

## Biomorphodynamics: Physical-biological feedbacks that shape landscapes

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[1] Plants and animals affect morphological evolution in many environments. The term “ecogeomorphology” describes studies that address such effects. In this opinion article we use the term “biomorphodynamics” to characterize a subset of ecogeomorphologic studies: those that investigate not only the effects of organisms on physical processes and morphology but also how the biological processes depend on morphology and physical forcing. The two-way coupling precipitates feedbacks, leading to interesting modes of behavior, much like the coupling between flow/sediment transport and morphology leads to rich morphodynamic behaviors. Select examples illustrate how even the basic aspects of some systems cannot be understood without considering biomorphodynamic coupling. Prominent examples include the dynamic interactions between vegetation and flow/sediment transport that can determine river channel patterns and the multifaceted biomorphodynamic feedbacks shaping tidal marshes and channel networks. These examples suggest that the effects of morphology and physical processes on biology tend to operate over the timescale of the evolution of the morphological pattern. Thus, in field studies, which represent a snapshot in the pattern evolution, these effects are often not as obvious as the effects of biology on physical processes. However, numerical modeling indicates that the influences on biology from physical processes can play a key role in shaping landscapes and that even local and temporary vegetation disturbances can steer large-scale, long-term landscape evolution. The prevalence of biomorphodynamic research is burgeoning in recent years, driven by societal need and a confluence of complex systems–inspired modeling approaches in ecology and geomorphology. To make fundamental progress in understanding the dynamics of many landscapes, our community needs to increasingly learn to look for two-way, biomorphodynamic feedbacks and to collect new types of data to support the modeling of such emergent interactions.

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### 1. Introduction

[2] Before plants and animals invaded the land (~400 Ma, in the Devonian Period), a geomorphological researcher would have beheld a landscape adorned with loose sediment: naked clasts making their way down highly incised hillslopes, sand and silt blowing free or piling up in ubiquitous dunes, most rivers braiding with abandon... Those of us who study landscape processes today often

pine for such a vista and field area (or seek them out in arid, arctic and alpine environments), where physics rules without the interference of biology. Purely physical morphodynamic interactions, the couplings between fluid flow, sediment transport, and morphological evolution, produce many rich and fascinating phenomena. The conservation of momentum, energy and mass, represented in various ways, often provide elegant and trustworthy treatments of the processes involved (although sediment transport presents a notable exception).

[3] Aggregates of biological organisms are, on the other hand, more difficult to treat starting with  $F = ma$ . Organisms operate within physical laws, of course, but reducing to basic physics how they grow and respond to the environment is exceedingly difficult (and likely not the most effective approach). Researchers interested in morphodynamics can be forgiven for traditionally neglecting the effects plants and animals can have on flow and sediment transport, because to the first approximation, many morphodynamic phenomena can be addressed with only physical interactions; biological effects are not needed to explain the formation of bed forms in river, estuarine and coastal

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environments, for example. However, the differences between the pre-Devonian landscape and what we see over much of the Earth's surface suggests that vegetation and creatures play an important role in many surface processes. The morphological evolution of some landscapes cannot be understood even approximately without considering the two-way coupling between physical and biological processes.

[4] Tidal marshes provide a striking example: Marsh vegetation depends on the physical processes in several ways, starting with the fact that colonization cannot occur unless a (previously unvegetated) surface is sufficiently high in the tidal range. In turn, marsh vegetation exerts first-order controls on flow, sediment transport, and morphological change within a marsh and tidal creek system. Addressing the long-term evolution of a marsh environment requires a consideration of both physical and biological processes, and how they interact.

[5] We argue here on the basis of a few select examples that such two-way couplings fundamentally shape many landscapes. Studies of systems in which biological-morphological coupling and feedback is important, which we term "biomorphodynamic", are beginning to blossom, and in our opinion this trend should accelerate. (The terms "ecomorphodynamic", "biogeomorphology", and ecogeomorphology have also been used [Fagherazzi et al., 2004; Hupp et al., 1995; Naylor et al., 2002; Stallins, 2006; Viles, 1988, 1990], and the latter two might be applied more broadly than the restricted sense of two-way coupling we suggest for biomorphodynamics.)

[6] Quantitative morphodynamic models have not included biological or ecological processes very often until recently, possibly because representing them in a quantitative framework has not seemed as straightforward as it is for many physical processes. Sediment transport also proves difficult to pin down, but because this challenge is impossible to avoid in morphodynamics, parameterizations for bulk sediment transport have been devised (with moderate quantitative success). Incorporating biological or ecological processes requires new parameterizations. As has occurred in the history of sediment flux parameterizations, continued modeling of small-scale processes and continued empirical studies will improve the accuracy of the representations of biological interactions in biomorphodynamic models. However, simple first guesses at the unknown forms of parameterizations, often called "rules", will go a long way in the initial stages of exploring poorly understood phenomena [Murray, 2003, 2007a], those of biomorphodynamic systems in this case. New parameterizations or rules are needed for both (1) biological effects on flow and sediment transport and (2) how biological communities or ecosystems evolve as functions of morphology, flow, and sediment transport.

[7] In the last decade or so, studies have sprung up addressing biomorphodynamics in many environments. We focus here on selective, illustrative examples of such studies concerning terrestrial and coastal environments in sections 2 and 3, pointing out common threads and highlighting their implications. In section 4 we discuss some possible reasons that biomorphodynamic studies are becoming much more common in recent years, and in section 5 we suggest some research strategies that we believe will enhance

the future progress of biomorphodynamics and landscape evolution generally.

## 2. Terrestrial Biomorphodynamic Studies

[8] Recent terrestrial studies show that biophysical feedbacks can take many forms, from biothermal effects in arctic and alpine patterned ground [Daanen et al., 2006] to arid regions ecohydrologic interactions that can lead to vegetation patterns [Porporato and Rodriguez-Iturbe, 2002; Rodriguez-Iturbe and Porporato, 2004]. We will concentrate here on investigations of how biomorphodynamic interactions can sculpt topography in eolian dunes, fluvial landscapes, and river channels.

### 2.1. River Channels

[9] Research documenting one-way couplings between physical and biological processes in river channels abounds. A considerable body of work concerns how physical processes and morphology in river channels determines the suitability of these environments as habitats [Buffington et al., 2004; Kondolf and Wollman, 1993; Merz et al., 2006; Pasternack et al., 2004; Suttle et al., 2004]. Animals and plants on hillsides and in drainage basins affect the rate that sediment enters a river [Liebault and Piegay, 2002; Piegay et al., 2004; Yoo et al., 2005], therefore affecting river morphology. Although two-way biophysical feedbacks likely influence river channel and river bed morphology on various scales, to date studies identifying them have been rare.

[10] One such study [Murray and Paola, 2003] involves river channel patterns, specifically, the difference between single- and multiple-channel rivers. This work is embedded in the context of many studies that have suggested that channel bank vegetation affects plan view channel pattern [Brice, 1964; Mackin, 1956; Millar, 2000; Nevins, 1969; Paola, 2001]. Vegetation increases the erosion resistance of banks both directly, through the sediment strengthening and flow diverting effects of plant roots, and indirectly, by trapping fine-grained sediment that adds cohesion [Knighton, 1984; Smith, 1976]. Field observations suggest that if these bank stabilization effects are strong enough, they can produce a single-channel pattern, where a multiple-channel, braided pattern (Figure 1) would otherwise exist [Brice, 1964; Nanson and Knighton, 1996; Mackin, 1956; Nevins, 1969]. Millar [2000] analytically showed that the degree of vegetation-influenced bank strength could discriminate between the two end-member channel patterns. Murray and Paola [2003], using a biomorphodynamic numerical model, added to this concept the idea that not only the vegetation effects on physical processes, but also the influences the physical processes exert on the plants, are important.

[11] The background for this modeling study starts with a purely physical model. Murray and Paola [1994, 1997] proposed that a simple pair of morphodynamic feedbacks cause the basic phenomenon of braiding. This potential explanation, embodied in a simple numerical model (the "MP" model), only requires a dominance of bed load transport (with its nonlinear dependence on local flow strength), and channels with noncohesive banks. The apparent robustness of the mechanism in the MP model raised the question of why braided rivers are not more common:



**Figure 1.** Braided rivers in the New Zealand Alps. Note vegetation growth (darker areas) in parts of the braid plain not recently active. (Darker areas in the foreground are cloud shadows.)

why are they restricted largely to arid, arctic, and high-alpine environments? The weak influence of vegetation in these harsh environments, relative to that in more temperate climates, offers a possible answer.

[12] To explore the plausibility of this hypothesis, these authors added plant effects on sediment transport to their original braided-stream model. However, in the dynamic setting of migrating, bifurcating, and avulsing channels in the model, some treatment of the kinematics of plant growth and death was also needed. As a simple first guess, where both local erosion and deposition rates in the model fall below specified thresholds, the degree of vegetation influence (which can be interpreted as biomass density) grows linearly with time, until a maximum is reached. Either erosion or deposition rates above the plant-destroying thresholds reset the vegetation density to zero. (The plant growth rate, a free parameter that can be varied to represent different vegetation types or environments, turns out to be important, as discussed below).

[13] Plants affect sediment transport in this model in two ways. The threshold flow strength (stream power) for sediment transport increases linearly with vegetation density. And gravity-driven transport, such as on channel banks, decreases with increasing vegetation density, representing the sediment stabilizing effects of roots and possibly cohesive sediment trapped by the plants. (The original MP model included a simple parameterization for the down-slope component of bed load transport that occurs wherever a noncohesive bed slopes in a direction oblique to the flow direction [Parker, 1984]. With plants added to the model, this sediment flux component decreases as vegetation density increases. This simple parameterization represents only the main effects of a complicated set of processes involved in vegetation channel stability interactions [Abernethy and Rutherford, 2000; Simon and Collison, 2002].)

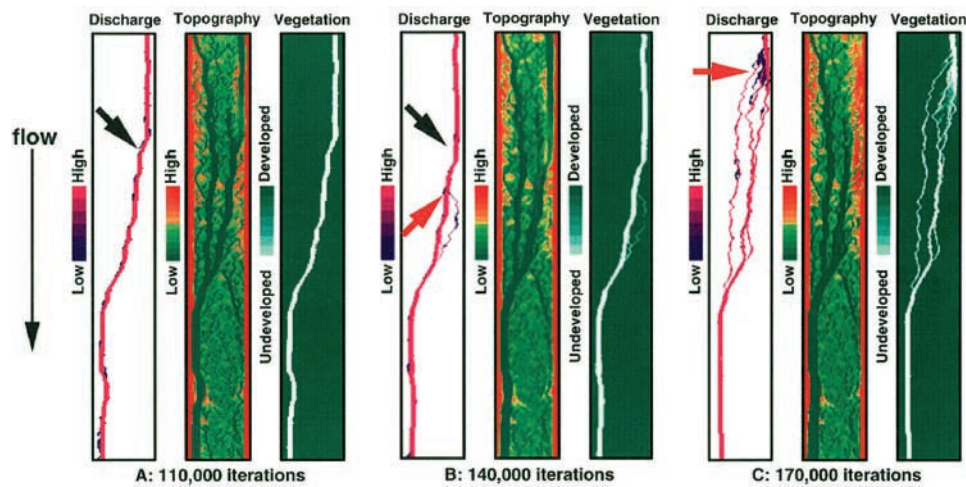
[14] The effect on sediment transport thresholds turns out not to affect the channel patterns in the model significantly, although the reduction of gravity-driven transport can change the model outcome qualitatively. When areas (model

cells) adjacent to an active channel are vegetated, bank erosion rates can be reduced enough to prevent channels from bifurcating. To understand this interaction, we need to consider why bifurcations develop in the model in the absence of plants. Where flow is spreading laterally over an incipient midchannel bar and therefore flow strengths are decreasing downstream, bed load sediment flux converges (because sediment flux depends nonlinearly on flow strength, whether flow strength is measured by bed shear stress or stream power [Murray and Paola, 1994, 1997]). The flux convergence causes the bar to grow, increasing the lateral flow divergence. Eventually, the flow may be diverted around an emergent bar. However, for this to happen, the diverted flows must shift laterally. Vegetation strengthened banks in the model tend to limit lateral flow divergence in a channel, which can inhibit the bifurcation feedback.

[15] The inclusion of plants, however, does not necessarily prevent bifurcations and braiding in the model. If the plant growth rate is slow relative to the rate that channels shift around in the absence of plants, erosion and deposition prevent plants from becoming well established on channel banks. On the other hand, rapidly growing plants that exert a significant influence on bank erosion can cause a single-channel pattern, rather than a braided one, to evolve in the model (Figure 2).

[16] This exploratory modeling exercise suggests that braiding results where (1) vegetation grows slowly or is sparse (and therefore weakly affects sediment transport), as in harsh arid and arctic environments, or (2) where high discharges or steep regional slopes cause high sediment fluxes, and therefore channel rearrangements that occur on a timescale shorter than that of plant growth, as in some alpine environments where water and sediment discharges from nearby glaciers are often high (Figure 1).

[17] This model serves only as a start in the effort to understand the biomorphodynamics in this system, suggesting a possible minimal set of key interactions. It does not include vegetation effects on flow, for example, and the



**Figure 2.** (a-c) Output of the biomorphodynamic channel pattern model, showing three snapshots from a dominantly single channel run [after Murray and Paola, 2003]. The dark arrows in Figures 2a and 2b show the location of minor channel migration; the lighter arrows in Figures 2b and 2c point out avulsions. The multichannel state in Figure 2c is a transient effect of the avulsion.

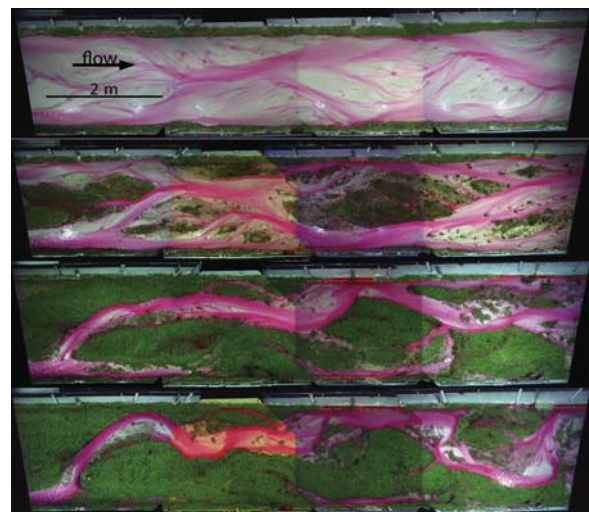
highly simplified forms of the interactions, while maximizing the clarity of potential insights [Murray, 2003, 2007a], are certainly not quantitatively accurate. Future numerical models will likely involve a greater quantitative fidelity as field and laboratory studies provide the bases for more empirically based parameterizations of the interactions between vegetation, flow and morphological evolution improved.

[18] Gran and Paola [2001] and Tal and Paola [2007] have experimentally explored vegetation channel pattern interactions in a laboratory flume by growing alfalfa sprouts on an initially unvegetated braided channel. Gran and Paola [2001] demonstrated that densely vegetated experiments produced channel patterns resembling single-thread rivers more than braided ones, with narrower, deeper, and less mobile channels. The next set of experiments [Tal and Paola, 2007] showed how the system evolves dynamically from braided to single-thread when the discharge is fluctuated and vegetation is added over many repeated cycles (Figure 3). This set of experiments presently underway investigates the dependence on the ratio between channel change and plant growth timescales suggested by the numerical model. Because the rate of plant growth is fixed in these experiments, Tal and Paola are changing the timescale for channel reworking. In one run, a flood lasting one hour occurs every 6 days, and the flow the rest of the time is considerably lower. In subsequent runs, the floods become more frequent or longer in duration, and in the limit that the channel is rearranged rapidly enough to significantly inhibit vegetation establishment, a braided pattern is expected to persist.

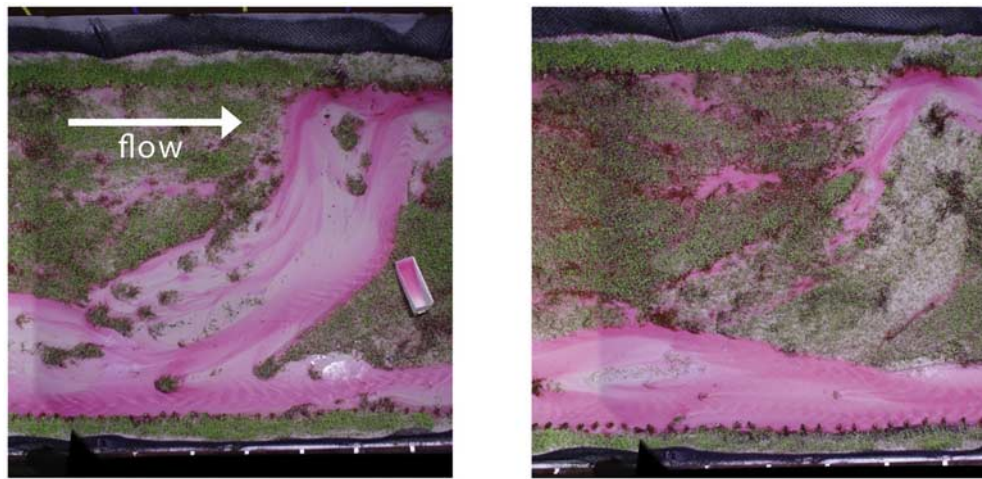
[19] These laboratory experiments suggest another key mode of interaction between vegetation and flow/sediment transport: vegetation encroachment of inactive low-flow channels. During periods of low flow, vegetation can become established in minor channels with little or no discharge. Once the plants become dense enough to divert the flow away from that channel at high flows, it becomes inactive (Figure 4). This interaction augments channel bank stabilization, strengthening the tendency for a single-channel

nel pattern to develop. Tal *et al.* [2004] also found results similar to those in the laboratory and numerical models in field settings where human-influenced increases in vegetation have decreased braiding intensity and channel mobility.

[20] The relationship between these studies of vegetation and river pattern illustrates what is likely a common theme. The studies that address a one-way influence of biology on physical processes (roots affecting bank strength in this case) [Brice, 1964; Nanson and Knighton, 1996; Knighton, 1984; Mackin, 1956; Millar, 2000; Nevins, 1969; Paola, 2001], while valuable and correct within their scope, elucidate a subset of the interactions involved. When the temporal evolution of the system is considered, the importance of the physical effects on biology becomes more evident. The resulting feedbacks occur over the timescales involved in the formation of the pattern, as morphological changes impact habitats of the plants or animals involved.



**Figure 3.** A laboratory experiment involving the growth of alfalfa, showing progressive times starting with the initial unvegetated state.



**Figure 4.** Successive times in laboratory experiment in which vegetation colonizes a channel with weaker flow during low-flow intervals.

These relatively long-term feedbacks will often, as in this river example, be difficult to address solely with field observations that constitute snapshots in the pattern development. Thus, biophysical interactions that appear to be one way on first impression may prove to be part of a more interesting biomorphodynamic evolution on longer timescales.

## 2.2. Fluvial Landscape Evolution

[21] Geomorphologists studying hillslopes and drainage basins have long recognized that biology affects sediment production and transport [Lancaster *et al.*, 2003; Langbein and Schumm, 1958; Wilson, 1973; Yoo *et al.*, 2005] and landscape morphology [Hack and Goodlett, 1960]. (See *Istanbulluoglu and Bras* [2005] for a more inclusive review.) Ecologists and some geomorphologists, on the other hand, study how topography and geomorphic processes affect biology [Bendix, 1997; Parker and Bendix, 1996; Stallins, 2006]. One series of modeling studies steps back from the details observed in particular field sites to undertake an initial exploration of how the physical and biological processes and morphology all coevolve over long timescales in fluvial landscapes [Collins *et al.*, 2004; *Istanbulluoglu and Bras*, 2005; Tucker and Bras, 1999; Tucker *et al.*, 2001].

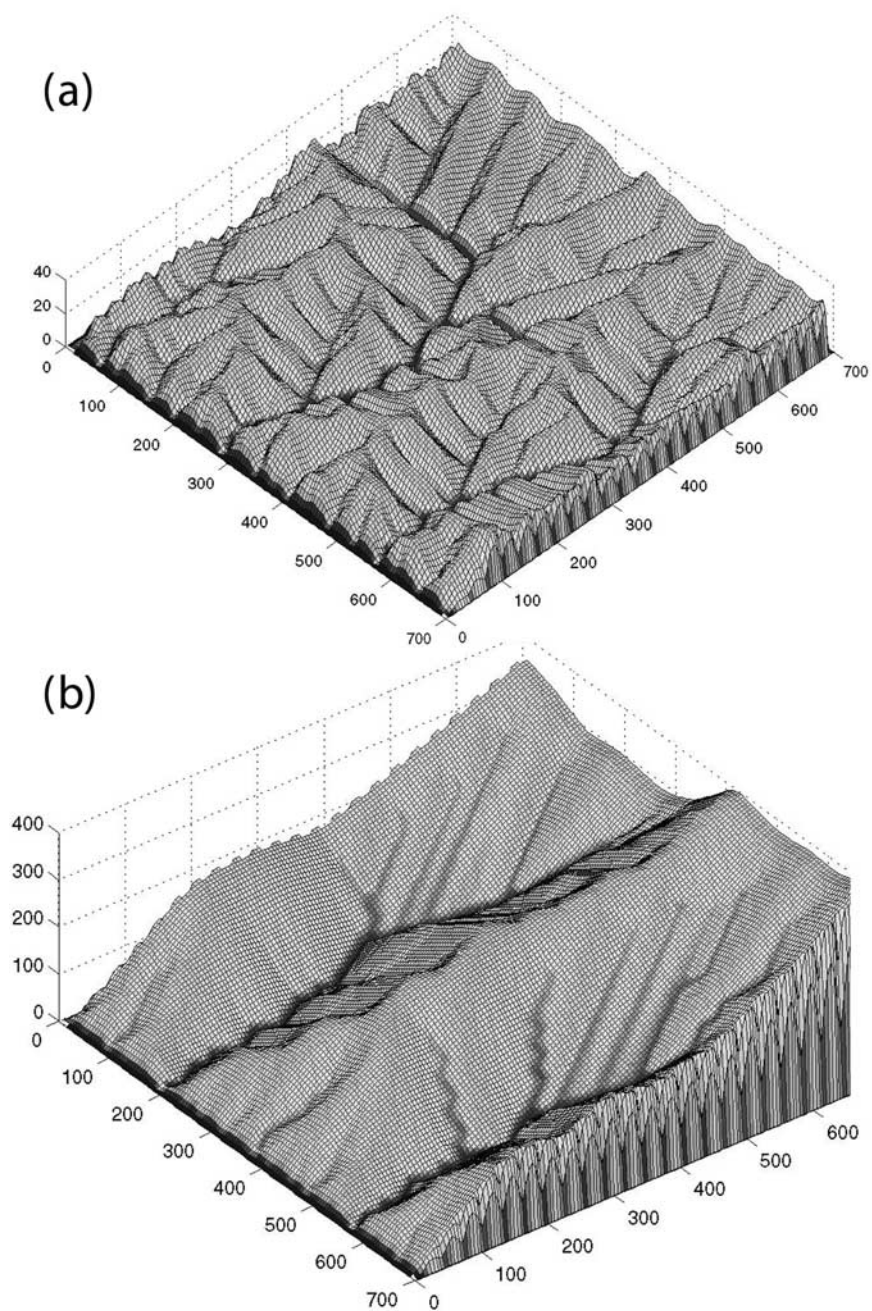
[22] *Tucker and Bras* [1999] incorporated representations of vegetation growth, and the consequent decrease in sediment transport by surface runoff, into a landscape evolution model: the Channel Hillslope Integrated Landscape Development (CHILD) model [Tucker *et al.*, 2001]. Collins *et al.* [2004] used this model to investigate how the simple reduction in fluvial sediment transport affects relief and drainage density in a small (1 km  $\times$  1 km) model catchment. When vegetation is present, steeper slopes and/or greater drainage areas are needed for channel head incision (i.e., for divergence of fluvial transport to outpace hillslope “creep” diffusion, which tends to fill in fluvial incisions). In model runs driven by constant uplift, vegetation produces a much steeper steady state topography (nearly an order of magnitude steeper), with a less extensive channel network. This modeling effort left out other ways that vegetation affects sediment transport processes, and

vice versa, so that the effects of the simple interactions addressed would be clear.

[23] *Istanbulluoglu and Bras* [2005] added to CHILD several biological and sediment transport processes, including: hillslope diffusivity that decreases with increasing vegetation cover; landsliding that occurs when a critical slope is reached; and the possibility that vegetation can be killed by landsliding and wildfires as well as by fluvial erosion. A decrease in hillslope diffusion, which tends to slow the filling of fluvial incisions, favors increasing drainage density with increasing vegetation cover. *Istanbulluoglu and Bras* [2005] showed analytically that, assuming vegetation density can be treated as an independent variable, drainage density could increase or decrease with increasing vegetation, depending on: the uplift rate (which affects steady state slopes); the initial vegetation density; and how effective vegetation is at retarding creep (which varies with vegetation type).

[24] To investigate what happens when vegetation density is allowed to vary dynamically (i.e., when vegetation density is treated as a dependent variable), *Istanbulluoglu and Bras* [2005] turned to the numerical model. Using forcing conditions representing the Oregon Coast Range in the USA, they first reproduced the basic results of Collins *et al.* [2004] by imposing a static vegetation cover and comparing the outcome to that without vegetation (Figure 5). Then *Istanbulluoglu and Bras* [2005] allowed runoff and landsliding to locally and temporarily kill vegetation (which then tends to grow back gradually). Figure 6 shows the results of that model experiment, and comparing Figure 6 with Figure 5 shows that, as in the river channel example, the effects that physical processes have on plants is approximately as important as the effects plants have on physical processes; the relief and drainage density in the dynamic vegetation case (Figure 6) is dramatically different than in the static vegetation case (Figure 5b). This modeling exploration suggests that the cumulative effects of local and temporary disturbances to vegetation can play a first-order role in long-term, regional landscape evolution.

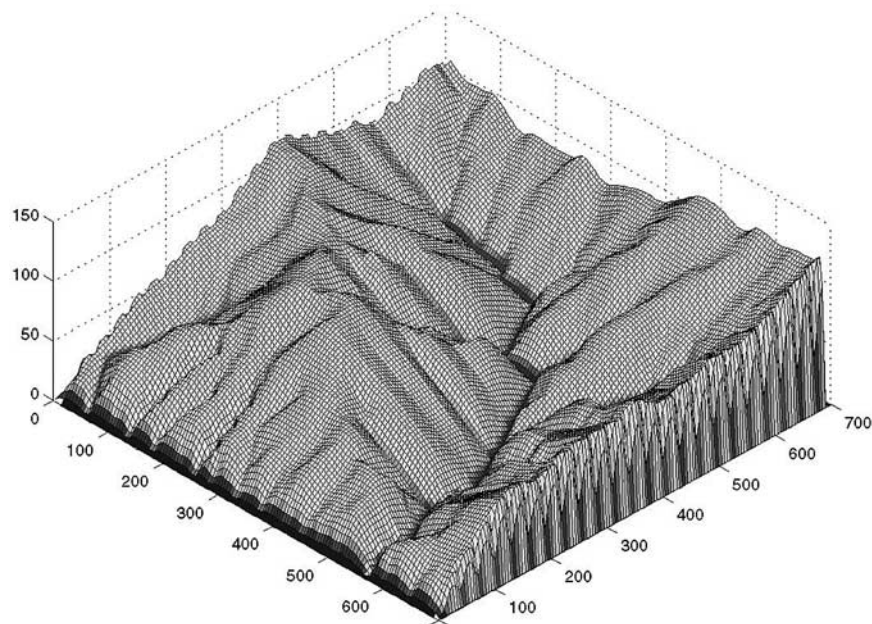
[25] *Tucker et al.* [2006] have taken these ideas into the field, examining spatially intermittent arroyo formation in a semiarid grassland in the Colorado high plains, USA. On



**Figure 5.** Results of the CHILD model, with a  $700\text{ m} \times 700\text{ m}$  domain [from *Istanbulluoglu and Bras, 2005*] with (a) no vegetation present and (b) complete and static vegetation cover. Note the different vertical scales; vegetation tends to make the landscape considerably steeper. Both cases show snapshots of dynamic equilibria, in which erosion driven by stochastic climate forcing balances uplift in the long term.

the basis of a simplified version of the vegetation-erosion relationships in CHILD and on field observations, they propose that arroyo formation is temporally as well as spatially intermittent, driven by biomorphodynamic feedbacks. Starting from an established cover of grass, it requires concentrated runoff from isolated convective storms to locally destroy the vegetation, which triggers a positive feedback. The underlying sediment or friable rock has a lower erosion threshold (critical shear stress) than the grass cover, so that overland flow will rapidly erode down

into the substrate. This process leads to the formation of the characteristic arroyo headcuts and plunge pools, which tend to migrate upstream. As the nick point deepens, several negative feedbacks become effective in countervailing the positive feedback, including channel widening and the tendency for vegetation to regrow in the time between runoff events. If the characteristic timescale of convective storms is much less than that of vegetation growth, arroyos will be spatially and temporally rare. However, when the two timescales are commensurate, the modeling [Tucker *et*



**Figure 6.** Results of the CHILD model, with a  $700\text{ m} \times 700\text{ m}$  domain [from *Istanbulluoglu and Bras, 2005*]. In contrast to the results in Figure 5b, vegetation cover is dynamic; vegetation is disrupted locally by water erosion and landsliding and tends to grow back to a saturated density. Note that the vertical scale is different than that in Figure 5b; the effects of physical processes on vegetation change the way the system organizes, leading to lower relief (and higher drainage density). As in Figure 5, the model is in dynamic equilibrium, with erosion balancing uplift in the long term.

*al.*, 2006] predicts rich dynamics. Those authors suggest that over long timescales, the repeated cycles of arroyo formation and annealing, of local and temporary disturbances to vegetation, have created the valleys that make up the larger-scale landscape, which evolves on a timescale much larger than that of the transient arroyos.

### 2.3. Vegetation and Eolian Dunes

[26] Vegetation can clearly affect eolian dune dynamics. When climate or land use changes allow vegetation to increase [Tsoar, 2005], mobile sand dunes can become stabilized. However, vegetation often only partially stabilizes a dune field, leading to a characteristic “parabolic” dune shape, with a concave-upwind, upwind-facing area of mobile sand surrounded by vegetated lee slopes and vegetated arms extending upwind (Figure 7a), rather than the transverse or barchan dunes that form in the absence of vegetation (Figure 7b). Conceptual [Hesp, 2004; Tsoar and Blumberg, 2002] and numerical [Baas, 2007; Baas and Nield, 2007; de Castro, 1995; Duran and Herrmann, 2006; Nishimori and Tanaka, 2001] models attribute the shape and dynamics of parabolic dunes to a competition between vegetation and eolian sand transport. If plants can grow, they tend to locally decrease sediment flux, trapping sand [Tsoar and Blumberg, 2002]. However, excessive deposition or erosion rates will kill vegetation [de Castro, 1995]. Erosion and deposition rates depend on dune migration rate, which is determined by the characteristic sediment flux and dune size. Dunes that migrate sufficiently rapidly can remain plant free [Duran and Herrmann, 2006], even if precipitation is sufficient for plant growth otherwise [Tsoar, 2005]. In the limit of fast plant growth relative to dune

migration rate, extensive plant cover can reduce eolian sediment fluxes to negligible values.

[27] Between these two limits, the shape of isolated dunes can shift from barchanoid to parabolic as vegetation is able to take hold where erosion and deposition rates are lowest. This occurs along the crest (the points on longitudinal cross sections where instantaneous bed-level changes approach 0 as the dune shape propagates), and along the lateral flanks, where wind is not sped up as it is over the higher parts of the dune. The growth of vegetation, reducing local sediment fluxes, retards the migration of the flanks of a dune, leading to the upwind-pointing appendages of parabolic dunes (Figure 8), in contrast to the downwind-pointing horns of a barchan dune (Figure 7b) (which occur because sediment flux is not trapped in the recirculation zone associated with the slip face). The vegetation along the crest of a parabolic dune decreases overall migration rates compared to barchan dunes [Duran and Herrmann, 2006], and makes parabolic dunes steeper [Tsoar and Blumberg, 2002].

[28] Baas and Nield have added an additional biodynamic interaction: they differentiate between grass and woody vegetation [Baas, 2007]. The marram grass they represented in this modeling does not increase in density on a static sandy surface, requiring moderate deposition rates to thrive. (Deposition reduces the impact of soil pathogens and parasites; see references in work by Baas [2007].) The woody vegetation grows more slowly than does the grass, and is less tolerant of erosion and deposition. In these model experiments, the woody vegetation cannot survive on the crests of the parabolic dunes that emerge, although it outcompetes the grass along the trailing arms (Figure 8). The increased realism of biological interactions in this model produces a richer set of behaviors than in previous models,



(a)



(b)

**Figure 7.** (a) Parabolic dunes on the Israel coast. Prevailing wind is approximately from left to right. View is from near the crest inside of one parabolic dune, with the vegetated outside of another showing in the background, past the researchers (Haim Tsoar and Hezi Yizhaq). (b) Barchan dunes in southern Morocco. Prevailing wind is from left foreground to right background.

including the self-organization of parabolic dunes from localized vegetation disturbances (“blow outs”), and the formation of sediment mounds behind individual bushes (“nebkhas”) [Baas and Nield, 2007].

[29] These initial dune vegetation studies provide a stark example of landforms that would not arise without a two-way interplay of physical and biological processes. These studies also will likely form a foundation for future science and management of arid regions, where changes in land use and climate will continue to drive hysteretic switches between mobile and stabilized eolian landscapes [Tsoar, 2005].

### 3. Coastal Biomorphodynamic Studies

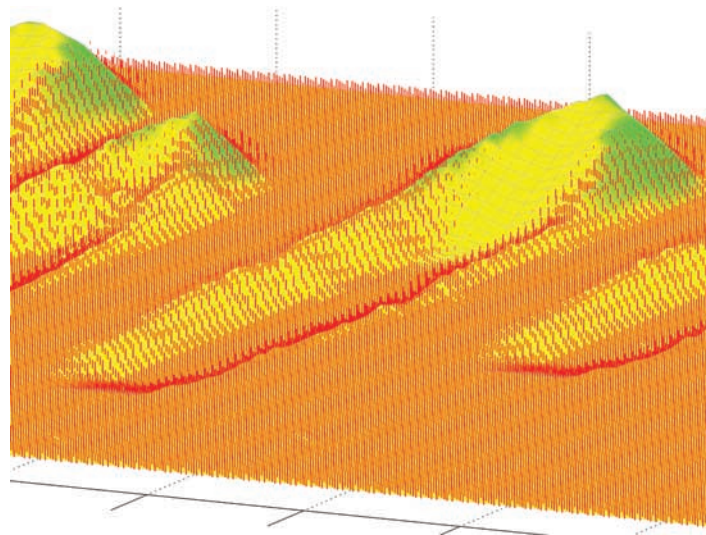
#### 3.1. Tidal Marshes and Channel Networks

[30] Research concerning the biomorphodynamics of salt marshes and the intertwining tidal channel networks

(Figure 9) has exploded in recent years. On vegetated tidal marsh platforms, a two-way biophysical coupling stands out perhaps more obviously than in any other environment. Dense marsh grasses slow tidal flows and wave orbital velocities across the platform and reduce near-bed turbulence and shear stress [Ghisalberti and Nepf, 2006; Leonard and Luther, 1995; Nepf, 1999], enhancing deposition of suspended sediment. Grasses also contribute belowground organic sediment. Thus, the rate at which a marsh platform aggrades depends on the density of vegetation, as well as on suspended-sediment concentration [Allen, 1990, 1997; Morris *et al.*, 2002]. On the other hand, the density and type of vegetation depends on the platform’s elevation relative to high-tide level [Morris *et al.*, 2002]. Therefore, even just considering the vertical dimension, a vegetation morphology feedback presents itself.

[31] Morris *et al.* [2002] analytically modeled this feedback, using parameters based on field measurements of a





**Figure 8.** Parabolic dune development in the Baas and Nield model after 60 seasons [from Baas, 2007] (with permission from Elsevier) started from a flat, fully vegetated surface with a few bare oval patches. Green gradation indicates grass “density” (vegetation effectiveness), and red sticks indicate woody shrub density. Transport direction is from bottom left to top right (unidirectional).

marsh dominated by *Spartina alterniflora* in South Carolina, USA. They investigated how platform aggradation rate adjusts to relative sea level rise rate. Because *Spartina* biomass increases with platform depth below high tide (up to a limit), a stable, equilibrium depth results, in which aggradation rate equals sea level rise rate. Perturbing this equilibrium by making the platform deeper (shallower) increases (decreases) biomass and aggradation rate, restoring equilibrium. (Above some sea level rise rate, which depends on suspended sediment concentration, the vegetation-enhanced deposition cannot keep up, and the marsh will drown.) This feedback helps explain why elevations tend to be constant across wide expanses of tidal marshes (where the vegetation type is consistent).

[32] Coupled parameterizations for vegetation change and sedimentation rate like those in the Morris *et al.*, 2002] model allow the development of spatially extended models addressing interactions between different parts of the system. Tidal channels deliver water and sediment to the marsh platform; suspended sediment concentrations and therefore aggradation rates tend to decrease moving away from channels [Friedrichs and Perry, 2001]. Mudd *et al.* [2004] constructed a model that extends in one horizontal direction, perpendicular to the axis of a channel. They examined how the morphology and biomass density pattern of the platform evolve under various rates of sea level rise, showing the development of subtle levees adjacent to channel banks where sediment concentration is highest. These authors also showed that marshes that accrete primarily through organic deposition do not exhibit significant levees, because in that case deposition is not affected by variations in suspended-sediment concentrations.

[33] D’Alpaos *et al.* [2007] perform a similar model analysis, but treating a spatial domain extended in both horizontal directions. They assume that a tidal channel network evolves on a timescale shorter than that for the evolution of platform morphology and vegetation cover, and then remains relatively static; they treat a tidal network as a

boundary condition for modeling the platform processes. (D’Alpaos *et al.* [2005] model channel network development as a separate morphodynamic exercise.) Using this platform model, D’Alpaos *et al.* [2007] explore how including multiple species of marsh vegetation alters the platform biomorphodynamics. Higher marsh elevations typically feature different plant species than lower ones, and different species have different effects on platform aggradation. Allowing multiple species, varying as a function of local platform elevation, produces different morphologies than those produced under a single-species assumption (Figure 10). For example, the density of high-marsh species increases as depth below high tide decreases (the opposite of the relationship for *Spartina alterniflora*), tending to produce elevations that emerge above high-tide level [D’Alpaos *et al.*, 2007] where high-marsh species take over. Although most of the experiments with this model to date have involved a static sea level, D’Alpaos *et al.* [2007] have begun to explore the platform biomorphodynamics under a rising sea level.

[34] The Mudd *et al.* [2004] and D’Alpaos *et al.* [2007] models involve the effects channels have on platforms through their sediment delivery function. But tidal channels are in turn affected by the platform evolution. For example, as high-tide platform depths decrease, tidal prisms flowing through the channel network decrease [Allen, 1997]. D’Alpaos *et al.* [2006] modeled the coupling between vegetated platform and channel evolution in a cross section perpendicular to the channel axis, examining how channel deposition and erosion rates and morphology change as vegetation enhances platform aggradation. Kirwan and Murray [2005, 2007, 2008] have developed a different three-dimensional model that complements those developed by D’Alpaos *et al.* [2006, 2007]; it features an additional level of coupling between vegetation and morphology, related to further coupling between the platform and channel network. The Kirwan and Murray model includes gravitationally driven sediment transport, representing pro-



**Figure 9.** Vegetated marsh and tidal channel network in Plum Island estuary, Massachusetts, USA (from <http://ecosystems.mbl.edu/pie/default.htm>). Darker marsh corresponds to low-marsh vegetation (*Spartina alterniflora*). The linear patterns in parts of the marsh are old mosquito ditches.

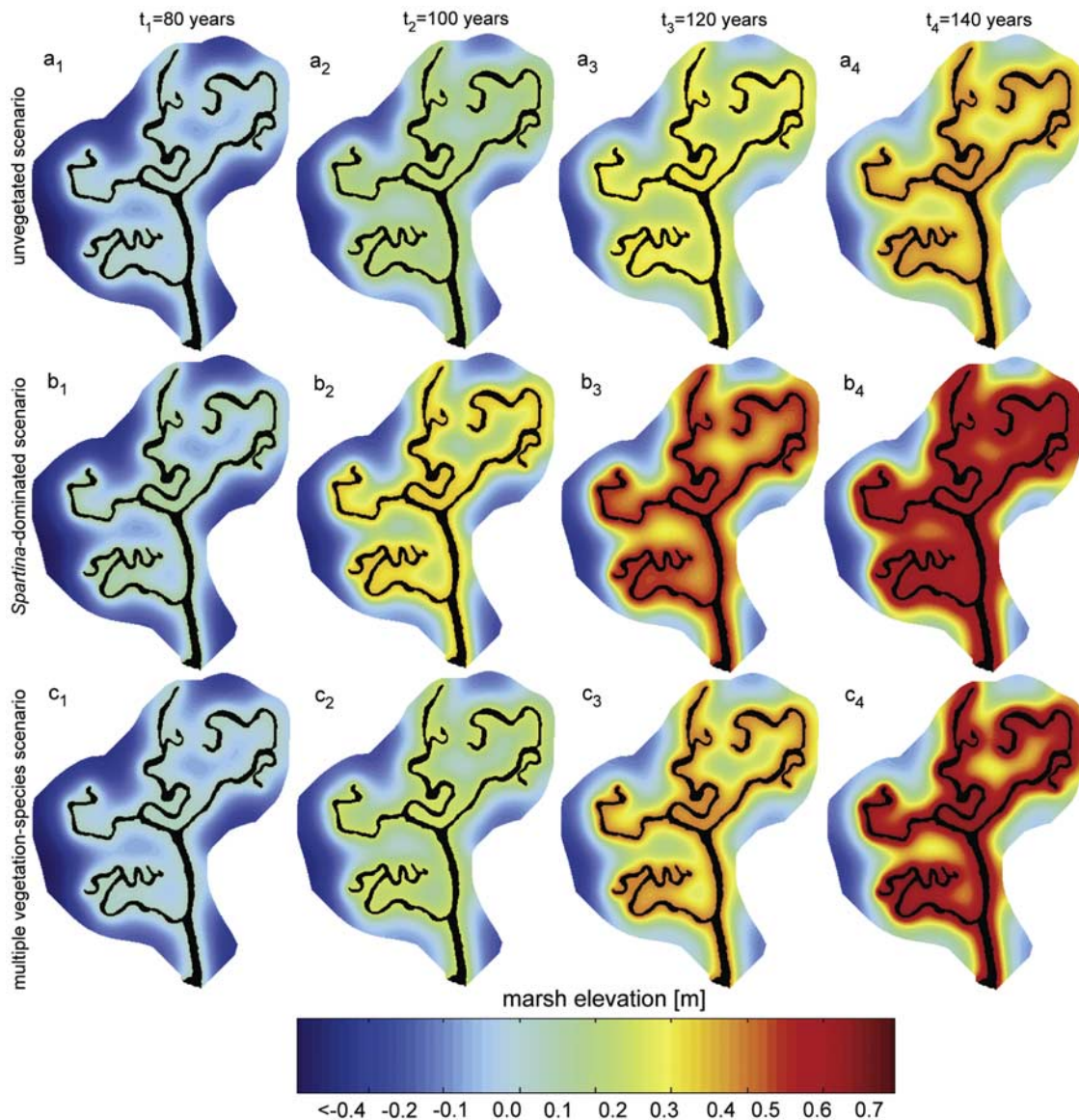
cesses including channel bank slumping, which tends to widen channels while making them shallower. This downslope (topographically diffusive) sediment flux decreases with local biomass density, representing the bank stabilization effect of grasses and their roots. As in the *D'Alpaos et al.* [2006] model, channel bed erosion, which tends to deepen channels, is explicitly included on the basis of local discharge and channel depth.

[35] Although the parameterizations in the Kirwan and Murray model are crude, the holistic treatment of the marsh and channel system allows the qualitative exploration of additional aspects of the biomorphodynamics. When vegetation effects are not included in the model, a morphology resembling tidal flats evolves; a network of channels with sloping banks grade into subtly curved platform-like areas between channels (Figure 11a). Under a low rate of sea level rise (1 mm/a), this morphology reaches an equilibrium in which the net aggradation from depth-dependent deposition rate and erosion rate equals sea level-rise rate everywhere. When vegetation effects are included, a 1 mm/a sea level rise rate also produces an equilibrium morphology, but one in which the platform is essentially flat (with subtle levees near channels), and the channels are steep banked and

narrow (Figure 11b). The sharp boundary between channels and platform, distinctive of tidal marshes, contrasts with the smoother transition without vegetation.

[36] Starting from the vegetated equilibrium developed under 1 mm/a sea level rise (Figure 11b), and increasing the sea level-rise rate to 10 mm/a causes a new equilibrium morphology to develop, which resembles the old one, but with some differences: The platform high-tide depth increases, as does the biomass density (Figure 11c), as could be predicted by the Morris et al. accretion model which is embedded in the Kirwan and Murray model. The consequently increased tidal prisms tend to cause channels to erode. The channels deepen (and extend headward slightly). However, the vegetation and its inhibition of gravitationally driven sediment transport, prevents the channels from widening significantly (Figure 11c).

[37] Starting from the unvegetated 1 mm/a equilibrium and increasing sea level-rise rate to 10 mm/a produces a drastically different result; equilibrium elevations become subtidal everywhere in the domain. Thus, while a vegetated marsh in this model is highly resilient to a moderate sea level-rise increase, under the higher sea level-rise rate the system is metastable; if vegetation were removed, the



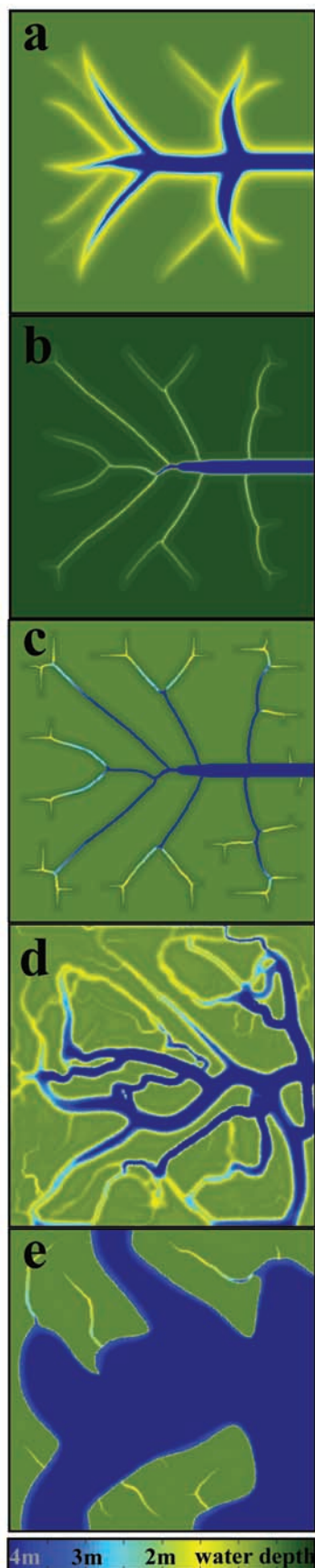
**Figure 10.** Model experiments in which vegetation influences marsh platform evolution [after *D'Alpaos et al., 2007*]. Reading across, each plot represents a different experiment, and reading down, each plot shows successive times. The tidal channel network is based on one measured in the Venice Lagoon.

system would irreversibly revert to a subtidal basin, with bed elevations too low to allow vegetation to come back.

[38] Murray and Kirwan have performed model experiments to explore whether localized and temporary vegetation disturbances can cause the system to switch to the open-water state. In these experiments, vegetation is removed from only portions of the platform (randomly selected model cells), and is allowed to regrow after 1–10 years. Figure 11d shows that even when 50% of the platform is disturbed at any time (and each disturbance lasts for 5 years), a vegetated platform persists under a 10 mm/a sea level–rise rate. The channel network, however, expands considerably (Figure 11d). Recent experiments suggest that under 10 mm/a sea level rise and even minor vegetation disturbance, if the sediment supply (the suspended-sediment concentration in the channels) is decreased, much of the vegetated marsh disappears. (Figure 11e). This experiment

may be relevant to deteriorating marshes in Louisiana and Chesapeake Bay, USA, where relative sea level rates are high, and land use changes have decreased the rate sediment is delivered to coastal wetlands. The result that temporary and local disturbance to vegetation can drastically affect the holistic behavior of the system echoes the findings of *Istanbulluoglu and Bras [2005]* and *Tucker et al. [2006]* regarding fluvial landscapes, discussed in section 2.2.

[39] Animals, as well as plants, can significantly affect tidal wetland morphology. Rapid widening of tidal creeks and consequent marsh erosion in southeast England appears to result from an increase in the population of polychaete worms [*Hughes and Paramor, 2004*]. The worms, likely by disrupting algal mats, make the channel bed sediment easier to erode, as well as discourage plant development by eating seeds. Crabs can inhabit marshes and channel banks in amazing densities, and their burrowing activity can contrib-



ute to the initiation of tidal channels [Perillo and Iribarne, 2003]. Muskrats may play a similar role in some marshes (M. L. Kirwan, unpublished observations, 2006). Grazing by cattle or geese [Miller *et al.*, 1996] reduces vegetation, which in turn restricts sedimentation and increases salinity [Bakker, 1985], preventing marshes from turning into dry land. Depending on the grazing intensity the marsh vegetation will recover or disappear leading to marsh erosion [Miller *et al.*, 1996]. To date studies have pointed to only one-way couplings in which animals affect morphology, although feedbacks from morphology to animal populations seem likely as well.

### 3.2. Tidal Flats and Subtidal Beds

[40] Biomorphodynamic feedback may be responsible for the repeated erosion cycles observed on some marsh-fringing tidal flats. Periods in which vegetation colonizes the tidal flat adjacent to the marsh, extending the marsh basinward, alternate with periods in which wave action produces a marsh-bounding scarp that retreats landward. These cycles could reflect changes in the physical forcing, such as shifts in major subtidal channels and shoals that alter the wave energy impacting the marsh edge. Or, the cycles may arise from dynamics internal to the marsh–tidal flat boundary [van de Koppel *et al.*, 2005a, 2005b]. Vegetation colonizing the tidal flat brings into play the sedimentation biomass elevation feedbacks that tend to rapidly elevate the marsh-fringing tidal flat toward marsh level. However, this elevation creates an increasingly steep slope between the newly vegetated area and the unvegetated tidal flat. The steepness of the slope concentrates wave energy dissipation there, which could eventually initiate another feedback in which erosion further steepens the boundary, leading to a vertical cliff eroding under the wave impact. Simple modeling shows that this scenario is plausible [van de Koppel *et al.*, 2005a, 2005b], although more work is needed before firm conclusions can be reached.

[41] Temmerman *et al.* [2006] have begun to explore feedbacks that occur as plants colonize a tidal flat further from a marsh edge. As patches of vegetation appear on a current-swept tidal flat, the vegetation locally enhances sediment deposition and aggradation, of course. In addition, the enhanced flow resistance in the patches diverts the flow around them, concentrating the currents between the patches, and enhancing erosion there. In numerical modeling including detailed hydrodynamics and vegetation effects [Temmerman *et al.*, 2006], a series of channels self organize from an initially random arrangement of plant colonization. Observations suggest that this interaction can also occur on natural tidal flats [Temmerman *et al.*, 2006]. Because of the demands of the detailed hydrodynamics simulations, the spatial scales represented in these initial experiments are limited. Further work will be needed to examine the channel

**Figure 11.** Numerical experiments involving (a) no vegetation and 1 mm/a sea level rise; (b) vegetation and 1 mm/a sea level rise; (c) vegetation and 10 mm/a sea level rise; (d) 10 mm/a sea level rise and vegetation disturbance (50% of platform cells disturbed, 5 year durations); and (e) 10 mm/a sea level rise, mild vegetation disturbance (5% of platform cells disturbed, 1 year durations), and reduced sediment supply.

spacing formed by this feedback on a more extended tidal flat domain, and to assess a possible connection between these tidal flat channels and the channel networks in fully developed marshes.

[42] Researchers have begun to investigate the substantial effects algae and animals can have on intertidal and subtidal beds [Paarlberg *et al.*, 2005]. Algae enhance bed resistance to erosion by binding the surficial sediments together [Widdows *et al.*, 2000], and by reducing the bed roughness [Lucas *et al.*, 2003]. Many animals, including birds [Davey and Partridge, 1998], shellfish, and worms [Widdows *et al.*, 2000] tend to reduce bed resistance to erosion and increase bed roughness by disturbing surficial sediments. The local mix of organisms can determine the mix of grain sizes and cohesiveness of the surficial sediment [Paarlberg *et al.*, 2005; van de Koppel *et al.*, 2001]. Long-term morphological feedbacks seem almost certain. For example, algae, which tend to trap and bind fine sediment and which flourish in shallow water, could facilitate the growth and stabilization of shoals. Paarlberg *et al.* [2005] and Lumborg *et al.* [2006] have begun to explore such interactions, numerically modeling the effect of spatially variable biology on morphological evolution. Marani *et al.* [2007] use an elegant 1-D vertical analytical model that can be expressed as a stability diagram to investigate the interactions between deposition, wave erosion, and biological influences (marsh vegetation bed-stabilizing organisms). (The Marani *et al.* model is similar to the purely physical model developed by Fagherazzi *et al.* [2006].) All of these factors depend on depth, and the model shows that multiple stable equilibrium states are possible, corresponding to marshes and tidal or intertidal flats. Spatially extended modeling including the effects of evolving morphology on the biology will likely follow.

[43] Bivalves of various sorts can form patches that stabilize the bed. They also strongly affect local hydrodynamics and sedimentation. van de Koppel *et al.* [2005a, 2005b] show that the feedback between mussels, hydrodynamics and soft sediments leads to pattern formation which enhances local sedimentation and productivity of the mussel bed. Coco *et al.* [2006] have modeled the feedbacks arising from bivalves affecting suspended-sediment concentration, and suspended sediment concentration affecting bivalve physiology, feedbacks that could help determine the density of bivalves within patches. On longer timescales, these patch dynamics must couple to morphological evolution, another topic ripe for future elucidation.

[44] Many of the stabilizing and destabilizing effects on sediment beds also occur on shallow continental shelves. Documentation of these biophysical interactions is rarer for shelf environments, possibly because of the difficulty of direct observation, relative to tidal flat and shallow estuarine settings. Baptist *et al.* [2006] show that the abundance of benthic fauna is larger in the troughs than on the crests of large sand waves. Knaapen *et al.* [2003] suggest that a related feedback may influence the sand wave morphology. However, off of open ocean coastlines, where wave energy is much higher than in protected estuarine environments, biological effects may be relatively less important for morphological evolution. For example, on shorefaces, while biological erosion is likely to play a significant role in transforming the underlying material (rocks or partially lithified sediments) into mobile sediment, the common

concave shape of the cross-shore profile can be explained invoking only wave forcing and sediment transport processes.

### 3.3. Coastline Dynamics

[45] On sandy coastlines, dune grasses and coastal dunes evolve symbiotically, as described in section 2.3. Stallins and Parker [2003], on the basis of field studies, suggest that a further biomorphodynamic interaction occurs for beach-backing dunes. Where wave and storm energy is relatively high, such as on an undeveloped barrier island in North Carolina, USA, dunes are frequently knocked down during storms and spread into a low-lying overwash deposit (Figure 12). In this environment, grass species that thrive when periodically buried dominate. However, Stallins and Parker's [2003] observations suggest that the biology also feeds back on the physical processes; the burial tolerant species form horizontally extensive root networks, which tend to create a relatively flat morphology. Thus, low-relief overwash deposits tend to be stabilized in such environments, favoring future overwash events and perpetuating the feedback. On a lower-energy coastline (Sapelo Island, Georgia, USA), less horizontally extensive dune grasses tend to build taller dunes that inhibit the already infrequent overwash events, allowing bushes in the swales to further stabilize that morphology [Stallins and Parker, 2003].

[46] However, where wave and/or tidal energy is high, the longer-term, larger-scale plan view coastline morphodynamics are probably not substantially affected by vegetation or small animals. Figure 13 shows that where an eroding beach meets a forest on a low-wave energy temperate coastline, erosion proceeds despite the trees. The fallen trees on the beach must affect alongshore currents and alongshore transport. However, the persistence of a sandy beach suggests that gradients in sediment flux still determine the evolution of the coastline, and that the vegetation effects may not play a crucial role in that evolution.

[47] In tropical settings, however, biology can exert a stronger influence. Mangrove ecosystems shows close links between geomorphology and vegetation assemblage [Souza Filho *et al.*, 2006]. Souza Filho *et al.* [2006] observe a significant reduction in coastal erosion in the presence of mangroves. The trees reduce wave action on the coast and enhance sedimentation of the bed by sediment trapping and deposition of organic matter. Mangrove ecosystems are sensitive to environmental change and harvesting. Disappearance of the mangroves results in significant coastal erosion [Souza Filho *et al.*, 2006]. Storlazzi *et al.* [2004] describe an Hawaiian coral reef system in which the wide shallow coral reefs suppress tidal flow and nearshore wave energy. As a result, a muddy flat had developed landward of the reef. It is likely that phytoplankton can thrive from the nutrient rich mud in relatively cool deep ocean waters and with plenty of sun light available. In return the production of organic matter is a welcome nutrient source for the reef plankton. Although two-way biophysical coupling in the morphological evolution has not been studied in these environments to date, such coupling seems likely.

[48] One species of large animals, however, exerts a first-order influence on many sandy coastlines in all climate zones: humans. Coastal engineers and scientists have extensively studied the ways that human shoreline stabilization activities (e.g., beach "nourishment" and or sea walls) affect local and adjacent shoreline segments. Slott *et al.*



**Figure 12.** Overwashed sand and gaps in the dune line on Ocracoke Island, North Carolina, USA, after Hurricane Isabel in 2003. Bulldozers clearing the road and rebuilding a dune line give the scale.

[2006] have also begun to study how anthropogenic stabilization in one location can influence coastline morphodynamics at more remote locations. The biophysical coupling obviously extends both ways; if coastline changes were not affecting people, they wouldn't act to stabilize the shoreline. However, this biomorphodynamic system involves additional complications compared to systems affected chiefly by grasses, worms, or even crabs. Human intentionality, economic analysis, and the shifting social and macroeconomic contexts need to be included in an exploration of the coupled human-coastline system. *Werner and McNamara* [2007] have taken an initial step, numerically modeling coupled barrier island-coastal development interactions and the resulting behaviors. *Slott et al.* [2008] have begun to model how beach nourishment decisions are coupled to shoreline evolution, with the goal of exploring the biomor-

phodynamics on extended coastline domains. Despite the challenges in parameterizing the interactions within the human component of the system (involving intentionality, cultural trends and tastes, etc.), the importance of coastal environments to society makes further attempts along these lines inevitable. Of course, coastlines constitute only one example of critical human-landscape interactions likely to be analyzed in the near future. The U.S. National Science Foundation's Coupled Human-Natural Systems program ([http://www.nsf.gov/funding/pgm\\_summ.jsp?pims\\_id=13681](http://www.nsf.gov/funding/pgm_summ.jsp?pims_id=13681), formerly a focal area within the Biocomplexity program) illustrates the societal impetus for such studies.

#### 4. Discussion

[49] Why has this flurry of biomorphodynamic work appeared recently? Part of the answer may be simply a



**Figure 13.** Coastal erosion impinging on a forest in the low-wave energy setting of Hunting Island, South Carolina, USA. Photo taken at approximately high tide by Kelly Stewart.

nonlinear feedback in scientific fashion; interdisciplinary work has become popular within scientific communities, and funding agencies are encouraging it presently.

[50] However, underlying factors fuel this sociological phenomenon, starting with the accelerating pace of global change. Both climate change and increasingly pervasive direct human manipulations impact the ecosystems and environments human civilization relies on, increasing the demand for scientific understanding of these systems to facilitate managing environmental change. As the selective examples in this opinion article illustrate, understanding ecological and morphological change in many environments requires linked study of biological and physical processes.

[51] Recent trends in modeling approaches (conceptual, analytical and numerical), in both ecology and geomorphology, have also facilitated the rapid growth of biomorphodynamics. A tendency has long existed in physical science generally, and in studies of geomorphic systems in particular, to study processes at small scales in the field and laboratory. This tendency may be associated with the implicit assumption that addressing larger-scale, longer-term phenomena has to wait until the small-scale interactions are sufficiently understood. The tendency to build numerical models directly upon representations of processes at scales as small as is practical, “explicit numerical reductionism” [Murray, 2003], reflects this assumption. A complementary modeling approach has arisen in recent decades; a tendency to base conceptual and numerical models on interactions that occur on scales commensurate with those of the phenomena of interest (rather than on scales as small, or “fundamental”, as possible) [Murray, 2003, 2007a; Paola, 2000; Werner, 1999, 2003], sometimes called a “top-down” approach.

[52] This approach stems from developments in nonlinear dynamics and complex systems research, including the emergent-phenomena perspective, and the discovery that complicated behaviors could arise from simple interactions. Thus, a model of a complex geomorphic system may not necessarily need to be based directly on complicated, small-scale processes; a model based on the relatively simple, relatively large-scale interactions that emerge from the collective behavior of the small-scale components of the system is worth investigating. The large-scale phenomena that arise from these interactions then constrain what happens at the smaller scales, as the development of landscape topography does in examples discussed here, so that the smallest-scale processes are not necessarily more fundamental in the sense of determining the overall system behavior. In this perspective, study of small-scale processes are essential for understanding phenomena on those scales, and can provide the basis for parameterizations of larger-scale interactions in models of larger-scale phenomena. Such parameterizations can also be empirically based, or can represent initial conjectures (rules) when empirical data or rigorous syntheses of the large-scale effects of smaller-scale processes are not available.

[53] Some biological influences on physical processes are relatively easy to represent within familiar parameterizations. For example, the effects of plant stems and leaves on hydrodynamics can be represented in partial differential equations on the basis of analyses of small-scale interactions [Leonard and Luther, 1995; Nepf, 1999]. However, addressing two-way biophysical coupling requires modeling

changes in ecological systems as morphology and/or physical forcing changes, which poses more of a challenge to models based on small-scale processes. Complex systems perspectives have also influenced ecology, where top-down, holistic conceptual [Brown and Maurer, 1989] and numerical [Starfield, 1990; Starfield et al., 1989] modeling approaches have increased in popularity.

[54] This confluence of modeling approaches in geomorphology and ecology makes coupled modeling immediately feasible. Models of landscape-scale systems can be based on large-scale interactions within a “cellular” modeling framework. Decades of experience in complex systems research using cellular automata has shown that rich and unexpected behaviors can emerge in a spatially extended domain from simple, local interactions. Many geomorphic models in recent years descend from this perspective, even though such models form a continuum between cellular automata and more traditional, partial differential equation–based models. Rather than the single, discrete-valued variables in classical cellular automata, cellular geomorphic models often involve multiple, continuously valued variables, and some of the local interactions can be finite difference representations of PDEs. The flexibility of this modeling approach facilitates the inclusion of ecological and physical processes, allowing the results of their couplings to be explored [Fonstad, 2006].

## 5. Conclusions and Suggestions

[55] The effects that plants and animals have on sediment transport and morphological change have been studied in many environments for many years [Hupp et al., 1995; Viles, 1988]. However, recent work indicates that influences going in the other direction, sediment transport and morphological change impacting biological development, can be just as important in landscapes and their associated ecosystems. The resulting two-way couplings and feedbacks lead to interesting behaviors and steer landscape evolution in the pioneering studies of what we call biomorphodynamics. We strongly suspect similar two-way coupling is present in many other environments, and believe that Earth surface scientists should learn to look for such interactions, to propel our understanding of landscape (and ecosystem) processes forward.

[56] While the influences of biology on sediment transport and morphological change are relatively easy to recognize and measure, plant and animal communities change in response to physical influences on the timescales of the evolution of a landscape pattern, and are less obvious. The examples we cite here indicate that even local and temporary biological disturbances can, cumulatively, play a significant role in shaping large-scale, long-term landscape evolution. Thus, we feel that the incentives to look for two-way couplings are great, and opportunities likely abound for discerning such couplings where only one-way influences (biology affecting physical processes) have been recognized to date.

[57] Incorporating in numerical models the way ecosystems (and humans!) adapt to physical influences, as well as how they affect physical processes, seems to require a top-down, “synthesist”, “hierarchical” strategy [Murray, 2003, 2007a, 2007b; Paola, 2000; Werner, 1999, 2003], as is common in many complex systems studies. This requires

devising a broader array of parameterizations of interactions at scales commensurate with those of ecological and landscape change. In many cases, these scales will be larger than those for which well-established parameterizations are available. Although simple first guesses based on physical and ecological reasoning and the available data provide a good start in early, exploratory stages of understanding a phenomenon [Murray, 2003], the community will ultimately need to put biomorphodynamics models on solid empirical footing, both to test the validity of exploratory models and to provide more quantitative confidence [Murray, 2007a]. To accomplish this, as a complement to field and laboratory studies of relatively short-term and small-scale processes, we will need to focus on gathering field data concerning physical and ecological change at relatively large scales.

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