Buried Alive or Washed Away

The Challenging Life of Mangroves in the Mekong Delta

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Mangroves encroaching on mudflats
in the Mekong Delta, Vietnam.

ABSTRACT. Mangroves colonize tropical shorelines, protecting coastal communities and providing valuable ecosystem services. Mangroves associated with deltas cope with a very dynamic environment characterized by strong gradients in salinity, deposition triggered by sediment inputs, and erosion caused by waves and currents. Mangroves are adapted to this ever-changing landscape, with different species colonizing different elevations in response to inundation frequency. A series of feedbacks between hydrodynamics, sediment transport, and mangroves was observed in a fringe forest of the Mekong Delta, Vietnam. *Sonneratia* spp. rapidly encroach upon sandy areas because the stable substrate favors seedling establishment. In contrast, fewer seedlings are present in muddy locations where currents and waves frequently rework the bottom. Along muddy shorelines that are eroding, turbulence increases local scour near roots and trunks, undercutting the trees. Enhanced sediment accumulation due to delta progradation can smother the mangrove roots and lead to forest dieback. We find clear evidence that mangroves affect both hydrodynamics and sediment transport, thus engineering the landscape and enhancing sediment trapping and delta progradation. *Sonneratia* spp. are replaced by *Aegiceras corniculatum, Avicennia marina,* and *Nypa fruticans* when the seabed becomes high enough, indicating that ecological succession is present in a fast prograding deltaic environment. Thus, it is imperative to determine the small-scale feedbacks between mangroves, hydrodynamics, and sediment transport in order to build quantitative ecogeomorphic models of deltaic sedimentation that can be used to explain the distribution of mangrove species, the forest structure, and large-scale dynamics in a tropical deltaic setting.

INTRODUCTION

Mangroves can withstand inundation and high levels of salinity; as a result, they colonize many tropical shorelines, providing valuable ecosystem services. Complex aerial root systems or vertical pegs (pneumatophores) allow aeration of the roots even when the soil is submerged by tens of centimeters, thus allowing the mangrove trees to survive where other terrestrial plants cannot.

Mangroves enhance the resilience of coastal communities. They stabilize the shoreline, reducing erosion by waves and currents. They can also mitigate the devastating effects of tsunamis, thus protecting human dwellings, infrastructure, and agriculture. Recent studies show that mangrove soils store large quantities of organic material and therefore carbon, thus possibly offsetting anthropogenic carbon dioxide emissions and mitigating global warming (Alongi, 2012). Finally, mangrove forests provide habitat for many fish and other animal species, especially in juvenile stages,

which contributes to the world's biodiversity. In particular, the mangroves in the Mekong Delta, Vietnam, are a biodiversity hotspot. Unfortunately, mangrove forests are rapidly disappearing, mostly due to land reclamation, with conversion of these important ecosystems to shrimp ponds and agricultural fields. Between 1980 and 2000, the global area of mangroves decreased by about 35% (Valiela et al., 2001). Among the most threatened mangrove forests are those bordering large tropical deltas in Asia, such as the Mekong Delta in Vietnam, the Ganges Delta in India and Bangladesh, the Ayeyarwady Delta in Myanmar, and the Indus Delta in Pakistan (Alongi, 2008). Anthropogenic pressure is intense in these densely populated areas because more agricultural land is needed to feed increasing populations. Yet, mangroves are necessary for delta stability and shoreline protection, inspiring a series of restoration projects aimed at reintroducing mangrove forests or increasing their footprints (e.g., Schmitt et al., 2013).

Deltaic shorelines are dynamic environments, with sediment accumulation and shoreward expansion fueled by massive sediment loads carried by large rivers. This contrasts with shoreline erosion caused by waves and currents in other areas. This ever-changing landscape strongly impacts the establishment and survival of mangroves and affects the long-term evolution of fringe forests and their resilience to tropical cyclones and sea level oscillations. Understanding the feedbacks between mangroves and sediment dynamics in a tropical delta is therefore critical for the preservation and restoration of these delicate environments. By controlling shoreline stability, mangroves also determine the evolution of entire deltas, which nowadays are inhabited by millions of people and are threatened by sea level rise and reduced sediment inputs due to trapping by dams (Allison et al., 2017, in this issue).

Here we describe the dynamics of a fringe mangrove forest in the Mekong Delta, Vietnam, with particular emphasis on the feedbacks between vegetation and sediment dynamics. The study area is the mangrove fringe of the island of Cu Lao Dung, located at the mouth of the Song Hau (Bassac) River, one of the main distributaries of the Mekong Delta (Figure 1). Parts of the mangrove forest were converted to shrimp ponds and sugar cane fields, triggering erosion by waves, so more mangroves were planted in the 1980s to protect the shoreline. Sediment accumulation and delta progradation favored the expansion of the mangrove fringe, whose width reached 1 km in 2015 (Nardin et al., 2016a). The pioneer species *Sonneratia caseolaris* was planted at the shore, and other typical Southeast Asian mangrove species have colonized parts of the fringe with high bottom elevations. Currently, *Avicennia marina*, *Aegericas corniculatum*, and *Nypa fruticans* can be found in the interior parts of the fringe (Figure 2).

MANGROVE ZONATION

The presence of distinct vegetation species at different elevations or at different distances from the shore is typical of mangrove forests. There is a complex interplay between elevation, inundation regime, and geomorphic history of a site and the succession history and zonation of a mangrove forest. Although well understood in marsh environments, why zonation occurs in mangroves is still subject to debate.

Vegetation zones represent the range of possible physical conditions in which each mangrove species can thrive, as well as reflect competition effects. Early studies on mangrove zonation were based on the concept of vegetation succession, with pioneer species particularly adapted to surviving long periods of immersion and colonizing tidal flats or sand bars at the shore (Davis, 1940). The concept of succession is that a pioneer species modifies its environment to allow the establishment of secondary species. In an environment where the dominant control is inundation, succession is possible if pioneer species modify the water depth to reduce inundation times. The pioneer species accomplish this by promoting sediment accumulation that results in accretion and land building. When seabed elevations are high enough, new species that can only survive with shorter inundation periods replace the pioneer species. As a result, zonation is simply the expression of different stages of mangrove forest development. Mature forest starts at low elevation with pioneer species and higher inundation periods; vegetation composition changes several times during accretion until a vegetation cover typical of present bottom elevation is reached.

Today, many ecologists question the concept of mangrove succession, mostly because there is evidence in some places that mangroves merely adapt to the landscape without modifying it to favor the encroachment of new species (Lugo, 1980). Moreover, in many mangrove locations, sediment cores do not record the presence of pioneer species at lower elevations. Recent hypotheses for mangrove zonation rely on gradients in physiochemical soil properties, which relegate each species to a particular range of elevations (McKee, 1993); on competition among species that relegates outcompeted species to lower and less favorable locations (Ball, 1980); and on dispersal and sorting of mangrove propagules (Rabinowitz, 1978).

One important shortcoming of several ecological studies on mangrove evolution is the lack of geomorphological context (i.e., how a particular coastal location has evolved in time and what the implications are for mangrove establishment). For example, the concept of vegetation succession can only be applied to a system with substantial sediment availability that allows sediment accumulation at the shore. This situation is typical for the delta of a large river, such as the area studied herein. Conversely, a stable shoreline with limited sediment deposition or erosion does not favor a shift in vegetation cover and succession, because the underlying landscape does not change to allow variations in inundation regime. Therefore, coupling ecology and geomorphology in an ecogeomorphic framework (see Box 1) is essential for correct understanding of mangrove zonation and forest dynamics. Morphodynamics in fact regulate the evolution of the landscape and therefore the bottom elevations, which have been established as an essential control on hydroperiod and vegetation zonation. Thus, we should expect a mangrove forest colonizing a prograding (i.e., land-building) system to be different from a mangrove forest along a stable shore or in an area subject to erosion and shoreline regression. Yet, many ecological studies fail to determine the geomorphic shoreline conditions of the sites under investigation.

One of the pioneering works on the coupling between geomorphology and mangrove zonation was done by Thom (1967), who studied the Grijalva-Usumacinta Delta of Mexico. He showed that different landscape units of the delta, such as active lobes, levees of distributary channels, or abandoned deltaic lobes, were characterized by specific assemblages of mangrove species that were affected not only by local soil characteristics and elevations but also by the morphological evolution of the system. While it was the first to introduce the link between geomorphology and mangrove ecology, this

FIGURE 1. Evolution of the mangrove forest on the island of Cu Lao Dung, Mekong Delta, Vietnam, from 1984 to 2012 determined from Landsat images. The mangrove forest was converted to shrimp farms and sugarcane fields while a new forest developed at the shoreline due to sediment accumulation from the Song Hau River.

study did not identify nor quantify the physical mechanisms that affect specific mangrove species and regulate their spatial distribution. A process-based characterization of the feedbacks between hydrodynamics, sediment transport, edaphic conditions, and vegetation is necessary in order to apply the same scientific framework in different systems with disparate environmental conditions. This characterization is also needed for building models that investigate the long-term evolution of mangrove shorelines under a variety of scenarios, including accelerated sea level rise and reduced sediment availability. Such conceptual and numerical models are instrumental for understanding the vulnerability and resilience of salt marshes, ecosystems that are equivalent to mangroves but that live in temperate areas where mangroves cannot survive (Fagherazzi et al., 2012).

SEEDLING ESTABLISHMENT AND WINDOW OF OPPORTUNITY

A critical stage during the initial growth of a pioneering species in the deeper, more inundated zones is seedling establishment. Conditions surrounding establishment can be so adverse that this early stage can easily become a "bottleneck" to expansion (Friess et al. 2012). Most mangroves are viviparous, with seeds germinating while still attached to the parent plant. Propagules are then dispersed in the water, drifting by the action of tides and currents until reaching a location suitable for establishment. Recent results have shed light on the feedbacks between seedling establishment, local hydrodynamics, and sediment-transport processes. Balke et al. (2011) introduced the concept of window of opportunity—a lull between storms that rework the bottom sediments during which pioneer mangroves can establish. They in fact show that seedlings of *Avicennia alba* need to have roots sufficiently long to withstand moderate hydrodynamic forces and even longer to survive sediment erosion during energetic events. A mature mangrove tree can survive such adverse hydrodynamic and
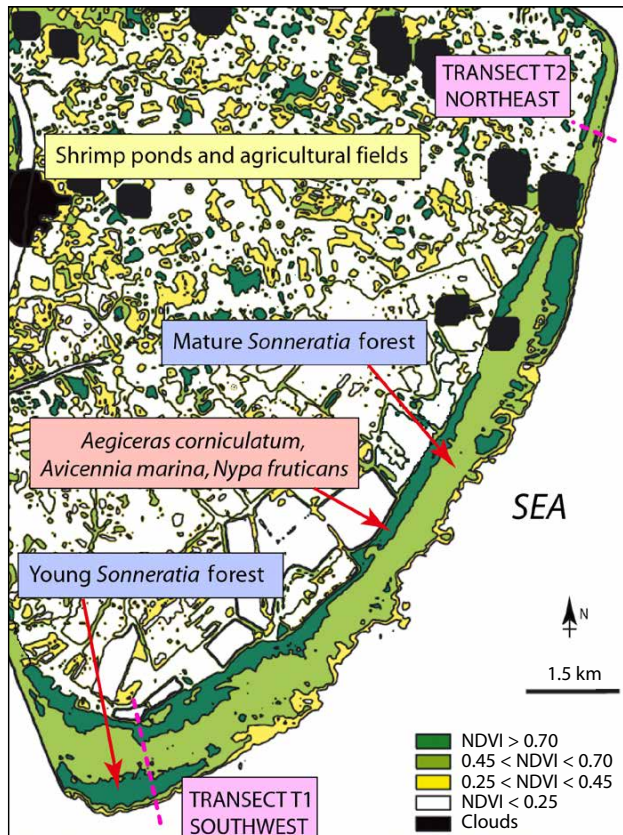

FIGURE 2. Distribution of the Normalized Difference Vegetation Index (NDVI) in the mangrove fringe forest of Cu Lao Dung. High NDVI values indicate either young *Sonneratia* trees encroaching on the tidal flats or secondary mangrove species (*Aegiceras corniculatum*, *Avicennia marina*, and *Nypa fruticans*) colonizing the interior forest at higher elevations. *Adapted after Nardin et al. (2016a)*

BOX 1. ECOGEOMORPHOLOGY

Ecogeomorphology is the study of the interactions between organisms and the development of the landscape. The emergence of life has affected Earth's surface immensely, and has left a distinct footprint in the landscape. It is widely accepted that vegetation strongly influences water and sediment transport, thereby influencing rock weathering, hillslope evolution, and fluvial/aeolian dynamics, among other processes. Animals have also been shown to influence Earth's morphology from the plot to the landscape scale. Conversely, the landscape and the processes that shape it have a great impact on biota. Research results in this area increasingly find their way into restoration projects. Despite these advances, our conceptualization and quantification of the processes, rates, and feedbacks between geomorphology and ecology is still limited. This lack of information is especially true for remote systems strongly affected by a changing climate, for instance, mountainous environments, deserts, and wetlands. Animals and plants influence geomorphic processes in a wide range of ways. For instance, plants with their roots and litter prevent soil erosion; biochemical compounds generated by vegetation increase the chemical weathering of bedrocks; trees can reduce possible landslides by stabilizing the underlying soil; and marine biota could cause the erosion of coral reefs. Dramatic changes in ecosystems and landscapes may drive the environment to diverse configurations through complex ecogeomorphological feedbacks.

Mangrove environments are among the most productive yet vulnerable intertidal ecosystems in the world. In coastal areas, mangroves are essential for erosion prevention, nutrient cycling, and habitat provision. However, in the Mekong River delta (Vietnam), where the sediment supply is great, positive ecogeomorphological feedbacks, such as sediment deposition, might drive the mangrove forest to collapse. In fact, rapid formation of cohesive sediment deposits can bury mangrove roots and lead to large-scale dieback.

erosive conditions, so there is a window of opportunity during which the mangroves can establish and grow strong enough to withstand subsequent disturbances.

These novel results are the first to link mangrove establishment to geomorphic processes by quantifying under what physical conditions mangroves can survive during early stages of development. Clearly, these feedbacks between mangrove physiology and physical disturbance have the potential to affect the large-scale evolution of entire mangrove fringes. Here, we will apply these concepts to the mangroves of Cu Lao Dung (Figure 2), generalizing the results for a prograding delta. Moreover, we will show that sediment dynamics and geomorphic processes affect not only mangrove establishment but also mangrove survival and zonation.

ECOGEOMORPHOLOGY AFFECTS LARGE-SCALE MANGROVE ENCROACHMENT IN A PROGRADING DELTA

Avicennia alba and *Sonneratia alba* seedlings (the latter grow in the Mekong Delta fringe) are sensitive to erosion during early establishment; they can only establish if the bottom substrate is stable. Balke et al. (2013) indicate that as little as 1–3 cm of vertical erosion can result in seedling failure. In addition, if a storm that produces strong currents hits the mangroves, the seedlings dislodge (Balke et al., 2011). Once established, mangroves grow and become more resistant to both erosion and currents. The concept of window of opportunity is supported by extensive laboratory and field measurements at a small scale (i.e., by studying the fate of single seedlings under different

disturbances). The question is whether this mechanism can affect the large-scale dynamics of an entire mangrove fringe. Field measurements along Cu Lao Dung show that a dense mangrove forest mostly formed of saplings has encroached upon the tidal flats in the southwest area, while large mature trees with few seedlings characterize the northeast fringe (Figure 3).

We ascribe this difference to bottom characteristics, with sandy sediments in the southwest providing a relatively stable substrate for mangrove expansion, while waves and currents erode the soft, muddy bottom of the northeast fringe, thus preventing establishment. This observation was corroborated by placement of erosion pins that showed erosion of less than 1 cm between September 2014 and March 2015 in the southwest area and 17 cm in the northeast.

The encroachment of mangroves and the differing erosion regimes along the fringe can be explained by the large-scale sediment dynamics of the Mekong Delta. During the high-flow monsoon season (July to October), the Song Hau River discharges large volumes of sediments in the nearshore. These sediments are stored on tidal flats and sand bars in front of river mouths and on the shelf (Eidam et al., in press), and then reworked by energetic storms that occur during January to April, when strong winds coming from northeast trigger large waves and longshore currents toward the southwest (Tamura et al., 2010). As a result, sand preferentially accumulates in front of the southwest fringe, forming shallow sand ribbons or aprons that in time merge with the shore and provide an ideal habitat for forest expansion. Fricke et al. (in press) used core records and ^{210}Pb geochronology to measure accumulation rates of 3–5 cm yr^{-1} at the front of the southwest fringe but only 1–3 cm yr^{-1} at the front of the northeast fringe during the past century. These observations are supported by spring-neap measurements of sediment fluxes that show sediment transport away from the northeast area and toward the southwest fringe.
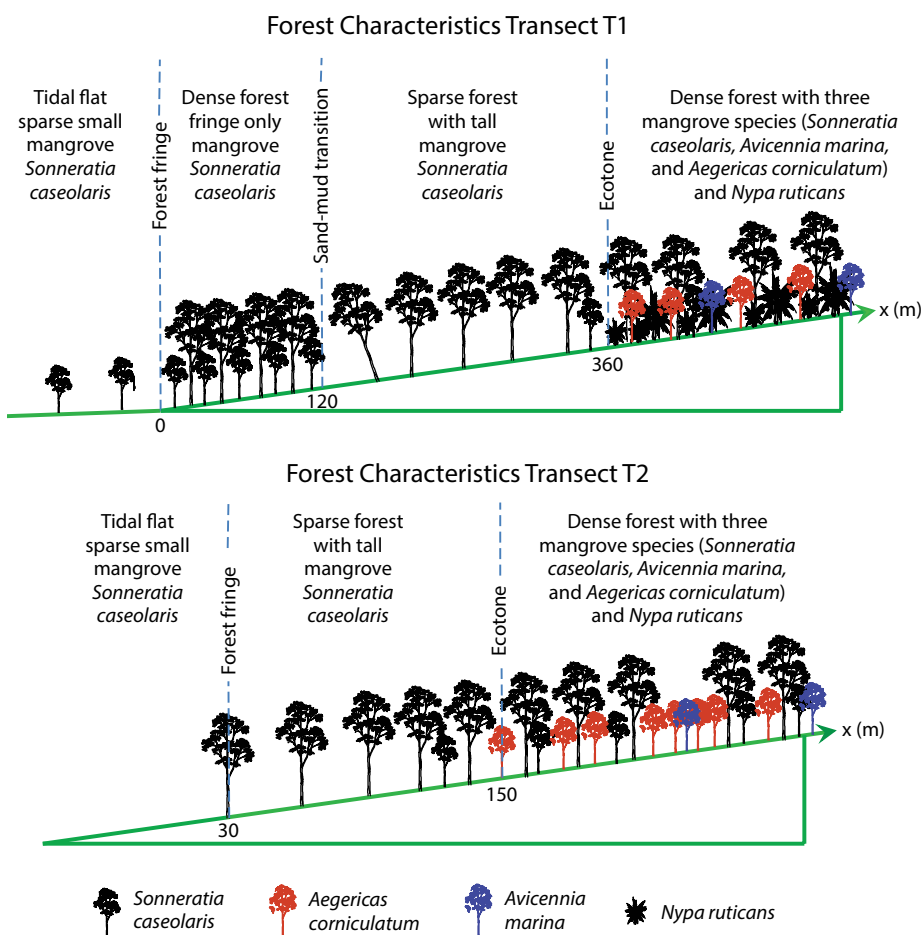

FIGURE 3. Distribution of vegetation species along two transects perpendicular to the forest boundary on Cu Lao Dung. The location of the transects is indicated in Figure 2. *Adapted after Nardin et al. (2016b)*

Sand deposits can also be moved inshore and emplaced during large and infrequent storms, forming shallow ridges typical of chenier plains (Tamura et al., 2010). The larger grain sizes of these sand deposits mean that they are relatively stable and can be remobilized only during infrequent storms, thus providing a long enough window of opportunity for mangrove encroachment. In the northeast, soft muddy sediments are instead deposited during calm weather conditions and partly eroded by waves during storms, creating large seasonal oscillations in bottom elevations that do not facilitate vegetation establishment. Sediment dynamics and the related response of the vegetation dictate the evolution of the entire fringe, with mangroves expanding and recruiting along the southwest sandy fringe while slightly contracting along the northeast muddy fringe. As a result, the shoreline is undergoing asymmetric progradation, with a wider fringe in the southwest (see Figure 1). A forest and bottom sediment survey carried out by Nardin et al. (2016b) in 2015 reports a significant positive correlation between percent of sand in bottom sediments and density of *Sonneratia* trees in the fringe forest. Moreover, remote-sensing color measurements show that the southwest forest is younger and faster growing, displaying a higher Normalized Difference Vegetation Index, or NDVI (Figure 2, see Nardin et al. 2016a).

## MECHANISMS OF SEDIMENT TRANSFER IN THE FOREST

It is not clear from the existing literature whether mangroves modify the landscape by favoring accretion and land building, or whether they respond passively by expanding into areas where the seabed is already accreting (e.g., Swales et al., 2015). If mangroves promote sediment accumulation, then the concept of succession could be applied to explain mangrove zonation along some shorelines. Recent high-resolution measurements in the Mekong Delta clearly show that the pneumatophores of *Sonneratia*

trees increase bottom drag (Mullarney et al., in press) and rates of turbulent dissipation (Norris et al., in press), possibly slowing the flow and creating suitable conditions for sediment deposition. At the same time, eddies detaching from the pneumatophores can lead to highly localized erosion near the roots. Moreover, waves are strongly dissipated in the forest fringe, thus reducing their erosive force (Massel et al., 1999; Henderson et al., in press). These effects of the vegetation canopy on hydrodynamics likely influence sediment transport and erosion/deposition patterns (Mullarney et al., 2017, in this issue). In the same forest fringe studied herein, Fricke et al. (in press) measured an accumulation rate of 5.1 cm yr⁻¹ in the forest interior and a rate of 3.0 cm yr⁻¹ near the boundary with the ocean. Other studies using sediment traps show that most sediment reaches the fringe environment (Adame et al., 2010), at least for temporary deposition. Clearly, evolution of the fringe depends critically on feedbacks between the vegetation-trapping ability and morphodynamic processes, the detail of which is more easily described by reviewing the processes that dominate a cross-shore

transect stretching from the unvegetated tidal flats to the landward edge of the mangrove forest (Figure 3).

In principle, the change of morphology along such an intertidal transect is controlled by the average, over many tidal cycles, of the subtle balance between erosion and deposition at each cross-shore location. Erosion will occur when the flux of sediment into a location is smaller than the flux out of that location, and deposition will occur during opposite conditions. A sediment flux can either be generated by advection from tidal currents or diffusion from eddies of suspended sediment in the water column (Figure 4). Therefore, the shape of the intertidal zone that ultimately evolves can be inferred by examining the processes that control the size of ebb and flood currents, and the processes that control the timing and magnitude of sediment suspension.

When only tidal currents are present, we can expect a convex profile to develop, where the water depth decreases quickly at the outer limit of maximum inundation, then more slowly near the upland. This profile forms firstly because tidal currents tend to be flood-dominated and secondly because they diminish
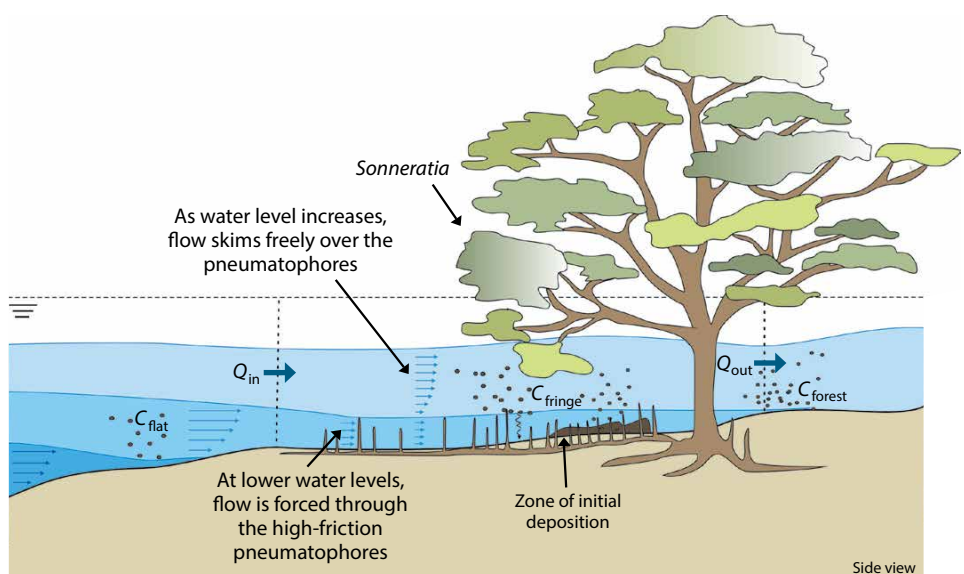
$(C_{flat} - C_{fringe}) \times Q_{in} < (C_{fringe} - C_{forest}) \times Q_{out}$ Erosion within fringe and increased supply to forest
$(C_{flat} - C_{fringe}) \times Q_{in} > (C_{fringe} - C_{forest}) \times Q_{out}$ Accretion within fringe and reduced supply to forest

FIGURE 4. Fluxes of sediments between ocean, mangrove fringe, and interior forest. Sediment flux across a boundary (e.g., vertical dashed line) is the product of sediment concentration C and water discharge Q.

shoreward due to the increased effect of friction as the water shallows (enhanced by the effect of vegetation). Therefore, sediment is not only more likely to suspend on the seaward extreme of the profile, it is also more likely to be transported landward rather than seaward.

To understand the conditions under which a concave profile might develop, we need to explore the effect of short-period waves, which can completely reverse the shoreward transport of sediment that accompanies tides in isolation. Short waves attenuate abruptly in the water column, so they do not affect the bottom if the water is very deep. Therefore, if wind waves are dominant, it is quite possible for the seaward ebb-tidal currents to carry much greater suspended loads than the flooding currents. This occurs even though the currents can have the same velocity, because the ebbing tide carries sediment that has been suspended by wind waves in the very shallow regions. In this case, sediment tends to be scoured from very shallow water, leading to a characteristic concave profile.

Similar considerations apply within estuaries (Hunt et al., 2015).

The differences in opinion on whether or not mangroves favor sediment deposition (e.g., Swales et al., 2015), and ultimately determine the shape of the profile, stem largely from the wide variations in density of structures near the seabed. First principles suggest that the role of mangrove vegetation in controlling the evolution of the morphology is twofold. First, vegetation dissipates wave and tidal currents, therefore increasing the natural effect of friction on diminishing tidal currents shoreward. Second, the vegetation provides a protective cover to the seabed so that the currents skim over the root structures (Figure 4) and are unable to entrain sediments beneath. In these cases, currents flowing from the more shallow vegetated areas may have less suspended sediment than flooding currents. Therefore, a convex profile should develop in the presence of vegetation because the flooding currents, and sediment loads they carry, should be enhanced. Indeed, the abrupt decrease

in intertidal slope that accompanies the onset of vegetation provides evidence of a change to much more accretionary conditions (e.g., examples provided in Lovelock et al., 2010, and in Vo-Luong and Massel, 2008)

However, much of our thinking about the role of vegetation in accretion comes from our understanding of salt marshes with very dense vegetation located in areas assumed to be entirely depositional. Surprisingly, at lower mangrove densities, the vegetation structures can increase the water-column turbulence so much that the eddies generated at the shear layer on top of the root structures can penetrate the vegetation (Mullarney et al., 2017, in this issue) and cause enhanced stirring at the bed that can largely compensate for the reduced current velocities. Laboratory experiments by Tinoco and Coco (2016) and later by Yang et al. (2016) show that the range of densities over which this stirring effect might be important is characteristic of mangroves, particularly fringing forest mangroves. Such an erosive fringing effect might explain the initial mound that often forms landward of mangrove roots. In fact, the fringing root structure causes local scouring, and the resulting sediment is immediately deposited where the currents flow into the denser vegetation. Our personal observations in the Mekong Delta also show that wind waves break at the seaward fringe as they interact with the high-friction pneumatophores, which would also contribute to a region of scour.

Mature mangrove trees are also subject to sediment dynamics. In the northeast part of our study area, the trunk and pneumatophores of *Sonneratia* spp. enhance water turbulence, producing local scour. Here, the entire substrate is slowly eroding and the fringe is retreating in time (Nardin et al., 2016a). If the bottom is muddy, local scour near the trunk and the root zone undermines the tree, which can eventually fall (see Figure 5c). Scour near the trunk is only present if the substrate is muddy; in a sandy substrate, a sediment mound forms near the trunk (Figure 6).
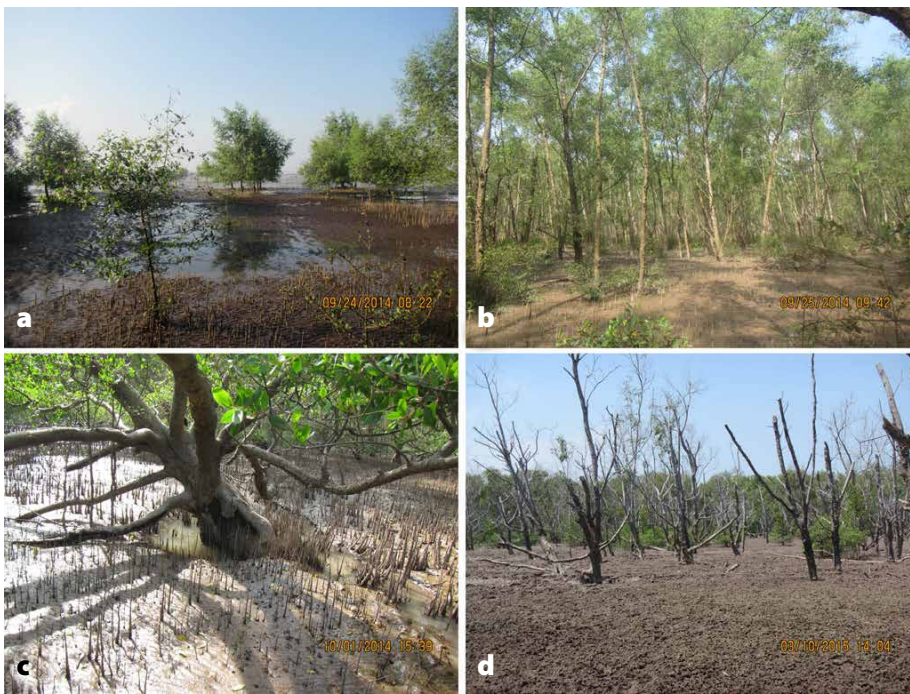

FIGURE 5. Examples of interactions between *Sonneratia caseolaris* trees and sediment dynamics. (a) Young forest fast encroaching upon a sandy tidal flat. (b) Mature forest in the fringe interior. (c) Mangrove tree that fell because of scour below the roots and the trunk. (d) Forest dieback caused by sediment burial.

Although not so well studied, the frictional effect of vegetation can also alter the shape and propagation characteristics of the tidal wave. Any nonlinear term within the momentum equations (which are essentially Newton's laws of motion applied to water) can cause transfer of energy and momentum from the main tidal wave to higher period harmonics. When combined with the main wave, this mechanism makes the wave more "sawtooth" in shape, with a steeper landward face. This can be explained by the crest (under which the water is deeper and so less affected by friction) moving more quickly and the trough (where friction plays a greater role) moving more slowly. The end result of this nonlinear effect is to enhance flood dominance and/or to cause the waves to shoal and increase in strength as they move over vegetated areas and counteract the effect of energy dissipation caused by turbulence within the vegetation. This nonlinear effect of friction was predicted by Parker (1984) and has been observed in manipulative numerical modeling studies that incorporate removal of mangroves (Li et al., 2014; van Maanen et al., 2015; Bryan et al., in press). Moreover, in some cases, enhanced ebb flows are also observed seaward of the vegetation (Lessa and Masselink, 1995) and in drainage channels (Wolanski, 1992), explained by the delayed draining of the vegetation caused by friction, which contributes to removal of sediments just seaward of the fringe.

In summary, both the shoaling and the scouring effects of vegetation mean that in some places the transition from bare tidal flat to vegetated forest does not always result in a convex or even flat-topped profile. Rather, a linear profile develops, which we observe along Cu Lao Dung, where the scouring effect diminishes gently landward as the tidal wave progressively loses energy. These results unequivocally indicate that mangrove vegetation does alter intertidal hydrodynamics and sediment transport, thus actively engineering the coastal landscape.

SEDIMENT ACCUMULATION, FOREST BURIAL, AND SPECIES SUCCESSION

It is clear that mangroves can modify sediment fluxes either directly by enhancing turbulence or through changing tidal characteristics to some extent. However, too much sediment accumulation overwhelms these effects by smothering the roots and causing dieback (Nardin et al., 2016b).

Once *Sonneratia* trees are established, they develop horizontal cable roots that allow the formation of vertical pneumatophores. Note that the tree needs to allocate a lot of biomass in developing these roots, so once they are developed, it is impossible to create new roots at different elevations. As a result, the tree is locked at that elevation, and too much sediment erosion or accretion will harm the plant. Once the tree is mature, it can only survive within a specific range of elevations centered around the depth of the roots.

There is an example of forest burial in the interior part of the southwest fringe of Cu Lao Dung, where the burial depth of the pneumatophores incrementally increases with distance from the shore. As a result, the forest density (measured with NDVI from remote-sensing images) decreases moving inland, whereas light availability increases because the forest becomes sparser (Nardin et al., 2016a).

Large and sudden sedimentation events can also cause large-scale dieback, with many trees buried in a short time frame (Figure 5d). Similar dieback has occurred along the Poring River in Indonesia, fueled by massive sediment loading from volcanic activity (Sidik et al., 2016).

Eventually, when the bottom elevation becomes high enough, new mangrove species colonize the fringe, partly taking advantage of the forest gaps and light availability caused by the forest burial and tree dieback (Bullock et al., in press).

Remote-sensing data can be used to track the effect of sediment burial on the forest in time. Satellite images are particularly suitable for monitoring forest dynamics in very remote and inaccessible areas. For example, Landsat satellites can provide a biweekly image of a forest at a spatial resolution of 30 m for the last 30 years. As a consequence, the use of remote sensing to map and study mangroves has become very common in many tropical and subtropical countries (Kuenzer et al., 2011).

A newly encroached forest is composed of young trees that appear very green in remote-sensing images (high NDVI). In time, the number of trees diminishes, with some trees growing tall and shading the surrounding ones, thus reducing the overall NDVI value. If intense sediment accumulation is present, the trees
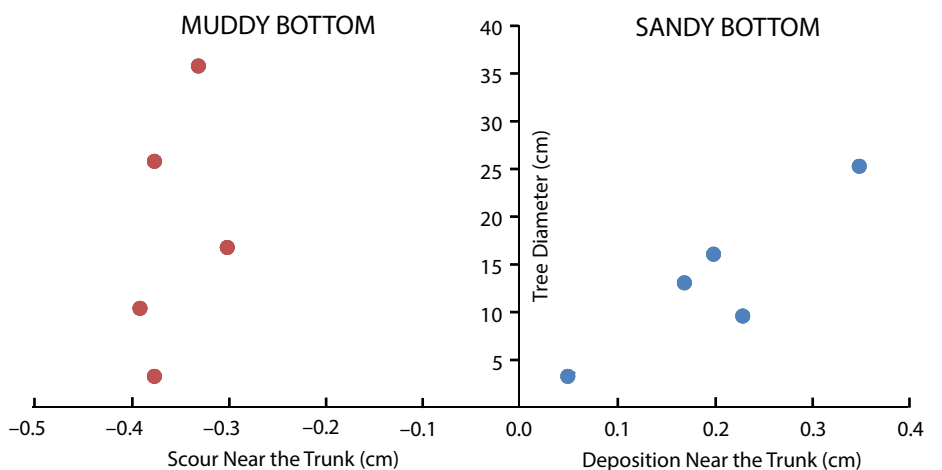

FIGURE 6. Example of ecogeomorphic feedback between *Sonneratia* mangroves and sediment transport. Turbulence during tidal flow causes erosion near the tree trunk where the bottom is muddy. In a sandy bottom, sediment accumulates near the trunk, possibly due to deposition during wave events.

are increasingly stressed, and the canopy is reduced along with the NDVI value. Some of the trees also die as a result of sediment burial. If the elevation of the forest is high enough, new mangrove species (*Aegericas corniculatum, Nypa fruticans*) can invade the stressed *Sonneratia* forest, producing a spike in NDVI. Therefore, we expect a decrease in NDVI through time within a *Sonneratia* forest where there is vertical accretion, followed by a sudden NDVI increase when new species arrive (Figure 2). In a prograding delta, these temporal dynamics also translate into a horizontal pattern by substituting space for time. The *Sonneratia* forest is very green at the shore, where it is young. The NDVI decreases inland where the forest is mature, and then sharply increases where new species are present. This pattern moves offshore through time, following the progradation of the entire delta (Bullock et al., in press). We can then monitor the encroachment of new species by tracking the zone of minimum NDVI through time.

As suggested by the evidence reported in the previous paragraph, for a prograding delta, *Sonneratia* mangroves favor sediment deposition. The higher elevations produced by this enhanced sedimentation allow encroachment of new species. Therefore, we conclude that

succession does exist in a prograding delta, with pioneer species engineering the landscape and thus facilitating the advent of secondary species. However, in the case of *Sonneratia spp.*, the replacement with secondary species is not only caused by competition but is also driven by sediment transport, and in particular by sediment burial of the already established forest.

Mangrove zonation is not always caused by succession. In a static landscape without accretion or erosion, different species likely colonize zones having specific elevations or distances from the shore in response to physicochemical gradients (Figure 7a). In such cases, pioneer species are not found because the timing of vegetation encroachment is not defined, and we do not have succession because upland species do not replace lowland species. Succession is only one of the possible outcomes, and perhaps the simplest, of ecogeomorphic feedbacks between sediment dynamics and forest growth (Figure 7b).

Many deltas are not simply prograding with a linear shoreline advancing in time. For example, distributary channels confined by natural levees characterize fluvially dominated deltas such as the Grijalva-Usumacinta in Mexico (Thom, 1967). Distributary channels bring water

and sediment to the coast, depositing bars at the mouth and creating large-scale depositional lobes (Fagherazzi et al. 2015). Avulsion can divert a distributary to another location by diverting sediment and sometimes causing a lowering of the abandoned lobe due to sediment compaction and subsidence. The only way to understand fully mangrove zonation in a complex evolving landscape is to first determine the morphodynamic evolution of the system as a whole (i.e., the accretion and depositional history) and to view the local processes in the overarching context of this history (Figure 7c).

Moreover, coastal landscapes with soft sediments are very dynamic, evolving in decades or even faster. Mangrove forest growth occurs on a similar time scale, and mature trees are usually more resilient and thus able to withstand more disturbance (i.e., they have longer roots and higher canopies). As a result, there is a strong legacy in vegetation distribution, with current tree zonation reflecting past states and therefore the history of the system.

In Soc Trang Province of the Mekong Delta, *Sonneratia* spp. are common on Cu Lao Dung and in nearby areas. Far from the mouths of the Song Hau River, *Rhizophora apiculata* and *Avicennia* spp. are predominant (Wölcke et al., 2016). Our results are therefore valid for mangrove forests near river mouths, where sediment supply and riverine flow are great.
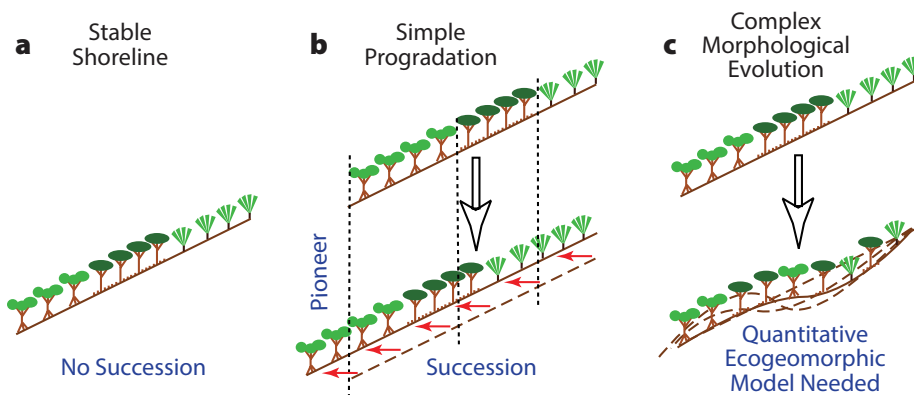
CONCLUSIONS

Through detailed observations of a fringe mangrove forest in Vietnam, we were able to identify a series of feedbacks between hydrodynamics, sediment transport, and mangrove trees (Figure 8). These feedbacks affect the large-scale evolution of the entire mangrove fringe. As a result, we find that mangroves do engineer the landscape, favoring sediment deposition and dissipating waves and preferentially colonizing sandy substrates.

In this simple configuration of a prograding shoreline, we observe vegetation succession, with the pioneering

FIGURE 7. Coupled evolution of shorelines and mangrove forests. (a) Along a stable shoreline, different mangroves are present at different elevations, but no succession occurs. (b) In a prograding shoreline, new pioneer species encroach upon the intertidal area while secondary species replace the pioneer mangroves at higher elevations (succession). (c) In a shoreline characterized by a complex morphological evolution, the distribution of mangrove species is controlled both by feedbacks between sediment dynamics and trees and by the history of the system. In this situation, only a quantitative model capturing all the feedbacks between physical and biological processes in mangroves can explain the distribution of mangrove species.

Sonneratia spp. colonizing tidal flats and trapping sediments by increasing drag and modifying the incoming tidal wave. Sediment accretion promoted by the *Sonneratia* forest creates suitable conditions for the encroachment of other mangrove species (species succession).

However, the morphodynamic evolution of tropical shorelines is almost always different from a simple, constant progradation. For example, in the Mekong Delta, sediment deposition is seasonal (see Fricke et al., in press) with sporadic wave events reworking bottom sediments and leading to local erosion. These cycles of erosion and deposition prevent the establishment of mangrove seedlings in soft muddy areas because vegetation prefers stable sandy substrates for encroachment. Moreover, species succession is not only caused by competition but also favored by sediment accumulation, tree-root burial, and smothering (Figure 8).

Therefore, succession is a simplistic explanation of mangrove zonation, which only applies to some simple coastal configurations. Very often the irregularity of deposition and erosion at the shore and the feedbacks among mangroves, hydrodynamics, and sediment transport lead to a complex forest structure that is difficult to decipher (Figure 7).

Only by understanding the small-scale feedbacks between mangroves and physical processes, and in particular sediment dynamics, is it possible to determine the evolution of the forest system and how the vegetation cover has changed in space and time (Figure 8). We need to quantify these small-scale feedbacks in order to mechanistically forecast vegetation distribution in time with physically based ecogeomorphic models.

The interpretations of ecogeomorphic processes reported herein were only possible because of the detailed sediment dynamic measurements made in the study area by an interdisciplinary research team (see Mullarney et al., 2017, in this issue). This type of interdisciplinary research is essential to understand the feedbacks between ecology and geomorphology.
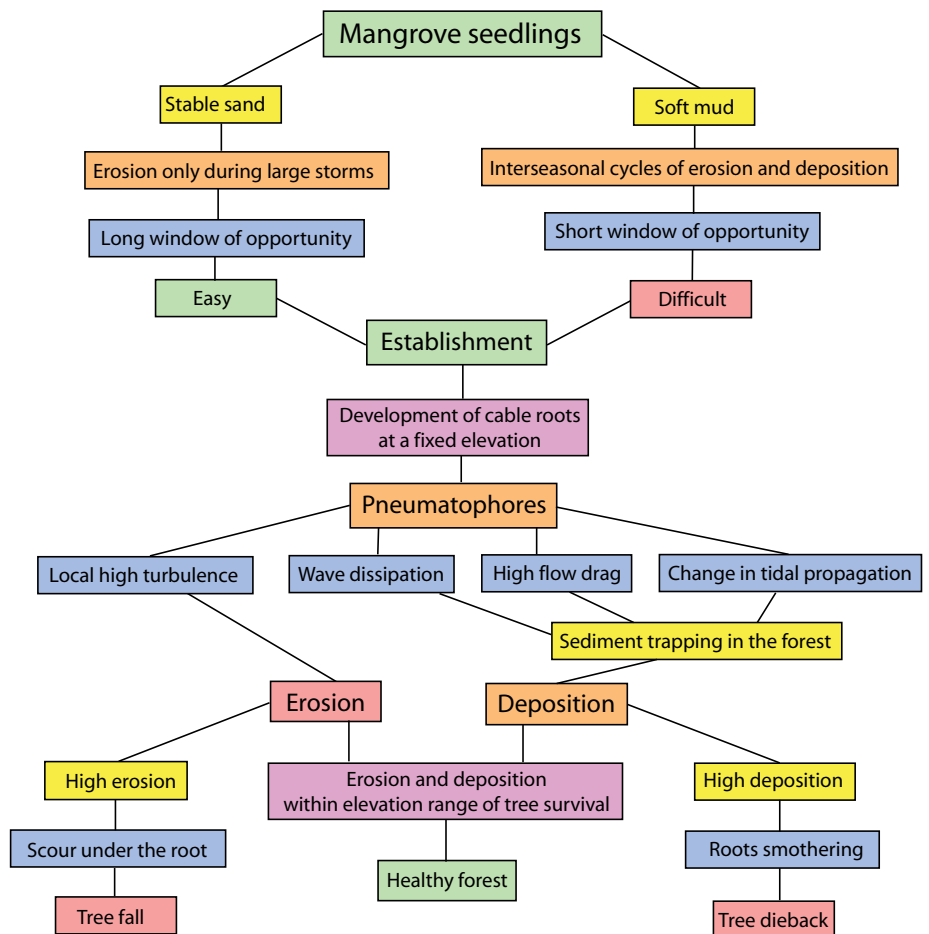

FIGURE 8. Feedbacks between physical and biological processes determined in a *Sonneratia caseolaris* mangrove forest.

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