



Behavioral self-organization underlies the resilience of a coastal ecosystem

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Self-organized spatial patterns occur in many terrestrial, aquatic, and marine ecosystems. Theoretical models and observational studies suggest self-organization, the formation of patterns due to ecological interactions, is critical for enhanced ecosystem resilience. However, experimental tests of this cross-ecosystem theory are lacking. In this study, we experimentally test the hypothesis that self-organized pattern formation improves the persistence of mussel beds (*Mytilus edulis*) on intertidal flats. In natural beds, mussels generate self-organized patterns at two different spatial scales: regularly spaced clusters of mussels at centimeter scale driven by behavioral aggregation and large-scale, regularly spaced bands at meter scale driven by ecological feedback mechanisms. To test for the relative importance of these two spatial scales of self-organization on mussel bed persistence, we conducted field manipulations in which we factorially constructed small-scale and/or large-scale patterns. Our results revealed that both forms of self-organization enhanced the persistence of the constructed mussel beds in comparison to nonorganized beds. Small-scale, behaviorally driven cluster patterns were found to be crucial for persistence, and thus resistance to wave disturbance, whereas large-scale, self-organized patterns facilitated reformation of small-scale patterns if mussels were dislodged. This study provides experimental evidence that self-organization can be paramount to enhancing ecosystem persistence. We conclude that ecosystems with self-organized spatial patterns are likely to benefit greatly from conservation and restoration actions that use the emergent effects of self-organization to increase ecosystem resistance to disturbance.

had very limited impact so far in conservation or restoration practices. For instance, the practice of dune restoration still applies an even spread of *Ammophila arenaria* plant propagules, disregarding the strong patchy to patterned distribution of *Ammophila* in many naturally emerging dune systems. Similarly, *Spartina alterniflora* propagules are typically planted at a constant and dispersed distance in salt marsh restoration projects, eliminating facilitation between out-plants and reducing overall yield (24, 25). To advance both fundamental and conservation science regarding self-organization, there is thus an urgent need for experimental tests of the emergent effects of spatial self-organization on ecosystem stability and persistence, using manipulative techniques.

In this study, we investigated the importance of spatial self-organization on the persistence of mussel beds in sandy intertidal ecosystems. Mussels in soft-sediment ecosystems form very large (1 to >10 ha), highly patterned beds in which self-organization occurs at two different scales (9, 13, 22). At a small scale, mussels make string-shaped clusters that form reticulate patterns (5–10 cm wide; Fig. 1D) as a result of behavioral aggregation, which is a fast process that can occur within the time frame of a single day (9). At larger scales, mussels organize in regularly spaced bands (5–10-m wavelength; Fig. 1E) perpendicular to water flow as a consequence of local facilitation and larger scale competition for pelagic algae (13). Comparative studies and theoretical models highlight that by organizing in a nested, two-scale pattern, mussels can maintain high

self-organization | resilience | multiscale patterns | ecosystems | mussels

Formation of regular spatial patterns by habitat-forming organisms, such as clumping and banding, have been observed in many different ecosystems, ranging from forests (1) to savannahs (2, 3), peat lands (4–6), and intertidal ecosystems (7–10). Theoretical studies have highlighted that local ecological interactions can explain the formation of large-scale spatial patterns through a process called spatial self-organization (9, 11, 12) (Fig. 1). In this process, regular patterns can emerge when organisms improve their growth conditions locally through habitat modification while inhibiting conspecifics at a larger scale due to competition for resources or other growth-restricting interactions (5, 7, 9, 10, 13–19). Other theoretical studies (6, 13) and a small number of comparative studies (2, 9) predict that formation of self-organized patterns enhances ecosystem persistence and stability (19–22). The ubiquity of self-organized spatial patterns across ecosystems worldwide (23) suggests that self-organization could be of universal importance in shaping ecosystem persistence and resistance to increasing anthropogenic stressors (24).

Despite well-developed theory predicting that self-organization can enhance ecosystem resistance to disturbance, there is currently no experimental evidence supporting this idea in any real-world situation. This lack of experimental support not only holds back further theoretical advance but also hampers its real-world application, potentially explaining why self-organization theory has

Significance

Theoretical models suggest that spatial self-organization enhances the resistance of ecosystems to disturbance. However, experiments investigating this important prediction are lacking. Our paper provides clear experimental evidence that spatial self-organization profoundly increases the ability of ecosystems to persist in the face of disturbance. The mechanisms underlying this positive impact of self-organization are driven by the combination of ecological and behavioral processes. Specifically, large-scale banded patterns in mussel beds created by ecological feedback processes facilitate fast behavioral aggregation of individual mussels into clumps, in turn improving mussel survival. Our study emphasizes the potential of harnessing spatial self-organization to enhance restoration success and persistence of threatened ecosystems.

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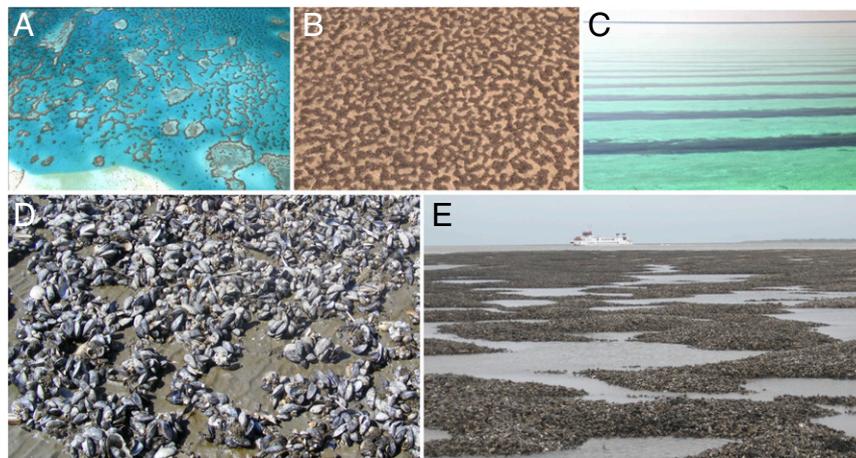


Fig. 1. Observations of self-organization in different ecosystems. (A) Spotted pattern of coral reefs in Australia (Copyright Google Earth). (B) Labyrinth pattern of bushy vegetation in Niger (Copyright Google Earth). (C) Banded patterns in seagrasses in Australia (Image courtesy of Marjolijn Christianen). (D) Small-scale self-organization in a mussel bed in The Netherlands. Mussels organize in strings (5–10 cm wide). (E) Large-scale self-organization in mussel beds in The Netherlands. Mussels organize in bands (5–7 m wide).

densities within the clusters, which provides safety against dislodgement and predation (26, 27). However, overall density remains sufficiently low in the nested pattern to avoid excessive competition (9, 13). Mussel beds provide a highly tractable system in which to test the general idea that self-organization can enhance ecosystem persistence. In addition, if this prediction holds, it has direct implications for the management and restoration of mussel beds, which act as a keystone habitat for provisioning of biodiversity (28), as well as being a marine food source.

Using manipulative experiments, we tested whether spatial self-organization affects the persistence of mussels within intertidal mussel beds under the natural influence of wave action and predation (29). In both June and October of 2012, we created artificial mussel beds with small-scale and large-scale spatial patterns, similar to the patterns found in natural conditions, and determined their effect on the persistence of mussels in the bed. This effect was tested with four controlled spatial organization treatments: (i) beds in which we made small-scale clusters, (ii) beds in which we made large-scale bands, (iii) a treatment in which we created both bands and clusters, and (iv) a control treatment in which we randomly scattered the mussels over the test plot (Fig. 2). To identify the mechanistic processes behind the differences in persistence in the experiment, we performed an analysis of mussel behavior in both the laboratory and the field. First, we analyzed how mussel movement on sandy substrates was affected by mussel density in both the laboratory and the field. In addition, we compared mussel behavior on sandy and rocky substrate in the laboratory. Our results provide important insights into the importance of spatial self-organization at multiple spatial scales for ecosystem persistence and how self-organization can be used to improve the restoration and conservation of natural ecosystems.

Results

Manipulation of the spatial patterns in artificial mussel beds revealed strong positive effects of self-organization on mussel bed persistence. During the first 6 d, cover in the control beds, which lacked any form of patterning, decreased twice as fast (4.98 ± 1.68 SE per day) relative to the plots with either small-scale or large-scale patterns, or both (0.87 ± 0.19 SE per day; Fig. 3A and B), with significant effects of both large-scale banding ($F_{2,32} = 6.19$, $P < 0.01$) and small-scale clustering ($F_{1,35} = 11.46$, $P < 0.01$). There was also a significant statistical interaction between the two scales of patterning ($F_{2,33} = 6.68$, $P < 0.01$); that is, the positive effect of both types of self-organization was statistically the same

when occurring either separately or in combination (Fig. 3A). The experimental results were consistent in both June and October, with no significant effect of season on the results. We observed that the loss rate of mussels decreased strongly over time ($F_{1,39} = 77.41$, $P < 0.001$), most likely because most of the remaining mussels in the treatments had organized into clusters after the first few days (Fig. 3C and D). This result highlights the importance of cluster formation for the resilience of mussel beds following experimental disturbance.

We conducted behavioral experiments both in the laboratory and in the field to unravel the importance of active mussel movement in cluster formation. The behavioral experiments revealed that the limited ability of mussels to move and aggregate on sand, which is crucial in determining clump size, underlies the lower resistance of mussels in unpatterned beds. The number of mussels in clumps was significantly higher in both the clustered and banded treatments ($\chi^2 = 78.44$, $P < 0.001$ and $\chi^2 = 106.59$, $P < 0.001$, respectively) compared with the unpatterned

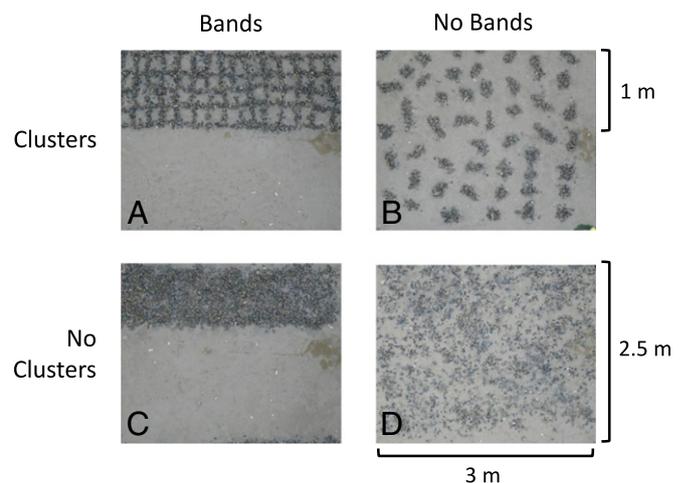


Fig. 2. Experimental setup to study the effect of spatial self-organization on persistence of mussel beds. Artificial beds were set up using a full-factorial design and four treatments: both bands and clusters (A), clusters but no bands (B), bands but no clusters (C), and mussels fully dispersed (D, control). Note that for each experimental plot, each treatment was repeated, making a 3- × 5-m plot.

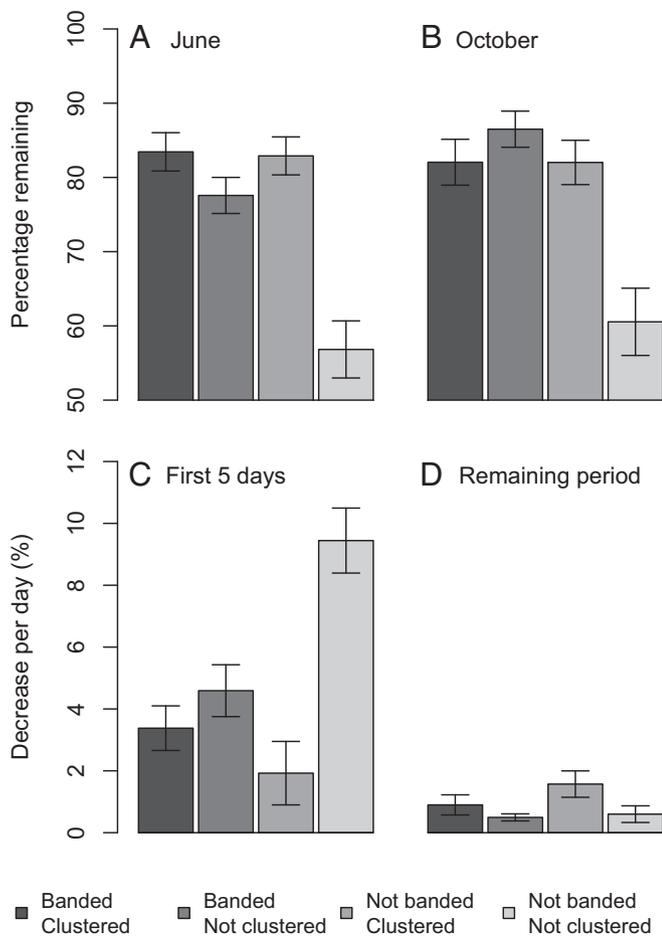


Fig. 3. Persistence of experimental mussel beds in the field over time. (A and B) Average cover decrease (percentage per day) over the course of the experiment for June and October. The decrease in cover (percentage per day) over the first 5 d (C) and in the remaining experimental period (D) is shown ($n = 28$; mean \pm SE).

controls, where average clump size was up to threefold smaller. Moreover, we found a significant statistical interaction between both treatments ($\chi^2 = 38.28$, $P < 0.001$), because both the banding and clustering treatments similarly facilitated aggregation (Fig. 4A). Hence, the effect of the two scales of self-organization proved nonadditive and complementary, with both converging to similar patterns of small-scale aggregation. Clump formation in the banded-not clustered treatment was as strong as in the clustered treatment, where we initially created clumps ourselves. In addition, we identified a significant interaction between the clustering treatment and the experimental setting ($\chi^2 = 11.10$, $P < 0.001$), because the effect of clustering was marginally lower in the field compared with laboratory conditions. Apart from forming smaller clumps, we also found two- to sevenfold more individual mussels out of clumps in the controls, as illustrated by a significant effect of the clustering and banding treatments, as well as their interaction, on the number of isolated mussels ($F_{1,32} = 34.96$, $P < 0.001$; $F_{1,32} = 43.93$, $P < 0.001$; and $F_{1,32} = 16.88$, $P < 0.001$, respectively; Fig. 4B). Similar to clump size, we also found a significant statistical interaction between bands, clusters, and location ($F_{1,32} = 7.65$, $P = 0.009$), because effects of self-organization were comparable but slightly lower in the field.

When the movement of mussels on sand is compared with the movement of mussels on rock in the laboratory, results show that the inability of mussels to move and aggregate on sand is the key

limitation explaining the low persistence of mussels in the control treatments, where patterns were absent. The clustering and banding treatments had no significant effect on mussel movement in terms of their average velocity, but mussels were found to move better on stone than on sand ($F_{1,609} = 109.23$, $P < 0.001$; Fig. 5). Furthermore, we found significant two-way interactions between banding and substrate and between clusters and substrate ($F_{1,609} = 16.91$, $P < 0.001$ and $F_{1,609} = 29.57$, $P < 0.0001$, respectively), as well as a three-way interaction between banding, clustering, and substrate ($F_{1,609} = 15.12$, $P < 0.0001$). Overall, these results, which highlight that when isolated, individual mussels can double their movement velocity when on rock, allowing for a fast behavioral response to isolation, are in agreement with observations in prior studies (9, 30). In contrast, the movement of mussels on sand is lowered by 26–39% when they are isolated. This finding highlights that when they are alone and on sand, mussels experience significant restrictions in their movement, preventing them from forming the clumps that are essential for survival and explaining the low persistence within the unpatterned mussel treatment, where mussels were scattered over the entire experimental area.

Discussion

Theoretical models predict that self-organized spatial patterns can have important emergent consequences for the functioning of ecosystems and their ability to resist disturbance (2, 6, 13, 22, 23, 31, 32). However, experimental validation of these emergent effects is lacking, restricting advancement and refinement of this cross-ecosystem

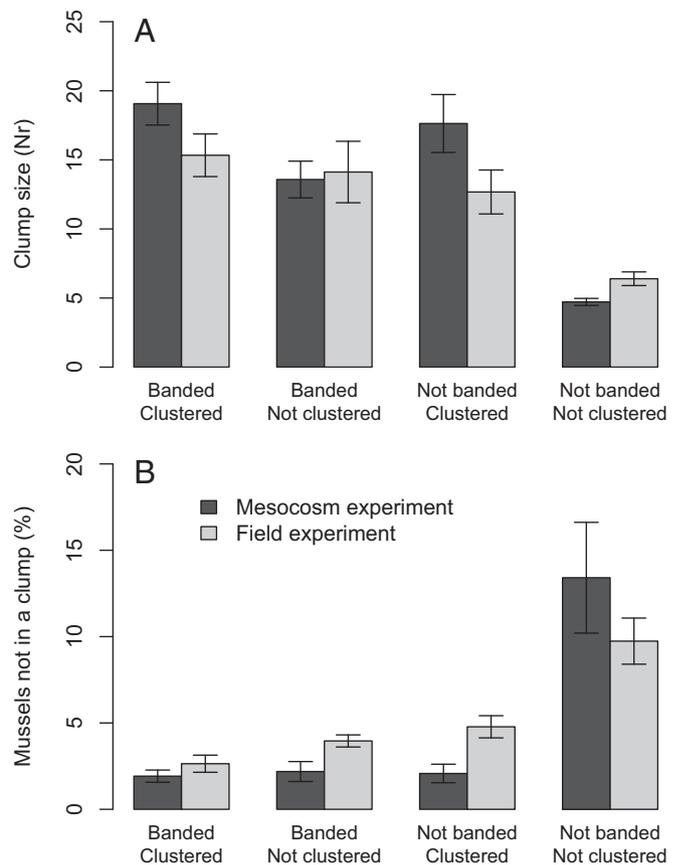


Fig. 4. Effect of experimental self-organization treatments on clump formation in laboratory and field conditions. (A) Average number (Nr) of mussels per clump (mean \pm SE). (B) Average number of loose individual mussels (mean \pm SE).

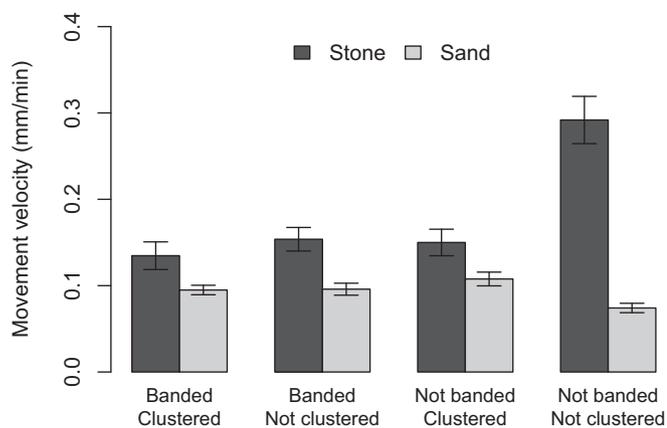


Fig. 5. Average movement velocity of an individual mussel under laboratory conditions (mean \pm SE). Isolated individual mussels on a rocky surface have increased velocity, whereas movement on sand under these conditions is hampered.

theory, as well as the application of self-organization concepts in the management and restoration of degraded ecosystems (24). In this study, we experimentally demonstrate that in mussel beds, self-organization processes enhance mussel resistance to disturbance, and thus the stability of this diversity-enhancing ecosystem on intertidal flats (33). This positive feedback occurs in our experiments regardless of whether a single scale of patterning or a combination is present, because all three patterned treatments either directly or indirectly facilitated small-scale mussel aggregation. Without any form of self-organization (i.e., in the fully dispersed treatment), the loss of mussels from the bed is 2.5-fold to fivefold higher compared with beds where mussels were aggregated in patterns of any sort. Here, small-scale, behavior-driven patterns proved crucial for mussel persistence, and by aggregating the mussels, the large-scale, banded patterns facilitated small-scale clump formation. In-depth laboratory analyses identify behavioral self-organization at a small spatial scale as the determining factor for the persistence of mussels on the beds; inability to move and aggregate into clumps in the treatments without any self-organization was found to underlie the high losses experienced in this treatment. Hence, our results provide unambiguous experimental support for the emergent effects of spatial self-organization in the mussel bed ecosystem and highlight the mechanisms that are behind this phenomenon.

Biological complexity at different spatial scales, driven by a multitude of behavioral, population-level, or ecosystem-level processes, is a defining characteristic of natural ecosystems (22, 34–36). A recent theoretical study highlighted that the interplay between two different self-organization processes created spatial patterns at two different scales in mussel beds, which proved a crucial factor in defining mussel bed persistence (22). Our results provide experimental validation of this prediction. The formation of small-scale, self-organized patterns proved to be crucial for mussel persistence because clumps increase resistance to disturbance, being either dislodgement or predation (9, 26, 27, 37–39). In our experiment, the large-scale spatial patterns were found to stimulate the formation of small-scale cluster patterns essential for survival: Without large-scale banded patterns, clump formation was hampered, leading to excessive mussel losses. When aggregated into bands, mussels could then form cluster patterns by using each other as a foothold, a behavior that becomes impossible when they are fully dispersed due to the low overall density. To summarize, the small-scale aggregation leading to high density improves mussel safety by reducing predation and wave dislodgement, a phenomenon already well-described in the literature (26, 27). High density, however,

would inevitably impose strong competition for food on the mussels. Competition can be avoided by forming banded patterns on a large scale, reducing overall density, and hence competition for food, yet preserving safety by maintaining a high local density within the bands (13, 40). Hence, the self-organization processes occurring at separate spatial scales, as we observed in our experiments, are important drivers of mussel bed persistence (22).

An unexpected result from our experiments was the clear importance of rapidly emerging behavioral self-organization in determining the persistence of mussel beds. Most studies of regular patterns in ecosystems suggest a scale-dependent interplay of facilitation and competition as the underlying process (5, 7, 10, 13, 19), a slow form of pattern formation that is akin to Turing's activator/inhibitor principle (41, 42). In mussels, however, the formation of small-scale patterns results from a behavioral process that is more similar to the physical process of phase separation (30). Phase separation occurs, for instance, during the formation of alloys, where separation between different types of molecules creates spatial patterns at a submillimetric scale, which boosts the material strength of alloys such as steel and bronze (43). Our results highlight that the patterns resulting from the behavioral self-organization in mussels (44) similarly determine the "strength" of mussel beds to resist predation and wave action. This finding highlights the importance of behavioral self-organization, driven by fast movement processes, as an underappreciated and understudied driver of the persistence of large-scale ecosystems.

Our study adds to a growing body of papers, theoretical or empirical, pointing to the importance of facilitation and self-organization for the resilience (13, 22), productivity (2), and biodiversity of natural ecosystems (33). In many, if not most, human-modified ecosystems, the natural spatial structure is altered or lost due to mowing, drainage, dredging, and other forms of interference. Moreover, in the coming decades, many ecosystems are expected to face further increases in disturbance as a result of global change (45, 46). Our results highlight that restoration of natural communities in these human-altered and homogenized ecosystems could be facilitated if (i) the original spatial structure is restored or conserved or (ii) the self-organization processes that generate these spatial patterns are restored to their former functioning. Such measures require a change in management perspectives and restoration approaches. It is likely insufficient to focus on improving abiotic conditions and removing dispersal barriers because these measures do not recover the facilitative processes that are characteristic to foundation species, such as mussels, cordgrasses, or marram grass (24, 25). Instead, restoration approaches should also aim to restore the functioning of internal positive feedback interactions to facilitate the persistence of the involved species. Recovery of the feedbacks can be achieved by reconstructing or approximating the self-organized spatial configuration of the ecosystem that has to be restored. Our study suggests that harnessing the emergent effects of spatial self-organization can make an important difference in the restoration of many marine and nonmarine ecosystems, such as salt marshes (24), seagrass beds (47), or arid bushlands (48).

There has been a recent global surge in promoting habitat restoration as a critical conservation approach to deal with both climate change and habitat degradation. At the 2014 United Nations Climate Summit, all nations present pledged to restore 350 million acres of degraded ecosystems actively by 2030. Critical to the success of this global pledge is (i) the facilitation of regrowth of ecosystems in degraded areas and (ii) the continued persistence of those systems once they are initially established. Although restoration of habitats dominated by ecosystem engineers has been prioritized (44, 49–52), large-scale restoration attempts of ecosystems such as coral reefs, shellfish reefs, and seagrasses is currently very costly and of limited success (53–57). Because many of these ecosystems are characterized by self-organized spatial patterns

generated by habitat-forming species, we argue that harnessing positive interactions and the resulting self-organization processes will be critical in developing more successful restoration and conservation practices (24, 25, 45, 46, 58). Our study provides a strong empirical basis for such a premise by experimentally demonstrating the importance of self-organization in mussel bed restoration. Moreover, it highlights the importance of the interplay between behavioral and ecological processes in driving ecosystem resilience. Our results point to the need for an integrated perspective on ecosystem restoration that not only addresses limitation in organism establishment but integrates the impact of organism behavior in terms of its effect on ecosystem resilience (22).

Materials and Methods

Ecological Field Experiment. To study the effect of self-organization on mussel bed persistence, we set up an experiment in which we tested the importance of pattern formation on the persistence of transplanted mussels in artificial beds. We tested for the effect of large-scale self-organization (bands) and small-scale self-organization (clusters) in a full-factorial design and then measured how treatments affected the persistence of the bed in the weeks after transplantation. In the first weeks, the impact of the patterns we have created on persistence is largest because, afterward, the mussels have either formed clumps and attached to others or been lost from the bed. In this way, our experimental transplantations mimic the effects of a natural disturbance, such as a storm, that dislodges and displaces mussels from the bed.

We set up the experimental beds (3 × 5 m) on the tidal flats near Schiermonnikoog, the eastern island of the Dutch Wadden Sea, in an area at the same elevation as natural beds (−0.5 m, coordinates: 53°27′9.91″N, 6°8′50.07″E). Using mussels from a nearby intertidal mussel bed, 12 plots were constructed using an overall density of 2.7 kg/m² (40 kg in total), which is similar to densities found in natural mussel beds (9). We applied four different spatial treatments in these experimental beds. The large-scale self-organization was represented by two bands sized 1 × 3 m. Within these bands, mussels were aggregated by hand in string and cluster patterns to reflect small-scale self-organization. In the first treatment (control; Fig. 2A), all scales of self-organization were present. In the second treatment (Fig. 2B), only clusters were made and no large-scale, banded patterns were used. In the third treatment (Fig. 2C), only bands were made, within which the mussels were fully dislodged. Finally, in the control treatment (Fig. 2D), neither large-scale nor small-scale self-organization was implemented and mussels were randomly dispersed on the plot. The treatments were not maintained, allowing the mussels to form their own patterns after transplantation. Plots were positioned along the low-water line, and the bands were orientated perpendicular to the dominant flow direction. The entire experiment was replicated four times in space, yielding 16 beds in total. To test for generality over time, the experiment was conducted twice, once in June and once in October. To measure the change of mussel cover in time, we took aerial pictures on a daily basis during the first 6 d and once every 12 d after that time, using a camera mounted on a telescopic pole. Pictures were transformed in black (mussels) and white (bare sand) images using ImageJ software (NIH). The proportion of black pixels was determined using ImageJ to provide us with an estimate of mussel cover for each plot. The development of cover over time was used as a measure of mussel persistence.

Behavioral Experiments. To investigate to what extent mussel movement behavior contributes to the observed differences in self-organization and subsequent persistence, we studied how mussel aggregative movement varied with the various densities of conspecifics in the different treatments. We first studied mussel aggregation under both natural and controlled conditions. In a second experiment, we analyzed aggregative movement in controlled laboratory conditions.

Mesocosm experiment. In the mesocosm, small artificial beds (40 × 40 cm) were set up in two polyester tanks (120 × 80 cm). As in the previous experiment, four spatial treatments were used with four replicates per treatment. To reflect the conditions within the bands of the large-scale, self-organization treatment used in the field, we used a high density of 5.6 kg/m². To reflect conditions without bands, we lowered the density to 2.5 kg/m². Both densities are within the range of densities found in natural mussel beds (9). In both densities, we mimicked small-scale self-organization by aggregating mussels by hand in clumps in half of

the units. In the other half, small-scale self-organization was removed by manually detaching the mussels and placing them randomly on the bed.

Early observations suggested that mussels appeared more restricted in their movement on sediment compared with the stone surfaces that had been used in prior experiments (9, 59). For this reason, we replicated the entire experiment on both solid and sandy substrate. The individual experiments were carried out in 80 × 120 × 10-cm tanks with a constant supply of fresh seawater. Each 100-L tank was divided into two equal areas in which a treatment was randomly applied to create four small artificial mussel beds. The bottom of the tanks was covered with either a 5-cm layer of sand or a 50- × 50-cm stone tile. Mussels were collected from wooden poles at the beach near Vlissingen (The Netherlands) a few days before the start of the experiments. Before the start of the experiments, the mussels were dislodged and added to one of the treatments. Each experiment was repeated three times.

Field experiment. Finally, to test whether laboratory results accurately reflected natural conditions, we repeated part of the laboratory experiments in the field. Pilot experiments revealed that visibility nearby the artificial beds on Schiermonnikoog was too limited to allow for reliable underwater camera observations. The experiment was therefore moved to a tidal flat in the Eastern Scheldt, in the south of The Netherlands (51°27′44.85″N, 4°4′51.75″E), where water clarity was much higher. We used the same plot size (~40- × 40-cm clumps within 50- × 50-cm plots) and aggregation treatments as in the laboratory and collected the mussels from the same site a few days before the start of the experiment. The experiment was set up in November 2013 and replicated two times.

Data collection. We tracked mussel aggregation and movement in the laboratory using Canon Powershot D10 cameras that were mounted over each tank. For the field, we used Canon Powershot S90 cameras within an Ikelite 6242.95 underwater housing (www.ikelite.com). The cameras took pictures every minute for 180 min. For each picture, we applied a pixel-to-centimeter conversion coefficient based on the distance of the camera from the bed and its angle. To analyze the effect of the treatments on the level of aggregation, we counted the number of clumps of at least two individuals, the number of mussels within the clumps, and the number of isolated mussels, after 24 h. In the laboratory, mussel movement velocity was quantified for 10 random mussels in each experimental unit. Images were processed in ImageJ and MATLAB (MathWorks) to determine the change in position (*x*-*y* coordinates) of the mussels, from which the distance traveled per unit of time was calculated.

Statistical Analyses.

Ecological field experiment. All statistical tests were run in R version 3.2.2. We used a generalized linear mixed model with a Gaussian distribution and Satterthwaite approximation of the degrees of freedom. Band, cluster, and day since start were included as fixed factors, and the month in which the experiment was carried out was included as a random factor. Furthermore, plot was nested within block as a random factor to account for block effects and repeated sampling within the plots, respectively. The decrease per day was calculated as the difference in cover between two sample dates divided by the number of days that had passed. The decrease in time was subsequently analyzed with the same analysis as above, but using “period” (0–5 d and the remaining time) instead of “day” as a fixed factor.

Mussel aggregation analyses. Differences in clump size (i.e., the number of mussels in a clump) were analyzed using a generalized linear model with a negative binomial distribution, using banding, clustering, and location (field or mesocosm) as fixed factors. The percentage of single, detached mussels was analyzed using ANOVA, with banding, clustering, and location (field or mesocosm) as fixed factors. The percentage of loose mussels was square root-transformed to obtain a normal distribution of the model residuals.

Aggregative movement analyses. Differences in movement on sandy vs. rocky substrate were tested using ANOVA, with the aggregation treatments and substrate as fixed factors. The data were square root-transformed to obtain normality of the model residuals.

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