REVIEW

Potential for landscape-scale positive interactions among tropical marine ecosystems

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ABSTRACT: Fluxes of energy, materials and organisms among ecosystems are consequences of their openness to exchange and lead to the consideration of reciprocal connections among adjacent ecosystems. Reciprocal connectivity may have implications for ecosystem functioning and management but it is generally studied only for a single factor, rather than for multiple factors. We examined the extent to which these fluxes may apply at the landscape scale for 3 ecosystems: mangrove forests, seagrass beds and coral reefs. From a literature review and analysis, we semi-quantitatively assessed fluxes based on attenuation of wave height and exchanges of sediments, nutrients and algivores. We found that coral reefs and seagrass beds significantly attenuated wave height and that this effect depended on specific physical conditions. In the case of coral reefs, the attenuation capacity depended on the section of the reef the wave breached, whilst for seagrass beds, we hypothesised that the density of the plants was the controlling factor. Mangrove forests' ability to reduce sediment fluxes was related to the mangrove forest area. Seagrass plants have a capacity to decrease sediments in the water column. Both mangrove forests and seagrass beds retained nutrients within the ecosystems, which was a positive interaction. Isolated reefs showed a decrease (30 to 95 %) in algivore biomass compared to situations where the 3 habitats were in proximity to each other. The findings show that there is potential for reciprocal connections among coastal ecosystems. Our results indicate that these exchanges at the ecosystem scale can be placed into the context of facilitation in the field of community ecology. Future research should focus on which natural and anthropogenic factors determine reciprocal facilitation between these ecosystems and determine how ecosystem-based management can be improved with this knowledge. The considerable potential for reciprocal facilitation implies that ecosystem managers may need to place greater emphasis on the landscape scale.

KEY WORDS: Mangrove forests · Seagrass beds · Coral reefs · Ecosystem engineering · Nutrients · Hydrodynamics · Sediments · Algivores

INTRODUCTION

Within the field of community ecology, positive interactions between species have an important impact on population establishment and thereby on overall community structure (Bertness & Callaway 1994, Silliman et al. 2011). Habitat-forming organisms (foundation species) that are able to change the physical conditions (i.e. ecosystem engineers cf. Jones et al. 1994, 2010) and buffer environmental stress can

become the dominant community-structuring force. By becoming the core species and changing the physical conditions within the habitat, ecosystem engineers can also change physical fluxes entering and exiting the system. Modifying these fluxes means that these species can also control connections between ecosystems and thus essentially form connective relationships between ecosystems.

All ecosystems are open to the exchange of energy, materials and organisms; ecosystems therefore are functionally connected in landscapes (Lovett et al. 2005). Understanding these connections is central to ecosystem-based management, particularly in the face of increasing human impacts. Connectedness relevant to management has been shown, for example, in riverine systems (Pringle 2001) (unidirectional), terrestrial ecosystems (Moilanen & Nieminen 2002) (unidirectional) and marine reserves (Kininmonth et al. 2011) (bi-directional). Two unconnected ecosystems can be managed as independent systems. If there is unidirectional influence, control over the donor ecosystem can be used in the management of the recipient ecosystem (e.g. hydrologic systems such as riparian/rivers) (Pringle 2001). When there are reciprocal interactions, however, management will be more complicated, particularly if these interactions involve multiple, mutually reinforcing exchanges between ecosystems. In such cases, each ecosystem can facilitate the establishment or functional persistence of the other, but the opposite can also occur. Small declines in the functioning of one ecosystem can lead to functional diminution in the other, and eventually this can result in a decline in the functioning of the entire landscape.

Despite the need for a better understanding of reciprocal connections among adjacent ecosystems as an aid to integrated management, quantitative analyses of reciprocal connections have seldom been conducted. Moreover, analyses are typically restricted to a single rather than multiple exchanges. To exemplify the importance of this concept, we review evidence for large-scale reciprocal interactions by multiple exchanges for 3 kinds of tropical ecosystems that often occur in close proximity: mangrove forests, seagrass beds and coral reefs. The co-occurrence is not invariably observed, even taking into account that present-

day observations are not always representative of historic connections. Large-scale positive interactions are defined as multiple connections, physical, biological or chemical, which help to improve adjacent ecosystems' growth or establishment conditions. We examine how ecosystems' spatial co-occurrence may influence mutual establishment and persistence via positive, landscape-scale interactions mediated through multiple exchanges of energy, materials (i.e. sediment and nutrients) and/or organisms.

Mangroves, seagrasses and coral reefs occur along a depth gradient from tidal flats to deeper (60 m) near-shore oceans (Fig. 1) (Ogden & Gladfelter 1983, Moberg & Folke 1999). Mangrove trees, seagrass plants and scleractinian corals are all foundation species that support entire ecosystems (Moberg & Folke 1999, Valiela et al. 2001, van der Heide et al. 2007). Via physical ecosystem engineering (Jones et al. 1994, 2010), nutrient uptake and organic matter production, these species can improve their own habitat and create the habitats and resources for many other species. Positive engineering feedbacks are important in the establishment and persistence of these foundation species, particularly under stressful conditions (Bruno et al. 2003, Halpern et al. 2007). Here, we review data on connections between these 3 kinds of ecosystems for 4 potentially important kinds of exchanges: wave height, sediment, nutrients and
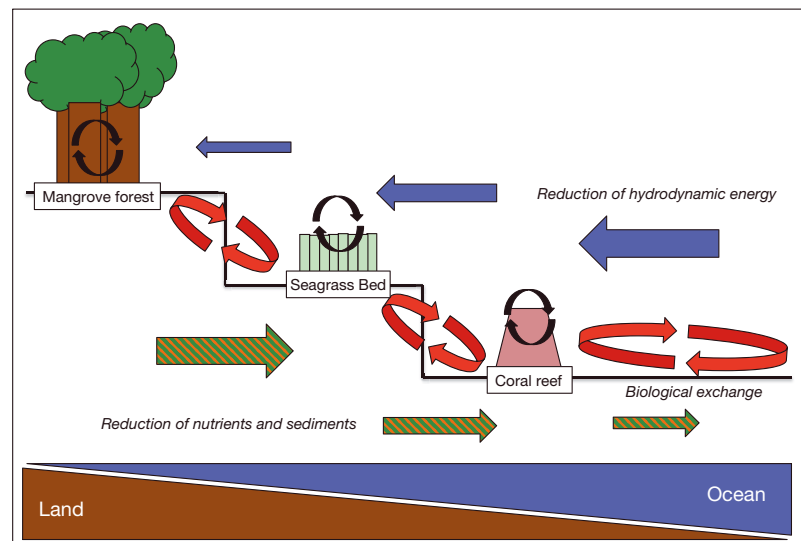

Fig. 1. Conceptualization of connections between land, mangrove forests, seagrass beds, coral reefs and ocean systems. Arrows indicate the direction and approximate magnitude (arrow width) for 4 exchange fluxes considered in the present review: sediment and nutrients (orange and green striped), hydrodynamic energy (blue) and organism movement (red). Black arrows within mangroves, seagrass and coral reefs indicate internal exchanges of nutrients, sediment, hydrodynamic energy and organisms within each ecosystem

organisms (Fig. 1). The first 3 exchanges largely derive from the extended spatial influence of physical ecosystem engineering by the foundation species within its ecosystem. This can then influence the establishment and persistence of recipient ecosystems. The fourth exchange derives from the creation of proximate habitat diversity in the landscape for other species occurring in >1 ecosystem type. Modification of these exchange processes by mangroves, seagrasses and/or corals can feed back to influence the establishment and persistence of the foundation species.

The potential for connections between mangrove forests, seagrass beds and coral reefs has been demonstrated in many studies conducted worldwide (Roberts et al. 1977, Alongi & Christoffersen 1992, Hemminga et al. 1994, 1995, Kitheka 1997, Lugo-Fernández et al. 1998, Koch 2001, Dorenbosch et al. 2004, Mumby 2006, Bouillon & Connolly 2009, Davis et al. 2009, Nagelkerken 2009). However, these studies did not investigate the potential for multiple, mutually reinforcing exchanges where one ecosystem changes the physical parameters to allow for the establishment of another. We define connectivity as a sub-set of positive reciprocal exchanges. Studies of tropical coastal ecosystems have highlighted the importance of landscape mosaic configuration in the management of tropical fisheries (Pittman et al. 2004, Grober-Dunsmore et al. 2009) and mangrove restoration (Thinh et al. 2008), but the importance of reciprocal exchanges — in particular their influence on recruitment, establishment and persistence of the foundation species — have not been considered. Coral reef, seagrass bed and mangrove forest structures decrease hydrodynamic energy (Roberts et al. 1977, Koch 2001), but it is not clear if such effects are sufficient to result in landscape-scale interactions. Sediment trapping by the extensive root systems of mangroves is thought to significantly buffer coastal oceans from terrestrial sediment runoff (Valiela & Cole 2002, Adame et al. 2010), but the implications for adjacent ecosystems have not been elaborated. Only a handful of studies have quantified the net exchange of nutrients between mangroves and seagrass beds (Hemminga et al. 1994, Hyndes et al. 2014), but these studies have not considered the potential for reciprocal exchanges. Studies investigating biological connectivity have largely focused on the importance of nursery and spawning sites (Mumby 2006, Nagelkerken 2009), but few studies have determined the degree to which high production rates in coral reefs are due to 'nursery' or other effects of adjacent eco-

systems or how such effects might influence reef persistence.

Here, our aims are to (1) identify the extents to which there are known physical, chemical and biological exchanges among adjacent mangroves, seagrass beds and coral reefs and (2) from this, deduce whether or not multiple, reciprocal interactions may exist among the ecosystem types when they co-occur in proximity. We use the literature to identify the optimum range of abiotic conditions for mangrove forests, seagrass beds and coral reefs for each kind of exchange variable. This capacity is reviewed from the literature, allowing a semi-quantitative assessment of (1) and (2) above. In the present paper, we hope to address the question regarding to what extent the proximity of ecosystems allows for connecting, mutually positive mechanisms between them.

CO-OCCURRENCE OF ECOSYSTEM TYPES AND CONSEQUENCES OF LOSS OF ONE TYPE

Spatial co-occurrence

The potential for reciprocal interactions will generally be restricted to situations where different ecosystem types occur in close proximity. For example, hydrodynamic energy effects via wave attenuation by coral reefs require the reefs to be close enough to seagrass beds and mangroves for waves not to build up again once they pass over the reef. Seagrass beds also have to be close to mangroves to have any influence on hydrodynamic energy exchange. Influence due to altered sediment and nutrient exchange will only occur if distances are short enough to 'carry over' changes in water quality before mixing from other areas 'dilutes' the impact. Biological effects require a sufficient proximity for juvenile and adult organisms to move between ≥2 of these ecosystem types, although this distance will vary substantially among species (Nagelkerken 2009).

Mangrove forests, seagrass beds and corals reefs have overlapping distributions across a latitudinal breadth encompassing East Asia, Australia, the Caribbean, the Red Sea and East Africa. The 3 types are often found together but do not always co-occur locally. For example, oceanic barrier islands often support only isolated mangrove ecosystems (Pilkey et al. 2009). Tropical seagrass beds exist in the absence of coral reefs (Orth et al. 2006). Atoll islands such as the Maldives have only a few co-occurrences of seagrass beds, and these habitats were introduced within the last 100 yr (Miller & Sluka 1999).

There has been a considerable global decline in occurrence and health of mangroves, seagrass beds and coral reefs over the last 100 yr. Worldwide, seagrass beds are thought to have been declining ~7% yr^{-1} since 1990 (Waycott et al. 2009). Mangroves are decreasing in surface area by 1 to 2% yr^{-1} (Valiela et al. 2001) and coral reefs by 1 to 7% yr^{-1} (Bellwood et al. 2004). Even though the high rate of destruction of coastal ecosystems makes it difficult to map where these ecosystems were once neighbours, mangrove forests, seagrass beds and coral reefs were much more widespread and the frequency of spatial co-occurrence was very likely much greater in the past than it is today.

Consequences of loss

Mangrove forests

Many mangrove forests have completely disappeared due to logging, coastal landfill and/or aquaculture (Valiela et al. 2001). Circumstantial evidence suggests that mangrove loss may have had functional consequences for neighbouring marine ecosystems, apart from their role in protecting terrestrial systems from major events such as tsunamis (Alongi 2008). For example, in Sabah, Malaysia, mangrove loss likely contributed to increased turbidity during the rainy season via increased terrestrial sediment runoff that, in turn, caused large scale disturbance to seagrass meadows within the area (Freeman et al. 2008). Cleared mangrove forests can alter the algae composition in adjacent ecosystems, such as coral reefs (Granek & Ruttenberg 2008). The algal species *Dictyota* sp. and *Acanthophora* sp. were found growing on dead and living patch corals, adjacent to cleared mangrove areas (Granek & Ruttenberg 2008). They were absent in the vicinity of intact mangroves. Valiela & Cole (2002) showed that mangroves could intercept and store large amounts of terrestrial nitrogen. Mangrove forests that received an input of <20 kg N ha^{-1} yr^{-1} intercepted all of it; this reduction in nitrogen load to the ocean positively correlated with increased seagrass biomass and reduced habitat loss (Valiela & Cole 2002).

Seagrass beds

Human activities in the coastal seascape can physically damage seagrass beds via coastal construction, boat movement, anchor damage and de-ballasting (Burkholder et al. 2007, Todd et al. 2010). Seagrass beds are susceptible to reduced light availability (Ralph et al. 2007, van der Heide et al. 2007) and to increases in nutrient concentrations and toxins (Orth et al. 2006, Freeman et al. 2008, Todd et al. 2010). Loss of seagrass beds has been associated with changes in neighbouring ecosystems. For example, in Motagu Bay, the Bahamas, the loss of patch reef over the last 50 yr is thought to be due to the loss of a seagrass bed (Sealey 2004). In Mauritius, many hotels are actively removing seagrass beds because they are deemed unsightly, and this has caused increased turbidity with potential damage to nearby corals (Daby 2003). Other negative impacts on seagrasses may also negatively affect linkages to coral reefs, such as the reduction in density or elimination of algivorous fish. Recently, it has been shown that seagrasses increase seawater pH, which in turn allows for an increase in calcification in corals of 18% (Unsworth et al. 2012). The rise in calcification of coral reefs only occurred when seagrasses were neighbouring coral reefs (Unsworth et al. 2012). It can be inferred that the loss of seagrass beds adjacent to coral reefs will cause a decrease in calcification rates. This especially has implications for anthropogenic impacts such as climate change, which can result in acidification of the ocean.

Coral reefs

Coral reef persistence is threatened by large-scale influences such as global warming, ocean acidification and deteriorating water quality (increased turbidity and eutrophication) that can result in reduced productivity, mass mortality and consequent habitat loss for other species (Moberg & Folke 1999, Bellwood et al. 2004). Destroyed or heavily damaged coral reefs no longer provide an effective wave barrier; this change results in increased coastal erosion. A study in the Seychelles (Sheppard et al. 2005) found that coral reef die-off caused in part by warming seas killed ~99% of hard coral cover. This mortality increased the depth of the coral flat, decreased roughness, reduced ecosystem complexity and increased wave energy on the shoreline, resulting in increased beach erosion. Although that study did not discuss a possible de-stabilizing effect on seagrass beds or mangroves, it does illustrate the importance of coral reefs in coastal protection from wave action. Recent work has also highlighted the importance of ecosystem structural complexity to ecosystem services, especially in coral reefs (Graham & Nash 2013).

Density and complexity of the coral reef was positively related to fish biomass (Graham & Nash 2013). Thus, a decrease in complexity will have concomitant effects on fish species, which connect coral reefs with seagrass beds and mangrove forests.

MATERIALS AND METHODS

We completed a literature search (using sources from 1947 to the present) on Web of Science and Google Scholar using keywords including, but not limited to, the following: connectivity, facilitation, positive interactions + coral reefs + seagrass beds + mangrove forests; facilitation, positive interactions + tropical coastal seascape; wave energy, wave height + coral reefs + seagrass beds + mangrove forests; alteration of hydrodynamic energy + coral reefs + seagrass beds + mangrove forests; turbidity, sedimentation rates + coral reefs + seagrass beds + mangrove forests; outwelling + mangrove forests; nutrient concentrations, fluxes + coral reefs + seagrass beds + mangrove forests; biological connectivity + coral reefs + seagrass beds + mangrove forests; nursery areas + coral reefs + seagrass beds + mangrove forests; and ecosystem based management + coral reefs + seagrass beds + mangrove forests. Not all topics of study were completed in the same time period. The relation between coral reefs and hydrodynamics was studied well before reports on other aspects (e.g. hydrodynamics and seagrass beds or mangroves) were present in the literature. In our supplementary tables, we indicate the time periods during which the results for different ecosystems and exchanges were published, but for the analysis we did not restrict the data used to a constrained time span.

We estimated the threshold value for sediment/ nutrient fluxes and wave height at coral reefs, seagrass beds and mangrove forests. This threshold value was the mean value from the literature review of fluxes under which the ecosystem engineers (stony corals, seagrass plants and mangrove trees) can survive (Table S1 in the supplement at www.int-res.com/articles/suppl/m503p289_supp.pdf, see also Tables 3 & 5). We decided to use a mean value as being the most representative because the range (minimum and maximum values) could be skewed by very high and low values being recorded for a specific site or species, which were not characteristic of the entire data.

In each of the literature studies, we searched for reductions in wave heights, sediment fluxes and nutrient fluxes as these passed through an ecosystem. This was done by comparing import and export per study. If an import value was not available but a retention rate was, we calculated import based on export and retention. Import and export of wave height, sediment or nutrients were plotted to establish if the ecosystem was reducing the flux and therefore providing a positive interaction. We also compared the export values from one system with the threshold values for the ecosystem engineers of the other systems.

Retention capacity of the different ecosystems was statistically analysed by regressing the export/import ratio versus area or length of the system with a Model II regression. To ensure normality and homogeneity of variances, the export/import ratios were log-transformed. This transformation also avoided any spurious correlation that could have been caused by a correlation between export or import and the dimensions of the system. Probability (p) was considered significant at $p < 0.05$. All statistical testing was completed in the R program.

ANALYSIS OF ECOSYSTEM EXCHANGES AND POTENTIAL INTERACTIONS

Attenuation of wave height

Habitat requirements of mangroves and seagrasses and ecosystem engineering feedbacks

Mangroves require low wave heights for seedling establishment and development of root systems (threshold wave height 0.5 m; Table 1, Table S1 in the Supplement) (Balke et al. 2011). Seagrass beds grow in shallow water environments. Similar to mangroves, they require calm conditions for initial establishment and expansion (threshold wave height 0.4 m; Table 1, Table S1) (van der Heide et al. 2007, Infantes et al. 2009). Along coastlines subject to strong wave action, mangroves and seagrass beds could benefit from the physical barrier provided by coral reefs (Ogden & Gladfelter 1983, Moberg & Folke 1999). Coral reefs at the edge of the coastal zone are a physical barrier between the land and the ocean (Moberg & Folke 1999). Coral reefs can persist at high levels of hydrodynamic energy (threshold wave height 0.9 m; Table 1, Table S1). The reef's physical structure is spatially complex, resulting in high friction with the water currents. As a result, coral reefs create calm lagoons on the landward side and can prevent shoreline erosion (Ogden 1988, Moberg & Folke 1999, Sheppard et al. 2005). Established seagrass beds can also attenuate wave energy

Table 1. Literature-based threshold values of wave height (m) and sediment (g m^{-2} d^{-1}), nitrogen (g N m^{-2} d^{-1}) and phosphorus (g P m^{-2} d^{-1}) fluxes at which mangrove forests (MF), seagrass beds (SB) and coral reefs (CR) can establish or persist. Values were calculated based on a literature review; the mean value of the literature review values was chosen as the threshold value (Table S1, Tables 3 & 5). Facilitation potential indicates whether one ecosystem type could positively affect the establishment and/or persistence of another by altering the corresponding abiotic variable (based on literature review); arrows indicate the direction of the facilitation potential. We have not considered differences in organic or inorganic nutrients and have combined all sources of N and P

Threshold variables	Mangrove forests	Seagrass beds	Coral reefs	Facilitation potential
Wave height (m)	0.5	0.4	0.9	CR→SB→MF
Total suspended sediment (g^{-1} m^{-2} d^{-1})	82	161	11.2	MF→SB→CR
Water column nitrogen (g N m^{-2} d^{-1})	0.07	0.04	0.009	MF→SB→CR
Water column phosphorous (g P m^{-2} d^{-1})	0.04	0.002	0.0002	MF→SB→CR

(Koch 2001, Bouma et al. 2005), but to a much lesser degree than coral reefs due to their flexible structure (Bouma et al. 2005, Infantes et al. 2009). In the present study, the data show that reduction of wave heights is species- and location-specific. Seagrass beds and corals can contribute to sediment accretion and stabilization, thus decreasing water depth toward the shore. This reduction in depth can also alter wave height, but we did not take this factor explicitly into consideration.

Positive interactions between coral reefs and seagrass beds under average conditions

Coral reefs reduce wave heights to a fraction of the incoming wave height (Fig. 2A, Table S2 in the Supplement). Assuming an initial wave height arriving at a coral reef of between 0.07 and 4 m, this would result in 0.02 to 0.8 m waves via attenuation of hydrodynamic energy (Fig. 2A, Table S2). There was no correlation between the distance the wave travelled and the retention capacity (linear regression $R^2 = 0.05$, p > 0.05). However, the data taken at the reef crest did show a negative relationship between export/import ratio and the distance the wave travelled (linear regression: $R^2 = 0.5$, p < 0.05). All studies showed a decrease in wave height between 20 and 97%; this indicates the ability of coral reefs to reduce

wave heights, thereby potentially facilitating the establishment of seagrass beds (Fig. 2A, Table S2).

After a wave passes a coral reef, seagrass beds will further reduce an initial wave height from 0.04–0.2 m down to 0.01–0.08 m (Fig. 2B, Table S2). The reduction ratio (export/import) was not related to the physical dimensions of the bed or to the density of the seagrass, possibly because of the small data set (Table S2). However, all values were well below 1, demonstrating that wave height reduction is a consistent feature of all seagrass beds studied. Overall, these studies (Table S2) show the potential of seagrass beds to attenuate wave height for neighboring ecosystems.

Positive interactions between coral reefs and seagrass beds in storms and hurricanes

Coral reefs may be exposed to recurrent tropical storms and hurricanes with high hydrodynamic energy. The main factor influencing coral reef capacity for wave height attenuation is the physical dimen-
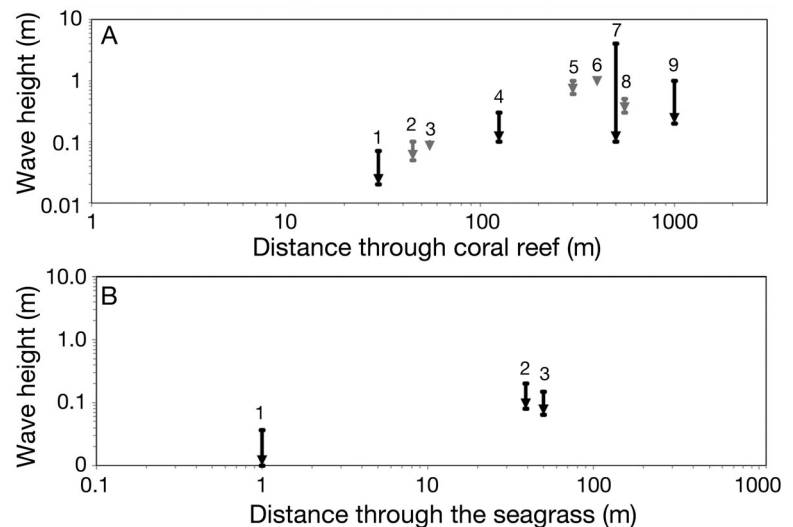

Fig. 2. Change in wave height (m) over a distance (ocean to shore) of (A) coral reef and (B) seagrass bed. Each line/arrow represents a different study, where the highest point is the initial wave height, and, following the direction of the arrow, the lowest point represents the end wave height. In panel (A), grey lines represent studies taken at the reef crest; black lines represent studies taken at the fore or back reef. Each study calculated a different percentage change of the wave height over a given distance; the number directly above the line indicates the study number in Table S2 in the Supplement

sion of the reef. Madin et al. (2006) reviewed various studies and found that 90% of wave height and velocity was reduced in the first 300 m of a fringing reef. Various wave heights during storm swells have been recorded: for example, 1 to 2 m in the South Pacific and Indian Ocean, 10 m in the North Pacific and 3 to 5 m at Hawaii (Dollar 1982). Based on Madin et al. (2006), such waves would be substantially reduced by coral reefs, although remaining waves would most likely still exceed normal threshold conditions for seagrass beds (Table 1). Thus, seagrass beds will be damaged by hurricanes even in the presence of coral reefs (Lugo 2000). However, given the transient character of storms, in most cases, these ecosystems will be damaged but not eliminated, given sufficient time for prior establishment and for recovery between storms (Uhrin et al. 2011). The storm surge created by Category 5 Hurricane Katrina (New Orleans, USA) was ≥5.6 m with a wind speed of 60 m s^{-1} (Knabb et al. 2005). This force was sufficient to damage coral reefs, increase wave energy and height in the lagoon and move coral reef debris toward the lagoon (Lugo-Fernández & Gravois 2010). Nevertheless, in the absence of coral reefs, damage to seagrass beds would most probably have been much greater. Healthy coral reefs are resilient to infrequent hurricanes, and if no additional major impacts occur immediately after the hurricane, they can continue to protect the shoreline (Lugo 2000).

Sediment exchange

Habitat requirements of coral reefs and seagrasses

With respect to total sedimentation and turbidity, the range of reported thresholds for establishment and/or persistence is lower in coral reefs than in seagrass beds and mangrove forests (Table 1, Table S3 in the Supplement). Suspended sediments can limit coral reef productivity by reducing light penetration (Erftemeijer & Lewis 2006, van der Heide et al. 2007, Todd 2008). High sediment loads can also bury coral reefs (Muzuka et al. 2010, Erftemeijer et al. 2012b). More modest sediment loads can also reduce coral energy reserves by creating a continuous demand for sediment clearing by coral polyps and can reduce reproductive success (Brown 1997, Todd 2008, Erftemeijer et al. 2012a). Because reduced sediment loads can benefit coral reefs, the potential for positive interactions will depend on the extent to which mangroves and seagrass plants can trap sediments.

Habitat modification by mangroves and seagrass beds

Sediment trapping is largely a consequence of hydrodynamic energy attenuation, hence physical structure. The extensive root systems of mangroves, along with their pneumatophores and stems, can result in sediment accumulation rates of 0.5 to 10 cm yr^{-1} (Wolanski et al. 1990, Adame et al. 2010). Therefore, the size of the forest may affect the capacity of mangroves to trap sediment. Because a greater amount of structure implies a greater reduction in hydrodynamic energy and more sediment accretion (Bouma et al. 2005), we expect mangrove forests with larger areas to trap more sediment; this results in greater potential for buffering of coral reefs.

Seagrass beds reduce hydrodynamic energy via leaf structure and stem density, which causes sediment deposition and reduced re-suspension (van der Heide et al. 2007). This could reduce sediment load and water turbidity of outgoing tides moving toward coral reefs (Koch 2001).

Positive interactions from mangroves and seagrass beds

From our review, all the mangroves reduced suspended sediment flux concentrations; the trapping capacity of the mangrove ranged from 1 to 90%, indicating large variability (Table S4 in the Supplement, Fig. 3). We realize that this variability can come from sediment fluxes over different time periods, but for simplicity, all data were transformed to g m^{-2} d^{-1} values, even when based on incomplete year cycles, as indicated in Table S4. We found a negative relationship between export/import ratio and area of mangrove forest (p < 0.05, R^2 = 0.7). This indicates that a larger mangrove forest has a greater relative retention capacity. In this analysis, we did not account for changes in fluxes of sediment from currents or increased water volume, which would certainly have an effect on the flux of suspended sediment in the water. Such analysis would require large-scale hydrodynamic modelling and is beyond the scope of this section. In conclusion, mangrove forests could provide a positive interaction with coral reefs via reduction in sediment load; however, further research is required on how the state (degraded or natural) of the mangrove forest could alter its ability to retain sediments.

Seagrass beds showed a reduction in turbidity (18 to 50%) (Hendriks et al. 2008, 2010). It is difficult to
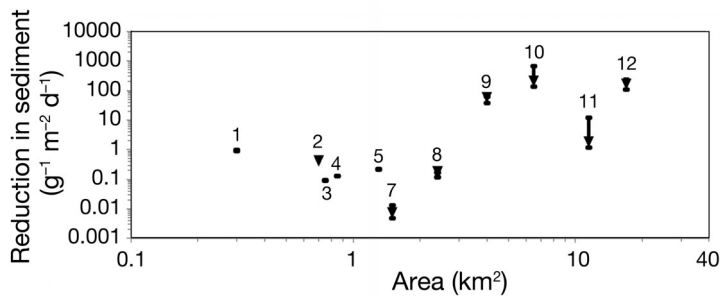
Fig. 3. Oceanward flux of total suspended solids (TSS; g^{-1} m^{-2} d^{-1}) from mangrove forests to the coastal ocean, as a function of mangrove area (km^2). Each line represents a different study, where the highest point is the initial sediment input, and, following the lines in the direction of the arrow, the lowest point represents the exported sediment (see Table S4 in the Supplement). Dash without arrow indicates no difference in imported and exported sediment. The number directly above the line indicates the study number in Table S4

draw firm conclusions because variability between studies is large and the data set is limited. For example, flume studies by Hendriks et al. (2008) show a very large initial concentration of sediment (1576 to 2575 g l^{-1}), which would not show any facilitative effect to coral reefs. Other ecological influences, e.g. local hydrodynamic conditions, nutrient status, disturbance, architecture of the seagrass canopy, resuspension potential and herbivory, are expected to affect the structures of the seagrass bed and therefore the perspective of positive sediment interactions from seagrass beds to coral reefs (Koch 2001, de Boer 2007, Infantes et al. 2009).

Nutrient exchange

Habitat requirements of coral reefs and seagrass beds

Corals reefs in pristine areas can be limited by nitrogen and/or phosphorus (Kuhlmann 1988, Hearn et al. 2001). Three major processes are involved in nutrient acquisition under these circumstances: nutrient depletion of the boundary layer; tight nutrient recycling within the ecosystem; and consumption of particulate matter (Kuhlmann 1988, Hearn et al. 2001, Todd 2008). Seagrass beds can also be limited by nitrogen and phosphorus in pristine areas (Lee et al. 2007) but are adapted to low nutrient availability. Seagrasses access the higher nutrient concentrations in sediment (Terrados et al. 1998) and can use organic sources as a nitrogen source both by trapping organic matter in porous sediment as well as by uptake of dissolved organic matter from the water column (Vonk et al. 2008a). Seagrass beds have

efficient nutrient recycling in the sediment that is enhanced by invertebrates such as burrowing shrimp (Vonk et al. 2008b).

Changes in land use in the last 100 yr have resulted in high nutrient inputs to the coastal seascape (Uriarte et al. 2010). Consequently, many coral reefs and seagrass beds are no longer nutrient limited (Schaffelke et al. 2005, Burkholder et al. 2007). Nutrient loading to seagrass beds, particularly of terrestrially derived nitrogen, has been found to initially increase seagrass productivity and biomass (Lee et al. 2007). However, increased loading for longer periods generally causes a decrease in leaf density and cover, followed by shifts to macroalgae-dominated systems (Burkholder et al. 2007). Many studies of coral reefs have found that high nutrient concentrations have detrimental effects, including growth of macroalgae (Todd et al. 2010), increased occurrence of exotic species (Dubinsky & Stambler 1996) and physiological changes (e.g. in feeding strategies, reproductive abilities and zooxanthellae photosynthesis) (Tomascik & Sander 1985, 1987).

In general, coral reefs have greater exposure to low nutrient ocean water than seagrass beds (Table 1, Table S5 in the Supplement). Because reduced nutrient loads can benefit seagrasses and coral reefs, the potential for positive interactions will depend on the extent to which mangroves (for seagrasses and reefs) and seagrass beds (for reefs) affect nutrient loads.

Habitat modification by mangroves and seagrass beds

The mangrove outwelling hypothesis (Odum 1968, Lee 1995) postulates that detrital export supports adjacent ecosystems and food webs. For example, mangrove detritus has been found up to 3 km away in nearby seagrass beds (Hemminga et al. 1994, Lee 1995, Bouillon et al. 2007). Here, however, we focus on the reverse influence: can mangroves buffer seagrass beds, and possibly even coral reefs, from excess terrestrial nutrients? These forests receive nutrients from a variety of oceanic and/or terrestrial sources (Vilhena et al. 2010). Mangrove ecosystems are biogeochemically complex, with high nutrient processing and outputs by associated fauna (Lee 1995, Kristensen et al. 2008). For example, invertebrates feeding on mangrove particulate organic matter can account for 10 to 80 % of exported carbon (Robertson 1986). Microbial activity has also been found to uti-

lize up to 20% of particulate organic matter, and microbial mineralization, nitrogen fixation and denitrification are significant processes within the nitrogen budget (Kristensen et al. 2008). High rates of biogeochemical cycling within mangrove ecosystems imply that nutrient export will be constrained to that exceeding internal requirements or that which cannot be retained at high discharge or under storm conditions (Boto & Wellington 1988).

Seagrass beds are known to trap and mineralize mangrove particulate organic matter and seston (Bouillon et al. 2007). Seagrass beds export nutrients via leaf shedding — enhanced during strong hydrodynamic events — and via marine herbivore consumption (Hemminga et al. 1994). In pristine seagrass beds, we expect most nutrients to be retained (Vonk et al. 2008b).

Positive interactions from mangroves and seagrass beds

Mangroves have been shown to be able to retain up to 100% of terrestrial nitrogen import (Valiela & Cole 2002), making it important to understand which factors affect mangrove retention. We have collected data regarding nutrient retention in mangrove forests; many of these studies were using very different methods of measurement. To give broad understanding of nutrient retention in mangroves, we compared all these studies, despite the limitations in this analysis. Eight studies (Table S6 in the Supplement, Fig. 4A) reported less export than import of dissolved nitrogen in the water column (N, DIN + DON, TN), indicating a potential facilitative effect to seagrass beds (Table S6, Fig. 4A). Two other studies showed a higher export than import of nitrogen in the water column (Table S6, Fig. 4A). No relationship was seen between mangrove area and retention capacity ($R^2 = 0.1$, $p > 0.05$). This could not be explained by any environmental influence that the authors were aware of for these studies. The same pattern was not seen with respect to fluxes of dissolved phosphorus in the water column (P, TP, DIP + DOP, DOP + PO_4)

(Table S6, Fig. 4B); all studies retained phosphorus. However, there was no correlation between mangrove areas and export/import ratio for phosphorus ($R^2 = 0.1$, $p > 0.05$).

Seagrasses absorb dissolved nitrogen and phosphorus from the water column and sediment porewater, and they export nutrients primarily as organic detritus. All the studies showed seagrass retaining dissolved nutrients in the water column, with retention rates of 5 to 79% for nitrogen and 35% for phosphorus, indicating a large range (Table S7 in the Supplement, Fig. 5). No relationship was seen between the retention capacity for nitrogen and the area of the seagrass beds ($R^2 = 0.1$, $p > 0.05$). In part, this is because the experiments were incubations or flumes, and therefore, the area is not a controlling variable. We did not complete statistics for phosphorus as there was only 1 data point.

Epiphytes also strongly contribute to nutrient retention in seagrass beds. Cornelisen & Thomas (2006) found that seagrass epiphytes absorb 43 to 47% of nitrogen from the water column. If seagrass beds and their associated epiphytes were the only buffer between coral reefs and the land, they obviously would provide an important service in absorbing nutrients, especially in the event of pulse nutrient enrichment. Nutrient-rich conditions in seagrass beds are mainly the result of increased organic matter concentrations (McGlathery et al. 2007). Organic matter addition ex-
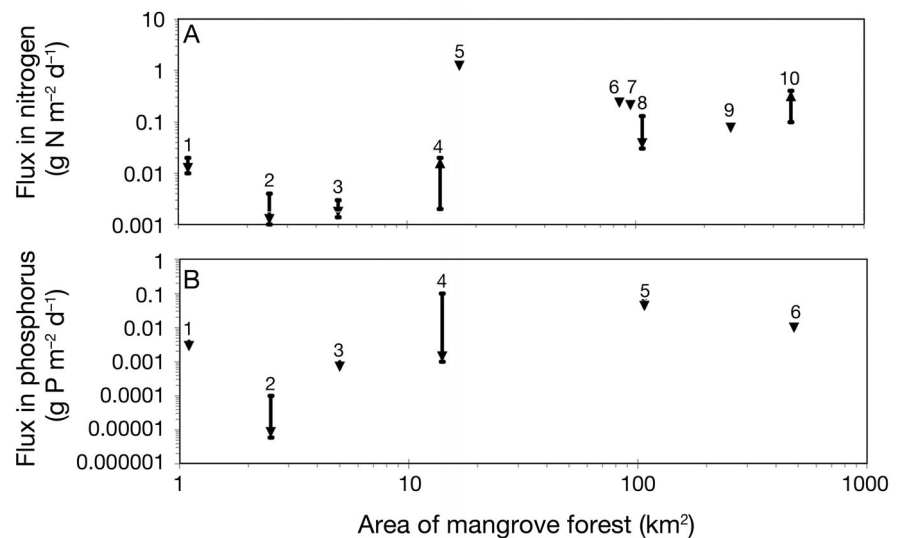

Fig. 4. Fluxes of dissolved (A) nitrogen (g N m^{-2} d^{-1}) and (B) phosphorus (g P m^{-2} d^{-1}) from and within mangroves forests with different surface area (km^2). Each line/arrow represents a different study, where the initial flux is represented by the highest point, and the end concentration flux is indicated by the arrow (see Table S6 in the Supplement). The arrow also shows if the nutrient flux is increasing (facing upwards) or decreasing (pointing downwards). Decreasing fluxes indicate that the mangrove forest is net absorbing nutrients; increasing fluxes indicate that it is net exporting. The number directly above the lines indicates the study number in Table S6
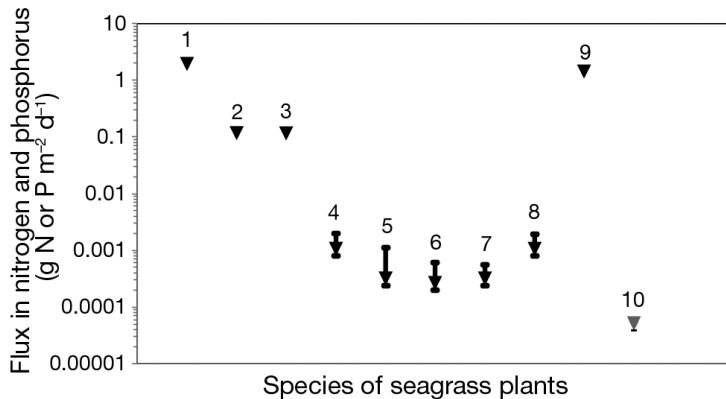
Fig. 5. Reduction of dissolved nitrogen (black) and phosphorus (grey) fluxes (g N or P m^{-2} d^{-1}) via uptake from seagrass plants. Each line/arrow represents a different study, where the highest point is the initial flux; following the arrows down, the lowest point represents the end concentration flux (see Table S7 in the Supplement). Each study calculated a different percentage change of nutrient uptake for a given species of seagrass bed, which we re-calculated to a flux; the number directly above the lines correlates with the study number in Table S7. Studies 1 & 2 refer to *Cymodocea* sp., Study 3 is a *Halodule* sp., Studies 4 & 5 refer to *Posidonia* sp., Studies 6–8 refer to *Thalassia* sp., and Studies 9 and 10 are both *Zostera* sp.

periments have shown a decline in above- and below-ground biomass (20 to 50%) due to plant mortality and greater leaf abscission (Perez et al. 2007). The resulting increase in particulate organic matter, along with sediment destabilization, would likely lead to greater export to mangroves or coral reefs under these conditions. Note that reduced aboveground biomass will reduce the potential of seagrass to attenuate hydrodynamic energy and to retain sediment.

Organism exchange

Increased densities of algal consumers can affect coral reefs and seagrass beds

As noted earlier, corals and seagrasses require relatively high light levels and are adapted to low nutrient conditions. In nutrient-rich environments, they can be overgrown by algae and epiphytes, which may compete for light (Ralph et al. 2007, van der Heide et al. 2007). For example, Heck & Valentine (2006) showed that seagrass declined due to surface epiphyte overgrowth following nutrient enrichment. The latter was especially problematic when no epiphytic grazers were present, as grazers can reduce epiphyte biomass by up to 30% (Neckles et al. 1993). Moreover, a small increase in grazing can result in a substantially greater resilience of coral reefs (Mumby & Hastings 2008, Berkström et al. 2012). Algivores (e.g. some spe-

cies of juvenile butterflyfish, goatfish, surgeonfish and parrotfish) can thus play a major role in maintaining the vigour of coral reefs and seagrass beds (Neckles et al. 1993). Thus, the presence of adjacent ecosystems may have facilitative effects on another ecosystem by enhancing populations of mobile algivores and thereby algal consumption. Piscivores/invertebrate feeders can also utilise all 3 systems as juveniles; 17 to 59% of these predator fishes use seagrass beds and mangrove reefs as nursery areas (Berkström et al. 2012). The predatory species can affect the stability of coral reefs via reduction of prey species such as sea urchins, starfish and gastropods, which can in large numbers cause bioerosion on stony corals (Berkström et al. 2012). However, based on available data, we will consider this question mainly for parrotfish, which are regarded as predominantly algivores with positive effects on seagrass and corals.

Positive interactions from mangroves and seagrass beds by enlarging algal consumer populations

Several studies in Tanzania and the Caribbean have shown increases in density of parrotfish when coral reefs were adjacent to mangroves and seagrass beds (Nagelkerken & van der Velde 2002, Dorenbosch et al. 2006); for example, parrotfish density increased >95% in Curaçao compared to coral reefs isolated from the other 2 systems (Fig. 6). The increased density of parrotfish for co-occurring ecosystems indicates a potential facilitative relationship for coral reefs and seagrass beds, as the fish can reduce algal loading via herbivory. Mumby et al. (2004) also found an increased biomass of reef fish when coral reefs were near to abundant mangroves, compared to coral reefs with few or no mangroves. Mangrove forests, seagrass beds and coral reefs are distributed across incremental depths from the land to the open ocean, and significant ontogenetic transfers from one ecosystem to another (i.e. juveniles to the shallows, mature organisms to the deep) (Kimirei et al. 2013) may occur in addition to transfer with daily tides (Forward & Tankersley 2001) and diurnal movements (Krumme 2009). With respect to the nursery function of adjacent ecosystems, Mateo et al. (2010) demonstrated that distance is not necessarily the primary influence on the origin of juveniles and that distance effects can be species-specific. Recent laboratory and *in situ* studies also find that juveniles of some fish
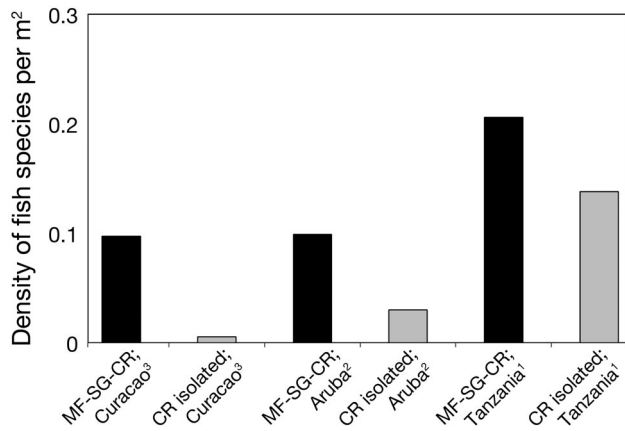
Fig. 6. Three examples of the positive effect of the co-occurrence of coastal ecosystems (MF: mangrove; SG: seagrass; CR: coral reef) on the density of parrotfish measured at the coral reef. MF-SG-CR indicates mangrove forests, seagrass beds and coral reefs occurring in close proximity (black columns); CR alone denotes coral reefs that have no other ecosystems nearby (grey columns). Data from [1]Dorenbosch et al. (2005), [2]Dorenbosch et al. (2007), [3]Nagelkerken et al. (2002)

species show strong preferences for specific habitats (Grol et al. 2011); this indicates that any potential for positive interactions would depend on a blend of species, distance and habitat types. Overall, it is clear that inland mangrove and seagrass bed areas form an important nursery habitat for parrotfish (Nagelkerken 2009) and that mangrove forests or mangrove-seagrass systems contribute high fractions of the populations of various reef fish species (Nagelkerken et al. 2002). Nursery or spawning areas in adjacent ecosystems may have lower predation risks for juveniles, which might explain why coral reefs close to nursery or spawning areas show enhanced species diversity or secondary production (Dorenbosch et al. 2004, Mumby et al. 2004, Nagelkerken 2009).

INTERACTING EFFECTS BETWEEN MULTIPLE FLUXES

The majority of previous studies have investigated single connections between systems (Hemminga et al. 1994, Bouillon et al. 2007, Nagelkerken 2009). We argue that multiple fluxes need to be taken into account in evaluating the importance of adjacent ecosystems. However, such multiple environmental factors may interact and thereby result in responses that differ from what would be expected based on a single factor. However, interactions between multiple fluxes are still too poorly studied to fully account for all in-

teractions within this perspective. It is clear that certain exchanges are likely to co-occur (e.g. high hydrodynamic energy and turbidity) (de los Santos et al. 2010). Wolanski (2007) showed that physical and chemical parameters are often linked to biological aspects of ecosystems. In the case of mangrove forests, the physical structure of mangroves will influence outwelling and consequently offshore fisheries.

Combining 2 factors may cause different types of interactions: synergistic, antagonistic and independent (de los Santos et al. 2010, La Nafie et al. 2012). A clear example of one exchange fully overruling a second exchange was shown by de los Santos et al. (2010), who demonstrated that light availability (related to turbidity) was much more important for seagrass health than changes in hydrodynamic energy. In contrast, La Nafie et al. (2012) showed that waves and high nutrient loads jointly decrease the survival but separately affect morphological and biomechanical properties of the seagrass *Zostera noltii*. Recent work has also shown that herbivores will limit the establishment of algae, in turn limiting sediment accumulation (Rasher et al. 2012). All of the factors mentioned above (light availability, hydrodynamic energy, nutrient loads, herbivore numbers and sedimentation) are critical for the growth and establishment of these ecosystems.

We have concentrated on the positive interactions, but there could be negative interactions as well. Fluxes leading to negative direct effects may have a positive indirect effect. For example, increased nutrient fluxes to coral reefs or seagrass beds, with negative effects due to eutrophication, may cause increased herbivore numbers, a positive effect. Some species of parrotfish *Leptoscarus vaigiensis* are known to only feed on seagrass leaves (Gullström et al. 2011). Thus, an increase in numbers for this specific herbivore because of proximity to a coral reef may cause a decrease in seagrass biomass and be therefore classified as a negative interaction. Furthermore, these potential negative interactions may be cancelled out, e.g. mega-herbivore grazing (green turtle) has been shown to increase seagrass tolerance to eutrophication (Christianen et al. 2012), and fish herbivore grazing has been shown to increase shoot density (Valentine et al. 1997, Heck & Valentine 2006). These simple examples illustrate the complexity of these ecosystems and how fluxes in both positive and negative interaction can have results not explicitly considered.

Obtaining a better understanding of multiple flux interactions is of vital importance for the future. Global climate change combined with anthropogenic

influences is likely to cause simultaneous changes in multiple factors in the near future and, as highlighted in the present perspective, the disappearance of one ecosystem can cause simultaneous changes in multiple fluxes with adjacent ecosystems.

PERSPECTIVES: LANDSCAPE FACILITATION?

The idea of facilitation is generally considered in ecological community theory (Bruno et al. 2003). The importance of the idea of facilitation or positive interaction in community ecology raises the question of whether this concept can be used as an analogy at the landscape level. Where ecosystems in close proximity are connected by flows of energy, materials and organisms, 3 minimal requirements must be met for landscape-scale positive interactions to occur. First, there should be a sufficiently large exchange between the systems of a relevant resource, such as nutrients, sediment, energy or organisms. This requires the systems to be close enough spatially, relative to the typical length scale governing dispersal and exchange mechanisms. Second, exchanges must have the potential to be beneficial to at least one of the systems, donor or recipient. Systems must either have a requirement for a specific resource or must be dependent on the stress-buffering capacity of another system. Third, the requirement for alteration in resources suggests that substantive ecosystem engineering by some species may well play an important role in landscape-scale facilitation. However, it is clear that only those ecosystems that cause a clear change in resources and/or stresses are relevant to consider and that such ecosystems may be expected to often contain strong ecosystem engineers.

This exploration of positive reciprocal interactions for mangrove forests, seagrass beds and coral reefs indicates a potential for landscape facilitation. We have shown that these systems show an exchange of relevant resources (nutrients, sediment, energy or organisms), that these exchanges can be beneficial to donor ecosystems (via sediment/nutrient buffers, wave reduction and nursery areas) and that a potential requirement is that ecosystem engineers are a substantial component of the donor or receiving systems (e.g. mangrove trees, seagrass plants and stony corals). Progress has been shown with regard to species interactions (Altieri et al. 2010) and more recently within habitat interactions (Thomsen et al. 2010) at the small scale; follow-up work should upscale and investigate multiple connections at the ecosystem scale. To our knowledge, quantitative analyses are typically only measured for single rather than multiple exchanges and more often for directional than reciprocal exchanges. Fortunately, interest in this type of research is gaining ground from the ecosystem services perspective (Barbier et al. 2008).

CONCLUSIONS

In the present review, we found that the changes in fluxes (wave height, sediment/nutrient and organismal exchange) will be vital for (1) establishment of foundation species and (2) when ecosystems are already under stress from eutrophic or natural affects. We acknowledge that threshold conditions may have already been surpassed before the interaction of the donor ecosystem. In many countries, these 3 ecosystems are managed by different entities. To ensure effective management, a more coordinated approach is required (Berkström et al. 2012). A priority should be ecosystem-based management (EBM), which is considered the most holistic approach to managing ecosystems (Mora et al. 2006, McLeod & Leslie 2009, Wilkinson & Salvat 2012). At present, it is highly speculative to generalize about the universal importance of ecosystem-level facilitation at the tropical coastal seascape. However, we suggest that the potential for the process is large and moreover that it may have substantial management implications.

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