of predator–prey encounters ([Lee, 2008](#)). Both prop roots and pneumatophores reduced the predation of small fishes and shrimps by larger fish ([Vance *et al.*, 1996](#); [Primavera, 1997](#)). The need for protection of soft-shelled crustaceans during ecdysis may explain the greater correlation between offshore catches and mangrove area observed for shrimp compared with fish ([Manson *et al.*, 2005](#)).

Are mangroves significant nursery sites?

The importance of mangrove nursery habitats for fish and shrimp populations is nevertheless still controversial ([Nagelkerken *et al.*, 2008](#)). On the one hand, more than

two-thirds of global fish and shellfish harvests have been linked directly to estuarine nurseries ([Robertson & Blaber, 1992](#)), and mangrove-related species contribute 30% of fish and 100% of prawn catches in Southeast Asia ([Rönnbäck, 1999](#)). Many studies showed a significant statistical relationship between catches of fish or shrimp and mangrove area (see the discussion by [Lee, 2004](#)) or length of mangrove-lined coastlines ([Staples *et al.*, 1985](#)). However, correlation does not mean causality, and juvenile abundance does not necessarily translate to adult catches ([Robertson & Blaber, 1992](#)). Furthermore, the analytical methods used to establish links between fish/prawn catches and mangrove/estuarine habitats suffer from: (1) temporal and spatial variability, (2) different scales, (3) use of only a few predictor variables, mainly area and latitude, and (4) autocorrelation and multicollinearity ([Lee, 2004](#); [Faunce & Serafy, 2006](#)).

When reviewing the densities of juvenile reef fish in the IWP, [Nagelkerken \(2009\)](#) found little indication for the nursery function of mangroves, although recently the same research team conclusively showed a nursery role of mangroves for reef fishes in the Indo-Pacific (Tanzania) ([Barbier *et al.*, 2011](#)). Furthermore, although many Caribbean mangroves are known to provide nursery functions for reef fish, [Halpern \(2004\)](#) found that the area of mangrove stands in the Virgin Islands and their proximity to adult reef habitats were not related to adult densities of two coral reef fish species, formerly thought to depend on mangrove nurseries. Finally, when assessing their nursery value for coral reef fishes at the community level, mangroves are insignificant either in the IWP or the western Atlantic ([Faunce & Layman, 2009](#)). In sum, the current literature clearly shows that the nursery value of mangroves is not ubiquitous.

What determines the nursery values of mangroves?

Using the same lens to look at different mangroves may explain the divergent findings about their importance as nurseries. The nursery value varies with spatial extent and temporal accessibility of mangroves, determined by factors such as shelf configuration, habitat configuration, hydrology ([Faunce & Layman, 2009](#)) and habitat connectivity (see below). Tidal regimes (both amplitude and semi-diurnal/diurnal, mixed tides) and forest type/area, often greatly differ between and within biogeographic regions; for example, in the AEP landward mangrove extension in macrotidal northern Brazil is c. 20 km, whereas forest fringes in the microtidal Caribbean Region are narrower. In areas with meso- and macrotidal regimes, mangrove forests are accessible only during tidal flooding. Hence, only biogeographic comparisons of sites with similar tidal regimes are valid and the particular environmental setting of each mangrove location strongly influences its nursery function.

Mangroves as part of a spatio-temporal mosaic of nursery areas

Species using mangrove forests exposed during low tide must as nurseries move to other 'playgrounds', i.e. adjacent ecosystems. Mangroves should thus be seen as a component of a

habitat mosaic, rather than in isolation, and the presence of alternative habitats may be critical. Even in almost permanently inundated mangroves, habitat connectivity may be crucial in exploiting complementary resources, for example when food becomes limiting. For example, the abundance of juvenile fish in Caribbean mangroves was related to overall landscape, rather than microhabitat features, demonstrating that a true nursery function is sustained by a spatial mosaic of nearshore habitats (Drew & Eggleston, 2008). Hence, the connectivity and complementarity of adjoining estuarine habitats enhance their nursery value through increased survival and productivity (Sheaves, 2005). Similar to salt marshes, mangroves can function as important links in a chain of habitats that provide complementary resources and benefits through the process of 'trophic relay' (Kneib, 1997). Ontogenetic movements of juveniles may be direct from mangrove–seagrass nurseries to deeper coral reefs or stepwise through shallower habitats in the Atlantic (Cocheret de la Morinière *et al.*, 2004). Both fish size frequency distribution and natural tags, i.e. otolith stable carbon and oxygen isotopes, strongly suggest ontogenetic habitat shift from mangroves and/or seagrasses to patch reefs and fore reefs (Mumby *et al.*, 2004; Barbier *et al.*, 2011). Such shifts reduce intraspecific competition and optimize growth and survival because the fish leaving nursery shelters are bigger and less vulnerable to predation in open waters (Manson *et al.*, 2005).

Interestingly, most, if not all, evidence for the habitat mosaic hypothesis comes from reef fishes. Marine shrimps, however, are associated with a single nursery habitat, e.g. *Penaeus monodon* and *Penaeus merguensis* in mangroves, and *Penaeus semisulcatus* and *Penaeus latissulcatus* in seagrass beds (Dall *et al.*, 1990). This probably relates to their smaller maximum sizes (generally 50–100 g, and *c.* 300 g for *P. monodon*) and shorter life spans (*c.* 3 years) precluding the need for multiple nurseries.

Data gaps and future research

The nursery-role hypothesis needs further testing by evaluating the contribution of recruits from mangroves to adult populations using tracer and tagging techniques (e.g. stable isotopes, microtags), measuring not only juvenile abundance and densities but also growth, survival and movements, over multiple time-scales (Heck Jr *et al.*, 2003; Faunce & Serafy, 2006; Nagelkerken, 2007). Recent advances using otolith microchemistry provide a powerful tool to further assess the nursery role of mangroves in nearshore fish assemblages for micro- and mesotidal areas (Gillanders, 2002, 2005; Kimirei *et al.*, 2013). By following cohorts over time, Jones *et al.* (2010) found evidence for mangrove–reef ontogenetic connectivity in four Caribbean reef fishes, highlighting the usefulness of this innovative longitudinal approach.

Recent studies suggest that juvenile nekton may actively seek out mangroves using olfactory or other cues (e.g. Huijbers *et al.*, 2008; Huijbers *et al.*, 2012), similar to the megalopae of larval-exporting mangrove crab species (e.g. Diele & Simith, 2007), and this ability could be impaired by ocean acidification (Munday *et al.*, 2009). Moreover, future studies should focus on

species with clearly separated adult and juvenile habitats, considering all potential nursery habitats. Such a seascape-scale approach will capture the influences of habitat connectivity (Meynecke *et al.*, 2007).

MANGROVES FOR COASTAL PROTECTION

Origin

The notion of a coastal protection function for mangroves dates back to the 1970s (Chapman, 1976). While support for this concept is mostly circumstantial (Alongi, 2008), there is empirical and/or modelling evidence of the protective role of mangroves during moderate events such as tropical storms (Braatz *et al.*, 2007; Granek & Ruttenberg, 2007; Zhang *et al.*, 2012). The wave energy of wind-generated surface waves is significantly attenuated by mangrove forests (Massel *et al.*, 1999) – a fully grown mangrove forest can reduce wave energy by 20% per 100 m (Mazda *et al.*, 1997a). Moreover, 54 papers published between 1972 and 2005 mentioned the ability of mangroves to act as a buffer between land and the sea (review by Dahdouh-Guebas & Jayatissa, 2009), while recent reviews highlight the role of ecosystems in coastal defence (McIvor *et al.*, 2012a, b). While these studies indicate a potential protective role for mangroves, the factors determining the degree of protection remain to be established. The degree of protection offered by mangrove forests can be analysed at three hierarchical levels (Dahdouh-Guebas & Jayatissa, 2009): (1) the landscape level – mangrove forest type and geomorphological setting, including landscape and geomorphological settings (Lugo & Snedaker, 1974; Thom, 1984; Dahdouh-Guebas & Jayatissa, 2009); (2) the community level – internal vegetation structure of the forest, including species-specific attributes of trees such as species composition, physiognomy silvometric parameters or the contribution to debris (Dahdouh-Guebas & Jayatissa, 2009; Ohira *et al.*, 2013); and finally (3) the species level – variation in root architecture of individual species/trees.

Attempts at modelling the resistance provided by mangroves to storm surges have considered individual trees to be cylinders, which is unrealistic (Iimura & Tanaka, 2012), particularly in the case of mangroves.

Current understanding

The extent to which mangroves provide coastal protection has been hotly debated for more than a decade, accentuated by extreme events such as the Indian Ocean tsunami in 2004. A chronology of mangrove–coastal protection research in post-tsunami publications and a few major storm events is provided as Appendix S1 in Supporting Information.

A more standardized approach to evaluating both the damage and protection offered by mangroves would assist in the evaluation of the protective role of mangroves. The coastal protection provided by mangroves is attributed to the following factors.

1. Energy of impact: protection against more common, low-energy events but not necessarily adequate protection against high-energy disturbances such as tsunamis.

2. Location: settlements in front of or very close to mangrove areas are not sufficiently protected or are even damaged by debris and flotsam as opposed to areas behind the mangroves.

3. Forest structure: the ecological status of the forest and anthropogenic pressure could play a role; for example, degradation of the forest due to selective logging or grazing may reduce the protective potential of the forest.

Protection is often dependent on the integrity of adjacent ecosystems (e.g. seagrass beds) beyond the immediate vicinity of the mangrove. This spatial integration is poorly understood and hardly ever tested. Protection by mangroves should not be considered only at the local scale or in the isolated context of the mangrove forest.

Data gaps and future research

Geomorphology and ocean currents

The protective function of mangroves is analysed by considering the characteristic waves or currents and the sediment transport/erosion pattern of water-related impacts (cyclones, sea-level rise, tides and heavy rains generated by El Niño-related events) (Wolanski, 1992; Mazda *et al.*, 1997b). For instance, mangroves may protect the coast against a discrete event such as a tsunami, but fail to withstand daily tidal erosion when too little sediment accretion takes place, or vice versa. The effect of floating debris (cf. Stieglitz & Ridd, 2001; Krauss *et al.*, 2005) on currents and waves should also be considered for mangroves (as a barrier and a source), as for other coastal vegetation (Bayas *et al.*, 2011).

Forest condition and threshold values

Mangrove extent has declined significantly in the last 50 years (Duke *et al.*, 2007; Spalding *et al.*, 2010). Remnant fragmented forests or individual trees may not provide the protection that a contiguous belt of pristine mangroves can. Mangrove areas degraded by human activities or natural hazards may be less functional in coastal protection due to 'cryptic ecological degradation' *sensu* Dahdouh-Guebas *et al.* (2005a), i.e. change in species composition but not forest cover. However, cryptic degradation is hard to detect by conventional remote sensing analysis, and was an important factor affecting the protection provided by mangroves against the 2004 tsunami (Dahdouh-Guebas *et al.*, 2005b). Such considerations of factors affecting the protective function will better inform restoration projects.

Empirical data on expected loss of function

The extrapolated loss of the protection function of mangroves on a global level is obscure. We postulate the following hypotheses.

1. Fragmentation of a mangrove-lined coast significantly reduces the coastal protection function of the mangrove system.

2. The functional ecological connectivity of littoral (mangroves, sandbanks or mudflats) to subtidal habitats (seagrasses and/or coral reefs) is crucial for maintenance of the coastal protection function. Degradation of the adjoining systems (e.g. due to harbour construction) may reduce the protection offered by mangroves.

3. Increased monetization and unsustainable valorization of mangrove resources (e.g. direct-use values such as timber extraction without sustainable forest management) would affect the ecological role of the forest including its coastal protection function.

4. Climate change will cause range shifts in species, which in turn may enhance the protection of coasts, either through mangrove colonization along a mangrove-free coast or through increase in the number of mangrove species along a mangrove-lined coast. Recent studies have demonstrated this by modelling the latitudinal limits of mangroves (Quisthoudt *et al.*, 2013; Record *et al.*, 2013).

5. Inappropriate planting schemes driven by scientifically unsound principles have a significant negative impact on the coastal protection function, with 'risky' consequences (loss of time, funds and public support for the plantation effort) (Lewis, 2005).

6. Deforestation or inappropriate management of mangrove catchment areas may silt up mangrove systems and affect their health status and regeneration, thus diminishing their protective function and ecosystem services (Wever *et al.*, 2012).

MANGROVES AS LAND BUILDERS: PARADIGM REVISITED

Origin

One of the first societal roles of mangroves mentioned in the literature was that of 'land builder' (Curtiss, 1888). Although land building is not an ecosystem service in a traditional sense, soil formation and vertical accretion are essential for maintenance of the mangrove habitat during sea-level rise and thereby ensure all other ecosystem services, including nursery support, carbon sequestration and coastal protection.

The idea that mangroves accumulate sediments and promote seaward land expansion, was enshrined in the scientific literature by John H. Davis (1940b) in a 74-page opus. He described mangrove vegetation associations common to Florida, USA and their successional relationships and also made some preliminary observations about the 'geologic role of mangroves' based on changes in land area and soil profiles showing mangrove peat layers below the tide range (indicating sea-level rise). These observations were interpreted, along with the Clementsian view of vegetation succession, as evidence of seaward progression of the mangrove community through land building. Previous and subsequent work by several investigators added to the land-building concept (reviewed by Carlton, 1974), but it was the classic work by Davis (1940b) that scientifically established the concept of mangrove land building.

The role of mangroves as geomorphic agents was later challenged by geologists, who argued that mangroves were not land builders but rather colonized land (e.g. intertidal mudflats) or retained land where it already existed and expanded only where sedimentation was high (Egler, 1952; Thom, 1967; Scholl, 1968; Bird, 1971). As summarized by Carlton (1974), two opposing viewpoints emerged from this literature: (1) mangroves act as a geomorphic agent by accreting inorganic sediments and/or organic detritus and by autogenic peat production and (2) mangroves are not geomorphic agents and can only modify the rate of land accretion.

In support of the second viewpoint, Egler (1952) argued that mangroves were soil *retainers* rather than soil builders. However, he did not present any new data to refute the land-building property of mangroves. In fact, a careful reading of this and other reports shows that few of Davis's critics offered contradictory data as extensively detailed or impressive as those presented in his classic works (Davis, 1940a, b). Some critics even acknowledged that under certain conditions, mangroves did contribute to vertical accretion by *in situ* peat formation and/or by affecting inorganic sedimentation rates (e.g. Scholl, 1964; Thom, 1967; Bird, 1986). Despite such examples, however, most critics argued that land building by mangroves was not a general phenomenon. Over time, the concept of mangroves as opportunistic colonizers with little to no land-building capacity became entrenched in reviews and textbooks. For example, in the text *Wetlands* (Mitsch & Gosselink, 2007), we find: 'It is no longer accepted dogma that mangroves are "land-builders" . . . '.

Current understanding

Arguments against mangroves as land builders focused, in part, on the requirement for an existing platform to support the lateral movement of mangroves. Mangroves cannot colonize or spread seaward unless surface elevations support seedling establishment and subsequent plant growth. If water depths are too great, seedlings cannot gain a foothold and/or cannot survive excessive flooding once embryonic reserves are depleted (Krauss *et al.*, 2008). The land platform must first build vertically, either by inorganic or organic deposition, to support mangrove expansion in the horizontal plane. The question is whether such a platform is ever built through the direct influence of mangroves.

Along muddy coasts, vertical accretion and lateral progradation are driven mainly by physical processes, and mangroves may passively follow the developing landform (e.g. Woodroffe *et al.*, 1985; Lovelock *et al.*, 2010). By comparison, there is little evidence for a direct role of mangroves in lateral land expansion, as envisioned by early workers. A number of studies have described mangrove retreat or expansion in response to sea-level rise or fall (e.g. Ellison, 1993; Parkinson *et al.*, 1994; Saintilan & Rogers, 2013) and in relation to salt marsh vegetation (Krauss *et al.*, 2011), but lateral movements were assumed to be driven by external drivers that altered physical or chemical conditions influencing plant growth. A few studies have documented lateral expansion of mangroves onto adjacent mudflats or sandy shoals but did not demonstrate

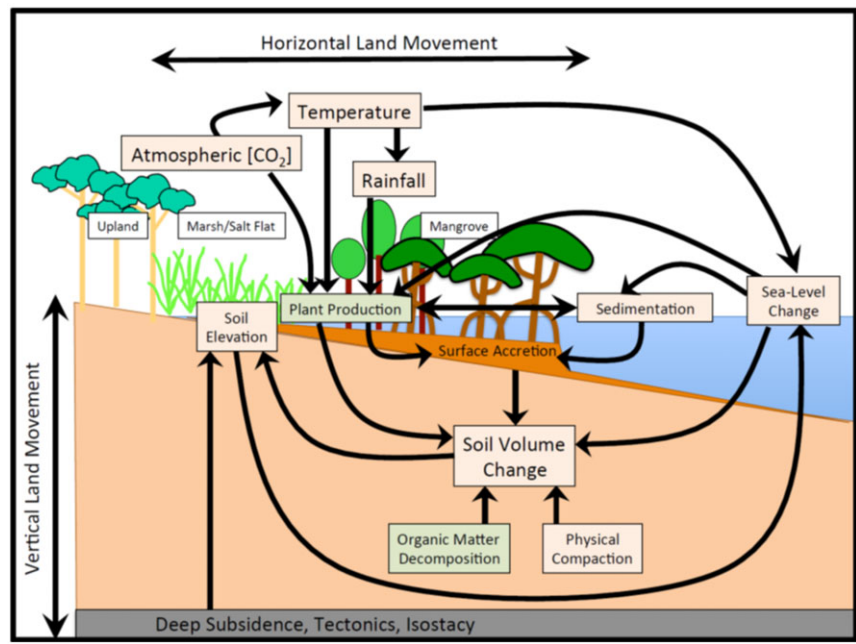
experimentally any accretionary influences by mangroves associated with this colonization (e.g. Panapitukkul *et al.*, 1998; Balke *et al.*, 2011).

Many researchers currently accept the role of mangroves as land stabilizers (e.g. Kathiresan, 2003; Alongi, 2008). Mangroves and their root systems promote sedimentation (Krauss *et al.*, 2003) by slowing water velocities (Mazda *et al.*, 1997b) and by trapping and preventing sediment resuspension (Scoffin, 1970). Even early workers who criticized the notion of mangroves as land builders agreed with this interpretation (Egler, 1952; Thom, 1967; Bird, 1986). The view of mangroves only as land stabilizers, however, neglects their role in promoting inorganic sedimentation as well as in autogenic soil development and resultant vertical land building.

Although empirical data are lacking in support of an active role by mangroves in lateral expansion, there is ample evidence for a direct contribution of mangroves to accretion in the vertical plane through peat formation. The occurrence of peat strata in sediment cores has been described for many locations in Florida and the Caribbean region (e.g. Davis, 1940a; Scholl, 1964; Parkinson *et al.*, 1994; McKee & Faulkner, 2000; McKee *et al.*, 2007). The presence of peat in the stratigraphic record is evidence of an autogenic process that has contributed to vertical accretion at some time in the past. One of the most impressive examples of mangrove peat accumulation and its role in vertical land development was reported for offshore islands in Belize where sequences of mangrove peat up to 10-m thick accrued over 7000–8000 years (Macintyre *et al.*, 2004). Moreover, recent studies experimentally demonstrated the above- and below-ground contribution of mangrove tissues (particularly roots) to autogenic accretion and elevation gain in Belize and Florida (McKee, 2011). The key role of mangroves in soil formation and elevation change was further evidenced in a peat-forming mangrove system in Honduras. When mangrove stands on the island of Guanaja were killed by Hurricane Mitch, peat collapse occurred, leading to a loss in soil elevation (Cahoon *et al.*, 2003). The work conducted in Belize and other locations with limited sediment supplies thus showed that *in some settings* mangroves can contribute directly to vertical land building by adding organic matter to soil volume and at rates comparable to global sea-level rise (McKee *et al.*, 2007).

We conclude that the early view of mangroves as land builders, especially in reference to lateral expansion, was not based on solid evidence and is not generally applicable to all settings. However, multiple lines of evidence indicate that mangroves can be important agents in vertical accretion by enhancing sedimentation and/or by direct organic contributions (Fig. 1). A key point is that the increase in soil volume is driven by mangroves (accelerated sedimentation, sediment trapping, organic matter input) and results in expansion of the land mass in at least one dimension. This viewpoint contrasts with the prevailing paradigm of mangroves as stabilizers or retainers of land and instead considers mangroves to be *integral* and *active* contributors to land formation, mitigating sea-level rise. The relative contribution of mangroves to land formation probably varies with geomorphic and sedimentary settings, but little progress will be

Figure 1 Conceptual model illustrating how physical and biological processes interact to control vertical and lateral land development. Physical processes include changes in sedimentation, sea level, air and sea temperatures and atmospheric [CO₂], which by accelerating inorganic sedimentation, trapping and retaining deposited sediment and/or by directly adding organic matter to soil volume (peat formation). The interaction between biological and physical processes creates a sensitive feedback relationship allowing adjustment of the landform (in both the vertical and horizontal planes) to changes in sea level may directly or indirectly affect mangrove growth. Mangroves, in turn, contribute to land building.



made without further investigation into such variation as well as the nature of the underlying biophysical processes.

Data gaps and future research

Work showing the contribution of mangroves to accretion, either by peat formation or by accelerating inorganic sedimentation, indicates that biotic processes are key to vertical land development and the accommodation of rising sea level in some locations (Cahoon *et al.*, 2003; Krauss *et al.*, 2003; McKee *et al.*, 2007; McKee, 2011). Such studies, however, are limited in scope and geographic extent and need to be repeated in a range of geomorphic settings to assess the broader role of mangroves in land development. Models to predict future mangrove expansion/retreat also need to include external drivers associated with climate change (e.g. temperature, rainfall, atmospheric [CO₂]). Our understanding of how such drivers interact with internal ecological processes (e.g. plant competition, above- and below-ground production–decomposition) in mangrove systems (Fig. 1) is rudimentary and mostly based on work conducted in terrestrial habitats (see review by McKee *et al.*, 2012). Although several studies have emphasized the relative contribution of surface and subsurface processes to maintenance of mangrove soil elevations in relation to relative sea-level rise (McKee *et al.*, 2007; Krauss *et al.*, 2010; Lovelock *et al.*, 2011; McKee, 2011) such work is limited because it does not span the range of settings in which mangroves occur. Further research is needed to address these gaps in our understanding of how mangroves contribute to sedimentation and soil development, how biological processes interact with physical processes to accommodate sea-level rise and how processes operating at different spatial and temporal scales lead to landscape-level changes in mangrove extent.

SYNTHESIS AND CONCLUSION

Decades of empirical research have clarified many of the ecological processes underlying the capacity of tropical mangroves to deliver essential ecosystem services such as fish production and shoreline protection (Table 1). However, the nexus between mangrove science and management is still weak. With increasing expectations from the general public as well as governments for tangible ecosystem services as the basis for conserving and managing mangroves, answers to questions such as how much removal of mangroves may result in detrimental impacts on coastal fisheries, or location-specific assessments of the capacity of mangroves for C sequestration remain elusive. A few issues contribute to this inadequacy.

While significant progress has been achieved in identifying drivers, characterizing processes and ascertaining the direction of relationships, management-relevant and quantitative knowledge of thresholds, spatio-temporal scaling and variability is still largely missing. For example, data on the C sequestration potential are highly patchy and often derived from a small number of cores at centimetre scales of sampling but extrapolated to cover large (> km) spatial scales. Similarly, data on how juvenile nekton locate mangrove nursery habitats, assessment of the interconnectivity of habitats and food web analysis of mangrove-dominated estuaries need to be linked with secondary production patterns at a landscape scale. Although most ecological and biogeochemical processes are expected to vary with habitat area, the relationships are unlikely to be linear (Barbier *et al.*, 2008). Thresholds or tipping points therefore exist for most habitat–function or diversity–function relationships. Further, the ecological and physical processes underpinning essential ecosystem services (e.g. shoreline protection, sediment accretion) may vary spatially and temporally (Barbier

Table 1 Biogeographic, physical geographic and socio-economic/anthropogenic factors influencing the delivery of ecosystem services by mangroves.

Service	Biogeographic	Physical geographic	Socio-economic/anthropogenic
C export/ storage	Difference in floral and faunal species richness may result in different forest productivity/biomass/C dynamics	Tidal regime combined with local geomorphology determines the balance of organic matter export/storage Local climate regime, e.g. amount and distribution of rainfall, influences riverine export of mangrove C Significant occurrence of microtidal regimes (e.g. the Caribbean) reduces C movement	Local management practice, e.g. biomass harvesting or pollution, influences forest productivity/biomass/C dynamics Anthropogenic forest degradation reduces forest performance Conversion to aquaculture ponds or agriculture reduces C storage capacity and increases C emission Urbanization introduces additional/alternative C sources to estuarine food chains Valuation of C capital associated with mangroves will drive management practices, e.g. reforestation, REDD+ approaches
Nursery function	Connectivity between nursery and adult habitats is higher in regions with microtidal regimes (e.g. the Caribbean) High local tree species diversity in IWP might improve the attractiveness of forest to larvae through habitat structural or trophic effects	Well-connected estuarine habitat arrays promote nursery function Local tidal regime determines access to mangroves by larvae	Removal of mangroves reduces nursery area; conversion to aquaculture ponds put further pressure onto remaining mangroves for natural larval stock
Coastal protection	Dominance by different species with different above-ground architecture may influence the coastal protection function	Value of mangroves accentuated in areas prone to tsunami/cyclone attack	'Coastal squeeze' limits width of mangrove belt and thus capacity for protection Degradation of forest reduces capacity for protection Replanting/rehabilitation increases capacity for protection
Land building	Dominance by different species with different aerial root architecture may influence sediment-trapping capacity Species differences in below-ground root production-decomposition rates may influence peat formation rates (e.g. in the Caribbean region)	Supply and delivery of inorganic sediment depends strongly on local geomorphology and rainfall/tidal/wind/storm regimes Geographic variation in nutrient, salinity and flooding regimes may influence biological processes controlling organic contributions to vertical land building (e.g. in the Caribbean region)	Anthropogenic erosion increases sediment supply, which may facilitate mangrove spread and colonization; however, excessive sedimentation may negatively impact existing mangroves through burial Barriers (dams, levees, seawalls) to water movement may decrease sediment supply and/or delivery Removal or degradation of mangroves may reduce vertical land development driven by biogenic processes (peat) Anthropogenic climate change and associated factors (sea-level rise, elevated CO ₂) and coastal eutrophication may have variable effects on land-building capacity through changes in mangrove growth

et al., 2011). Loss of the same ecosystem service may therefore be mediated by disturbance to different ecological processes or components (e.g. removal of forest versus degradation).

Some of the drivers influencing the delivery of key ecosystem services by tropical mangroves differ between the two broad biogeographic regions: diversity and abundance of keystone fauna (e.g. low brachyuran crab diversity in the AEP; Lee, 2008) and anthropogenic threats (aquaculture ponds in IWP versus oil pollution and urbanization in AEP) (Ellison & Farnsworth, 1996; FAO, 2007; Spalding *et al.*, 2010). The effect of the fundamental difference in mangrove species richness (and the key fauna they support) between the AEP and IWP has never been

assessed in the light of recent concepts and data on biodiversity–ecosystem function relationship and cascading effects along the food chain (e.g. Duffy, 2002; Hector & Bagchi, 2007; Naem *et al.*, 2012). The large spatial scale characteristic of marine ecosystem processes creates practical challenges for the experimental testing of the biodiversity–function relationship (Naem, 2006). Diversity effects may also differ between top-down (consumer-driven) and bottom-up (resource-driven) scenarios in detritus-based systems (Srivastava *et al.*, 2009; Kominoski *et al.*, 2010). To what extent and how mangrove and keystone consumer diversity drive ecosystem processes, and thus services, differently in the two mangrove biogeographic regions,

demands attention from global collaborative research. The replanting efforts currently popular in Southeast Asia, often replacing the diverse original forests with monospecific stands, may present opportunities for evaluating this relationship. Assessment of rehabilitated habitats thus far mainly focuses on a return of structure rather than function, let alone services.

This review further shows that mangrove ecosystems functioning is also subject to local physical, and increasingly socio-economic, setting. The capacity of mangroves for sediment trapping and accretion, for example, is strongly responsive to local erosion and hydrologic regimes (e.g. availability of sediment, wave action), the species composition and the condition of the forest (e.g. degree of degradation). While this variability cautions against simple generalization of mangrove ecosystem services, it also encourages the application of knowledge of the response of mangroves to environmental drivers in maximizing services.

Managing mangroves for key ecosystem services

The uncertainty associated with the future of complex ecological systems (e.g. mangrove forests) is a key challenge to incorporating the value of ecosystem services into informed environmental decision-making. The coupling of ecosystem service valuations with simulations of possible future management scenarios offers a promising tool to guide complex decision-making related to ecosystem management (Daily *et al.*, 2009), but requires reliable and compatible data encompassing a wide range of physical, biological and socio-economic scenarios. There is a strong need for a global network of consistently collected data for scaling up to ecosystem-level analyses at greater geographic coverage. This network could be similar to existing large-scale forest plot measurements (e.g. the United States Forest Inventory and Analysis programme, the Smithsonian Institute Global Earth Observatory (SIGEO)). While technol-

ogies such as remote sensing reduce the effort required for studying spatially extensive processes (e.g. nutrient export from mangrove-lined estuaries into the nearshore environment; Naeem *et al.*, 2012), the network needs to incorporate the range of variation in mangrove species and assemblage distribution in local hydrologic as well as broader biogeographic settings. This could present a challenge to global mangrove analysis and management, as the greatest mangrove resources are predominantly in developing countries where mangrove destruction is most rapid (FAO, 2007).

Challenges and opportunities

Mangroves, urbanization, agriculture (e.g. rice farming) and coastal aquaculture often compete for the same space in tropical estuaries (the majority of the world's 'megacities' are located on the coast; Martinez *et al.*, 2007), making science-based management of tropical mangroves a challenging but strategic opportunity in securing ecosystem services such as C sequestration. Replacing mangroves with intensive aquaculture ponds results not only in removal of the C sequestration capacity of mangroves but also significantly increases C emission to levels beyond most agricultural practices following forest clearance (Sidik & Lovelock, 2013). Both abiotic (e.g. hydroperiod, tidal strength, salinity) and biotic (e.g. *in situ* consumption, bioturbation) drivers influence the balance between C storage and mineralization. As many of the drivers for storage or mineralization can be manipulated (Table 2), mangrove resources in tropical estuaries can theoretically be managed for C storage to partly offset anthropogenic C emissions in urbanizing estuaries.

Only 6.9% of global mangrove area is covered by the existing protected areas network (Giri *et al.*, 2011) due to financial and other limitations, hence prioritizing valuable areas becomes important. A mosaic of connected habitats contributes to nursery value (Sheaves, 2005) and a broad diversity of habitats is

Table 2 Drivers of mangrove C dynamics that may be manipulated for maximizing the C sequestration potential of mangroves.

Drivers	Promotes	Main abiotic/biotic agent	Intervention method	Reference
Tidal amplitude	Mineralization/storage	Tidal regime, geomorphology, access by nekton	Dyking, sluice gates, drainage network	Lee (1990), Dittmar and Lara (2001)
Hydroperiod	Mineralization/storage	Tidal connectivity, geomorphology	Dyking, sluice gates, drainage network	Ellison and Farnsworth (1997), Davis <i>et al.</i> (2005), Krauss <i>et al.</i> (2006)
Aeration	Mineralization, outgassing	Bioturbators, tidal and wave regimes	Artificial burrows and exclusion of bioturbators	Stieglitz <i>et al.</i> (2000), Kristensen (2008)
Nutrient level	Productivity, above- to below-ground biomass, decomposition rate	Mangrove plants	Fertilization, diversion of effluents from urban and aquaculture wastes	Tam and Wong (1995), Lovelock (2008)
Fauna/microbes	Consumption, bioturbation, mineralization	Crabs, meiofauna, bacteria and fungi	Limit hydrological connectivity; nutrient level	Kristensen (2008), Lee (2008), Andreetta <i>et al.</i> (2014)
Vegetation	Mineralization/storage	Mangrove plants, seagrasses	Afforestation	Bosire <i>et al.</i> (2005), Huxham <i>et al.</i> (2010), Kumara <i>et al.</i> (2010)

essential for completing fish life cycles (Meynecke *et al.*, 2007). Conservation efforts should protect connected mangrove–seagrass–coral reef corridors rather than identify representative areas of each habitat in isolation (Mumby *et al.*, 2004) as well as mangrove catchment areas. Whether the single- or mosaic-habitat approach is adopted, and despite the paucity of direct evidence to support fisheries–mangrove dependence, the studies so far infer a linkage and highlight the need to reverse mangrove loss (Nagelkerken *et al.*, 2008).

Irrespective of the debate in science, the impact of the coastal protection paradigm on policy has been substantial. In the recent World Conservation Congress (September 2012), the head of the International Union for the Conservation of Nature stated that mangroves are better than human-made structures in protecting coastlines threatened by climate change. Moreover, there have also been large-scale projects funded by international agencies to support mangrove plantations based on this paradigm (Feagin *et al.*, 2010), but success is often hampered by a lack of reference to substrate and hydrological requirements for mangrove establishment (Lewis, 2005). Even as early as the 1970s, the Philippines and other typhoon-prone countries started to embed mangrove greenbelts in various laws premised on their coastal protection function, although enforcement has been wanting (Primavera, 2000, 2005). With proper implementation, such environmental laws provide an excellent demonstration of damage prevention and mitigation, for example the Trinity Inlet Management Plan (which covers 3600 ha of mangroves) during the destructive Cyclone Larry that hit Australia in 2006 (Williams *et al.*, 2007).

The concept of mangroves as key biotic agents involved in geomorphic processes is important to conservation and restoration efforts. Seeing mangroves as passive players in coastal dynamics, and especially with respect to counterbalancing sea-level rise, may weaken arguments for their protection. More importantly, the assumption that mangroves are not inherently involved in land development may lead to faulty management plans and decisions that threaten habitat stability. A better understanding of geographic variation in the contribution of mangroves to soil accretion and elevation dynamics is essential to enhancing the resilience of mangrove coastlines. In addition, information about differences among sedimentary settings will allow plans that are better tailored to a particular situation. The ecosystem service of land building can only be maximized if the processes (physical and/or biological) relevant for a particular setting are protected or restored. For example, peat-forming mangroves may be more responsive to changes affecting the accumulation of organic matter. Mangroves in other sedimentary settings may be more affected by changes in sediment supplies or barriers to sediment delivery. Recognition of such differences will be critical in properly managing mangroves and the ecosystem services they provide.

Implications for local communities

Traditional approaches to managing goods and services derived from mangrove productivity have focused on subsistence to

local communities, for example artisanal fishing and harvesting of mangrove products. Unsustainable intensive aquaculture driven by commercial investment often results in long-term depletion of the capacity of mangrove productivity to maintain these services to local communities. The C sequestration capacity of global forests to ameliorate anthropogenic emissions has prompted international efforts such as REDD+, with major implications for how tropical forests are governed and managed: a shift from local subsistence to a 'pay for ecosystem services' model. Tropical mangroves offer significant potential for REDD+ implementation due to their high C sequestration rate and the high C stock (up to 10 times those of terrestrial forests; Donato *et al.*, 2011) but are currently not receiving corresponding attention. Future governance and management models of tropical mangrove productivity must integrate local and global ecosystem services such that ecological as well as socio-economic benefits are returned to local communities for objectives such as poverty alleviation.

Although the fisheries maintenance value of mangroves is only US\$708–987 ha⁻¹ compared with \$8966–10,821 ha⁻¹ for coastal protection (Barbier *et al.*, 2011), it is critical to the survival of sustenance fishers who are often landless and marginalized, with no other means of livelihood. Yet the continuing decline of mangroves compromises their nursery, coastal protection and other ecological services. The major threats to mangroves, currently estimated at 14–15 million ha world-wide (Spalding *et al.*, 2010; Giri *et al.*, 2011), are overharvesting for fuelwood and construction, and conversion to resorts, housing projects, agriculture and aquaculture (Ellison & Farnsworth, 1996). In particular, shrimp pond culture accounted for 38% of global decline of more than a third of mangroves in the 1980s and 1990s (Valiela *et al.*, 2001). However, some aquaculture systems manage to integrate mangroves and aquaculture (Primavera, 2000), among which the mixed mangrove–shrimp ponds in Vietnam operated by small farmers have evolved and expanded in area (Bush *et al.*, 2010). With the high export value of shrimp – 15% of the US\$125 billion global trade in fisheries products in 2011 (FAO, 2012) – and a growing international market for 'organic products', the Vietnamese government plans to convert all shrimp farms on the southern Ca Mau Peninsula to an integrated landscape of 'organic coasts' by 2015 (Ha *et al.*, 2012). Research on the connectivity of juvenile habitats is needed to determine how much pond area can be integrated in mangroves, and in what patterns, without compromising the nursery functions of the latter. For example, conserving an ample seaward mangrove belt of fringing forests (Primavera, 2005; Primavera & Esteban, 2008) gives greater nursery functionality because of the edge effect by which the mangrove–water interface provides access to juvenile shrimp and fish (Vance *et al.*, 2002). Developing brackish water ponds in the landward zone provides a win–win solution of food production from aquaculture compatible with the nursery and coastal services of mangroves (Primavera *et al.*, 2007).

Apart from integration, restoration and protection are the other management options for mangrove conservation. In the case of rehabilitation, science-based protocols, monitoring and

evaluation of whether and how replanted mangroves function as nurseries for shrimps and fish need to be in place (Walton *et al.*, 2006; Crona & Rönnbäck, 2007; Primavera *et al.*, 2012a). To ensure success, such initiatives should be community based (Primavera *et al.*, 2012b) and incorporate mechanisms by which the community, as *de facto* mangrove managers, are granted tenurial rights (Primavera & Esteban, 2008; Wever *et al.*, 2012). In other governance contexts, for example in Kenya, legally based co-management structures for resources like the beach management units may be the way forward to reconcile and mutually strengthen local livelihood and mangrove conservation. Likewise, ecoparks managed by local cooperatives may serve to protect remaining pristine mangroves while providing a livelihood.

The future of mangrove ecosystem services

Continual rapid urbanization of the coastal zone will compromise the capacity of tropical mangroves to offer ecosystem services through direct habitat reduction and degradation due to pollution and other disturbances. The former not only reduces the amount of all services derived from mangroves, but also increases the vulnerability of coastal communities to extreme physical events. Indirect impacts such as eutrophication decrease the survivorship of mangroves already stressed by salinity and aridity through reduction of the root to shoot ratio (Lovelock *et al.*, 2009). This response illustrates the complex nature of management decisions about ecosystems subject to multiple natural and anthropogenic threats, as attempts to maximize one service (e.g. nutrient removal) may compromise another (e.g. C sequestration). Further, these threats will help drive vicious circles of accelerated mangrove destruction and diminishing ecosystem services, potentially culminating in the disappearance of a unique global habitat (Duke *et al.*, 2007).

Global climate change plays a vital role in moderating the capacity of mangroves for ecosystem services. Mangroves respond and adjust to sea-level rise through root production, which may be influenced by nutrient availability (McKee *et al.*, 2007). While mangroves generally are able to keep pace with the anticipated increased inundation (Alongi, 2008), sea-level rise may significantly reduce world mangrove area due to 'coastal squeeze', which also seems to affect mangrove stand structure and potentially function (Heatherington & Bishop, 2012). Intrusion of mangroves into salt marshes occurs where these habitats coexist; the latter will likely disappear because of continual coastal infrastructure development.

Finally, future management of tropical mangroves must recognize the changing socio-economic drivers of coastal resource management. To date, tropical mangroves have largely been managed for goods and services targeting local subsistence but their roles in C sequestration, sustenance of coastal fish production, coastal protection and sediment dynamics have regional if not global environmental and socio-economic significance. Just as the adverse impact of global climate change is predicted to be strongest in less polluting tropical developing economies (Wittman & Caron, 2009), a similar imbalance exists between

the burden on those managing environmental assets (e.g. mangroves that reduce C emission, thus providing a solution) and those generating the problem (e.g. C emission from rapid industrialization). Successful and sustainable management of tropical mangroves as a global resource must involve political and socio-economic partnerships between countries with and without mangroves, underpinned by sound science cognizant of thresholds, scales and variability.

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Additional references may be found at the end of Appendix S1 in the online version of this article.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Chronology of key research publications on the protection function of mangroves after the Indian Ocean tsunami in 2004 and other notable ocean surges.

BIOSKETCH

S.Y.L. led the overall conception and manuscript writing, and the C dynamics section; J.H.P., F.D., and K.M. and I.M. led writing of the nursery, coastal protection and sedimentation sections, respectively; all other authors contributed to ideas presented and writing of the manuscript.

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