

## Research

### Large-scale ecosystem engineering by flamingos and fiddler crabs on West-African intertidal flats promote joint food availability

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Although the ecosystem engineering concept is well established in ecology, cases of joint engineering by multiple species at large scales remain rare. Here, we combine observational studies and enclosure experiments to investigate how co-occurring greater flamingos *Phoenicopterus roseus* and fiddler crabs *Uca tangeri* promote their own and each other's food availability by creating a spatially complex mosaic of depressions (bowls, gullies) and hummocks (plateaus, mounds) in the intertidal zone. This results in a mosaic of microhabitats with different tidal inundation regimes. These microhabitats are spatially organized with labyrinth-like patterns in the high intertidal zone and spotted patterns in the lower intertidal, both of which likely arise from biophysical interactions between these organisms and hydrodynamic forces. We show that the resulting spatial complexity is vital for biofilm production. The depression microhabitats were wetter and richer in organic matter and biofilms compared with hummocks. Excluding flamingos and crabs resulted in an increase in biofilm biomass over the shorter term (six months), but a decrease over the longer term (after one year). Moreover, our results strongly suggest that these biogeomorphological microhabitats in the mosaics were maintained by the feeding activities of flamingos and to a lesser extent crabs. During a period of flamingo exclusion, all the spotted patterns filled up with sediment, while the exclusion of crabs led to gradual sediment accumulation in the labyrinth-like patterns. Collectively, these findings provide empirical evidence for large-scale joint promotion of food availability by multiple taxa in a marine ecosystem.

Keywords: Banc d'Arguin-Mauritania, biofilms, biogeomorphic, ecological autocatalysis, facilitation, feedback loop, spatial patterns

#### Introduction

Ecosystem engineers have a remarkable ability to modify abiotic conditions to their own benefit (Jones et al. 1994), thereby facilitating other organisms as a side effect (Donadi et al. 2015). Their activities often launch a network of (positive or negative) biogeomorphic feedback loops that may significantly alter ecosystem processes and

services (Olf et al. 2009). Although the ecosystem engineering concept is well established and has been intensively studied over the last two decades (Wright and Jones 2006), ecologists have mainly focused on engineering by a single species and have rarely studied ecosystem engineering across species networks (but see Caliman et al. 2011, Largaespada et al. 2012, Donadi et al. 2015). As species are often embedded in complex interaction networks (Montoya et al. 2006), an understanding of natural systems may require a more holistic approach.

Ecosystem engineering could have the following benefits: ensure safety (the beaver *Castor canadensis*; Wright et al. 2002), create shelter (shelter-building caterpillars; Lill and Marquis 2003), improve living conditions (seagrass; Bos et al. 2007), ensure food availability (sprouting seeds by bristle worms; Zhu et al. 2016), and promote the quality of food (through soil compaction; Veldhuis et al. 2014). Food supply is a key determinant of habitat choice (Piersma 2012) and consumer demographics (Krebs 1996). In marine intertidal systems where tidal cycles drive food availability (Iriarte et al. 2003, Bulla et al. 2017), animals experience high variation in daily and seasonal food supply (Beukema et al. 1993). In these cyclic habitats, ensuring a reliable food supply through engineering activities can make a crucial difference. Here, we present a study on joint engineering by two marine ecosystem engineers, greater flamingos *Phoenicopterus roseus* and fiddler crabs *Uca tangeri*, which have the potential to enhance biofilm production (Fig. 1) through biogeomorphic

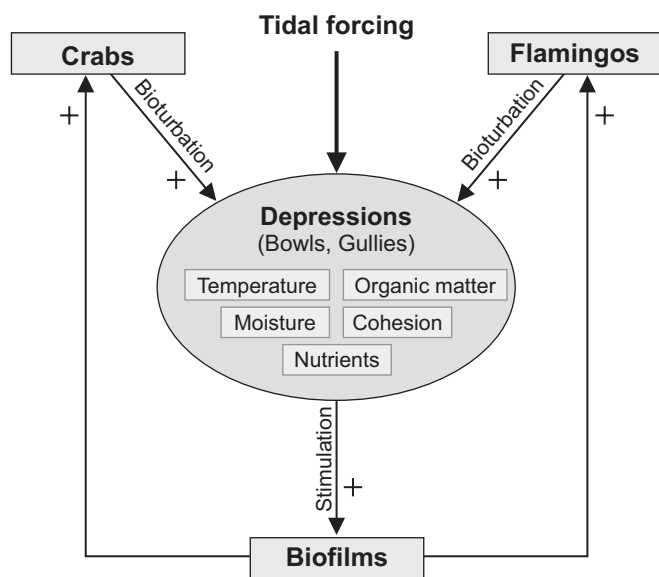


Figure 1. Conceptual model of the proposed biophysical feedback mechanisms characterising the ecosystem engineering by flamingos and crabs to ensure their own food supply in the mosaic system of Banc d'Arguin (Fig. 2). The feeding activities of flamingos (sediment compaction) and crabs (sediment loosening and transport) together with tidal forcing result in patterned depressions (bowls and gullies) in the mudflats (Fig. 2). Tidal flooding of these depressions favours the conditions for biofilm development, which are in turn fed upon by flamingos and crabs.

feedback loops at the landscape-scale in Parc National du Banc d'Arguin, Mauritania (Fig. 2). Together, flamingos and crabs appear to improve their food supply by creating an irrigation system (dense mosaics of contrasting depressions and hummocks) at the landscape scale, which subsequently boosts the biofilms that they both feed upon (Robertson et al. 1981, Krienitz et al. 2016).

Flamingos are well-known ecosystem engineers that can modify sediment characteristics, microtopography and benthic communities (Glassom and Branch 1997a, b, Rodríguez-Pérez and Green 2006, Scott et al. 2012). Greater flamingos have been reported to create distinct donut-shaped depressions (also known as craters) due to their circular filter-feeding behaviour while remaining standing at a single location (Rodríguez-Pérez and Green 2012, Gihwala et al. 2017). Fiddler crabs are also effective ecosystem engineers in coastal systems due to their feeding and intensive burrowing activities (Kristensen 2008, Smith et al. 2009, Holdredge et al. 2010). Their deposit-feeding and sediment reworking activities are likely to impact sediment characteristics (Kristensen and Alongi 2006, Kristensen 2008) and primary production (Smith et al. 2009, Holdredge et al. 2010). During low tide, fiddler crabs constantly collect sediment balls from the gullies (Ens et al. 1993), carry them up and process them next to their burrows, resulting in a constant directional flow of sediment. This behaviour allows them to quickly retreat into their burrows at the approach of predators like whimbrels *Numenius phaeopus* and gull-billed terns *Gelochelidon nilotica* (Zwarts 1985, Zwarts and Blomert 1990, Stienen et al. 2008). Biofilms (such as diatoms and cyanobacteria) also have important ecosystem engineering effects by gluing the top layer of sediment together via the excretion of extracellular polymeric substances (EPSs) in intertidal ecosystems (Smith and Underwood 1998, Flemming and Wingender 2010). Biofilm layers trap fine sediment and prevent sediment erosion by increasing sediment cohesion and smoothness of the sediment surface (Grant et al. 1986, Gerbersdorf et al. 2008). Abundance of biofilm is typically greater in winter than in summer (Jackson et al. 2010, Orvain et al. 2014) and we therefore expect that the activities of flamingos and crabs in the mosaics will intensify during the cool months of the year.

The aim of this study is to test whether these three ecosystem engineering species mutually benefit each other through the formation of an irrigation mosaic. We explore if the interactions between feeding activities of flamingos and crabs in association with tidal hydrodynamics create and maintain spatial depressions on intertidal flats (Fig. 1). To analyse these three focal interactions, we ask the following questions: 1) whether geomorphology and topographical elevation affect sediment characteristics and biofilm biomass, 2) whether the feeding activities of flamingos and crabs affect the spatial heterogeneity and the topography of the mosaics, 3) whether foraging flamingos and crabs can change biofilm biomass, and 4) whether these effects vary between the different elevational zones of the mosaic. We explored the combined and separate effect of flamingos and crabs on

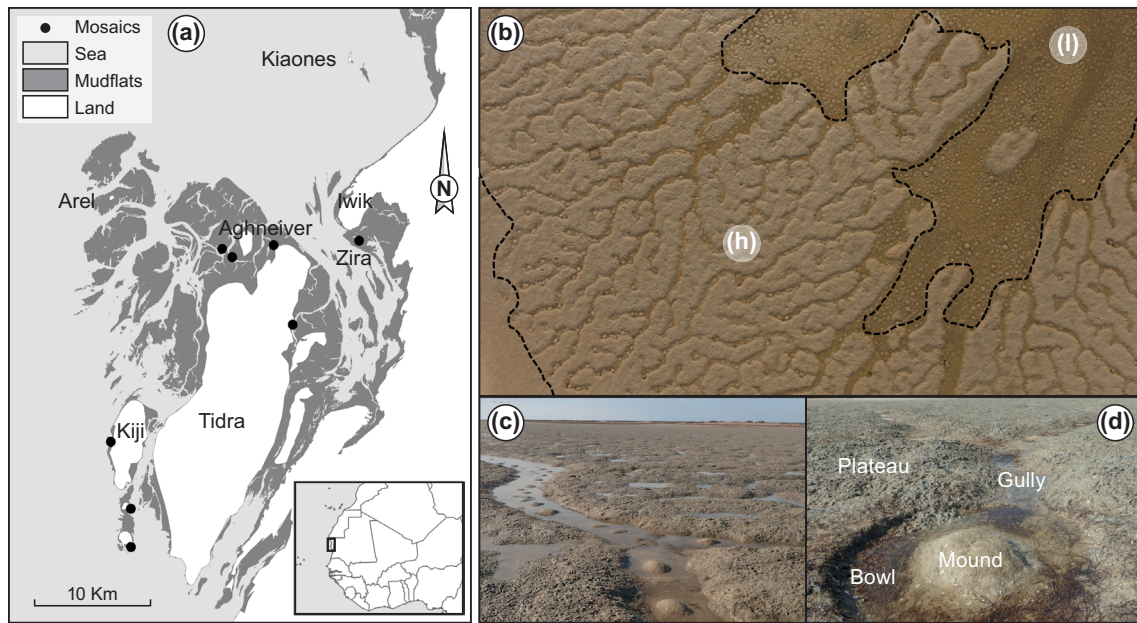


Figure 2. (a) Map of the study area showing different mosaics in Banc d'Arguin. (b) Aerial view of the Zira mosaic showing the two elevational zones as well as the different patterns: the high zone (H) where both flamingos and crabs coexist, and the low one (L) where only flamingos are active. (c) Closer view of the contrast between hummocks and depressions in the high zone. (d) Photo illustrating the four different microhabitats (bowl, mound, gully, plateau) with the bowl-like microhabitats created by flamingos and debris trapped in the bowls. Top-right photo by Laura Soissons.

landscape morphology and microphytobenthic by experimentally excluding flamingos and crabs from two different elevational zones and measuring microphytobenthos biomass and morphological changes in the sediment. The two zones served to compare areas only used by flamingos with those used by both flamingos and crabs.

## Material and methods

### Study system

We conducted our study on the intertidal mosaic formations on the islet of Zira, one of several mosaics that can be found across Parc National du Banc d'Arguin (PNBA), Mauritania (Fig. 2a). The mosaics are complex spatial landscapes comprising microhabitats of different elevations (Fig. 2b, c): depressions (gullies and bowls) and hummocks (plateaus and mounds). The elevational differences between microhabitats results in great variation in tidal inundation regimes among them (about 80 min, based on camera observations). These mosaics are intensively used by greater flamingos and fiddler crabs (Supplementary material Appendix 1). For greater flamingos, the Banc d'Arguin ecosystem is one of the most important breeding and wintering sites in West Africa (Cézilly et al. 1994, Diawara et al. 2007). At least 15 000 pairs breed on the Kiaone islands, 14 km north of the Zira study site (Campredon 2000). Fiddler crabs are by far the most abundant mobile organisms in the mosaics of Banc d'Arguin with densities of  $33.5 \pm 9.5$  (mean  $\pm$  SE) individuals

per  $m^2$  near the islet of Zira and  $7.3 \pm 4.4 m^2$  near the islet of Aghneiver (Fig. 2a). Crab densities were measured every 2 m along two transects (ca 150 m) per site by counting the active burrows within a  $50 \times 50$  cm PVC frame.

The mosaic at Zira (6.8 ha) is composed of two zones with different elevations and biota, and is characterised by a labyrinth-like pattern in the highest zone and a spotted pattern lower down the gradient (Fig. 2b). The highest zone on average (including all microhabitats) had an elevation of  $-13.12 \pm 2.6$  cm compared with average sea level, while the lowest one had an average elevation of  $-5.9 \pm 4$  cm. The lowest zone is used mainly by flamingos and can be recognised by signs of flamingo feeding: extensive circular pits of up to 1.4 m in width (Gihwala et al. 2017) with a sand heap in the middle that are clearly visible even on aerial photos (area L in Fig. 2b). These pits persist over at least several weeks, and flamingos return to them on a daily basis to feed on the biofilm biomass that has accumulated during low tide. In the higher zone, flamingos and crabs co-occur up to the elevation of the highest neap tide. This zone is characterised by complex mosaics of hummocks and gullies filled with flamingo pits (area H in Fig. 2b). On a small scale, four different microhabitats can be distinguished within the mosaics, especially in the high zone: mounds and bowls are formed by flamingo feeding activities (Fig. 2c–d), and gullies and plateaus probably result from long-term interactions between crab foraging and tidal water flow (Fig. 2c–d). Fiddler crabs make their burrows on the plateaus, but seem to prefer to feed in bowl and gully microhabitats. These preferences result in the



continuous transport of sediment from gullies to plateaus, causing a net 'digging out' of gullies and building up of plateaus over time.

### Exclosure experiment on landscape formation

To evaluate the importance of biophysical interactions versus only hydrodynamics for the formation of the spatial patterns in the mosaic, the level of the sediment bed was flattened in January 2015. We then set up two crab exclosures, two flamingo exclosures and two controls (total of six experimental plots of  $1.5 \times 1.5$  m, with two replicates per treatment) in the high zone. This additional pilot experiment was visited on four occasions (2–3 days each) over two years to score visually the recovery of the spatial patterning. In the exclosure plots, flamingos were excluded with rope set at the height of 50 cm, while crabs were excluded by burying wire mesh in the ground to prevent their settlement. In the set of control plots, we only flattened the plots and marked them without setting up exclosures.

### General survey on daily and seasonal biotic activities

To monitor the biotic activities in the mosaics, three time-lapse Bushnell Trophy Cam HD cameras were fixed securely to a vertical wooden pole at 1.5 m above ground at different places to cover the entire study area. Cameras were set to take a photo, a short video (10 s) and log air temperature ( $^{\circ}\text{C}$ ) at 15-min intervals over a 24-h period. The presence/absence of flamingos and crabs was scored every 15 min during the study time by visually inspecting photos and videos from the three cameras. Animals were considered present when they appeared in at least one of the cameras during a time interval, timed to the nearest quarter of an hour. Very dark images and videos were excluded from analysis.

### Exclosure experiment on primary production

To investigate the effect of the feeding activities of flamingos and crabs on the geomorphology and biofilm biomass in the different elevational zones, a second exclosure experiment was established in mid-January 2015 and measured on three occasions during the subsequent year: January–February 2015, May–June 2015 and January–February 2016. In this experiment, flamingos and crabs were excluded using two different sets of exclosures with minimum change to the existing geomorphology of the plot. To exclude flamingos, we used exclosures ( $1 \times 1 \times 0.5$  m) consisting of four upright PVC tubes connected tightly with rope at a height of 50 cm. To exclude crabs, we established chicken-wire cages ( $1 \times 1 \times 0.3$  m) with a mesh size of 1 cm. Crab exclosures also excluded flamingos. Control plots were marked only with small PVC tubes. All plots were placed (10 m apart) to capture the different microhabitats in the different zones. In total, 50 plots were established over five randomly selected blocks; each block covered the two different elevational zones. This randomized block design was used to reduce unexplained variation due

to other heterogeneity than the main elevational gradient. In the low zone, where crabs are absent, only flamingo exclosures (10 replicates) were used (area L in Fig. 2b), and in the high zone (area H in Fig. 2b), where both species coexist, we combined both flamingo and crab exclosures (10 replicates for each). Each exclosure was paired with a control treatment without exclosure (20 controls).

### Measuring topographical profiles, sediment characteristics and biofilm biomass

To assess the impact of the engineering activities of flamingos and crabs on the geomorphology of the mosaic, topographic changes were measured as the vertical height difference between the initial bed level (soil surface elevation) and the bed level at the end of the experiment. The differences in elevation between plots and the different microhabitats were measured using the real time kinematic global positioning system (RTK-GPS). Elevational measurements (with an accuracy of 0–8 mm) were taken twice (at the start of the experiment and a year later) and calibrated against an absolute known level at Zira.

To investigate the effect of the geomorphology on the prevailing sediment conditions of the mosaics that could potentially affect biofilms (reviewed by Gerbersdorf and Wieprecht 2015, Ansari et al. 2017), the following parameters were measured in the control plots where all microhabitats remained visible at the end of the experiment. The sediment critical shear-strength was measured three times during the year with a Pocket Vane Tester (14.10) as a proxy for sediment stability and cohesion. A Pocket Vane Shear Tester is a simple instrument that measures the force needed to disturb the sediment surface, by pushing a circular plate with ribs on it into the sediment surface and turning it until the plate starts to move. Soil temperature ( $^{\circ}\text{C}$ ) was also measured multiple times over the year with an Actpe portable handheld non-contact infrared digital thermometer sensor. To investigate the sediment properties, a sediment sample of the upper 5 cm was taken from each microhabitat type in all the plots at the end of the experiment. Water content in the sediment was determined for each habitat by weight loss after oven drying ( $75^{\circ}\text{C}$ , 72 h). Subsamples of the sediment were analysed for organic matter content as loss on ignition (LOI; 4 h,  $550^{\circ}\text{C}$ ).

To study the effects of elevational variation and of excluding flamingos and crabs on the biofilms, we estimated the biomass of diatoms, cyanobacteria and green algae densities ( $\mu\text{g cm}^{-2}$ ) in all microhabitats using a 'BenthosTorch', a fluorescence-based optical technique. In a methodological study, Kahlert and McKie (2014) showed that the biomass of the total microphytobenthos obtained with a BenthosTorch is similar to those obtained via conventional methods; however, values for the relative contribution of the different microphytobenthos groups should be used with caution. Thus, we used the biomass of the entire community (diatoms, cyanobacteria and green algae) as our measure of biofilm abundance. Biomass measurements (one estimate per microhabitat per

plot during each sampling event) captured different daily as well as monthly tidal cycles, including neap and spring tides, on the following dates: winter 2015 (18, 21, 23, 26 January; 1, 4, 10 February); spring 2015 (21, 29 May); and winter 2016 (26 January).

## Statistical analyses

Normality and homogeneity of variance were ensured for each variable by visual inspection of Q–Q plots and Levene's test, respectively, and appropriate transformations were used when necessary. We used circular statistics to quantify how flamingo and crabs activities were clustered relative to the diurnal tidal (12 h) as well as the semilunar tidal (15.8 days) amplitude cycles. Activities were plotted on circular plots as an angle (in degrees) relative to the tidal amplitude or lunar cycle. We used the Rao spacing test for circular uniformity to determine whether crab and flamingo activities were unevenly distributed around the circles. Watson's two-sample test for homogeneity for circular data was used to compare between flamingo and crab activities in winter and spring. Tests were performed using the R package 'circular'. In all tests, a  $p$ -value  $<0.05$  was considered significant. To investigate the effects of temperature as well as daily and monthly tidal cycles on the activities of flamingos and crabs, a multinomial logistic regression was applied to determine whether the probability of being active is affected by the explanatory variables. The effects of temperature and tide on flamingo and crab activities during the different seasons (winter, spring) were tested separately using different multinomial models. The best model for each season was identified using backwards step-wise model selection.

The effects of the geomorphology on sediment conditions were assessed only on control plots (20), where all four microhabitats remained visible over the period of observation. Moreover, initial analyses showed that measurements of the same microhabitat did not differ between zones. Therefore, sediment conditions of the controls were pooled together in this analysis. The effect of geomorphology on sediment water content, organic matter content, sediment critical shear strength and temperature were analysed with one-way ANOVA, followed by Tukey's HSD post hoc comparisons. Sediment critical shear strength data taken during January 2016 could not be normalised, and thus were analysed using the Kruskal–Wallis test with the Dunn comparison test.

The effects of ecosystem engineers on the geomorphology were investigated by studying changes in bed level over one year. Only one measurement per microhabitat per plot was taken at the start and at the end of the experiment, and differences in bed level change (initial–end) per microhabitat were averaged and compared across replicate plots. Changes in all microhabitats upon excluding flamingos and crabs were analysed using Student's  $t$ -tests (two-tailed) in the low zone and with ANOVA in the high zone.

Finally, to examine the effects of grazing activities of flamingos and crabs on biofilm biomass, linear mixed-effects

models (LMER) using restricted maximum likelihood fitted with enclosure and microhabitats as fixed effects and blocks as random effects were conducted with the lme4 package in R (Bates et al. 2015). Parametric assumptions were tested on the residuals. To demonstrate the magnitude of differences in biofilm biomass between enclosures and controls in the same block, effect size (Hedges et al. 1999) was calculated as the natural log of response ratios,  $LRR = \log(\text{treatment/control})$ , following Borenstein et al. (2009). Mean effect sizes with their bootstrapping CI of treatments were calculated using the R package 'Metafor' (Viechtbauer 2010) and were considered significant if the 95% CI did not overlap with zero.

All statistical analyses were performed in R ver. 3.4.3 ([www.r-project.org](http://www.r-project.org)).

## Data deposition

The University of Groningen has implemented a strict data archiving system since 2013. All research data including the data used in this article will be archived in the University of Groningen Research Data Repository ([www.rug.nl/research/gelifes/research/data-management/repository?lang=en](http://www.rug.nl/research/gelifes/research/data-management/repository?lang=en)) (El-Hacen et al. 2018).

## Results

### Enclosure experiment on landscape formation

The initial spatial pattern of the mosaic did not recover in the enclosure, at least during the first two years, after flattening of the surface (Supplementary material Appendix 2 Fig. A1). Control plots, on the other hand, showed a slow recovery of the original pattern, which was visible after two years (Supplementary material Appendix 2 Fig. A2). Thus, the presence of the excluded biota appears to be a requirement for pattern formation.

### General survey on daily and seasonal biotic activities

Analyses of camera time-lapse data revealed strong seasonal patterns in the activities of flamingos and crabs in the mosaic found in Zira. Multinomial logistic regression models showed that seasons, monthly and daily tidal cycle, and air temperature jointly determined the activities of both flamingos and crabs in the mosaic (Supplementary material Appendix 3 Table A1-b, Fig. A3, A4). Overall, flamingos were mostly active during the hours of incoming and high tide (Rao spacing test,  $U = 355$ ,  $p < 0.001$ ) and more present in spring compared with winter (Watson–Williams test,  $F = 1.3$ ,  $p < 0.001$ ; Supplementary material Appendix 3 Table A1, Fig. A3). In spring, flamingos were present in the mosaic over the entire monthly tidal cycle (Rao spacing test,  $U = 354$ ,  $p < 0.001$ ; Supplementary material Appendix 3 Fig. A3). In winter, however, flamingos seemed to use the mosaic only for a few days after spring tides (Rao spacing test,  $U = 340$ ,  $p < 0.001$ ;

Supplementary material Appendix 3 Fig. A3). The presence of flamingos was positively correlated with air temperature in winter, but negatively correlated in spring (Supplementary material Appendix 3 Fig. A4).

Crabs were active during the hours of low and outgoing tide (Rao spacing test,  $U = 357$ ,  $p < 0.001$ ; Supplementary material Appendix 3 Fig. A5). In winter, crabs were active after spring tide (Rao spacing test,  $U = 353$ ,  $p < 0.001$ ). In spring, however, they were active for a few days before the spring tide (Rao spacing test,  $U = 352$ ,  $p < 0.001$ ; Supplementary material Appendix 3 Fig. A5). The proportion of active crabs was positively correlated with air temperature (Supplementary material Appendix 3 Table A3b, Fig. A6).

### The effects of the geomorphology on sediment conditions

We found that depression microhabitats (bowls and gullies) were generally wetter than the hummocks (mounds and plateaus), but only bowls were significantly different from the hummocks ( $F_{3,106} = 24.3$ ,  $p < 0.001$ ; Fig. 3a). Temperature in the microhabitats showed seasonal patterns: in winter, only gullies showed a significant increase in temperature compared to mounds ( $F_{3,1236} = 3$ ,  $p = 0.03$ ; Fig. 3b), while in spring, plateaus were significantly warmer than the other microhabitats ( $F_{3,164} = 61.86$ ,  $p < 0.001$ ; Fig. 3c). The values of the sediment cohesion index in the microhabitats also showed a distinct seasonal pattern (Fig. 3d) with bowls and gullies having

significantly lower values of the sediment cohesion index than plateaus during winter (January 2015:  $H_{3,176} = 53.6$ ,  $p < 0.001$ ; January 2016:  $H_{3,113} = 143.9$ ,  $p < 0.001$ ). In spring, however, bowls and gullies had significantly higher values of the sediment cohesion index than mounds and plateaus ( $H_{3,164} = 31.8$ ,  $p < 0.001$ ). Sediment organic matter contents were different among the different microhabitats ( $F_{3,66} = 9.97$ ,  $p < 0.001$ ; Fig. 3e): mounds were significantly lower in organic matter than the other microhabitats. Gullies showed a trend of being the richest in sediment organic matter, although this was not statistically significant (Fig. 3e). Finally, prior the establishment of the enclosures biofilm biomass of the microhabitats was significantly higher in depressions than on hummocks ( $F_{3,106} = 167$ ,  $p < 0.001$ ; Supplementary material Appendix 3 Fig. A7).

### The engineering effects of flamingos and crabs on biogeomorphology

During the experiment, we did not observe any evidence of flamingos entering the crab or flamingo enclosures at any time by way of footprints or signs of foraging activity. We observed that after excluding flamingos, the mound and bowl microhabitats completely disappeared through sediment accretion in the low zone (Fig. 4a). Crabs, especially the small ones, could not be fully excluded. There were on average  $21.73 \pm 13.62$  active burrows in the enclosure at the end of the experiment compared with  $33.5 \pm 9.5$  active burrows in the controls. After excluding both flamingos and crabs in

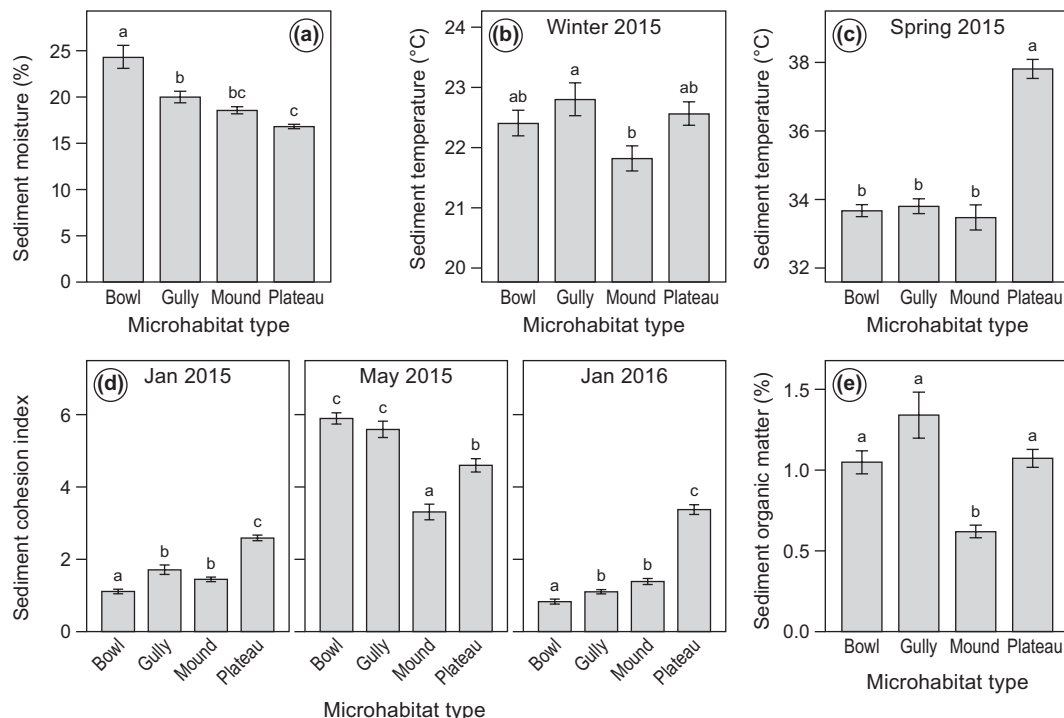


Figure 3. Comparisons of the (a) sediment moisture content, (b) sediment temperature in January–February 2015, (c) sediment temperature in May 2015, (d) sediment critical shear strength, and (e) sediment organic matter content of the different microhabitats in the mosaics. All bars show mean  $\pm$  SE; significant differences between habitats are depicted with lower-case letters ( $p < 0.05$ ).

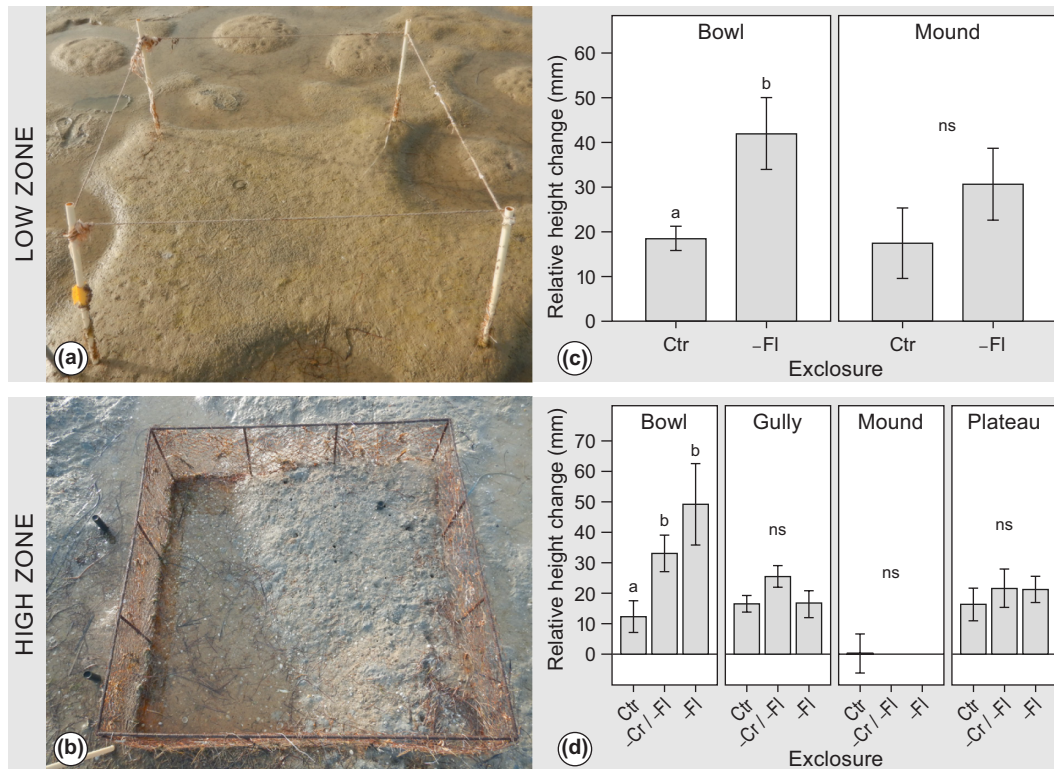


Figure 4. The state of representative (a) flamingo and (b) crab exclosures one year after establishment in the low and high zones, respectively. All the original microhabitats such as mounds and bowls had disappeared. (c) Changes in mean ( $\pm$ SE) relative bed level over one year in bowl (left panel) and mound microhabitats (right panel) found in control (Ctr) plots and flamingo exclosures (-Fl) in the low zone. (d) Changes in mean ( $\pm$ SE) relative bed level over one year in all microhabitats of the control (Ctr) plots and crab exclosures (-Cr/-Fl) in the high zone. Significant differences between microhabitats are depicted with lower-case letters ( $p \leq 0.05$ ).

the high zone, gully and plateau microhabitats remained visible at the end of the experiment, although gullies had accumulated slightly more sediment than in controls. Bowl and mound microhabitats, however, disappeared in the exclosures (Fig. 4b).

Topographic elevational changes showed that most of the microhabitats in exclosures experienced more sediment accumulation than in the control plots although not always significantly different (Fig. 4c-d). Bed level change for bowl microhabitats in the low zone was significantly higher in exclosures than in controls (Fig. 4c;  $t = -2.72$ ,  $n = 18$ ,  $p = 0.013$ ). Unlike bowl microhabitats, the bed level of mounds was not significantly different between treatments in the low zone (Fig. 4c;  $t = -1.16$ ,  $n = 18$ ,  $p = 0.2$ ). In the high zone, bed level change for bowl microhabitats was significantly higher in exclosures than in controls (Fig. 4d;  $F_{2,25} = 4.72$ ,  $p = 0.018$ ). Gully bed levels were only marginally different between crab exclosures ( $25.5 \pm 3.66$  mm) and controls ( $16.5 \pm 2.88$  mm) (Fig. 4d;  $t = -1.4$ ,  $n = 18$ ,  $p = 0.06$ ). Plateau microhabitats showed similar response in both control and exclosure treatments (Fig. 4d;  $F_{2,27} = 0.2$ ,  $p = 0.7$ ). Finally, excluding flamingos and crabs resulted in the disappearance of all mound microhabitats from the high zone (Fig. 4d).

### The effects of flamingo and crab grazing on biofilm biomass

All exclosures showed increases in biofilm one month and six months after their establishment, followed by a decrease one year later in both the high zone (LMER: January 2015:  $F_{2,878} = 19.7$ ,  $p < 0.001$ ; May 2015:  $F_{2,190} = 5$ ,  $p < 0.01$ ; January 2016:  $F_{2,190} = 5$ ,  $p = 0.08$ ; Fig. 5) and low zone (LMER: January 2015:  $F_{1,161} = 1.5$ ,  $p = 0.2$ ; May 2015:  $F_{1,73} = 0.9$ ,  $p = 0.3$ ; January 2016:  $F_{2,73} = 24$ ,  $p < 0.001$ ; Fig. 6). In the high zone, biofilm biomass increased within the first six months by  $56\% \pm 33\%$  in flamingo exclosures and by  $81\% \pm 33\%$  (mean  $\pm$  CI) in crab exclosures compared with controls (Fig. 5). A year later, however, depressions in flamingo and crab exclosures showed a reduction by  $32\% \pm 11\%$  and  $28\% \pm 11\%$ , respectively (Fig. 5). A similar trend was found in the low zone, where only flamingo exclosures had been erected, with an increase in biofilm biomass over the first six months by  $83\% \pm 26\%$ , and a reduction by  $53\% \pm 17\%$  a year later relative to controls (Fig. 6). Generally, in the high zone – where both flamingos and crabs were foraging – crab exclosures seemed to have had a stronger effect on biofilm densities than flamingos (Fig. 5). In agreement with our prediction on biomass levels among microhabitats, biofilm



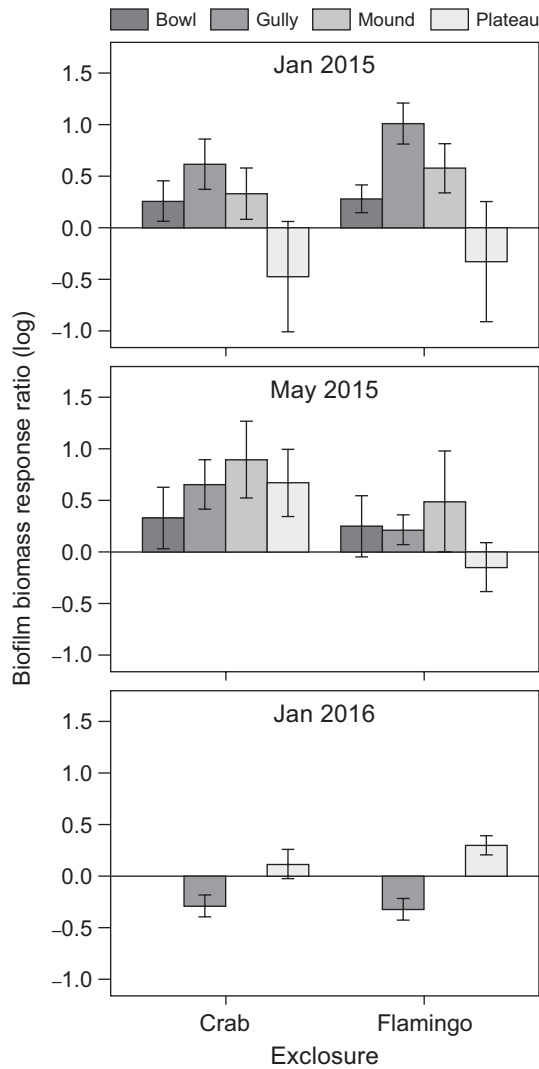


Figure 5. Differences between exclusions and controls in biofilm biomass found in the different microhabitats in the high zone. Data were collected over three time intervals. The bars represent mean effect sizes (log response ratios, LRR) with error bars representing the 95% CI. The zero line indicates no effect, and the significance of mean effects is indicated when the 95% confidence interval does not overlap with zero.

biomasses were significantly higher in depressions than hummocks (Fig. 5, 6).

## Discussion

In this study, we observed that within the two years after experimental removal of the microhabitat mosaics, recovery only occurred in the control areas. Where flamingos and crabs were excluded, these mosaics did not return. Also, the exclusion of flamingos and crabs caused the mosaics in undisturbed plots to disappear. Biofilm, the food for flamingos and crabs, was higher in depressions than on hummocks. This suggests that the joint feeding activities of flamingos and

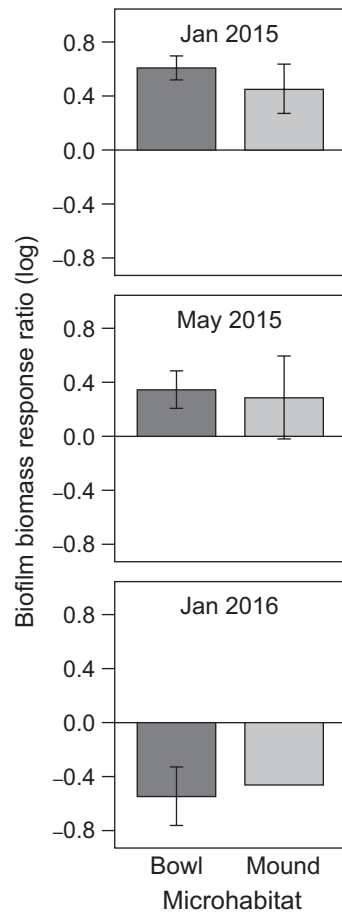


Figure 6. Differences between exclusions and controls in biofilm biomass found in the different microhabitats in the low zone. The bars represent mean effect sizes (LRR) with 95% CI. The zero line indicates no effect, and the significance of mean effects is indicated when the 95% confidence interval does not overlap with zero.

crabs create and maintain the microhabitats crucial for biofilm production.

In this case, both species most likely profit from each other's ecosystem engineering activities. This suggests a link to the concept of ecological autocatalysis, in which multiple coexisting species promote each other through resource manipulation feedback loops, increasingly drawing in and retaining resources in the loop, thus increasing system-level productivity (Veldhuis et al. 2018). Our study system can be considered as a marine example of such an autocatalytic loop, where flamingos and crabs on one side and biofilms on the other mutually promote resource recycling and productivity.

Over the last decade, considerable emphasis has been placed on the integration of non-trophic interactions, especially ecosystem engineering, into studies on ecosystem functioning (Olf et al. 2009, Bascompte 2010, Kéfi et al. 2012, Sanders et al. 2014, Genrich et al. 2017). The present findings reinforce the role of feedbacks and engineering networks across multiple trophic levels. If we had only examined the effects of flamingos and crabs on the



geomorphology and/or the effect of microhabitats on biofilm production in the present study, we would probably have missed the underlying engineering-feedback loop that controls the functioning of the mosaics. Understanding such mechanisms yields crucial insights into improving the conservation and management of ecosystems and species (Polis 1998, Olff et al. 1999, 2009, Lohrer et al. 2004, Suding et al. 2004, Largaespada et al. 2012). Loss of feedback loops could degrade ecosystem resilience and promote regime shifts (Scheffer and Carpenter 2003, Rietkerk et al. 2004, Nyström et al. 2012, van de Koppel et al. 2012, Bertness et al. 2015). Our results confirm earlier empirical evidence on the importance of joint ecosystem engineers in modulating intertidal ecosystem functioning (Caliman et al. 2011, Largaespada et al. 2012, Donadi et al. 2015). It has been shown that co-existing benthic engineers can determine the large-scale structure of intertidal communities (Lohrer et al. 2004, Donadi et al. 2015) and nutrient fluxes (Caliman et al. 2011, Largaespada et al. 2012).

### **The effects of biogeomorphology on sediment conditions**

The microhabitats within the mosaic strongly differ with respect to the sediment characteristics that might affect biofilm production. Depression microhabitats (bowls and gullies) were wetter than plateaus and richer in organic matter than mounds (Fig. 3). Depressions were also richer in biofilm than hummocks (Supplementary material Appendix 3 Fig. A7), indicating that the creation and maintenance of bowl and gully microhabitats is vital for biofilm as well as for the grazers who engineered them. The spatial heterogeneity of the mosaics creates an irrigation system where tidal water and debris are trapped in bowl and gully microhabitats, thus enhancing the moisture and organic matter contents. The sediment cohesion index showed clear seasonal patterns with a two-fold increase in spring compared with values in winter per microhabitat (Fig. 3d), perhaps reflecting an increase salt-crust induced by evaporation (Geng and Boufadel 2015, Geng et al. 2016).

Soil temperatures remained moderate in depression microhabitats in both winter and summer (Fig. 3b–c). Plateau temperatures were much higher than the temperatures in bowl and gully microhabitats in spring, which may explain why waders tend to use the depression microhabitats in spring and summer to avoid overheating (Verboven and Piersma 1995). Thus, depressions provide an intertidal irrigation system with low wave energy, moderate temperatures even in the warm season, and sediment that is rich in organic matter and nutrients; all these factors are known to favour biofilm growth and establishment (reviewed by Gerbersdorf and Wieprecht 2015).

### **The engineering effects of flamingos and crabs on biogeomorphology**

We tested whether excluding flamingos and crabs would lead to the disappearance of the microhabitats of the mosaics. Excluding flamingos and crabs resulted in the loss of the

bowl and mound microhabitats and a slight increase in the bed level of gully microhabitats. This was probably due to excluding the effects of trampling by flamingos, and digging and transport of sediment by crabs. At the end of the experiment both bowl and mound microhabitats were still absent from the exclosures. In the low zone, a plateau without any patterning started to develop in flamingo exclosures. In the high zone, however, gullies remained visible and active even though a thick layer of sediment had settled over the bowls. The effects of excluding flamingos on the topography are remarkable (Fig. 4a–c), and the accumulation of sediment can only be attributed to the absence of flamingo feeding.

In the high zone, however, the results of excluding both crabs and flamingos on topography, especially gully (almost significant  $p=0.06$ ) and plateau microhabitats, might have been affected by two contrasting effects. First, we failed to exclude all crabs from the plots. This certainly prevented the settlement of even more sediment in the gullies, as the caged crabs would have removed a larger part to the plateaus. In fact, this may explain why the differences in plateau bed levels between treatments remained non-significant. Plateaus receive sediment from the crabs through processed sediment balls collected in the depressions. These balls fall apart during the incoming tide and the fine particles may go into suspension and end up on the beach, while the remaining sand will settle down on the plateau. Thus, the sediment accumulation in the plateaus is predicted to be a slow and long-term process. Second, in direct contrast to the effect of crabs, the sediment accumulation in depressions might have been enhanced by the cages used as exclosures hindering water flow and thus increasing rates of sedimentation within the cages.

Previous studies in the marine systems have shown that cages could affect microphytobenthos biomass (Schrijvers et al. 1998, Como et al. 2006, Abdullah and Lee 2016) as well as sediment characteristics (Virnstein 1977, Piersma 1987, Felsing et al. 2005, Gallucci et al. 2008). Our experimental design, however, makes it unlikely that the cages caused major artefacts. The reported unwanted effects of cages are typically related to small mesh-size ( $<6$  mm) and shading (Reise 1977, Virnstein 1977, Como et al. 2006). Such artefacts should be minimal in our system, as we used a 1-cm mesh size and had no shading due to the open top of the exclosures (Fig. 4b). Unlike in other reported systems, the mosaics in our study are characterised by very low hydrodynamics and extensive shallow seagrass beds in front of them, which trap much suspended sediment before it reaches the mosaics (Folmer et al. 2012). The combination of using a large mesh size (i.e. 1 cm) in an area with low sediment suspension, as present in the mosaics, makes a cage effect unlikely. The 1-cm mesh offers plenty of space for the gentle flow to pass through freely. This was confirmed by visual observations during incoming and outgoing tide, during which there was no sign of flow deflection by the cages. We thus expect that the lack of full crab exclusion is likely to have caused more sediment removal than the enhanced sediment accretion due to a possible cage artefact. Indeed, we did not observe any odd sedimentation patterns in the

enclosures close to the edges of the cages. This might explain why there was no significant topographical change in plateau microhabitats between controls and crab enclosures in the high zone (Fig. 4d).

### The effects of flamingo and crab grazing on biofilm biomass

We found that the exclusion of flamingo and crab consumption enhanced the biofilm abundance over the short term (Fig. 5, 6) but impaired biofilm production over the long run. This means that these grazers stimulate biofilm productivity over the long term. This is likely the result of topographic changes through sediment accumulation, which subsequently alters sediment moisture content and surface temperature. Generally, microhabitats within crab enclosures accumulated slightly more biofilm compared with the ones in the flamingo enclosures. This accumulation was only significant in comparisons within gully microhabitats, suggesting the importance of gullies for food production to crabs. This importance of crabs becomes even more evident when taking into account that the crab enclosure treatment was in reality only a 1/3 'crab-reduction' treatment.

Flamingos and crabs seem to use different tidal phases to feed in the mosaic (Supplementary material Appendix 3 Fig. A3–A5). Flamingos use mostly the high tide hours, while crabs use the low tide ones. Both species, however, co-feed on biofilms during the outgoing tide. In the warm season, crabs also have been observed to move in huge numbers to feed in bowl microhabitats in the low zone where normally only flamingos feed. Crab burrows have never been observed in the low zone during our study period. In fact, crabs showed escape behaviours toward incoming tidal waters. The observed avoidance of crabs to burrow in the low zone could be due to water temperature and/or predators arriving with the tide. The low zone seems also unsuitable place for plateau formation due to increasing water flow with increasing tidal slope, which might inhibit the settlement of sediments and hence the divergence of plateaus and depressions. The observed differences in the use of tidal phases by flamingos and crabs are likely caused by their feeding habits. Flamingos are filter-feeders and thus need some tidal water to stir up the sediment with their feet to harvest buried microphytobenthos (Gihwala et al. 2017). This motion will prevent the settlement of new sediment and maintains the bowls and mound structures, which seems to create a favourable conditions for the growth of biofilms (Gerbersdorf and Wieprecht 2015). Crabs, on the other hand, are deposit-feeders that forage on the sediment surface around their burrows. The large number of constantly feeding of crabs the depressions is manifested in the sediment heaps that can be seen on a daily basis in the mosaic. These sediment heaps may be shifted elsewhere with the incoming tide, which will help maintain the structure of gullies and plateaus on the long-term.

### Generalisations and conclusions

We observed that hydrodynamic processes alone are unlikely to be responsible for creating the mosaics. The enclosure experiment demonstrated that the mosaics of Banc d'Arguin are the result of three-way biogeomorphic engineering loops between flamingos, crabs, biofilms and hydrodynamics. Our study on this biofilm-engineering network gives empirical support for interspecific engineering at the scale of many hectares, with consequences for several other species. Our work, together with previous studies on ecosystem engineering (Caliman et al. 2011, Largaespada et al. 2012, Donadi et al. 2015), identifies engineering networks as a driver of feedbacks between community structure and ecosystem processes in marine systems.

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*Author contributions* – HO, EME, TP and TB conceived the ideas and designed methodology; EME, HO, PO and TB collected the data; EME, PO and HO analysed the data; EME, HO, TP and TB led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

### References

- Abdullah, M. M. and Lee, S. Y. 2016. Meiofauna and crabs in mangroves and adjoining sandflats: is the interaction physical or trophic? – *J. Exp. Mar. Biol. Ecol.* 479: 69–75.
- Ansari, F. A. et al. 2017. Factors affecting biofilm formation in vitro and in the rhizosphere. – In: *Biofilms in plant and soil health*. – Wiley, pp. 275–290.
- Bascompte, J. 2010. Structure and dynamics of ecological networks. – *Science* 329: 765–6.
- Bates, D. et al. 2015. Fitting linear mixed-effects models using lme4. – *J. Stat. Softw.* 67: 1–48.
- Bertness, M. D. et al. 2015. Indirect human impacts turn off reciprocal feedbacks and decrease ecosystem resilience. – *Oecologia* 178: 231–237.
- Beukema, J. J. et al. 1993. Year-to-year variability in the biomass of macrobenthic animals on tidal flats of the Wadden Sea: how predictable is this food source for birds? – *Neth. J. Sea Res.* 31: 319–330.
- Borenstein, M. et al. 2009. *Introduction to meta-analysis*. – Wiley.
- Bos, A. R. et al. 2007. Ecosystem engineering by annual intertidal seagrass beds: sediment accretion and modification. – *Estuar. Coast. Shelf Sci.* 74: 344–348.

- Bulla, M. et al. 2017. Marine biorhythms: bridging chronobiology and ecology. – *Phil. Trans. R. Soc. B* 372: 20160253.
- Caliman, A. et al. 2011. Bioturbating space enhances the effects of non-additive interactions among benthic ecosystem engineers on cross-habitat nutrient regeneration. – *Oikos* 120: 1639–1648.
- Campredon, P. 2000. Between the Sahara and the Atlantic: Banc d'Arguin National Park, Mauritania. – FIBA, La Tour du Valat.
- Cézilly, F. et al. 1994. Observations on the breeding of the greater flamingo, *Phoenicopterus ruber roseus*, in the Banc d'Arguin National Park, Mauritania. – *Colon. Waterbird* 17: 181–183.
- Como, S. et al. 2006. Caging experiment: relationship between mesh size and artifacts. – *J. Exp. Mar. Biol. Ecol.* 335: 157–166.
- Diawara, Y. et al. 2007. Nouvelles données sur la reproduction et l'hivernage des flamants roses en Mauritanie et confirmation d'échanges avec les populations méditerranéennes. – *Ostrich* 78: 469–474.
- Donadi, S. et al. 2015. Multi-scale habitat modification by coexisting ecosystem engineers drives spatial separation of macrobenthic functional groups. – *Oikos* 124: 1502–1510.
- El-Hacen, E. M. et al. 2018. Data from: large-scale ecosystem engineering by flamingos and fiddler crabs on West-African intertidal flats promote joint food availability. – Univ. of Groningen Research Data Repository, <www.rug.nl/research/gelifes/research/data-management/repository?lang=en>.
- Ens, B. J. et al. 1993. Flocking and feeding in the fiddler crab (*Uca tangeri*): prey availability as risk-taking behavior. – *Neth. J. Sea Res.* 31: 477–494.
- Felsing, M. et al. 2005. Preliminary study on the effects of exclusion of wild fauna from aquaculture cages in a shallow marine environment. – *Aquaculture* 243: 159–174.
- Flemming, H. and Wingender, J. 2010. The biofilm matrix. – *Nat. Rev.* 8: 623–633.
- Folmer, E. O. et al. 2012. Seagrass–sediment feedback: an exploration using a non-recursive structural equation model. – *Ecosystems* 15: 1380–93.
- Gallucci, F. et al. 2008. Caging experiment in the deep sea: efficiency and artefacts from a case study at the arctic long-term observatory Hausgarten. – *J. Exp. Mar. Biol. Ecol.* 354: 39–55.
- Geng, X. and Boufadel, M. C. 2015. Impacts of evaporation on subsurface flow and salt accumulation in a tidally influenced beach. – *Water Resour. Res.* 51: 5547–5565.
- Geng, X. et al. 2016. Evidence of salt accumulation in beach intertidal zone due to evaporation. – *Sci. Rep.* 6: 31486.
- Genrich, C. M. et al. 2017. Duality of interaction outcomes in a plant–frugivore multilayer network. – *Oikos* 126: 361–368.
- Gerbersdorf, S. U. and Wieprecht, S. 2015. Biostabilization of cohesive sediments: revisiting the role of abiotic conditions, physiology and diversity of microbes, polymeric secretion and biofilm architecture. – *Geobiology* 13: 68–97.
- Gerbersdorf, S. U. et al. 2008. The engineering potential of natural benthic bacterial assemblages in terms of the erosion resistance of sediments. – *FEMS Microbiol. Ecol.* 66: 282–294.
- Gihwala, K. et al. 2017. Differential impacts of foraging plasticity by greater flamingo *Phoenicopterus roseus* on intertidal soft sediments. – *Mar. Ecol. Prog. Ser.* 569: 227–242.
- Glassom, D. and Branch, G. M. 1997a. Impact of predation by greater flamingos *Phoenicopterus ruber* on the macrofauna of two southern African lagoons. – *Mar. Ecol. Prog. Ser.* 149: 1–12.
- Glassom, D. and Branch, G. M. 1997b. Impact of predation by greater flamingos *Phoenicopterus ruber* on the meiofauna, microflora, and sediment properties. – *Mar. Ecol. Prog. Ser.* 150: 1–10.
- Grant, J. et al. 1986. The interaction between benthic films and sediment transport diatom. – *Estuar. Coast. Shelf Sci.* 23: 225–238.
- Hedges, L. V. et al. 1999. The meta-analysis of response ratios in experimental ecology. – *Ecology* 80: 1150–1156.
- Holdredge, C. et al. 2010. Fiddler crab control of cordgrass primary production in sandy sediments. – *Mar. Ecol. Prog. Ser.* 399: 253–259.
- Iriarte, A. et al. 2003. Short-term variability in microbial food web dynamics in a shallow tidal estuary. – *Aquat. Microb. Ecol.* 31: 145–161.
- Jackson, A. et al. 2010. Latitudinal and environmental patterns in abundance and composition of epilithic microphytobenthos. – *Mar. Ecol. Prog. Ser.* 417: 27–38.
- Jones, C. G. et al. 1994. Organisms as ecosystem engineers. – *Oikos* 69: 373–386.
- Kahlert, M. and McKie, B. G. 2014. Comparing new and conventional methods to estimate benthic algal biomass and composition in freshwaters. – *Environ. Sci. Processes Impacts* 16: 2627–34.
- Kéfi, S. et al. 2012. More than a meal... integrating non-feeding interactions into food webs. – *Ecol. Lett.* 15: 291–300.
- Krebs, C. J. 1996. Population cycles revisited. – *J. Mammal.* 77: 8–24.
- Krienitz, L. et al. 2016. Food algae for lesser flamingos: a stocktaking. – *Hydrobiologia* 775: 21–50.
- Kristensen, E. 2008. Mangrove crabs as ecosystem engineers; with emphasis on sediment processes. – *J. Sea Res.* 59: 30–43.
- Kristensen, E. and Alongi, D. M. 2006. Control by fiddler crabs (*Uca vocans*) and plant roots (*Avicennia marina*) on carbon, iron, and sulfur biogeochemistry in mangrove sediment. – *Limnol. Oceanogr.* 51: 1557–1571.
- Largaespada, C. et al. 2012. Meta-ecosystem engineering: nutrient fluxes reveal intraspecific and interspecific feedbacks in fragmented mussel beds. – *Ecology* 93: 324–333.
- Lill, J. T. and Marquis, R. J. 2003. Ecosystem engineering by caterpillars increases insect herbivore diversity on white oak. – *Ecology* 84: 682–690.
- Lohrer, A. M. et al. 2004. Bioturbators enhance ecosystem function through complex biogeochemical interactions. – *Nature* 431: 1092–1095.
- Montoya, J. M. et al. 2006. Ecological networks and their fragility. – *Nature* 442: 259–264.
- Nyström, M. et al. 2012. Confronting feedbacks of degraded marine ecosystems. – *Ecosystems* 15: 695–710.
- Olf, H. et al. 1999. Shifting mosaics in grazed woodlands driven by the alternation of plant facilitation and competition. – *Plant Biol.* 1: 127–137.
- Olf, H. et al. 2009. Parallel ecological networks in ecosystems. – *Phil. Trans. R. Soc. B* 364: 1755–1779.
- Orvain, F. et al. 2014. Tidal and seasonal effects on the short-term temporal patterns of bacteria, microphytobenthos and exopolymers in natural intertidal biofilms (Brouage, France). – *J. Sea Res.* 92: 6–18.
- Piersma, T. 1987. Production by intertidal benthic animals and limits to their predation by shorebirds: a heuristic model. – *Mar. Ecol. Prog. Ser.* 38: 187–196.
- Piersma, T. 2012. What is habitat quality? Dissecting a research portfolio on shorebirds. – In: Fuller, R. J. (ed.), *Birds and*

- habitat: relationships in changing landscapes. – Cambridge Univ. Press, pp. 383–407.
- Polis, G. A. 1998. Stability is woven by complex webs. – *Nature* 395: 744–745.
- Reise, K. 1977. Predator exclusion experiments in an intertidal mud flat. – *Helgol. Wiss. Meer.* 30: 263–271.
- Rietkerk, M. et al. 2004. Self-organized patchiness and catastrophic shifts in ecosystems. – *Science* 305: 1926–1929.
- Robertson, J. R. et al. 1981. Chemical and live feeding stimulants of the sand fiddler crab, *Uca pugilator* (Bosc). – *J. Exp. Mar. Biol. Ecol.* 53: 47–64.
- Rodríguez-Pérez, H. and Green, A. J. 2006. Waterbird impacts on widgeongrass *Ruppia maritima* in a Mediterranean wetland: comparing bird groups and seasonal effects. – *Oikos* 112: 525–534.
- Rodríguez-Pérez, H. and Green, A. J. 2012. Strong seasonal effects of waterbirds on benthic communities in shallow lakes. – *Freshwater Sci.* 31: 1273–1288.
- Sanders, D. et al. 2014. Integrating ecosystem engineering and food webs. – *Oikos* 123: 513–524.
- Scheffer, M. and Carpenter, S. R. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. – *Trends Ecol. Evol.* 18: 648–656.
- Schrijvers, J. et al. 1998. The infaunal macrobenthos under East African *Ceriops tagal* mangroves impacted by epibenthos. – *J. Exp. Mar. Biol. Ecol.* 222: 175–193.
- Scott, J. J. et al. 2012. Impacts of flamingos on saline lake margin and shallow lacustrine sediments in the Kenya Rift Valley. – *Sediment. Geol.* 277–278: 32–51.
- Smith, D. J. and Underwood, G. J. C. 1998. Exopolymer production by intertidal epipellic diatoms. – *Limnol. Oceanogr.* 43: 1578–1591.
- Smith, N. F. et al. 2009. Fiddler crab burrowing affects growth and production of the white mangrove (*Laguncularia racemosa*) in a restored Florida coastal marsh. – *Mar. Biol.* 156: 2255–2266.
- Stienen, E. W. M. et al. 2008. Why do gull-billed terns *Gelochelidon nilotica* feed on fiddler crabs *Uca tangeri* in Guinea-Bissau. – *Ardea* 96: 243–205.
- Suding, K. N. et al. 2004. Alternative states and positive feedbacks in restoration ecology. – *Trends Ecol. Evol.* 19: 46–53.
- van de Koppel, J. et al. 2012. The influence of local- and landscape-scale processes on spatial self-organization in estuarine ecosystems. – *J. Exp. Biol.* 215: 962–967.
- Veldhuis, M. P. et al. 2014. A novel mechanism for grazing lawn formation: large herbivore-induced modification of the plant–soil water balance. – *J. Ecol.* 102: 1506–1517.
- Veldhuis, M. P. et al. 2018. Ecological autocatalysis: a central principle in ecosystem organization? – *Ecol. Monogr.* 88: 304–319.
- Verboven, N. and Piersma, T. 1995. Is the evaporative water loss of knot *Calidris canutus* higher in tropical than in temperate climates? – *Ibis* 137: 308–316.
- Viechtbauer, W. 2010. Conducting meta-analyses in R with the metafor package. – *J. Stat. Softw.* 36: 1–48.
- Virnstein, R. W. 1977. The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. – *Ecology* 58: 1199–1217.
- Wright, J. P. and Jones, C. G. 2006. The concept of organisms as ecosystem engineers ten years on: progress, limitations and challenges. – *BioScience* 56: 203–209.
- Wright, J. P. et al. 2002. An ecosystem engineer, the beaver, increases species richness at the landscape scale. – *Oecologia* 132: 96–101.
- Zhu, Z. et al. 2016. Sprouting as a gardening strategy to obtain superior supplementary food: evidence from a seed-caching marine worm. – *Ecology* 97: 3278–3284.
- Zwarts, L. 1985. The winter exploitation of fiddler crabs *Uca tangeri* by waders in Guinea-Bissau. – *Ardea* 73: 3–12.
- Zwarts, L. and Blomert, A.-M. 1990. Selectivity of whimbrels feeding on fiddler crabs explained by component specific digestibilities. – *Ardea* 78: 193–208.

Supplementary material (available online as Appendix oik-05261 at <[www.oikosjournal.org/appendix/oik-05261](http://www.oikosjournal.org/appendix/oik-05261)>). Appendix 1–3.