Self-organization of a biogeomorphic landscape controlled by plant life-history traits

Christian Schwarz[1,2]*, Olivier Gourgue[2], Jim van Belzen [2,3], Zhenchang Zhu[3], Tjeerd J. Bouma[3], Johan van de Koppel[3], Gerben Ruessink[1], Nicolas Claude[4,5] and Stijn Temmerman[2]

Feedbacks between geomorphology and plants are increasingly recognized as key drivers shaping a variety of landscapes. Most studies of biogeomorphic interactions have focused on the influence of physical plant characteristics, such as stem and root density, on landscape morphodynamics without considering the role of life-history traits. However, pioneer plants can have very different colonization behaviours. Fast colonizers are characterized by a high number of establishing seedlings that produce homogenous vegetation patterns. In contrast, slow colonizers are characterized by a low number of establishing seedlings that are able to expand laterally, resulting in patchy vegetation patterns. Here we combine biogeomorphic model simulations and field observations in the Western Scheldt Estuary, the Netherlands, to show that colonization behaviour can influence the evolution of wetland landscapes. We find that colonization by fast colonizers favours stabilization of pre-existing channels and consolidation of the landscape configuration. In contrast, colonization by slow colonizers facilitates the formation of new channels and thereby actively facilitates further landscape self-organization. Our findings underline the key role of life-history traits in steering landscape self-organization across different biogeomorphic systems, and potentially the long-term resilience of these landscapes to disturbances.

A major advancement in landscape morphodynamics over the past decade is the increasing recognition of the key role of vegetation–landform interactions. Prominent examples are alluvial river landscapes, where vegetation colonization has been shown to instigate a shift from multiple braiding to single meandering channel patterns[1–3]; coastal intertidal landscapes, where vegetation triggers the formation of dense, efficient drainage channel networks[4–6]; fluvial and semiarid hillslopes where vegetation modulates hillslope channel drainage density[7,8]. While theory on biogeomorphological landscape formation is now widely adopted[9], there is little consistent understanding on how species-specific plant traits shape landform patterns or influence landscape self-organization, the process whereby small-scale localized interactions among components of a system generate complex spatial structures at large spatial scales[10].

In this study, we show that plant life-history traits modulate the formation of biogeomorphic landscapes using tidal marshes as model systems. We hypothesize that life-history-mediated colonization rates and patterns are more important in governing the formation and evolution of landforms than previously studied physical plant properties, such as stem density, stiffness and height. Colonization of an initially bare landscape is controlled by two plant life-history traits: (1) establishment probability (that is, chance of appearance of plants on initially bare substrate, for example, by seedling establishment) and (2) subsequent lateral expansion rate (that is, expansion of existing vegetation patches to directly adjacent bare substrate, for example, by tillering). We define life-history-mediated colonization as a combination of these two traits leading to fast homogenous and slow patchy colonizers. We found that fast and slow colonizers cause differences in local-scale vegetation–flow interactions that generate large-scale self-organization effects on tidal channel evolution

and channel geometric properties. Geometric properties are a major determinant for key ecosystem functions of intertidal landscapes, such as biological productivity, sediment and nutrient supply and deposition, and the capacity of tidal wetlands to sustain sediment accretion rates in pace with sea-level rise[4–6,11–14].

We focus on the initial phase of intertidal landscape development where a transition from an initially bare state to a vegetated state occurs. During this phase, the effect of vegetation establishment on channel incision is linked to vegetation colonization rates and patterns. Fast and massive colonization results in a stabilized physical landscape, while slow and patchy colonization results in a self-organized biogeomorphic landscape. Two distinct feedback processes caused by isolated patches (of a few metres square) of primary colonizing vegetation occur: local facilitative (positive) and long-distance hampering (negative) feedbacks[15]. Within vegetation patches, the aboveground plant biomass exerts a drag force slowing down water flow, which diminishes its sediment transport capacity and stimulates sediment deposition[16]. Concurrently, the belowground plant biomass enhances substrate resistance against erosion[16], which in turn facilitates plant growth[15] (that is, local positive feedback). However, the elevated drag force within vegetation patches leads to the rerouting of flow alongside the edges, where increased flow velocity leads to erosion[17,18], hampering recruitment and establishment[15,19] (that is, long-distance negative feedback). The combination of these two processes leads to so-called scale-dependent biogeomorphic feedbacks, which can trigger the initiation of tidal channels in between laterally expanding pioneer vegetation patches and the emergence of self-organized channel networks and physical landscapes[4,6,10]. However, although it is now generally accepted that plants can strongly influence geomorphic processes, little attention has been given to the importance of specific

[1]Department of Physical Geography, Faculty of Geosciences, Utrecht University, Utrecht, Netherlands. [2]Ecosystem Management Research Group, University of Antwerp, Wilrijk, Belgium. [3]Royal Netherlands Institute for Sea Research (NIOZ), Department of Estuarine and Delta Systems, Utrecht University, Yerseke, Netherlands. [4]Laboratoire d'Hydraulique Saint-Venant, Université Paris-Est, ENPC, EDF R&D, CEREMA, Chatou, France. [5]EDF R&D Laboratoire National d'Hydraulique et Environnement (LNHE), Chatou, France. *e-mail: c.s.schwarz@uu.nl
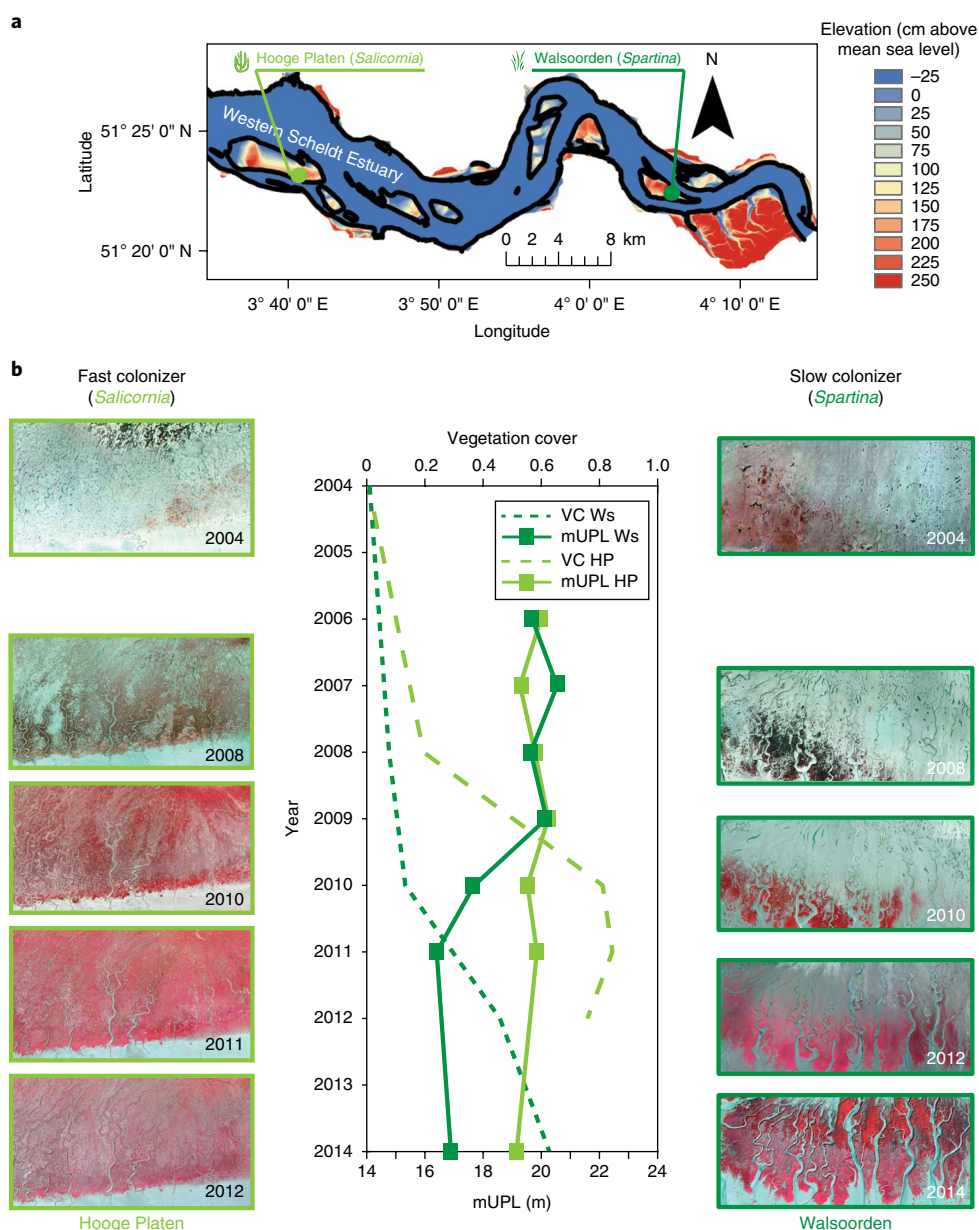
Fig. 1 | False-colour aerial images showing the vegetation and channel development at reference field sites. a, Location of reference sites used for validation for numerical experiments located in the Western Scheldt Estuary, the Netherlands. **b**, Right: Walsoorden (Ws, shown extent 600 m × 300 m), characterized by establishment through slow-colonizing *Spartina*. Left: Hooge Platen (HP, shown extent 600 m × 400 m), characterized by establishment through fast-colonizing *Salicornia*. Pink colour denotes vegetation presence. Numbers in the lower-right corner indicate the year the aerial image was taken. Middle: development of vegetation cover (VC) and the mUPL during vegetation colonization. Dark green, *Spartina* on Walsoorden; light green, *Salicornia* on Hooge Platen.

life-history traits on the resulting self-organization of channel and physical landscape geometric properties.

Primary colonizers of salt marsh ecosystems have developed certain physiological traits to persist in anoxic and regularly inundated soils[20]. These primary colonizers can be grouped based on their life-history strategy-elicited colonization behaviour: as fast-colonizing and slow-colonizing plant species. Fast-colonizing species are characterized by high rates of initial establishment through large seed output and high seedling survival per unit biomass and time. In life-history terms, this can be expressed by a low ratio between lateral expansion rate (LER) and establishment probability (EP). Slow-colonizing species are characterized by either low seed recruitment through low seed output/survival per biomass and time and/or paired with a high LER through vegetative growth[21]. In life-history

terms, this can be expressed by a high ratio between LER and EP. The ratio between LER and EP is further referred to as the colonization dominance index (CDI). A low CDI indicates fast homogenous colonization being dominated by recruitment from seeds and high CDI means slow patchy colonization being dominated by lateral expansion (equation (1)).

$$CDI = \frac{LER}{EP} \qquad (1)$$

where LER and EP are expressed as the fraction relative to the slow colonizer (for details see Supplementary Section 1).

We compare the impact of life-history strategies versus physical plant properties on landscape development by using the fast-colonizing
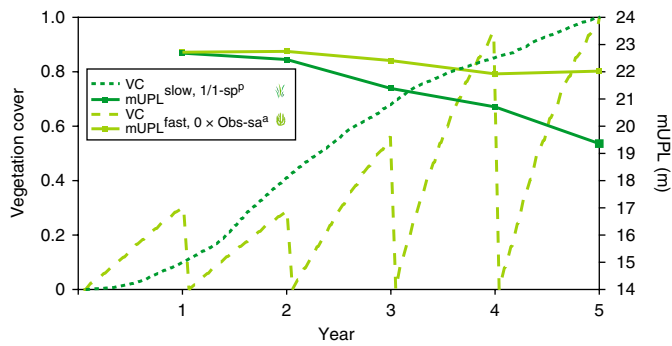
Fig. 2 | Numerical model results (N1) show the development of vegetation cover and mUPL over a five-year simulation period for fast and slow colonizers. The fast colonizer is simulated using the physical properties of *Spartina* (sp) and life-history traits with a CDI = 1 (1/1-sp[p], dark green lines). The slow colonizer is simulated with the physical properties of *Salicornia* (sa) and life-history traits with a CDI = 0 (0 × Obs-sa[a], light green lines), including vegetation die-off at the end of each year with increasing recruitment from years 1 to 5 mimicking recruitment in the field (Supplementary Sections 1 and 5). The initial bathymetry is based on Hooge Platen in 2006. Superscript designations: [p]perennial; [a]annual.

annual *Salicornia europaea* (hereafter referred to as *Salicornia*) and the slow-colonizing perennial *Spartina anglica* (hereafter referred to as *Spartina*) as references (Fig. 1a). Both are dominant pioneer species in northwest European salt marshes, and are very related to other *Salicornia* and *Spartina* species that grow in salt marshes across the globe. The fast-colonizing *Salicornia* is characterized by a high EP, but not capable of lateral expansion leading to a homogenous vegetation pattern (low CDI). Their high EP is achieved by a high seed output and viability, paired with seeds being able to germinate in seawater optimizing their chance for long-distance dispersal and recruiment[22,23]. The slow-colonizing *Spartina* is characterized by a low EP caused by the low percentage of viable seeds produced[24], and a strong root system with a high capability for lateral expansion through tillering, leading to a patchy vegetation pattern (high CDI)[4,6,23,25,26]. We assume that the selection between the two life-history strategies, resulting from environmental conditions such as inundation duration, salinity, soil anoxia or geographic region, has already taken place[23,27–29]. We focus on the fundamentally different effect that the two life-history strategies have on biogeomorphologic landscape development through model simulations and field observations.

Disentangling physical and life-history traits

We first investigate landscape dynamics instigated by colonization of two reference plant species in the field. We then proceed by carrying out numerical simulations (N1), where colonization of our two reference species is modelled through their corresponding life-history strategies and physical plant properties. This showed (1) that landscape dynamics are induced by the properties of the colonizing vegetation species and (2) that our model is able to reproduce vegetation-induced landscape dynamics observed in the field (Fig. 1a,b) (Supplementary Section 2). Thereby the effect of vegetation colonization on landscape development is assessed by calculating the mean unchannelled path length (mUPL). The mUPL is a measure of the distance a drop of water has to travel until it reaches the closest channel. mUPL is a good indicator for drainage network efficiency[5]. Subsequently, we disentangle the importance of life-history strategies and physical plant properties on landscape development by conducting another set of numerical simulations (N2). In N2, various combinations of life-history strategies (modelled through varying EPs and LERs, CDI) and physical plant properties (modelled through varying stem height and density) are tested.

Field observations at two field sites with pre-existing channels dominated by either fast-colonizing *Salicornia* (Hooge Platen) or slow-colonizing *Spartina* (Walsoorden) show contrasting landform dynamics (Fig. 1). The two field sites are very similar in hydrodynamics and sediment characteristics and mainly differ in the colonizing plant species (see Supplementary Section 3). Comparisons of the mUPL show a stable mUPL for the fast-colonizing site (2006–2014) and a decreasing mUPL for the slow-colonizing site (2006–2011) (Fig. 1). A constant mUPL indicates no change in drainage network after plant colonization (stabilization), whereas a decreasing mUPL indicates an increased drainage network through vegetation-induced channel incision. The field data further reveal that it took the slow-colonizer *Spartina* five years to cover the whole area, whereas it took the fast-colonizer *Salicornia* at maximum two years to cover the whole domain.

The conducted simulations were set up following the averaged field site conditions present at intertidal bars in the Western Scheldt Estuary (Hooge Platen and Walsoorden, the Netherlands) before plant colonization (Fig. 1, see Methods for details and Supplementary Sections 3 and 4). The hydrodynamic model (TELEMAC2D) solves the shallow water equations. This is coupled with a sediment transport model (SISYPHE), where sediment transport rate is calculated as a function of excess bed shear stress using the van Rijn transport formula[30,31]. Although winds and fine cohesive sediments have an important control on bar dynamics in various estuarine systems, at the current investigated model systems fine cohesive sediments only become dominant several years after establishment of pioneer vegetation, which was also previously observed in salt marsh systems across the Netherlands and China[12,32]. Wind waves only play a very limited role due to a limited fetch caused by prevalent southwest wind directions[33] (Supplementary Section 3).

This morphodynamic simulation was coupled with a vegetation model, to simulate the biogeomorphic landscape development. The vegetation model resolves spatiotemporal vegetation dynamics (establishment, growth and mortality) governed by stress exerted from currents and water level (see Supplementary Section 1)[4]. The vegetation model only simulates the plant growth season, assuming that the vegetation configuration during winter remains dormant (constant). Additional tests on the impact of different overwintering strategies on morphological development were conducted (Supplementary Section 5). The effect of vegetation is parameterized through flow resistance, using separate expressions for flow resistance due to submerged versus emerged vegetation, following the approach of Baptist et al.[34]. The capacity of the model to reproduce plant–flow interactions due to the contrasting physical plant properties of both species was verified through a calibration step using the results of previously published flume experiments[17,18] (see Supplementary Section 2).

Effects of life-history traits on landscape self-organization

Similar to what we found in the field, our model predicted a strong difference in drainage channel patterns between the fast-colonizing and the slow-colonizing plants (Figs. 1 and 2 (N1) and Supplementary Section 1). The fast-colonizing scenario shows little initiation of new channels, observable through an almost constant mUPL (22.7 to 22.5 m) over the five-year modelling period, indicating only stabilization of pre-existing channels and no formation of new channels (Fig. 2). The slow-colonizing scenario, in contrast, shows that the patchy establishment of vegetation induces formation of new channels in between vegetation patches paired with stabilization (inheritance) of existing channels, observable through a decrease in mUPL from 22.7 to 19.3 m (Fig. 2). The reduction in mUPL following plant colonization demonstrates self-organized landscape development through biogeomorphic feedbacks, while constant mUPL demonstrates stabilization of the pre-existing landscape.

Model analysis (N2) highlighted the importance of life-history strategies on physical landscape evolution, relative to physical plant
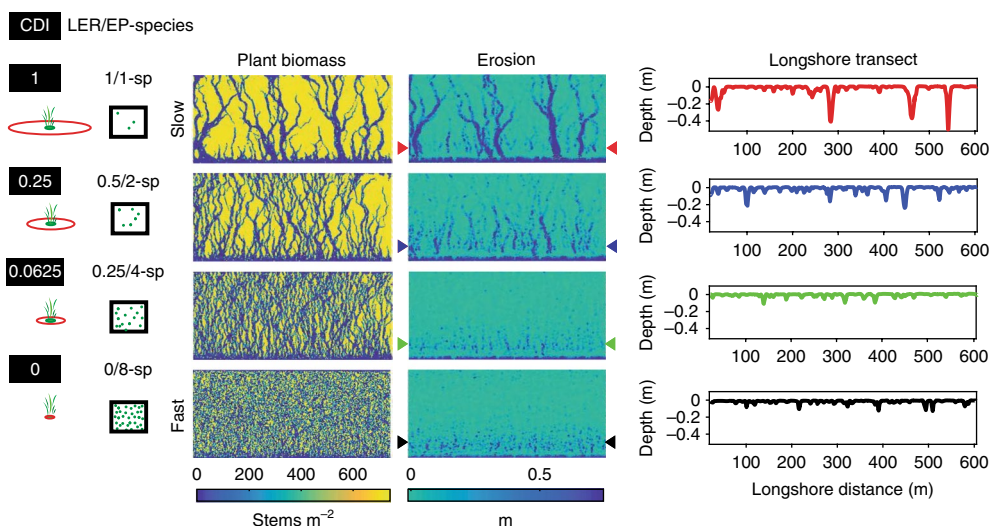
Fig. 3 | Numerical model results (N2) disentangling the effect of life-history strategies and physical plant properties for *Spartina*. Model scenarios of varying life-history strategies (that is, fast-colonizing (1×1) to slow-colonizing (0×8)) with *Spartina* (sp) physical plant properties. Left: model scenarios. Middle: plant biomass and topography. Right: longshore transect over the topography as indicated by arrows in the middle plot.
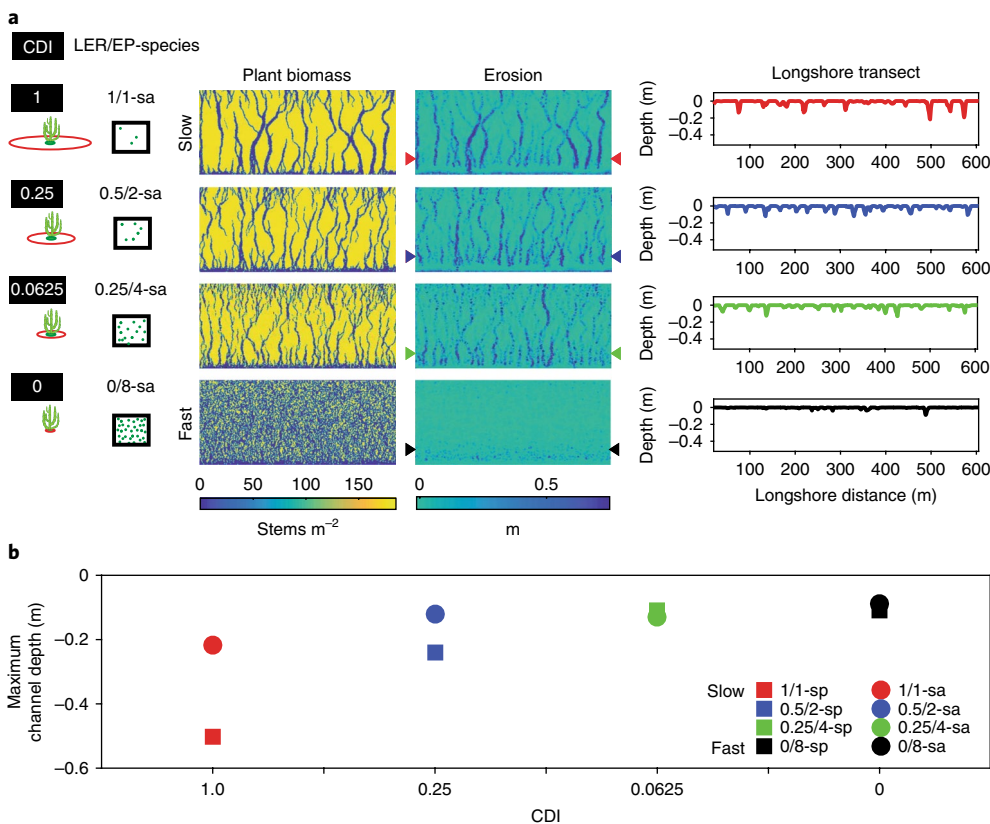
Fig. 4 | Numerical model results (N2) disentangling the effect of life-history strategies and physical plant properties for *Salicornia*. a, Model scenarios of varying life-history strategies (that is, fast-colonizing (1×1) to slow-colonizing (0×8)) with *Salicornia* (sa) physical plant properties. Left: model scenarios. Middle: plant biomass and topography. Right: longshore transect over the topography as indicated by arrows in the middle plot. **b**, Comparison between maximum channel depths of all eight different scenarios, with the CDI plotted on the *x* axis.

properties (Figs. 3 and 4). When we impose a transition in LER and EP from slow-colonizing (CDI=1) to fast-colonizing (CDI=0) characteristics (Figs. 3 and 4), this is the main factor driving channel drainage density, regardless of physically plant properties (Figs. 3 and 4; *Salicornia* versus *Spartina*). A decrease in LER paired with

an increase in EP means a reduction in CDI, indicating a transition from slow- to fast-colonizing life-history strategy. This clearly increases the number of shallow narrow channels, while reducing the number of deep wide channels (Figs. 3 and 4). No channel incision is simulated when the LER is reduced to zero and EP is eight
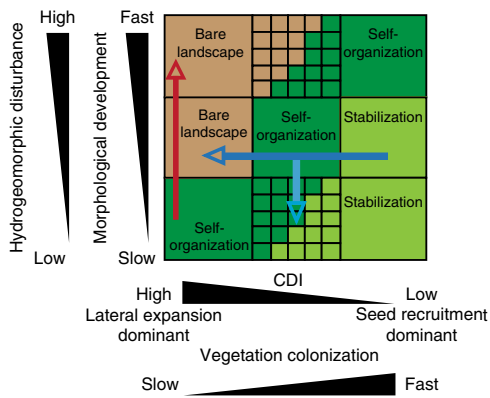
Fig. 5 | Conceptual models showing equivalent timescales between vegetation colonization and morphological development are required for the emergence of self-organized dynamics. A transition from high to low vegetation colonization rate (that is, low to high CDI) at an intermediate morphological development rate shifts the system from stabilizing to self-organizing to eventually bare (dark blue arrow). A reduction in morphological development rate with constant vegetation colonization rate instigates a shift from self-organized to stabilized dynamics (light blue arrow, Supplementary Section 7). Low vegetation colonization rates with increasing morphological development rates instigate a transition from self-organizing to bare system dynamics (dark red arrow).

times the value for the slow colonizer (CDI = 0). This pattern is consistent for simulations that use either physical plant properties of slow or fast colonizers, which highlights the dominant role of life-history strategies in landscape development (Supplementary Section 1). Simulations further show that physical plant properties of the fast colonizer (*Salicornia*) generally result in slightly lower channel depths. Lower channel depths are due to the lower biomass and hence weaker effects on flow and morphodynamics induced by *Salicornia* compared with *Spartina*[17]. In short, these numerical experiments suggest that colonization by plants with differing physical plant properties (*Salicornia*, *Spartina*) evoke similar morphological patterns (emerging channels), whereas plants with differing life-history strategies (specifically LER and EP) induce different morphological patterns (presence/absence of channels) (Figs. 3 and 4).

Slow-colonizing life-history strategies (Figs. 3 and 4: CDI = 1, Supplementary Section 1) lead to a patchy vegetation patterns, facilitating the formation of new channels between laterally expanding vegetation patches that have a low chance of initial establishment. This behaviour is caused by the scale-dependent feedbacks between plant growth, water flow diversion and sedimentation–erosion dynamics, which has been validated at salt marsh ecosystems in the Netherlands and China[4,18,19,35]. The fast-colonizing cases (Figs. 3 and 4: CDI = 0) are characterized by a spatially homogenous vegetation pattern and show no new channels emerging on the initially flat landscape and only little change in mUPL on the initially heterogeneous (channelled) bathymetry (Fig. 2). We propose that, with fast colonization paired with zero (or very slow) LER (CDI = 0), establishing patches remain small and porous, and therefore stay below the size and density threshold for flow acceleration to occur around patches (Figs. 2–4).

Colonization by slow colonizers (*Spartina*) exhibited the emergence of new vegetation-induced channels paired with stabilization of pre-existing channels leading to self-organized biogeomorphic landscapes (bio-self-organized). In contrast, primary colonization by fast colonizers (*Salicornia*) showed exclusively channel template-controlled landscape development, stabilizing pre-existing channels without, or with very little, initiation of new channels

(bio-stabilized) (Figs. 3 and 4). This insight was also confirmed by observed fast colonization of an intertidal bar in the Chinese Liaohe Estuary. There, *Sueada heteroptera*, a fast-colonizing primary colonizer comparable to *Salicornia*, inhabited the bar in about three years[36]. This rapid colonization event lead to a bio-stabilized system where most of the mudflat channels where stabilized after plant colonization (Supplementary Section 6).

We propose the difference between bio-self-organized or bio-stabilized landscape dynamics is determined by the ratio between the timescale of morphological development (influenced among other factors by hydrodynamic forcing, sediment supply and composition) and the timescale of vegetation colonization, which is influenced by life-history strategies shown in the conceptual model in Fig. 5. Our numerical experiments show that with a constant morphological development rate, a reduction in vegetation colonization rate (increasing CDI) changes the system from stabilized to self-organized and eventually to bare (without vegetation) (Figs. 3 and 4 (N2) and Fig. 5 dark blue arrow). This is in agreement with previous insights at alluvial river and delta systems[37–39]. At alluvial rivers, slow vegetation colonization on bars facilitates a more dynamic channel behaviour (for example, creating downstream migrating lobate bedforms), whereas fast vegetation colonization precipitates more stable channel behaviour with only limited morphological change[37,38]. A study on the effect of plant colonization on large-scale delta dynamics found that rapid vegetation colonization enhanced deposition but inhibited vegetation-mediated channelization leading to bio-stabilized landscape dynamics[39].

To study the influence of morphological development on landscape dynamics (*y* axis in Fig. 5), we altered the morphological development timescale in our numerical simulation by reducing the morphological acceleration factor. This lead to a diffuse plant pattern interjected by numerous narrow channels, which compared with our numerical experiments N2 indicated a transition from self-organizing to stabilizing behaviour as observed in Figs. 3 and 4 (Fig. 5 light blue arrow, Supplementary Section 7). Previous research on alluvial rivers where an accelerated morphological development rate at a low constant vegetation colonization rate changed the system from self-organized to bare supports our conceptual model[38,40] (Fig. 5 red arrow).

Implications across biogeomorphic systems

Accordingly, we propose that self-organizing landscapes require equivalent timescales in morphological development and vegetation establishment. When timescales differ, either bare or full vegetated landscapes emerge, with little effect on drainage channel formation. This is either due to the dominance of physical sedimentation–erosion processes preventing vegetation development (bare) or due to the dominance of vegetation colonization processes preventing scale-dependent feedbacks leading to landscape stabilization. The addition of life-history strategies governing vegetation colonization rate and therefore the potential for landscape self-organization, opens new perspectives in evaluating landscape adaptability and re-organization in the face of global change. Morphological development is related to the frequency and magnitude of hydrogeomorphic disturbances. Thus, global change-induced alterations in morphological timescales might influence recolonization behaviour of biogeomorphic systems and ultimately their long-term resilience (the disturbance a system can withstand before shifting its state). For instance, when salt marshes pass through recolonization–erosion cycles[41], increased morphological timescales could reinforce salt marsh erosion. Our proposed conceptual framework could also be used as an indicator system evaluating changes in morphological or colonization timescales and further applied as early warning signals (Fig. 5) of tipping points in landscapes.

Our study emphasizes the importance of the life-history traits of specific species in shaping the physical landscapes of intertidal

systems. This has two important implications. First, for many ecosystems, human-induced change in abiotic conditions triggered by engineering works, such as the salt content of the water in estuaries, may influence landscape evolution even when abiotic conditions are unaffected, because of a shift in the dominant species and life-history strategy. Second, on a more fundamental level, it highlights the importance and control of evolutionary processes in shaping the physical landscape, as plants traits are shaped by natural selection. This implies that landscape features such as marsh creeks reflect how evolutionary processes have shaped biogeomorphological systems that characterize our planet.

Methods

Methods, including statements of data availability and any associated accession codes and references, are available at https://doi.org/10.1038/s41561-018-0180-y.

References

1. Tal, M. & Paola, C. Dynamic single-thread channels maintained by the interaction of flow and vegetation. *Geology* **35**, 347–350 (2007).
2. Gibling, M. R. & Davies, N. S. Palaeozoic landscapes shaped by plant evolution. *Nat. Geosci.* **5**, 99–105 (2012).
3. Braudrick, C. A., Dietrich, W. E., Leverich, G. T. & Sklar, L. S. Experimental evidence for the conditions necessary to sustain meandering in coarse-bedded rivers. *Proc. Natl Acad. Sci. USA* **106**, 16936–16941 (2009).
4. Temmerman, S. et al. Vegetation causes channel erosion in a tidal landscape. *Geology* **35**, 631–634 (2007).
5. Kearney, W. S. et al. Salt marsh vegetation promotes efficient tidal channel networks. *Nat. Commun.* **7**, 12287 (2016).
6. Schwarz, C. et al. Impacts of salt marsh plants on tidal channel initiation and inheritance. *J. Geophys. Res. Earth Surf.* **119**, 385–400 (2014).
7. Collins, D. B. G., Bras, R. L. & Tucker, G. E. Modeling the effects of vegetation–erosion coupling on landscape evolution. *J. Geophys. Res.* **109**, F03004 (2004).
8. Saco, P. M. & Moreno-de las Heras, M. Ecogeomorphic coevolution of semiarid hillslopes: emergence of banded and striped vegetation patterns through interaction of biotic and abiotic processes. *Water Resour. Res.* **49**, 115–126 (2013).
9. Corenblit, D. et al. Feedbacks between geomorphology and biota controlling Earth surface processes and landforms: a review of foundation concepts and current understandings. *Earth Sci. Rev.* **106**, 307–331 (2011).
10. van de Koppel, J., Bouma, T. J. & Herman, P. M. J. The influence of local- and landscape-scale processes on spatial self-organization in estuarine ecosystems. *J. Exp. Biol.* **215**, 962–967 (2012).
11. Ganju, N. K. et al. Spatially integrative metrics reveal hidden vulnerability of microtidal salt marshes. *Nat. Commun.* **8**, 14156 (2017).
12. Schwarz, C. et al. On the potential of plant species invasion influencing bio-geomorphologic landscape formation in salt marshes. *Earth Surf. Process. Landf.* **41**, 2047–2057 (2016).
13. van Maanen, B., Coco, G. & Bryan, K. R. Modelling the effects of tidal range and initial bathymetry on the morphological evolution of tidal embayments. *Geomorphology* **191**, 23–34 (2013).
14. Fagherazzi, S. et al. Numerical models of salt marsh evolution: Ecological, geomorphic, and climatic factors. *Rev. Geophys.* **50**, RG1002 (2012).
15. van Wesenbeeck, B. K., van de Koppel, J., Herman, P. M. J. & Bouma, T. J. Does scale dependent feedback explain spatial complexity in salt marsh ecosystems? *Oikos* **117**, 152–159 (2008).
16. Bouma, T. J. et al. Spatial flow and sedimentation patterns within patches of epibenthic structures: combining field, flume and modelling experiments. *Cont. Shelf Res.* **27**, 1020–1045 (2007).
17. Bouma, T. J. et al. Organism traits determine the strength of scale-dependent bio-geomorphic feedbacks: a flume study on three intertidal plant species. *Geomorphology* **180**, 57–65 (2013).
18. Vandenbruwaene, W. et al. Flow interaction with dynamic vegetation patches: implications for biogeomorphic evolution of a tidal landscape. *J. Geophys. Res. Earth Surf.* **116**, F01008 (2011).
19. Bouma, T. J. et al. Density-dependent linkage of scale-dependent feedbacks: a flume study on the intertidal macrophyte *Spartina anglica*. *Oikos* **118**, 260–268 (2009).
20. Friess, D. A. et al. Are all intertidal wetlands naturally created equal? Bottlenecks, thresholds and knowledge gaps to mangrove and saltmarsh ecosystems. *Biol. Rev.* **87**, 346–366 (2012).
21. Huston, M. & Smith, T. Plant succession: life history and competition. *Am. Nat.* **130**, 168–198 (1987).
22. Heukels, H., van der Meijden, R. & Bruinsma, J. *Heukels' Flora van Nederland* (Wolters-Noordhoff, Groningen, 1990).
23. Wolters, M., Garbutt, A., Bekker, R. M., Bakker, J. P. & Carey, P. D. Restoration of salt-marsh vegetation in relation to site suitability, species pool and dispersal traits. *J. Appl. Ecol.* **45**, 904–912 (2007).
24. Author, S., Marks, T. C. & Truscott, A. J. Variation in seed production and germination of *Spartina anglica* within a zoned salt marsh. *Source J. Ecol. J. Ecol.* **73**, 695–705 (1985).
25. van der Wal, D., Wielemaker-Van den Dool, A. & Herman, P. M. J. J. Spatial patterns, rates and mechanisms of saltmarsh cycles (Westerschelde, The Netherlands). *Estuar. Coast. Shelf Sci.* **76**, 357–368 (2008).
26. Balke, T. et al. Conditional outcome of ecosystem engineering: a case study on tussocks of the salt marsh pioneer *Spartina anglica*. *Geomorphology* **153**, 232–238 (2012).
27. Silvestri, S., Defina, A. & Marani, M. Tidal regime, salinity and salt marsh plant zonation. *Estuar. Coast. Shelf Sci.* **62**, 119–130 (2005).
28. Bertness, M. D. Zonation of *Spartina patens* and *Spartina alterniflora* in a New England salt marsh. *Ecology* **72**, 138–148 (1991).
29. Davy, A. J., Brown, M. J. H., Mossman, H. L. & Grant, A. Colonization of a newly developing salt marsh: disentangling independent effects of elevation and redox potential on halophytes. *J. Ecol.* **99**, 1350–1357 (2011).
30. Villaret, C., Hervouet, J.-M., Kopmann, R., Merkel, U. & Davies, A. G. Morphodynamic modeling using the Telemac finite-element system. *Comput. Geosci.* **53**, 105–113 (2013).
31. Van Rijn, L. C. *Principles of Sediment Transport in Rivers, Estuaries and Coastal Sea*s (Aqua Publications, Amsterdam, 1993).
32. Temmerman, S., Govers, G., Wartel, S. & Meire, P. Modelling estuarine variations in tidal marsh sedimentation: response to changing sea level and suspended sediment concentrations. *Mar. Geol.* **212**, 1–19 (2004).
33. Callaghan, D. P. P. et al. Hydrodynamic forcing on salt-marsh development: distinguishing the relative importance of waves and tidal flows. *Estuar. Coast. Shelf Sci.* **89**, 73–88 (2010).
34. Baptist, M. J. et al. On inducing equations for vegetation resistance. *J. Hydraul. Res.* **45**, 435–450 (2007).
35. Schwarz, C. et al. Interactions between plant traits and sediment characteristics influencing species establishment and scale-dependent feedbacks in salt marsh ecosystems. *Geomorphology* **250**, 298–307 (2015).
36. Jia, M. et al. Monitoring loss and recovery of salt marshes in the Liao River Delta, China. *J. Coast. Res.* **300**, 371–377 (2015).
37. Nicholas, A. P. Modelling the continuum of river channel patterns. *Earth Surf. Process. Landf.* **38**, 1187–1196 (2013).
38. Corenblit, D. et al. Engineer pioneer plants respond to and affect geomorphic constraints similarly along water–terrestrial interfaces world-wide. *Glob. Ecol. Biogeogr.* **24**, 1363–1376 (2015).
39. Piliouras, A., Kim, W. & Carlson, B. Balancing aggradation and progradation on a vegetated delta: the importance of fluctuating discharge in depositional systems. *J. Geophys. Res. Earth Surf.* **122**, 1882–1900 (2017).
40. Bertoldi, W. et al. Modeling vegetation controls on fluvial morphological trajectories. *Geophys. Res. Lett.* **41**, 7167–7175 (2014).
41. Bouma, T. J. et al. Short-term mudflat dynamics drive long-term cyclic salt marsh dynamics. *Limnol. Oceanogr.* **61**, 2261–2275 (2016).

Acknowledgements

Author contributions

C.S, O.G., N.C. and J.v.B. designed the model experiments and analysed the data. Z.Z., G.R. and J.v.d.K. contributed to interpreting the paper. C.S., S.T. and T.J.B. wrote the paper.

Additional information

Methods

Life-history strategies. Primary colonizers of salt marsh ecosystems can be grouped based on their life-history strategies. Fast-colonizing plants are characterized by high seed output and viability able to produce large transient seed banks[42]. Examples are *Salicornia procumbens*, *Salicornia europea* and *Sueda maritima*[20,23,27,43], which typically are able to rapidly colonize large areas, but without the ability to produce lateral tillers. Slow-colonizing plants are characterized by low recruitment from seeds but able to reproduce both sexually through seeds and asexually by producing clonal tillers, leading to lateral expanding plant patches. Although these plants are able to use both proliferation strategies, previous studies have shown that their colonization pattern is mainly determined by a low initial establishment chance but extensive clonal growth of the few established patches[23]. Examples are *Spartina anglica*, *Spartina alterniflora*, *Sarcocornia perennis* and *Puccinellia maritima*, to name a few dominant species in northwest Europe, the United States and China[23,44].

Model set-up. We used the hydrodynamic module TELEMAC2D coupled two-way with the morphodynamic and sediment transport module SISYPHE to compute flow, sediment transport and morphology in our intertidal environment. The model solves the two-dimensional depth-averaged equations for momentum and continuity for unsteady incompressible turbulent flow (shallow water equations). The hydrodynamic and morphodynamic modules are fully coupled, which means that the flow field adjusts immediately as bed topography changes. For our study, we focus only on erosional properties, although sedimentation is possible in our model environment, the sediment boundary conditions were set to maintain a boundary equilibrium concentration, resulting in very little additional sediment input for inorganic sedimentation[30].

The model domain represents an initially uncolonized intertidal bar, present in the Western Scheldt Estuary, the Netherlands, in 2006, called Hooge Platen (51° 23′ 04″, N 3° 40′ 50″ E) (Supplementary Section 4). Hooge Platen experienced massive plant colonization by *Salicornia* from bare to complete cover over a period of five years (2006–2011), subsequently also used for model validation. For numerical model simulations, N2, an idealized averaged field bed topography was used with a slope of 0.001 m m⁻¹ (average elevation 1.4 m above mean sea level). At the southern end of the domain (near the open boundary), the slope was increased to 0.005 m m⁻¹ representing the adjacent channel of the Scheldt Estuary (Supplementary Section 4). For numerical simulations, N1, a real initial bathymetry (with pre-existing channels) was used based on the field bathymetry measured using lidar at Hooge Platen in 2006 (Supplementary Section 4). The model domain consists of a 600 × 600 m unstructured grid composed of 80,643 triangular elements with a 600 × 300 m area of interest and an average mesh resolution of approximately 2 m (Supplementary Section 4). The open boundary is located at the southern side of the model domain (Supplementary Section 4). At each computational time step, the coupled hydrodynamic–morphodynamic model is solved using an average semi-diurnal tidal forcing (main tidal harmonic component at this location) with a time step of 6 s fulfilling the Courant–Friedrichs–Lewy condition. Tidal action was simulated by imposing a sinusoidal water-level fluctuation (M2) at southern open boundary of the domain representing average field conditions (amplitude, 2.4 m; period, 745 min). The simulation is run for 20 d, which is then multiplied online with a morphological factor of 91.25 at each time step to simulate a morphodynamic development of five years. For additional information about the model behaviour, please refer to Supplementary Section 8.

For sediment transport, we use the van Rijn sediment transport formulation for non-cohesive sediments, based on available data of bottom sediment properties at the period of interest provided by the Dutch authorities (Rijkswaterstaat, RWS.nl) (Supplementary Section 3). Although there might be fine sediment available for suspended transport, as the bottom sediment showed a non-cohesive character, the van Rijn transport formula was chosen (for further details see Supplementary Section 3)[45]. The above-described hydromorphodynamic model is coupled online to a spatiotemporal vegetation-growth module (for details see 'Vegetation-growth module'). The bed evolution is calculated using the mass-conservation equation of Exner. The effect of aboveground plant structures on tidal flow was incorporated by following the approach of Baptist et al.[34] in our TELEMAC2D depth-averaged model environment. This method treats vegetation stems as uniformly spaced rigid vertical cylinders, where flow velocity through the stems is assumed to be uniform within the vegetation after passing the vegetated–unvegetated boundary. The effect of vegetation is parameterized through the flow resistance, with separate expressions for flow resistance due to submerged and non-submerged vegetation. The extra drag force exerted by vegetation results in momentum loss, which reduces the basal shear stress on a vegetated bed representing the impact of vegetation on sediment transport[46–48]. The two investigated plant species (*Spartina* and *Salicornia*) differ in physical plant properties (such as stiffness, stem density, maximum height and stem diameter) and life-history strategies (Supplementary Section 1). For this reason, we used data gathered during the HYDRALAB III[17,18] experiment, a medium-scale flume experiment on vegetation patch–flow interactions, to validate the simulated species-specific physical plant properties governing plant–flow interactions (for details refer to Supplementary Section 2).

How different life-history strategies are incorporated in the model is described below (see 'Vegetation-growth module').

Vegetation-growth module. The model simulates spatiotemporal changes in stem density with a constant year-averaged stem height, diameter and drag coefficient for *Spartina* and *Salicornia* following previously proposed processes (for details on the model equation please refer to Supplementary Sections 1 and 2)[4,6]. Vegetation is treated as uniformly spaced vertical cylinders, assumed to induce uniform flow within vegetation stems. Shear stress acting on vegetation results in a loss of momentum, which reduces shear stress on the bed, but can lead to flow acceleration between neighbouring vegetation patches. Initial plant establishment on bare grid cells is modelled stochastically with a user-defined initial minimum plant cover. Lateral expansion of plants to neighbouring cells is modelled through a diffusion equation. Plant mortality is determined by the tide integrated tidal flow stress and by tidal averaged inundation stress following ref. [4]. For details on the parameter settings please refer to Supplementary Section 1.

Different life-history strategies are modelled by adapting the plant EP and LER. The slow-colonizing scenario simulates physical plant properties (*Spartina*) and a life-history strategy able to reproduce from seeds and by tillering through a relatively low EP (0.01 yr⁻¹ referred to as 1 in Fig. 2) and a relatively high LER (0.2 m² yr⁻¹ referred to as 1 in Supplementary Section 1)[4,6,47]. Temporal dynamics assumes an extended growth cycle, by removing the dormant winter season as done at different numerical salt marsh experiments[4,6]. The fast-colonizing scenario simulates physical plant properties (*Salicornia*) and life-history traits only able to recruit from seeds from a relatively high seed EP with no LER and annual field observation-based temporal dynamics (Supplementary Section 1). At field observation-based annual temporal dynamics (0 × Obs-sa[a]), vegetation biomass die-off occurs at the end of every simulated morphological year with increasing EPs of 8, 16 and 24 over time. The EPs were adapted following the measured aboveground biomass development at Hooge Platen (Fig. 1), with an EP during years 1 and 2 of 8 times, during year 3 of 16 times and in years 4 and 5 of 24 times the EP of *Spartina*. These values were chosen to reach the desired recruitment rate as observed in field observations (Fig.1). This increased recruitment between years could be caused, for instance, by gradually improving environmental conditions, which, however, exceeds the scope of the study.

To disentangle the effect of different combinations of LERs and EPs on morphological development, simulations using fractions and multiples of field values for LERs (1×, 0.5×, 0.25×, 0×) and EPs (1×, 2×, 4×, 8×) of *Spartina*[23] were conducted, varying the CDI from 1, 0.25, 0.0625 to 0. Previous studies showed that LERs and EPs of 1 × 1/0 × 8 are a good representation of growth strategies of *Spartina/Salicornia*, respectively[4,23].

The minor impact of different seasonal dynamics on the of the annual species was shown through conducted pre-experiments (see Supplementary Section 5).

The vegetation module is coupled with the hydromorphodynamic module (biomorphodynamic model) twice per M2 tidal cycle. One year in morphological and vegetation time is defined by four hyrdrodynamic days or eight vegetation couplings (4 hydrodynamic days × morphological factor 91.25 = 365), which is sufficient to track biogeomorphic vegetation development. Establishment and expansion strategies are based on the literature[4,23,49] (see Supplementary Section 2). The biomorphodynamic model was simulated over a period of five years, which according to pre-tests has shown to be sufficient to reach dynamic equilibrium. As the main focus lies on the final channel configuration, dynamic equilibrium was defined as bed level changes <0.1 mm yr⁻¹. A control run with no vegetation was computed showing no morphologic adaptations over the simulation period.

Vegetation cover calculations. We calculated vegetation cover from available false-colour aerial photographs of the Western Scheldt. Vegetation cover was calculated applying a supervised classification algorithm of ArcGis 10.2 using clear distinguishable vegetation tussocks as sample datasets.

Drainage network delineation and mUPL. Post-processing was done using MATLAB and Blue Kenue. The channel networks were extracted using the TopoToolbox[50], previously used for the extraction of terrestrial channel networks. The UPL is a measure of the distance a particle of water at any point of the platform has to travel on before reaching a channel[5]. After we divided the marsh platform in subbasins using the TopoToolbox UPL for the seven biggest subbasins was calculated by fitting a probability density function to the scalar field and determining the slope of the linear part[5,51]. Subsequently the mUPL for the entire marsh platform was calculated by averaging the UPLs over these subbasins.

References

42. Adam, P. *Saltmarsh Ecology* (Cambridge Univ. Press, Cambridge, 1990).
43. Marani, M., Lanzoni, S., Silvestri, S. & Rinaldo, A. Tidal landforms, patterns of halophytic vegetation and the fate of the lagoon of Venice. *J. Mar. Syst.* **51**, 191–210 (2004).
44. Shumway, S. W. & Bertness, M. D. Salt stress limitation of seedling recruitment in a salt marsh plant community. *Oecologia* **92**, 490–497 (1992).
45. van Ledden, M., van Kesteren, W. G. M. & Winterwerp, J. C. A conceptual framework for the erosion behaviour of sand–mud mixtures. *Cont. Shelf Res.* **24**, 1–11 (2004).
46. Vargas-Luna, A., Crosato, A., & Calvani, G. Representing plants as rigid cylinders in experiments and models. *Adv. Water* **93**, 205–222 (2016).
47. Nardin, W. & Edmonds, D. A. Optimum vegetation height and density for inorganic sedimentation in deltaic marshes. *Nat. Geosci.* **7**, 722–726 (2014).
48. Meire, D. W. S. A., Kondziolka, J. M. & Nepf, H. M. Interaction between neighboring vegetation patches: impact on flow and deposition. *Water Resour. Res.* **50**, 3809–3825 (2014).
49. Ungar, I. A. Population characteristics, growth, and survival of the halophyte *Salicornia europaea. Ecology* **68**, 569–575 (1987).
50. Schwanghart, W. & Kuhn, N. J. TopoToolbox: a set of Matlab functions for topographic analysis. *Environ. Model. Softw.* **25**, 770–781 (2010).
51. Marani, M., Lanzoni, S., Zandolin, D., Seminara, G. & Rinaldo, A. Tidal meanders. *Water Resour. Res.* **38**, 1225 (2002).