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Ecosystem services of the tropical seascape: interactions, substitutions and restoration

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Abstract

The tropical coastal "seascape" often includes a patchwork of mangroves, seagrass beds, and coral reefs that produces a variety of natural resources and ecosystem services. By looking into a limited number of attempts at substitution and restoration of ecosystem services (e.g. artificial reefs, aquaculture in mangroves, artificial seawalls), we address the questions: (1) To what degree can technologies substitute for ecosystem services in the seascape? (2) How can ecosystem restoration reestablish not only the functions of direct value to humans, but also the ability of the systems to cope with future disturbance? Substitutions often imply the replacement of a function provided free by a solar powered, self-repairing resilient ecosystem, with a fossil-fuel-powered, expensive, artificial substitute that needs maintenance. Further, restoration usually does not focus on large-scale processes such as the physical, biological and biogeochemical interactions between mangroves, seagrass beds and coral reefs. Nonetheless, restoration might be the only viable management alternative when the system is essentially locked into an undesired community state (stability domain) after a phase-shift. We conclude that ecosystem services cannot be readily replaced, restored or sustained without extensive knowledge of the dynamics, multifunctionality and interconnectedness of ecosystems.

1. Introduction

The tropical coastal "seascape" often includes a mosaic of mangrove forests, seagrass beds, and coral reef ecosystems [1–4]. This tropical seascape is one of the richest repositories of marine biodiversity and provides a number of natural

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resources and ecosystem services that are vital to human survival and well-being [5–7].

The pressure on coastal ecosystems from growing populations, new technologies and changing lifestyles is particularly evident throughout the tropics [8]. More than 50% of the world's mangroves have been removed [5], and in Asia and the Pacific region there is an estimated areal loss of at least 1% /year [9]. Diversion of freshwater flows, deteriorating water quality caused by pollutants and nutrients, overharvesting of fuelwood and timber as well as conversion into development activities like agriculture, aquaculture, mining, salt extraction and infrastructure all contribute to the degradation and deforestation of mangrove ecosystems [10,11]. There have been substantial losses of seagrass beds throughout the world. Although natural events, such as severe storms, may account for some of the reported seagrass losses, the increasing input of anthropogenic materials into the coastal zone seems to be a major factor behind the worldwide decline in seagrasses [12,13]. It has been suggested that human activities have altered natural disturbance regimes of coral reefs and added many new disturbances not earlier experienced by reef systems [8]. Nearly 60% of the world's coral reefs have been classified as threatened by overfishing, coastal development, and other human activities [14]. In addition, during 1997–1998 elevated sea-surface temperatures, possibly linked to global warming and one of the strongest El Niños of this century, resulted in the most geographically widespread coral bleaching event ever recorded [15].

Humanity has been more successful in simplifying (degrading and reducing biodiversity) than in reconstructing ecosystems, and the many efforts to replace degraded ecosystem functions by technical substitutions have often proven to be expensive failures in the long term [16–19]. These kinds of management alternatives usually imply the substitution of a natural ecosystem function, provided free by a solar-powered, self-repairing and resilient ecosystem, with a fossil-powered, expensive, artificial substitute that needs to be repaired and maintained [20,21]. This substitution can never replace the full array of services of the previously multifunctioning ecosystem [16,17]. There are efforts to restore degraded ecosystems and their production of ecological goods and services, but restoration of services into processes of the greater landscape (e.g. if interactions between ecosystems have been reestablished or not) has so far not been analysed to any larger extent [22,23]. Mangroves, seagrass beds and coral reef ecosystems are not autonomous units, but rather integral parts of a "seascape" interlinked by ecological and hydrodynamic processes [2,3,24,25].

This article adopts a landscape/seascape approach attempting to answer the complex questions: (1) To what degree, and at what scale, can human technologies substitute for ecosystem services in the coastal zone of the tropics? and (2) How can ecosystem restoration be more effective in restoring not only the functions of direct value to humans from a short-term anthropocentric viewpoint (sometimes called regreening or rehabilitation; [26]), but also the ecosystem resilience (*sensu* Holling [27,28]) of the systems to buffer future disturbances?

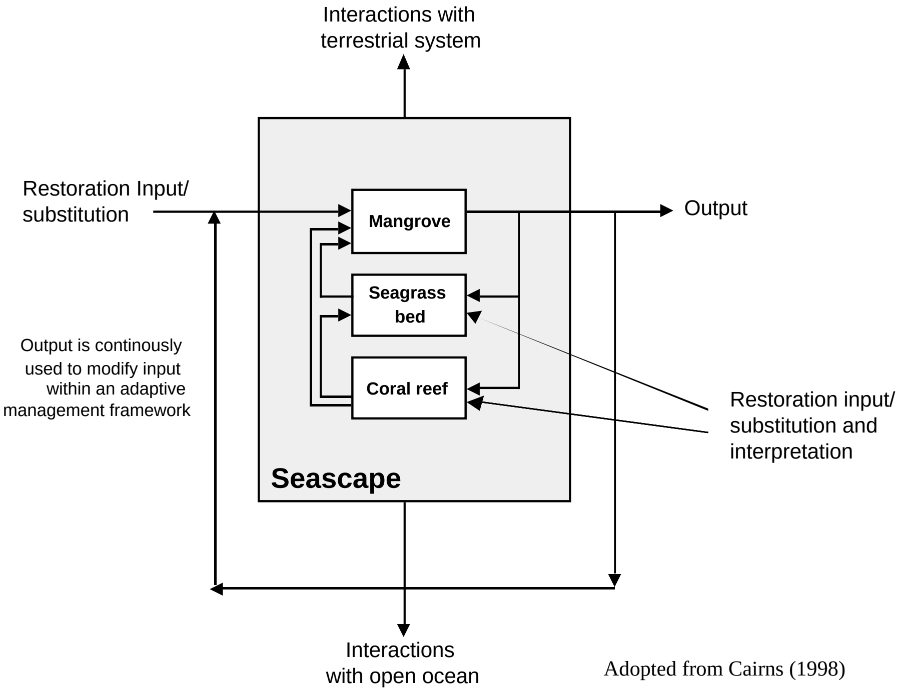
First, we give a presentation of the ecosystem services provided by the subsystems in the seascape and the major interlinkages between these systems. Secondly, we look into a number of attempts at replacement and restoration of ecosystem services in the seascape. These examples range from single-service replacement to restoration efforts aimed at restoring the functions, structure and resilience that characterised the system prior to degradation. We focus mainly on two ecosystems of the tropical seascape, i.e. mangroves and coral reefs. These ecosystems form the physical boundaries for the seascape: mangroves at the transition zone between terrestrial and aquatic environments and coral reefs at the interface between coastal areas and the open sea.

2. The seascape

Numerous physical, biological and biogeochemical interactions have been identified among mangroves, seagrass meadows and coral reefs [1–3,6,7,25]. These interconnected systems are sometimes called the *seascape*, meaning a complex, dynamic patchwork of mangroves, seagrass beds and coral reefs [3] that in some settings are so interdependent that they can be regarded as "mutual and symbiotic" [4]. The seascape is not an isolated entity. Rather it is influenced by terrestrial as well as open ocean activities (Fig. 1).

Coral reefs physically dissipate the force of currents and waves, creating over geologic time scales calm lagoons that are suitable environments for seagrass beds and mangroves. Mangroves and seagrass beds prevent shoreline and riverbank erosion and increase the residence time of water, which enable the assimilation of inorganic nutrients and entrapment of particles and pollutants carried by rivers. These ecosystem services stabilise coastal water quality, create relatively clear, nutrient poor water that favours the growth of coral reefs [24,29,30]. The biological interactions arise from dispersal of larvae (fish and coral), seeds (seagrass), propagules (mangroves), but also more active animal migrations of transient fish and invertebrate species. These species that link different ecosystems can also be called "mobile links" [6]. Many fish and shellfish species utilise mangroves or seagrass beds as nursery grounds [7,31], and this abundance of young organisms also attract larger carnivorous fish from surrounding systems such as coral reefs [1]. Coral reef fish and invertebrate communities also include herbivores, whose feeding migrations are quantitatively important wherever reefs and vegetated habitats co-occur [2,32]. These migrations of herbivorous fishes and sea urchins also influence plant community structure in the adjacent vegetated habitats [2]. Another biological link is the input of nutrients and organic matter as excretory and faecal products from migrating fish that may enhance the growth of reef corals [33]. There are also links in terms of chemical contaminants. For example, if mangroves are degraded this may entail exposure of coral reefs and seagrass meadows to metals and organic compounds that were previously bound in mangrove sediments [29,30]

There are numerous settings where the seascape as described by, e.g., Ogden [3] is not as developed and, of course, several places where coral reefs, mangroves and seagrass ecosystems occur in relative isolation. For example, mangroves underlain by a carbonate limestone platform are more likely to have strong interconnectedness



Adopted from Cairns (1998)

Fig. 1. A heuristic figure of the interactions among the subsystems in the seascape. Management activities (e.g. restoration or substitutions) should be interpreted in the larger context of the seascape/landscape, e.g. if interactions between ecosystems have been reestablished after a restoration or maintained after a substitution.

with adjacent seagrass beds and coral reefs, compared to large river deltas where mangroves develop on accreting sediments and reefs are not found in the immediate vicinity. In these settings, the influence of unvegetated shallow habitats, i.e. mud- and sandflats, on coastal ecosystem dynamics is likely to be more significant.

3. Ecosystem services

3.1. *Mangroves*

Mangroves have been classified as keystone ecosystems [34], as they are important for other ecosystems and generate a wide range of natural resources and ecosystem services (Tables 1 and 2). Ecosystem services like protection against floods and hurricanes, reduction of shoreline and riverbank erosion and maintenance of biodiversity are key features that sustain economic activities in coastal areas throughout the tropics [7,10]. Mangrove forest products like construction materials, charcoal, tannins, medicines and honey are vital to subsistence economies and

Table 1
Ecosystem services of the tropical seascape. Adopted from [6,7,37].

	Mangrove	Seagrass	Coral reef	Single-service substitutions
Erosion control	**	*		a
Storm and flood protection	**	*	**	a
Nursery, feeding and breeding ground	**	*	**	b
Maintenance of biodiversity and genetic resources	*	*	**	
Interrupts fresh water discharge	**			
Trap sediments and pollutants	**	*		c
Nutrient filter	**	*		c
Remineralisation of organic and inorganic matter	**	*	*	
Export of organic matter	**	*	*	
Carbon dioxide sink	**	*		
Oxygen production	**	*		
Top soil formation	**			
Water catchment and groundwater recharge	*			
Climate, pollution record			**	
Educational and scientific information	*	*	**	
Support recreation	*	*	**	
Habitat for indigenous people	**			
Sustaining the livelihood of coastal communities	**	*	**	
Cultural, spiritual and artistic values	*		*	

*—significant and **—very significant.

[a] Artificial seawall.

[b] Aquaculture.

[c] Water treatment plant.

Table 2
Ecosystem goods of the tropical seascape. Adopted from [6,7,37].

Mangrove	Seagrass	Coral reef
Seafood, honey, sugar, fruits, animal fodder, alcohol, vinegar, fur, aquarium industry products, traditional medicine, tannins, lime, timber, thatch, firewood, etc.	Seafood, agar, manure, carageenan, animal fodder, traditional medicine, paper, etc.	Seafood, traditional medicine, building material, aquarium industry products, lime, agar, manure, fertilisers, ornamentals, snakeskins, etc.

provide a commercial base to local and national economies (Table 2). Fish and shellfish constitute the major value of marketed products from unexploited mangroves, and the support to commercial, recreational and subsistence fisheries is well documented [7,35]. For instance, 80% of all marine species of commercial or recreational value in Florida, USA, have been estimated to depend upon mangrove estuarine areas during some stage in their life cycles [36].

3.2. Seagrass beds

The recent degradation of a number of important seagrass habitats has resulted in a growing awareness of the functional roles of these communities [12]. The leaf canopy of the seagrasses reduces the velocity of water currents and particle resuspension and, together with the extensive network of roots and rhizomes, stabilise coastal sediments [12]. Many commercial fish species utilise seagrass beds as nursery or feeding ground during some life stage [3]. Seagrasses also serve as critical habitat for dugongs, turtles and birds, and provide a list of habitat-specific goods and ecosystem services, e.g. species used in traditional medicine, sea food, animal fodder, manure, agar, carageenan, paper, flour, assimilation of domestic waste and aquaculture effluents [12,37] (Table 1 and 2).

3.3. Coral reefs

Coral reefs have the highest species diversity of all explored marine habitats supporting up to one-quarter of all marine fish species [38]. Healthy reefs can produce up to 35 metric tonne of fish/km^2 year [39]. It has been estimated that the catch from coral reef fisheries may constitute up to 10% of the world fisheries catch [40] and in some developing countries 25% of the fish catch is taken from coral reef ecosystems [41]. These figures pinpoint the importance of coral reefs to the livelihood of coastal communities in the coral reef literature. The ecosystem services (and goods) provided by coral reef ecosystems have been discussed in more detail by Moberg and Folke [6]. These include not only fish and shellfish, but also recreational possibilities, coastal protection, nutrient cycling, medicines, climate change information, ornaments, building material as well as aesthetic and cultural benefits (Table 1 and 2).

4. Single-service substitutions

In this section, we go through a number of cases where humans have tried to substitute or replace a service provided by an ecosystem in the seascape with technological substitutes. This is mostly done as a response to degradation and following economic losses due to the loss of a particular ecosystem service when natural recovery of the former ecosystem functions is unlikely to occur. The first case, however, is the deliberate substitution of mangrove ecosystems by shrimp aquaculture to optimise the output of one service. The sun still provides the basic energy for these kind of “subsidised solar powered systems” [20], but this source is augmented by human labour, machines, pesticides and fertilisers, much of which is derived directly or indirectly from fossil fuels.

4.1. Shrimp aquaculture systems substituting the natural production of fish and shellfish in mangroves

The worldwide decline of ocean fisheries stocks [42] has provided impetus for rapid growth of aquaculture. Shrimp farming makes up only 3–4% of global aquaculture production by weight but almost 15% by value [42]. The conversion of mangrove forests into shrimp ponds has during the last decades constituted the main threat to mangroves in many countries [43]. For example, between 1951 and 1987 the Philippines lost 67% of their mangroves, of which the development of brackishwater ponds accounted for approximately half of the loss [44]. As a paradox, the productivity, sustainability and profitability of these aquaculture systems are heavily dependent on viable mangrove ecosystems, which provide ecosystem services like water quality maintenance and buffer against natural disturbances, as well as products like seed, spawners and feed from mangrove-associated fisheries [7,45]. Failure to acknowledge this life-support function of mangroves is one explanation for the boom-and-bust pattern of shrimp aquaculture. In Thailand, 70% of previously productive ponds have been abandoned [46] due to self-pollution and disease problems that restrict the lifespan of most intensive shrimp ponds to 5–10 years [47]. The socio-economic unsustainability of this industry has also been widely debated and criticised [43,44].

Apart from problems with long-term sustainable shrimp production, the contribution to net animal protein production from this single-service technological-subsidised substitute is open to debate. Compound feeds of semi-intensive and intensive shrimp farms contain large amounts of fish meal and fish oil extracted from wild caught fish. The production of 1 kg of farmed shrimp has been estimated to require an input of 2.8 kg fish [48]. The net loss of animal protein to the society as a whole becomes even more pronounced when the foregone benefits of converting mangroves are accounted for. Each square kilometre of mangroves can generate a fishery production of 90–280 tonne annually, based on their role as critical habitat for fish, crustaceans and molluscs [7]. Hence, the mangrove is nature's own 'aquaculture system' with a number of advantages. Whereas a single-service artificial system, i.e. the aquaculture ponds, enjoys relatively easier harvest and selection of species, the natural system is multifunctional as well as more resilient and less susceptible to disease and epidemics [49].

4.2. Coastal storm, flood and erosion protection by mangroves

The massive deforestation and degradation of mangroves during the last decades has impaired the generation of many life-supporting functions. The loss of protection against storms, floods and erosion is perhaps the most alarming example. Fosberg [50] suggested that the loss of hundreds of thousands of lives in Bangladesh in 1970 following a hurricane and tidal wave might have been reduced had large areas of mangroves not been converted into rice paddies. Primavera [51] proposed that thousand of deaths and damage to property in the Philippines, inflicted by typhoons that hit the archipelago every year, could be reduced by the presence of a mangrove protective belt. In some areas in the Upper Gulf of Thailand coastlines have been eroding at 28 m/year between 1969 and 1987 [52], owing to a large extent to massive mangrove losses. The replacement cost of building hard protective structures to replace the coastal protection service once generated by mangroves can be significant. For example, in Peninsular Malaysia, Chan et al. [53] estimated this cost at US$3 million/km coastline. Furthermore, these single-service artificial seawalls have limited lifetime and need continual maintenance. This stands in sharp contrast to mangrove forests, which aside from forming cost-free, self-repairing barriers also generate an array of goods and other ecosystem services.

4.3. Coastal storm protection by coral reefs

One of the many processes provided by coral reefs that have a social value is the provision of a natural self-repairing breakwater that protects the shoreline from ocean surf, waves of storms, hurricanes and typhoons. These benefits to society in terms of protection from erosion of valuable land can be worth up to US$1,000,000/km coastline over a 25-year period in areas with major infrastructure [54]. Moreover, reefs also create calm lagoons suitable for a number of human activities, e.g. transportation, fishing and gleaning of molluscs and seaweeds [38]. Shoreline erosion is increasing around the world where reefs have been degraded, and possibly also due to global sea level rise. The replacement cost of reefs in such areas is high and most structures built only replaces one service of the reef ecosystem. In addition, they are ultimately undermined and broken apart by wave actions, and must be rebuilt at great expense [55]. In Fiji where coastal erosion has been significant for some 40 years seawalls that have been constructed to date have displayed many inappropriate elements in design and materials [56]. Artificial breakwater substitutes can cost from US$246,000 to $5 million/km depending on material, labour, transport, etc. [54,57]. In contrast to seawalls or piers the construction of artificial reefs may replace more of the services that a coral reef generate and initiate or mimic natural succession to produce a more self-sustained and multifunctional reef (see further in Section 5.2).

5. Restoration

Restoration might provide hope that natural ecosystems and their production of ecological goods and services can be reestablished, and consequently human-induced ecological damage becomes reversible. However, as seen in the following cases many restoration attempts are still in a trial-and-error stage and depend heavily on nearby healthy assemblages of plants and animals that can recolonise the damaged area after transplants or propagules are in place. Moreover, restoration efforts often lead to failures in the long run if they aim at recreating short-term anthropocentric functions instead of restoring ecosystem resilience so that the long-term provision of ecological goods and services can be sustained.

5.1. *Mangrove restoration and afforestation*

As a result of growing awareness regarding the ecological and socio-economic importance of mangroves, a number of countries have initiated mangrove replantation programs in degraded mangrove systems or abandoned shrimp ponds [46,58]. In developing countries, the one-time cost of restoring mangroves is some few hundred USD/ha [59]. The fact that the market value of one single good, i.e. fisheries, has been valued at US$800–12,000/ha mangrove annually [7] suggests that there are substantial economic benefits to be gained.

Mangroves can also be established through afforestation on unvegetated intertidal flats and other areas where they would not normally grow. Perhaps the most impressive mangrove afforestation programme on accreting mudflats has been in Bangladesh [60,61]. The coastal areas of Bangladesh suffer severe annual storm and cyclone damage, and in 1970, a particularly violent storm caused the deaths of more than 300,000 people [60]. To protect the lives and properties of the coastal communities from cyclone and storm damage, an afforestation programme was initiated in 1966. By 1990, an area of 120,000 ha (29% of total mangrove area in Bangladesh) of this newly accreted land had been afforested. Because of the highly dynamic nature of the Bangladesh coastline, survival of the planted mangroves was generally poor and repeated replacement planting often had to be carried out for periods of up to 3 years. Out of the 27 species of mangroves that occur in Bangladesh, only two species, *Sonneratia apetala* and *Avicennia marina*, showed encouraging survival rates on the mudflats, and consequently these two species dominate the mangrove replantations. However, these low diverse plantations were susceptible to two insect pest species, one stem borer and one leaf defoliator [60]. Hence, incompletely restoring or creating a habitat may lead to a spatially uniform ecosystem with low diversity within functionally groups that is more sensitive to disturbances that otherwise could have been absorbed.

While the initial objective of the mangrove afforestation programme was to provide storm protection, a number of other goods and services were generated by this multifunctional system. The fisheries production potential has most certainly increased significantly. Furthermore, it is estimated that the plantations have provided 600,000 m^3 of forest products, and have generated more than 5 million mandays of employment for coastal communities, and thereby contributing substantially to the local economy. The creation and stabilisation of new lands is another aspect of immense importance in a country as densely populated as Bangladesh, where approximately 10 million people live in the coastal region and offshore islands [61]. During an intense cyclone in April 1991, many of the mangrove plantations were damaged, but later on showed signs of recovery, indicative of a self-repairing system. Given these ecological and socio-economic benefits, it is surprising to note that in a follow-up coastal embankment rehabilitation project supported by the World Bank (commenced in 1993), over 60% of the US$80 million budget was allocated for civil works (mainly repair and improvements of coastal embankments), while only 7% was set aside for afforestation of a 50–200 m wide belt of mangroves on the foreshore to reduce cyclone damage and embankment maintenance costs [62].

The choice of mudflats for the mangrove planting has the advantage of avoiding conflicting claims over land ownership and development. Such conflicts would most likely arise in efforts to restore mangroves in abandoned shrimp farm areas or former logging areas. Intertidal mudflats represent a rich and productive ecosystem in themselves, providing an important habitat that supports high densities of intertidal benthic invertebrates and fulfilling a range of key ecological functions [59]. During low tides, the intertidal mudflats serve as important feeding grounds for large concentrations of migratory shorebirds, while in many areas the mudflats are exploited by humans for bivalves and crabs, contributing substantially to their income and food. Consequently, the planting of mangroves on mudflats would represent a form of "*habitat conversion*" where one valuable habitat is transformed into another. Even if the afforestation is successful, the net gains in such a situation are likely to be less than in the case of restoration efforts in degraded former mangrove areas and abandoned shrimp ponds.

5.2. Artificial reefs—"artificial respiration" or success story?

Artificial reefs have been in use for centuries in Japan and India. Today artificial habitats are used for recreational diving, breakwaters, habitat restoration, scientific research and solid waste disposal [63]. Artificial reefs may mitigate the degradation of natural reefs if natural coral reef habitats are successfully imitated (structural heterogeneity important), without being used as an excuse for dumping garbage in the ocean such as wrecked cars, airplanes, ships, oil rigs, etc. [63,64]. The latter structures may indeed attract large fish schools if surrounding habitat provides inadequate shelter spaces, but may leak antifouling paint, and due to rust and corrosion they are not a suitable substrate for framework builders. Steel, concrete and plastics are not either any good substrates for the development of the important dynamics of bioerosion and carbonate deposition [64]. The question whether artificial reefs actually produce more fish biomass or simply aggregate them, making them easier to locate and catch is heavily debated, and difficult to answer since studies on larger spatial–temporal scales are too few to statistically distinguish impacts from natural variability [63]. This controversy became known as the attraction-production question [65]. The advocates of the production hypothesis assume that habitat is the limiting factor and that artificial substitutes will promote the growth and survival of juveniles. Polovina and Sakai [66] showed that adding artificial structures to soft bottom habitat increased refuge availability and as a consequence regional production of *Octupus dolfeini* in Japan. The prevalent opinion of reef fish ecologists, on the other hand, seems to be that most adult reef fish populations are limited by recruitment variability [65]. As a consequence, it has been argued that populations of fish already being overfished may be even more depleted due to the remaining individuals being concentrated to artificial reef structures and more vulnerable to fishing [67]. Nonetheless, artificial reefs may reduce the cost of fishing by increasing catch per unit effort, convenience and efficiency.

5.3. Restoration of coral reefs

Numerous attempts at restoring lost services in coral reef ecosystems are currently being undertaken, either through restoration, rehabilitation or creation [68]. However, coral reef restoration is still considered to be at the experimental, and trial-and-error stage [69]. In the ideal case restoration speeds up growth of corals and starts a succession to resemble a natural reef ecosystem. Growth rates of corals are generally slow and therefore most evaluations have documented at least a decade for reestablishment of coral abundance, and sometimes up to a century if it will occur at all [70]. Rehabilitation of degraded reefs through transplantation of corals has generally been based on labour-intensive methods, where corals are attached with expensive materials like cement mixture or underwater epoxy [71,72]. These techniques have been used to replace corals killed by pollutants, increase coral cover in areas for recreational purposes, to replenish populations of rare species and to restore reefs after ship-groundings and blast fishing. In general, corals should be collected from a habitat with similar disturbance history, depth, water quality and wave exposure to that into which they will be transplanted [71].

In many reef areas, small boat-groundings are chronic, as witnessed by the Florida Keys with 500 small vessel (<30 m)-groundings reported each year [73]. A restoration project, initiated after two ship-groundings in 1989 in the coral reef of the Key Largo National Marine Sanctuary, had funds exceeding US$3 million and required a flotilla of barges, tugboats, supply vessels and cranes. For example, the underlying reef framework had to be repaired by 40 10 tonne modules made of special marine cement and natural coral reef rock, after removing of coral rubble, and stabilising the underlying reef structure. Subsequent to this structural restoration corals and other reef-dwelling animals were transplanted onto the repaired habitats. These kinds of large-scale restorations after ship-groundings are extremely time, money, energy and labour consuming [68,73].

There have been experiments done using inexpensive and low-tech methods for transplantation of corals [74,75]. Near Mafia Island, Tanzania, a method of tying staghorn coral *Acropora formosa* together with strings and subsequent placement on the seabed, initiated colonisation of other species of hard and soft corals on reefs moderately exposed to water movements [75]. This method cost in the order of US$10,000/ha, which is considerably cheaper than many other restoration attempts ranging up to US$6,500,000/ha which is far beyond the financial capacity of many developing countries [72].

One way to restore reefs and enhance the calcification rate of reefs by human technology is the “mineral accretion technique” [76]. Electrolysis (low-voltage electrical currents) is used to create high pH at the growing mineral surface, leading to precipitation of limestone from seawater which can increase growth rates of calcareous organisms [64]. These structures are suitable for transplantation of corals and also for natural colonisation by organisms typical of healthy reef conditions that gain a competitive advantage over weedy organisms (algae) as long as they receive electrical current. Hence, it has been suggested that coral reefs might therefore be restored even in areas where water quality is rather poor, and algae otherwise would overgrow corals. This technique should of course be powered by some renewable source of energy, for example, solar panels, windmills, or water current generators. This alternative requires a great deal of management initially but if there is sufficient connectivity to other reefs, and secondary succession is initiated, the low voltage can be removed.

Another way to help restore reefs is research efforts to develop artificial substrates (larval "flypaper") containing purified immobilised morphogenic cue recognised by certain coral larvae to increase the settlement [77]. However, as discussed in the following sections, no matter which technique is applied, the chance for successful reef restoration in the longer-term requires a connection to ecosystem resilience and interlinkages to other reef communities and adjacent ecosystems in the seascape.

5.4. *Restoration of what?*

The meaning of the concept of ecosystem restoration must always be analysed and discussed prior to any investment in restoration management programmes. The objectives behind mangrove restoration and the evaluation of programmes are sometimes blurred due to the use of different terms and confusion in their meaning [78]. For instance, afforestation is a widely used term in forestry and refers to planting of trees in areas that have not previously been forested, and consequently restoration is not the objective. Rather, habitat substitution would be the correct ecological definition for mangrove afforestation.

When initiating a restoration programme, it is important to distinguish truly degraded habitats from the sometimes so-called degraded states that might be common stages in a succession initiated by natural disturbance [79]. The success of restoration is often measured as percent cover of living corals [70] or mangrove vegetation [58] of a site for a defined period of time, usually only 2–3 years (the lifespan of a development project or research grant) [58]. This implies that secondary succession or long-term dynamics is seldom included in evaluation processes.

Restoration of degraded marine habitats has been more successful in mangroves and seagrass beds than in coral reef environments [58,72]. Often the focus of restoration is on the success of restoring the functions of direct value to humans whereas the complex interactions among species responsible for building resilience and opportunity for renewal and evolution is often not recognised [26]. It may seem easier to restore some ecosystem services (functions) than ecosystem form (structure: species diversity, trophic structure) [80,81], but if the services are to be delivered long term under changing environmental and anthropogenic conditions the restored habitat must also attract a sufficiently high diversity of organisms to become resilient. Although there may be no real mechanistic relations between diversity and function, many authors have suggested the connection between biodiversity and ecosystem resilience to both man-made and natural disturbances, e.g. [82,83]. However, there is yet too little information from restoration projects in the tropical coastal zone to tell if the restored ecosystems resemble the natural ones in terms of ecosystem functioning, linkages to other systems and if they are able to respond to natural and human-induced disturbances as well as environmental changes over time without losing important functions [23,58]. This is not to say that restoration is always a failure or inherently unsustainable. Sometimes it might be the only way to proceed when the system is essentially locked into an undesired stability domain after a more or less irreversible phase-shift.

5.5. *Adaptive management in restoration*

There are many uncertainties associated with restoration efforts owing to spatial and temporal variations in hydrology, currents, weather and unpredictable patterns of disturbance in the surrounding seascapes or landscapes, and therefore it is almost impossible to predict the trajectory that succession processes will take after the intervention [23,84]. As a consequence, many authors have lately advocated the need for viewing restoration as experiments and adopt some "learning-by-doing" approach, often referred to as adaptive management [23,81,84,85]. This requires extensive monitoring and the building of ecological knowledge of ecosystem dynamics in order to learn and adapt in response to the observed outcome. The involvement of many different stakeholders to include many kinds of knowledge (scientific as well as local or traditional) is also emphasised in most adaptive management protocols, to be able to understand and respond in a flexible manner to the complexity that ecosystems display. The adaptive management framework also has the advantage of involving both the local users and government in the process with the anticipation of also sharing the benefits to be achieved [23].

6. Substitutions and restoration from a seascape perspective

As discussed above, most efforts to replace degraded ecosystem functions in the seascape by technical substitutions replace only one single service of the previously multifunctioning ecosystem. Unfortunately, when one of the ecosystems in the seascape is degraded the loss of biological, physical and biogeochemical linkages also tends to affect structure and functions in adjacent, interconnected systems (Fig. 1). For instance, in the reefs around Ishigaki island, Ryukyus in Japan, the average coral cover was higher where inland natural forest belts were intact compared to settings with low forest cover, probably due to the capacity of coastal forests to absorb harmful material from erosion, construction work, agricultural fertilisers, pesticides, etc. [29]. Also seagrass beds will suffer from indirect effects as a consequence of degradation of catchment and mangroves [4]. Increasing silt load and eutrophication have been reported to lead to changes in depth distribution, species composition, productivity and morphology of seagrasses [12]. The effects on interlinked ecosystems may also have severe economic implications as suggested in the often-cited study by Hodgson and Dixon [86] from Bacuit Bay in the Philippines. They estimated the economic losses from coral-reef-related tourism and fishing as a consequence of increased erosion from coastal logging leading to negative effects on the marine ecosystems via sedimentation. Their study demonstrated that continued logging was neither economically nor ecologically feasible. Moreover, it became evident that a landscape–seascape perspective, where the study area is considered to be a series of interlinked systems from mountaintop to seafloor, is a very effective, albeit difficult, way to evaluate management alternatives. Similarly, the success or failure of any restoration, replacement or substitution effort in the tropical coastal zone will largely be determined by the ability to acknowledge how it influences adjacent systems in the seascape and its surroundings (see Fig. 1).

A restoration attempt can be seen as an uncontrolled experiment in assembling a community [81]. After the initial intervention of propagules or transplants, the restored mangrove or reef habitat will start to attract other species and follow some successional pathway [23]. However, most mangrove restoration work has focused only on the techniques for growing mangrove trees with little attention paid to long-term community structure or linkages with other systems [58]. Rather than first assessing the reasons behind mangrove loss and working with the natural recolonisation processes, management has usually emphasised planting of mangroves as the primary tool of restoration [78]. Likewise, transplanting corals to restore a degraded reef to reestablish ecosystem functions and reintroduce species without taking into consideration the condition of adjacent mangrove ecosystems may lead to expensive failures because of reduced water quality. If the underlying cause of degradation was human impacts on catchment and mangrove vegetation, which increases both suspended sediments and nutrients in terrestrial runoff, there is no point in restoring a coral reef without rehabilitation of upstream ecosystems (e.g. improving water quality by replanting mangroves or by other means) [4]. These examples of "treatment-without-diagnosis" will in most cases be very inefficient and need continual maintenance.

Successful restoration projects have to date had the advantage of healthy assemblages of plants and animals in the surroundings that could recolonise the damaged area after transplants or propagules are in place and initiate one of many possible successional pathways to some acceptable stable state [81,87]. This secondary succession can also be deliberately utilised by the managers as in the case of restoring seagrass beds in the Florida Keys National Marine Sanctuary. A native pioneering seagrass species was planted initially to stabilise the site and prevent erosion while facilitating the natural recolonisation of the target turtlegrass (*Thalassia testudinum*) [88].

Stevenson [46] reported that recolonisation occur quite rapidly if hydrology is restored in, for example, reconnected abandoned shrimp aquaculture ponds if mangrove forests are present in the vicinity and natural production of propagules is sufficient. Hence, successful restoration efforts have to date been able to foster natural recruitment and allow the ecosystem to design itself over time [89]. In a world of human dominance, this kind of self-design by natural recolonisation can no longer be taken for granted [14,87]. Successional pathways may be lost owing to habitat fragmentation, pollution barriers or "upstream" systems being degraded due to human activities and thus not containing the full array of species needed for reestablishment of function and structure [14]. Consequently, transplants or propagules used in restoration might have to be collected from areas far from the affected site and might therefore be less adapted to the specific local conditions compared to the original flora and fauna. To reduce the negative effects on the area where coral transplants are collected, coral farming may be a source of seed colonies for coral transplantation and also a solution for diminishing pressure from coral collection for the curio and live coral trade [90].

However, irrespective of applied technique, reef restoration will only be successful in the long term if there are thriving upstream "source" reefs that can supply larvae to down-stream "sink" reefs [79,91], and if water quality (and global warming) can be controlled. Moreover, fishing pressure should be decreased or maintained on a low level so that diversity within the functional group of herbivores and associated grazing levels remain sufficiently high to maintain the substrate in a suitable state for coral larvae to settle [14]. Under these circumstances, coral reproduction and recruitment can occur and facilitate a secondary succession towards coral dominance after a disturbance and avoid phase-shifts to algal dominance.

7. Discussion and conclusions

In the introduction we asked, to what degree can human technologies substitute for ecosystem services in the coastal zone of the tropics? This question relates to a central issue in ecological economics: to what extent is human-made capital a substitute for natural capital that generates the flow of ecological goods and services [18]. From the information presented here it seems that replacing ecosystem services of the tropical seascape provided by self-repairing, resilient ecosystems with technological substitutes only provide some of these services, and often entails huge engineering and maintenance costs. Moreover, the loss of ecosystem interactions often leads to the loss of ecosystem services generated by the interconnected ecosystems in the seascape, with economic losses that can be substantial. In contrast, proactive management of multifunctional ecosystems, including efforts of restoration can be profitable. This is illustrated by for example White et al. [92] showing that the benefit/cost returns was about 30:1 for management of coral reef and mangrove resources of Olango Island in the Philippines.

If ecosystem services are to be substituted at all, this requires ecological knowledge and understanding of the multifunctionality and interconnectedness of ecosystems. For example, replacing natural fish and shrimp production with aquaculture must take into consideration the aquaculture industry's dependence on natural ecosystems and prioritise farming of low trophic level herbivorous fish, reduce fish meal and fish oil inputs in feed and develop integrated farming systems to minimise negative effects on interlinked ecosystems in the seascape [48,49]. For long-term sustainability, complex and resilient systems are required to respond to future environmental changes and disturbances, and to continue providing the ecological goods and services needed [93]. This relates to the second question posed in the introduction: How can ecosystem restoration be more effective in restoring not only the functions of direct value to humans from a short-term anthropocentric viewpoint, but also the ecosystem resilience? As highlighted in our examples, incomplete habitat restoration may lead to a more spatially uniform, less functionally diverse ecosystem, i.e. a system more sensitive to disturbances. Highly specialised and co-evolved interactions are often replaced with weedy species or managed landscapes [94]. There are many uncertainties associated with restoration and which trajectory that succession processes will take after the restoration is initiated. Hence, ecological restoration efforts should adopt an adaptive management approach and strive to shift from only reestablishing those functions easily perceived as ecosystem services to restoring also ecosystem resilience so that the services provided to humanity is secured in the long run.

With resilience as the ultimate goal of restoration the 'ecological memory' [95] of the area and the surrounding seascape should be considered. Ecological memory contains features that determine the capacity of ecosystems to reestablish former functions and avoid phase-shifts following disturbance (Bengtsson et al., MS [95]). Internal memory (or 'biological legacies') includes the species and biological structures and patterns that persist within the disturbed area and serve as foci for regeneration and allow species to colonise ([96,97]; Elmqvist et al., MS). The other important part of the ecological memory is the external memory that provides sources and support areas outside the disturbed area for species colonising disturbed patches. It consists of inflow of seeds, propagules, larvae and mobile links (species that spread from one area to another and contribute with important resources, genetic information or interactions; Lundberg and Moberg [98]) and their support areas. Hence, restoration efforts cannot rely on self-design without sufficient ecological memory, and therefore tend to be dependent on fossil fuel, money, and labour support to be sustained. The mangrove afforestation case of Section 5.1 highlights the problems associated with creating habitats in areas not earlier occupied by a similar ecological community, or areas where a large-scale disturbance have cleared the area, so that no internal memory (or biological legacies) is present for incorporation into the reestablishment of the ecosystem. Therefore, restoration efforts of an ecosystem in the tropical seascape should not be implemented in isolation from the surrounding landscapes and seascapes. Often it must be complemented by other management actions (e.g. reserves) to secure important ecosystem interactions, water quality and ecological memory. With this hindsight, restoration for sustainability is about reestablishing ecological memory for ecosystem resilience, natural successional processes and capacity for renewal (evolutionary opportunities). In this context, restoration aims at sustaining the capacity of ecosystems to provide essential ecological services. In conclusion, prevention seems always to be more effective than the cure. It is probably always cheaper to aim at preserving ecosystem functioning than trying to restore or substitute them when they have been degraded or lost.

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