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The influence of local and landscape-scale processes

on spatial self-organization in estuarine ecosystems

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1   **Summary**

2   Complexity theory proposes that spatial self-organization, the process where small-scale,

3   localized interactions among the components of a system generate complex spatial

4   structures at large spatial scales, explains the formation of autogenic spatial patterns in

5   ecosystems. We question this premise by reviewing three estuarine ecosystems - mussel

6   beds, mudflats and salt marshes - where self-organization has been put forward to explain

7   spatial patterns. Our review highlights that these self-organized estuarine systems are

8   shaped by the combination of small-scale interactions between ecological and physical

9   processes on the one hand, and large-scale physical forcing on the other. More

10   specifically, local interactions generate patchiness at small spatial scales, whereas

11   landscape forcing determines the shape and orientation of these patches in the landscape.

12   We present a framework that illustrates how self-organized ecosystems are shaped by

13   interactions between organisms and physical processes occurring at multiple spatial

14   scales. Moreover, the present review of estuarine systems underlines that scale-dependent

15   feedbacks are capable of explaining much more complex spatial patterns than the regular

16   patterns to which they have been applied so far.

17   **Introduction**

18   Many estuarine ecosystems are characterized by striking spatial patterns. From the air,

19   mussel beds can reveal stunning banded patterns that remain regular over an extensive

20   spatial ranges (Fig 1a). In mudflats, diatoms can generate patchy landscapes of elevated

21   hummocks covered by dense diatom biofilms (Fig 1b). Salt marshes reveal fractal like

22 creek structures along which vegetation patterns are aligned (Fig 1c). Recent research has

23 suggested that organisms within these spatial patterns do not simply follow landscape

24 features, but that an intricate interaction between ecological and physical processes is a

25 central explanation for the observed landscape complexity (Klausmeier, 1999; Van de

26 Koppel et al., 2005; Temmerman et al., 2007; Weerman et al., 2010). Similar spatial

27 patterns have been observed all over the world, in systems ranging from arid bush lands

28 to boreal peat lands (Rietkerk and Van de Koppel, 2008).

29 Complexity theory puts forward that small-scale, localized interactions between

30 components of a system can generate spatial patterns at larger spatial scales through a

31 process called spatial self-organization, even in the absence of external, landscape-scale

32 forcing (Levin, 1998). So what characterizes these "local" interactions? In estuarine

33 systems, organisms experience the direct and indirect effects of the tidal water. Whereas

34 water motion from currents and waves is an important supply of resources like e.g., food

35 and oxygen, it also imposes a force that can dislodge organisms. Especially wave action

36 during storm events can impose a strong disturbing force. Many organisms have special

37 adaptations or strategies to cope with these mechanical forces. Salt marsh plants form

38 dense clumps in which the effects of water flow are diverted. Mussels form mats by

39 binding to each other using byssus threads, preventing dislodgement by waves and water

40 flow (Waite and Broomell, this volume). Other organisms dig into the sediment, only to

41 come out when the tidal flow has subsided. These adaptations invoke a wide range of

42 ecological, physical and biomechanical interactions, which can have a profound influence

43 on how estuarine communities are organized. Many communities are characterized by

44 strong aggregation of the organisms, as is found in mussel beds, oyster beds, diatom

45 biofilms and salt marshes. The spatial structure of these intertidal communities was found

46 to be determined by the interplay of positive and negative interactions within the system

47 (Gascoigne et al., 2005; Van de Koppel et al., 2005; van de Koppel et al., 2008; Weerman

48 et al., 2010). A reoccurring feature is that intraspecific positive interactions act on a local

49 scale: organisms can resist mechanical forces by clumping direct to neighbouring

50 individuals, which for instance protects against wave action or stimulates sedimentation.

51 Negative interactions, however, such as competition for algae, predominate at a

52 somewhat larger spatial scale. The resultant of these interactions at different scales is that

53 positive interactions predominate at short distance from any individual, whereas negative

54 interactions mainly occur at larger distance. This scale-dependent interplay between

55 positive and negative interactions has been found to explain the formation of spatial

56 complexity in estuarine systems such as mussel beds and mudflats, but similarly in other

57 patterned ecosystems all over the world (Rietkerk and Van de Koppel, 2008).

58 We question the premise of complexity theory that self-organized spatial patterns are

59 primarily shaped by local interactions at scales below that of the observed spatial

60 patterns. Results from a number of spatially self-organized systems lead us to propose

61 that the shape of many self-organized spatial patterns is often determined by a

62 combination of local interactions and large-scale physical forcing. We therefore

63 hypothesize that small-scale interactions between organisms and physical processes can

64 break the symmetry of an ecosystem to initiate pattern, in terms of a concentration or

65 aggregation of individuals in clusters of a particular scale. How these feedbacks scale up

66 to determine ecosystem structure and functioning is determined by the physical

67 constraints on organism-environment feedback, set by the landscape. Hence, our

68 hypothesis implies that both local and landscape-level processes shape self-organized

69 spatial patterns in ecosystems.

70 Here, we review three estuarine ecosystems that illustrate how physical constraints at

71 large spatial scales determine the spatial complexity of an estuarine ecosystem. First, we

72 use mussel beds to show how the physical setting shapes spatial patterns that basically

73 originate from an ecological interaction. Second, we discuss a diatom-covered mudflat

74 ecosystem where interactions between the physical process of water drainage and

75 increased sedimentation by benthic diatoms generate a regular physical landscape.

76 Finally, we discuss how a scale- and density-dependent feedback induced by salt-marsh

77 vegetation interacts with the physical settings to generate a complex salt-marsh

78 landscape. Our examples demonstrate that, despite of their complexity, estuarine habitats

79 are shaped by simple, interactions between biology and physics operating at both local

80 and landscape scales.

81 **Mussel beds**

82 Mussel beds on soft sediment often have a patchy appearance, where dense aggregations

83 of mussels alternate with nearly bare sediment (Snover and Commito, 1998; Gascoigne et

84 al., 2005). When viewed from the air, the seemingly haphazard patchiness reveals itself

85 as being strikingly patterned: elongated mussel patches are aligned in a regular fashion

86 perpendicular to the incoming flood direction. In particular in young mussel beds that

87 have not gone through their first winter, regular patterning is strong and consistent over

88 extensive ranges. Older mussel beds can have a more fractal appearance, likely due to the

89 disturbing effects of strong wave action due to storms.

5

90   Can we explain the formation of regular patterns in mussel beds from the ecology of

91   mussels? Mussels are filter feeders that occur on concentrated beds in a wide range of

92   temperate intertidal systems. Mussels aggregate to form tight mats in which they bind

93   themselves together using byssus threads. In these mats, they are better protected against

94   predation and wave dislodgement (Bertness and Grosholz, 1985; Hunt and Scheibling,

95   2001, 2002), generating a direct positive interaction between neighbouring mussels via

96   byssus connection. Being filter feeders, however, mussels also interact by depleting the

97   algae in the lower water layers (Bertness and Grosholz, 1985; Newell, 1990; Svane and

98   Ompi, 1993), which can generate strong competition for food. Competition can act at

99   large spatial scales as the water flows over the mussel bed. Models have shown that this

100   interplay between facilitation via byssus connections on a small spatial scale and

101   competition for algae at a larger spatial scale generates spatial self-organization within

102   mussel beds that can explain the observed regular spatial patterns in mussel beds (Van de

103   Koppel et al., 2005).

104   The above described approach views pattern formation between mussels is to a large

105   extent an ecological process. However, comparison of mussel beds in different tidal

106   conditions reveals the effects of the large-scale physical setting in which a mussel bed

107   can be found. If water flow is minimal, as is for instance the case in the limfjorden in

108   Denmark, no consistent patterning is found at scales above one meter (Ysebaert et al.,

109   2009). In contrast, in intertidal areas with strong tidal currents, mussel beds typically

110   form banded patterns. Integral to these banded patters are the physical constraints set by

111   the flow rate causing the banded patterns to be aligned perpendicular to the flood

112   direction, as the incoming floods carry most of the algae.

Mudflat ecosystems

114   An close interaction between biology, hydrodynamics and geomorphology generating a

115   spatially patterned landscape is found in patterned, diatom-covered mudflat ecosystems.

116   On intertidal mudflats, spatial patterns can develop in the form of diatom-covered

117   hummocks alternating with water-filled hollows where diatom density is much lower.

118   Diatoms can form thick biofilms through the excretion of extracellular polymeric

119   substances (EPS), which form a smooth film on top of the sediment, trapping fine-grained

120   sediment particles and preventing them from being eroded by the shear stress imposed by

121   the tidal currents. As a result, sediment accumulates underneath these biofilms,

122   generating proto-hummocks on which thick biofilms can persist. However, this results in

123   water diverting away from these hummocks and accumulating in the hollows, which face

124   increasing water levels as they receive the drainage water remaining on the tidal flat after

125   the tides have receded (Fig 2). In this remaining water layer, EPS dissolves, reducing the

126   integrity of the biofilm, and making the sediment more vulnerable to erosion. As a

127   consequence of this interplay between diatom biofilm growth, sediment accumulation and

128   erosion, and water drainage, a regular landscape of hummocks develops interspersed with

129   gullies that form a drainage network. Hence, also in this mudflat, the interplay between

130   ecological and physical processes can explain self-organized patterns (Weerman et al.,

131   2010).

132   Although local diatom-sedimentation feedbacks form the central mechanisms behind the

133   observed patterns, the spatial characteristics of this hummock and hollow landscape is set

134   by the physical constrains determined by the landscape. If the tidal flat covers a large area

135 and is very flat, water flow can be very high once the system submerges, and near-linear

136 patterns of ridges and runnels emergence parallel to the flow direction, as is observed in

137 the Marenne-Oléron tidal flats in France (Laima et al., 1999) or the Humber estuary in

138 England (Blanchard et al., 2000). When flow rates are much reduced, more roundish

139 patterns become prominent, as was described in the Kapellebank tidal flat in the

140 Westerschelde, the Netherlands (Weerman et al., 2010). Again, although at its heart the

141 mudflat patterns are generated by a feedback that involves organisms, physical

142 constraints imposed by the landscape determine their final shape.

143 Salt marsh ecosystems

144 Among the most striking spatially patterned ecosystems found in estuaries are salt

145 marshes. Salt marshes are shaped by drainage creeks that form feather-shaped networks

146 removing the tidal water from the marsh during ebb periods. At the banks of the creeks,

147 increased sedimentation of sandy particles causes the formation of elevated levees. The

148 elevated marsh platform that forms due to increased sedimentation in between the creeks

149 hence gets bounded by levees, forming a basin. As a consequence, the areas in between

150 these levees drain less efficiently, generating a landscape with clear variation in

151 waterlogging of the soil (Allen, 2000). Hence, in salt marshes, variation in elevation and

152 water logging are the main drivers of salt marsh vegetation patterns, which can persist for

153 extended periods of time (Bertness, 1999; Allen, 2000).

154 At first glance, the vegetation may appear to just follow the variation in landscape

155 properties. A typical property of salt marshes, however, is that the landscape itself is

156 mostly biogenic, e.g. the formation of saltmarshes geomorphology is for a large part the

8

157 result of a close interaction between biology, hydrodynamics, and geomorphology (Allen,

158 2000). Salt-marsh vegetation attenuates both wave energy and water flow, which in turn

159 prevents erosion and stimulates the settlement of fine-grained sediment. As a

160 consequence, salt marshes typically increase in elevation during their development, and

161 can accumulate extensive amounts of sediment (Kirwan et al., 2010). This results in a

162 decrease of the influence of tidal flow and of salt water, and as a consequence the marsh

163 becomes more benign to plant growth (Allen, 2000).

164 Sediment accumulation on salt marshes does not occur homogeneously over space.

165 Initially, sediment-stabilizing plants such as *Spartina anglica* or *Puxinellica maritima*

166 establish in isolated patches, which develop dome-shaped hummocks over time due to

167 increased sedimentation. Water flow gets diverted around these hummocks, where water

168 flow rates increase, generating increased erosion, especially in high energy environment

169 (Fig 3a) (Bouma et al., 2007). Divergence of water flow around expanding vegetation

170 patches finally results in the formation of creek networks as the patchy salt marsh pioneer

171 zone develops into a mature marsh (Fig 4)(Temmerman et al., 2007). Hence, similar to

172 mussel beds and diatom-covered mudflats, the interaction between plant growth,

173 hydrodynamics and geomorphology that underlies salt-marsh formation is scale-

174 dependent, changing in nature from increased sedimentation within vegetation tussocks to

175 increased erosion at some distance.

176 An important question is why salt marshes reveal a much more complex spatial structure

177 compared to other estuarine systems, while the underlying interaction between plants and

178 sedimentation is a scale-dependent feedback similar to that found in mussel beds and

179 mudflats. First, the feedback processes that characterize plant-sediment interactions are

9

180　　strongly density-dependent (Fig 3B-C). In low density tussocks, plant density is

181　　insufficient to divert the water flow, and hence, no positive feedback develops locally,

182　　and the trembling of individual shoots in the flow may even cause increased erosion and

183　　plant dislodgement (Bouma et al., 2009). Hence, at very low density, feedbacks are

184　　predominantly negative. As density increases, the flow rate of the water is reduced as

185　　water flow is diverted laterally or over the vegetation, increasing sedimentation (Bouma

186　　et al., 2009). This effects introduces threshold dynamics, where salt–marsh plants have

187　　difficulty establishing, while clumps of marsh plants can persist and expand (van

188　　Wesenbeeck et al., 2008). As a consequence, salt-marsh pioneer zones are characterized

189　　by extensive patchworks, which slowly expand at their edges and can easily take decades

190　　to develop into semi-closed vegetation. Second, estuarine marshes are bounded primarily

191　　by terrestrial environments, with less that 30% of marsh boundaries lined by open water.

192　　This has important implications for the spatial structure of salt marshes. When not

193　　bounded by coastline, marshes develop a semi-regular spacing of creeks alternating with

194　　dense vegetation (Temmerman et al 2007). Hence, under these conditions, saltmarshes

195　　conform to the regularity that is predicted by models with a scale-dependent interaction

196　　of positive and negative feedback. When salt-marshes are enclosed by coastline, models

197　　of marshes predict more complex feather-shaped drainage canals, or fractal shapes if

198　　erosion is a dominant process (D'Alpaos et al., 2007; Kirwan and Murray, 2007). This

199　　suggests that the complexity that salt marsh ecosystems can exhibit not so much results

200　　from underlying complexity in governing processes, but results from a simple interaction

201　　between vegetation and morphological processes put into physically constraining

202　　landscape setting.

Scaling up local interactions between organisms and the physical world

A central premise in spatial ecology is that small-scale interactions explain patterns that occur at broad spatial scales, in a process called spatial self-organization (Levin, 1992; Wootton, 2001). This premise has been applied to a wide range of self-organized ecosystems, such as patterned arid bush lands, boreal peat lands, and seagrass beds (Rietkerk and Van de Koppel, 2008). In this paper, we argue that to explain the patterns observed in self-organized ecosystems, both processes occurring at small spatial scales, and processes occurring at the landscape scale need to be considered (Fig. 5). Small-scale processes occurring at the individual level are crucial in explaining the formation of aggregations of animals or patches of vegetation. These processes cause small inhomogeneity's in the distribution of organisms to increase and develop into clear aggregations, clusters, or patches (a symmetry breaking instability in mathematical terms). The combined studies reviewed in this paper demonstrate, however, that subsequently, landscape-level features such as the strength and direction of the tidal water flow or the slope of the underlying landscape shape these patterns, and determines the patterns as we see them, as being dotted or banded, regular or fractal shaped. Landscape-scale processes thereby shape and constrain these self-organized spatial pattern. Hence, localized interactions, in combination with landscape-level constraints, determine the development of self-organized patterns. When physical constraints are minimal, relatively simple spatial patterns can develop, like the striped patterns that are observed in mussel beds and mudflat systems. When landscape settings constrain the formation of spatial

11

225   structure, and multiple processes interact, more complex spatial structures can form, as is

226   found in salt marshes.

227   Although we support our argument using three patterned ecosystems that we ourselves

228   are most acquainted with (i.e., mussel beds, mudflats and salt marsh ecosystems), these

229   insights obtained are by no means limited to estuarine systems. For example, in patterned

230   arid bush land, the general slope of the landscapes dictates whether surface runoff of rain

231   is directional or not, which in term determines whether vegetation patterns are banded

232   (tiger bush) or have a dotted or labyrinth shape (leopard bush) (Klausmeier, 1999;

233   Rietkerk et al., 2002). Boreal peat land can develop ribbon-shaped vegetation patterns

234   that are aligned perpendicular to the direction of water drainage through the peat land, a

235   process that is dictated by the landscape (Rietkerk et al., 2004). Hence, the influence of

236   landscape-scale processes on pattern formation can be distinguished in patterned systems

237   all over the world, and we hypothesize that it is a general feature of self-organized

238   ecological systems.

239   **Conclusions**

240   From the above review of the processes that govern the development of spatial structure

241   in mussel beds, mudflats and salt marshes, it becomes evident that a close interplay

242   between ecological and physical interactions play a large part in causing the spatial

243   complexity that characterizes estuarine communities. Underlying this complexity are

244   sometimes very simple interactions between organisms and physical processes such as

245   tidal water flow and sedimentation, which trigger self-organization processes and

246   generate patterns at larger spatial scales. The complexity of these spatial patterns,

247 however, not only follows from the self-organization process, but is co-determined by

248 physical constraints that characterize the estuarine environment: directional tidal flow of

249 sea water, and constraining coastline features. More importantly, our review of estuarine

250 systems emphasizes that scale-dependent feedbacks are capable of explaining much more

251 complex spatial patterns than the regular patterns to which they have so-far been applied.

Acknowledgements

References

256 Allen, J. R. L. (2000). Morphodynamics of Holocene salt marshes: a review sketch from

257   the Atlantic and Southern North Sea coasts of Europe. Quaternary Science

258   Reviews 19, 1155-1231.

259 Bertness, M. D. (1999). The ecology of Atlantic shoreline. Sunderland: Sinauer

260   Associates.

261 Bertness, M. D. and Grosholz, E. (1985). Population dynamics of the ribbed mussel,

262   Geukensia demissa: the costs and benefits of a clumped distribution. Oecologia

263   67, 192-204.

264 Blanchard, G. F., Paterson, D. M., Stal, L. J., Richard, P., Galois, R., Huet, V., Kelly, J.,

265   Honeywill, C., de Brouwer, J., Dyer, K. et al. (2000). The effect of

266   geomorphological structures on potential biostabilisation by microphytobenthos

267   on intertidal mudflats. Cont. Shelf Res. 20, 1243-1256.

268   Bouma, T. J., Friedrichs, M., van Wesenbeeck, B. K., Temmerman, S., Graf, G. and

269   Herman, P. M. J. (2009). Density-dependent linkage of scale-dependent

270   feedbacks: a flume study on the intertidal macrophyte Spartina anglica. Oikos

271   118, 260-268.

272   Bouma, T. J., van Duren, L. A., Temmerman, S., Claverie, T., Blanco-Garcia, A.,

273   Ysebaert, T. and Herman, P. M. J. (2007). Spatial flow and sedimentation patterns

274   within patches of epibenthic structures: Combining field, flume and modelling

275   experiments. Cont. Shelf Res. 27, 1020-1045.

276   D'Alpaos, A., Lanzoni, S., Marani, M., Bonornetto, A., Cecconi, G. and Rinaldo, A.

277   (2007). Spontaneous tidal network formation within a constructed salt marsh:

278   Observations and morphodynamic modelling. Geomorphology 91, 186-197.

279   Gascoigne, J. C., Beadman, H. A., Saurel, C. and Kaiser, M. J. (2005). Density

280   dependence, spatial scale and patterning in sessile biota. Oecologia 145, 371-381.

281   Hunt, H. L. and Scheibling, R. E. (2001). Patch dynamics of mussels on rocky shores:

282   integrating process to understand pattern. Ecology 82, 3213-3231.

283   Hunt, H. L. and Scheibling, R. E. (2002). Movement and wave dislodgment of mussels

284   on a wave-exposed rocky shore. Veliger 45, 273-277.

285   Kirwan, M. L. and Murray, A. B. (2007). A coupled geomorphic and ecological model of

286   tidal marsh evolution. Proc Natl Acad Sci U S A 104, 6118-6122.

287   Kirwan, M. L., Guntenspergen, G. R., D'Alpaos, A., Morris, J. T., Mudd, S. M. and

288   Temmerman, S. (2010). Limits on the adaptability of coastal marshes to rising sea

289   level. Geophys. Res. Lett. 37.

290   Klausmeier, C. A. (1999). Regular and irregular patterns in semiarid vegetation. Science

291   284, 1826-1828.

292   Laima, M. J. C., Girard, M. F., Vouve, F., Blanchard, G. F., Gouleau, D., Galois, R. and

293   Richard, P. (1999). Distribution of adsorbed ammonium pools in two intertidal

294   sedimentary structures, Marennes-Oleron Bay, France. Mar. Ecol.-Prog. Ser. 182,

295   29-35.

296   Levin, S. A. (1992). The problem of pattern and scale in ecology. Ecology 73, 1943-

297   1967.

298   Levin, S. A. (1998). Ecosystems and the biosphere as complex adaptive systems.

299   Ecosystems 1, 431-436.

300   Newell, C. R. (1990). The effects of mussel (Mytilus edulis, Linnaeus, 1758) position in

301   seeded bottom patches on growth at subtidal lease sites in Maine. J Shellfish Res

302   9, 113-118.

303   Rietkerk, M. and Van de Koppel, J. (2008). Regular pattern formation in real ecosystems.

304   Trends Ecol Evol 23, 169-175.

305   Rietkerk, M., Dekker, S. C., Wassen, M. J., Verkroost, A. W. M. and Bierkens, M. F. P.

306   (2004). A putative mechanism for bog patterning. Am Nat 163, 699-708.

307   Rietkerk, M., Boerlijst, M. C., Van Langevelde, F., HilleRisLambers, R., Van de Koppel,

308   J., Kumar, L., Klausmeier, C. A., Prins, H. H. T. and De Roos, A. M. (2002). Self-

309   organisation of vegetation in arid ecosystems. Am Nat 160, 524-530.

310   Snover, M. L. and Commito, J. A. (1998). The fractal geometry of Mytilus edulis L.

311   spatial distribution in a soft-bottom system. J Exp Mar Biol Ecol 223, 53-64.

312   Svane, I. and Ompi, M. (1993). Patch dynamics in beds of the blue mussel mytilus-

313   edulis-L - effects of site, patch size, and position within a patch. Ophelia 37, 187-

314   202.

315   Temmerman, S., Bouma, T. J., Van de Koppel, J., Van der Wal, D. D., De Vries, M. B.

316   and Herman, P. M. J. (2007). Vegetation causes channel erosion in a tidal

317   landscape. Geology 35, 631-634.

318   Van de Koppel, J., Rietkerk, M., Dankers, N. and Herman, P. M. J. (2005). Scale-

319   dependent feedback and regular spatial patterns in young mussel beds. Am Nat

320   165, E66-E77.

321   van de Koppel, J., Gascoigne, J. C., Theraulaz, G., Rietkerk, M., Mooij, W. M. and

322   Herman, P. M. J. (2008). Experimental Evidence for Spatial Self-Organization

323   and Its Emergent Effects in Mussel Bed Ecosystems. Science 322, 739-742.

324   van Wesenbeeck, B. K., van de Koppel, J., Herman, P. M. J., Bertness, M. D., van der

325   Wal, D., Bakker, J. P. and Bouma, T. J. (2008). Potential for Sudden Shifts in

326   Transient Systems: Distinguishing Between Local and Landscape-Scale

327   Processes. Ecosystems 11, 1133-1141.

328   Weerman, E. J., van de Koppel, J., Eppinga, M. B., Montserrat, F., Liu, Q. X. and

329   Herman, P. M. J. (2010). Spatial Self-Organization on Intertidal Mudflats through

330   Biophysical Stress Divergence. Am Nat 176, E15-E32.

331   Wootton, J. T. (2001). Local interactions predict large-scale pattern in empirically

332   derived cellular automata. Nature 413, 841-844.

333   Ysebaert, T., Hart, M. and Herman, P. M. J. (2009). Impacts of bottom and suspended

334   cultures of mussels Mytilus spp. on the surrounding sedimentary environment and

335   macrobenthic biodiversity. Helgol Mar Res 63, 59-74.

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Figure captions

Figure 1: Self-organized spatial patterns as observed in estuarine ecosystems. A) represents a banded mussel bed, scale approximately 100 meters across. Source: Van de Koppel et al 2005, B) A regular spatial pattern on the Kapellebank mudflat in the Westerschelde, The Netherlands. Source: Weerman et al, 2010. C) Creeks patterns in a salt marsh. Source and location unknown.

Figure 2: A) Schematic representation of how the interaction between diatom growth, sediment accumulation and water diversion generate a positive feedback that can explain the formation of regularly spaced patches covered by a diatom biofilm. The difference in B) the diatom densities, as reflected by cholorophyll density, and C) erosion threshold, between hummocks. Redrawn from Weerman et al 2010.

Figure 3: A) a single tussocks of *Spartina alterniflora* demonstrates that the interaction between *Spartina* and sedimentation is both scale and density dependent. B) Relation between local density and net sedimentation within a tussock of Spartina, revealing clear density dependence. C) relation between within tussock density of shoots and erosion next to the tussock. Redrawn from Bouma et al 2010.

Figure 4: A spatially-explicit model of the interaction between *Spartina* vegetation, hydrodynamics, and sedimentation processes. A) represents the changes in the water flow field induced by a single round tussock of *Spartina*. B) A regular landscape of creeks alternating with vegetation-covered salt-marsh plateau's develops after 30 years as a result of scale-dependent feedback between sedimentation and plant growth. Redrawn from Temmerman et al 2007.

361   Figure 5: A schematic representation of how the interplay of local interactions and

362   physical forcing from the landscape generate spatial pattern and structure in ecosystems.

A: a patterned mussel bed
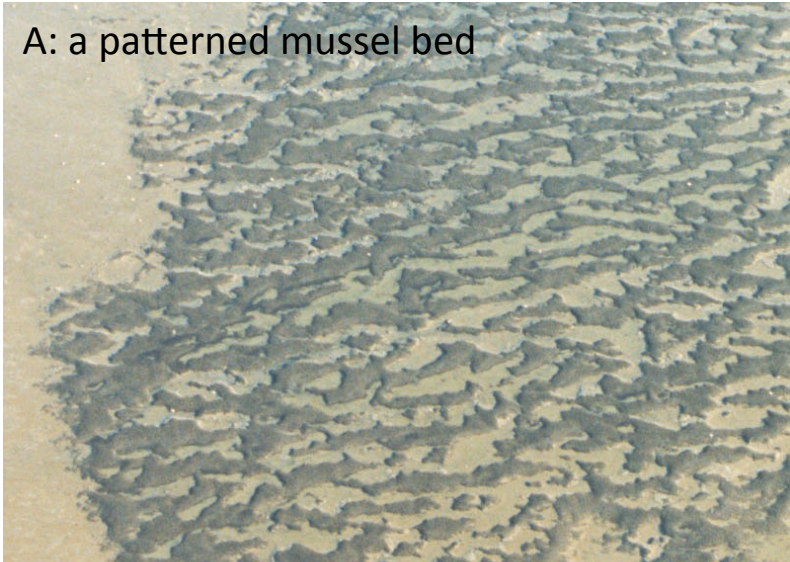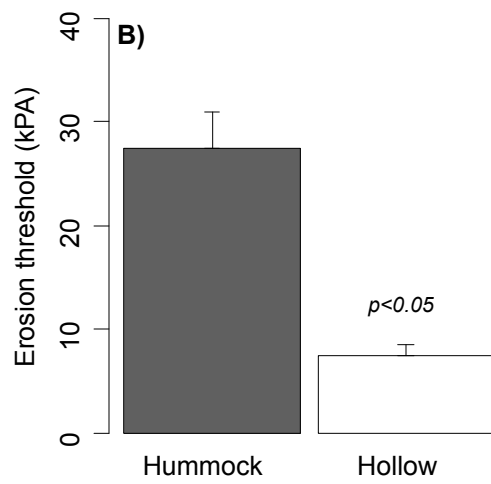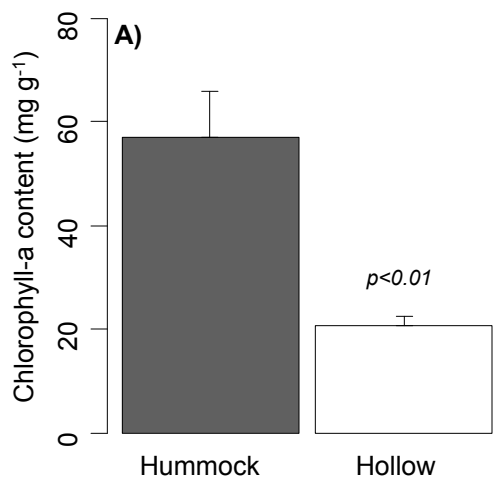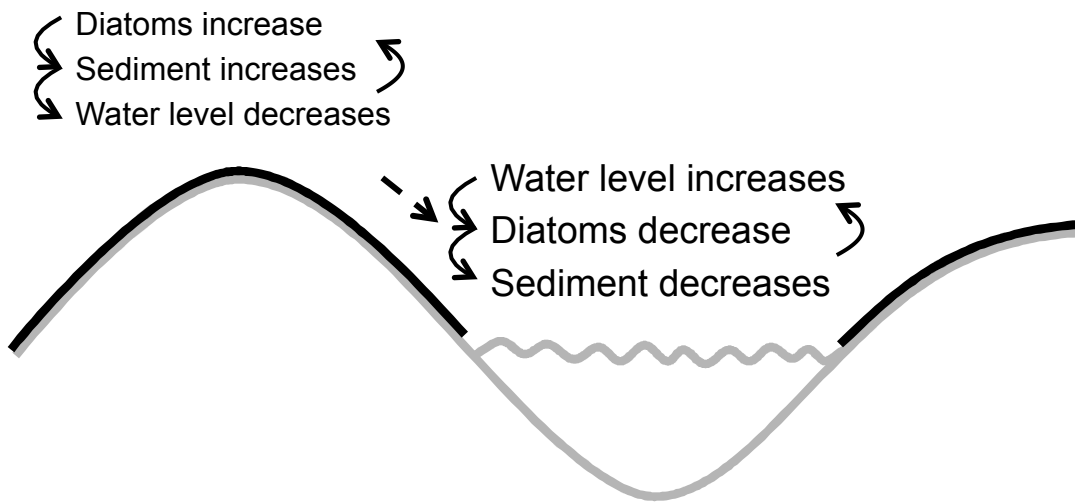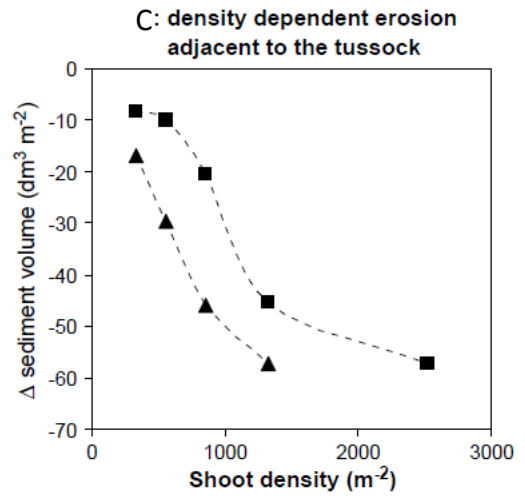
B: a patterned mudflat

C: Salt marsh

Figure 1

Diatoms increase
Sediment increases
Water level decreases

Water level increases
Diatoms decrease
Sediment decreases

A)

Chlorophyll-a content (mg g⁻¹)

p<0.01

Hummock   Hollow

B)

Erosion threshold (kPA)

p<0.05

Hummock   Hollow

Figure 2

A

B: density dependent sedimentation within the tussock

C: density dependent erosion adjacent to the tussock

Figure 3

A

bed shear stress (N m⁻²)

low density patch

flow direction

distance (m)

distance (m)

bottom elevation (m)

Figure 4

Figure 5