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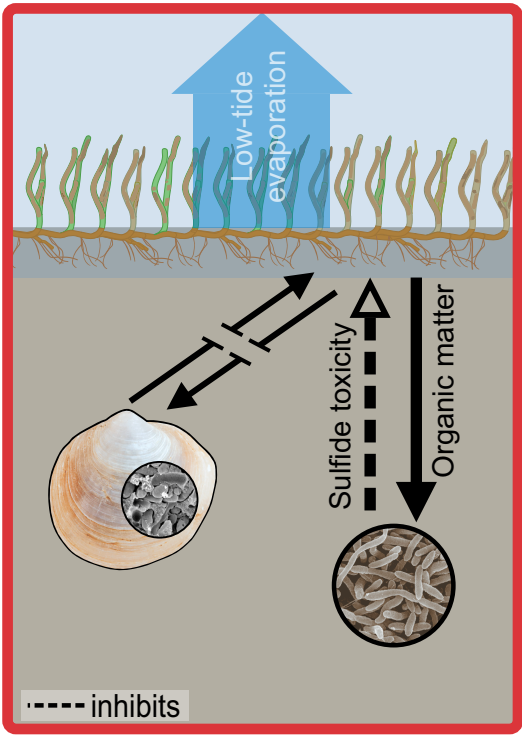
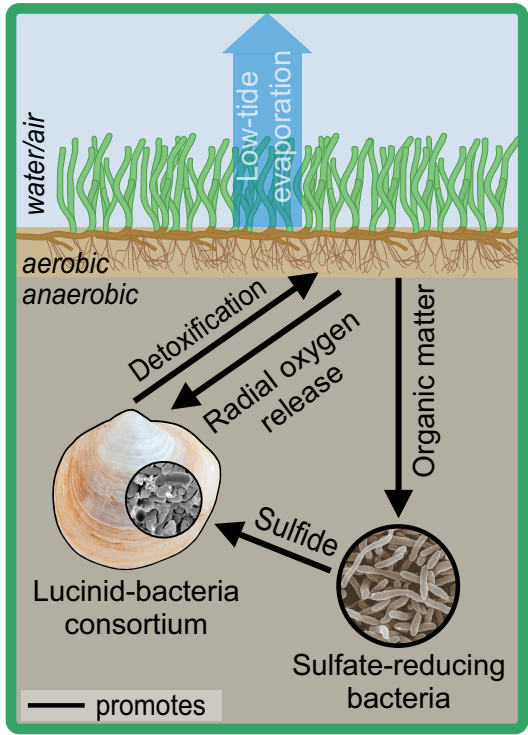
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Drought-induced mutualism breakdown and seagrass degradation

Healthy intertidal seagrass system



Drought, mutualism breakdown and landscape-scale degradation of seagrass beds

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Summary

In many marine ecosystems, biodiversity critically depends on foundation species such as corals and seagrasses that engage in mutualistic interactions [1-3]. Concerns grow that environmental disruption of marine mutualisms exacerbates ecosystem degradation, with breakdown of the obligate coral mutualism ('coral bleaching') as an iconic example [2, 4, 5]. However, as these mutualisms are mostly facultative rather than obligate, it remains unclear whether mutualism breakdown is a common risk in marine ecosystems, and thus a potential accelerator of ecosystem degradation. Here, we provide evidence that drought triggered landscape-scale seagrass degradation, and the consequent failure of a facultative mutualistic feedback between seagrass and sulfide-consuming lucinid bivalves that in turn appeared to exacerbate the observed collapse. Local climate and remote sensing analyses revealed seagrass collapse following a summer with intense low-tide drought stress. Potential analysis – a novel approach to detect feedback-mediated state shifts – revealed two attractors (healthy and degraded states) during the collapse, suggesting that the drought disrupted internal feedbacks to cause abrupt, patch-wise degradation. Field measurements comparing degraded patches that were healthy before the collapse with patches that remained healthy demonstrated that bivalves declined dramatically in degrading patches with associated high sediment sulfide concentrations, confirming the breakdown of the mutualistic seagrass-lucinid feedback. Our findings indicate that drought triggered mutualism breakdown, resulting in toxic sulfide concentrations that aggravated seagrass degradation. We conclude that external disturbances can cause sudden breakdown of facultative marine mutualistic feedbacks. As this may amplify ecosystem degradation, we suggest to include mutualisms in marine conservation and restoration approaches.

Results

Mutualisms are important drivers of global biodiversity and ecosystem functioning, as many organisms are directly involved in networks of beneficial interactions [4, 6, 7]. A vast majority of terrestrial plants depends on mutualistic partnerships [6, 7], and in marine ecosystems, ecosystem-structuring foundation species such as corals, kelp, salt marsh plants, mangroves, and seagrasses may depend on them to decrease physical stress or gain resources [1-3]. Mounting evidence suggests that global change can disrupt such mutualistic feedback loops [2, 4, 8, 9], potentially accelerating habitat degradation [1, 2, 4]. Coral bleaching events (i.e. expulsion of endosymbiotic algae) are an iconic example where environmental changes (e.g. global warming) lead to the breakdown of an obligate mutualism and ecosystem degradation [2, 5]. Similar to coral reefs, many other marine ecosystems shaped by mutualism-dependent foundation species also exhibit sudden and large-scale declines [10, 11]. However, in contrast to the obligate coral symbiosis, the mutualisms in these ecosystems are facultative [1], and can vary in strength depending on prevailing conditions [3]. Therefore, it remains unclear whether mutualism breakdown due to environmental change is a general risk inherent to mutualism-dependent marine ecosystems.

Here we investigate the hypotheses that (1) similar to the obligate coral symbiosis, climatic extremes can trigger sudden breakdown of a facultative mutualism between seagrass and sulfide-consuming lucinid bivalves, and (2) the loss of this self-sustaining mutualistic feedback has the potential to exacerbate seagrass ecosystem degradation. Seagrass beds are essential for coastal zones worldwide, because they provide coastal protection, act as carbon and nutrient sinks, and serve as vital habitat for many species [12-14]. Seagrass ecosystems are currently degrading at an accelerating rate worldwide [13], and losses are often typified by sudden die-off.

Such rapid declines have been attributed to climatic extremes such as storms, high seawater temperatures, and low-tide desiccation events in intertidal beds [12, 15-18], but also to the disruption of internal feedback mechanisms by environmental changes [11, 19]. Seagrass meadows increase water clarity by trapping suspended particles and stabilizing sediments, thereby facilitating their own growth [3, 11, 14]. This positive feedback, however, also results in a negative feedback as organic matter accumulates in the sediment, and its anaerobic decomposition involving sulfate-reducing bacteria yields toxic sulfide [3, 20, 21]. To prevent sulfide accumulation, seagrasses can engage (recently-discovered) mutualistic feedback loop with lucinid bivalves and their gill-inhabiting, sulfide-oxidizing bacteria [3, 12]. In return, the bivalves and their endosymbionts not only profit from sulfide that is indirectly provided by the seagrasses, but also from oxygen released by seagrass roots. [3, 22, 23].

To investigate our hypotheses, we studied a landscape-scale die-off event in the intertidal seagrass beds of Banc d'Arguin – a pristine Marine Protected Area in Mauritania (West Africa). In this tropical Sahara desert climate, low-tide desiccation is a common stressor for seagrasses [24], but in 2010 and 2011 the region experienced exceptional drought and heat (with anomalies of +2-3.5°C compared to long-term mean monthly temperatures) [25-27]. Using local climate data and remote sensing analyses of spatiotemporal seagrass dynamics, we investigated whether (1) the die-off could be related to low-tide desiccation stress caused by heat, wind, and/or drought extremes, and (2) if disruption of a feedback was an important accelerant of the observed decline. Finally, we carried out field measurements to examine the potential link between desiccation, seagrass die-off, and breakage of the mutualistic feedback.

Local climate analyses

Analyses of data from the nearest weather station suggest that in our study area, the summer of 2011 was exceptionally warm, windy and dry, leading to a high evaporative demand (Supplemental Experimental Procedures). The number of extreme days in the warmest three months (August-October) – defined as days over the 95% percentile – was higher for all four variables included in our analyses (Figure 1). The number of recorded extremely hot and windy days in the warmest months was at least 1.3 times higher in 2011 compared to other years. More importantly, however, the number of extremes in the two most direct proxies of evaporation, and thus low-tide desiccation stress – dew point depression and water vapor pressure deficit [28] – was over 5 times higher in 2011.

Remote sensing and potential analyses

To investigate spatiotemporal seagrass cover changes, we calculated the Normalized Difference Vegetation Index (NDVI) from Landsat imagery taken in 2007, 2009, 2011 and 2013, and combined these analyses with ground observations (Supplemental Experimental Procedures, Figure S1). NDVI data indicate that degradation of the intertidal seagrass beds was initiated in 2011. Following a small increase between 2007 and 2009, NDVI started to decrease, after which a system-wide 44% decline occurred in 2011-2013 (Figure 2A-E). This landscape-scale NDVI decrease was supported by ground observations that showed a 50% decrease in seagrass cover between 2009 and 2013 (Figure 2F).

Next, we used potential analyses to test whether disruption of internal feedbacks by for instance the drought, contributed to the sudden seagrass collapse. This analysis fits a probability density function to a state variable per interval along an environmental stress gradient. Potential analysis is based on the fact that, if distinct ecosystem states exist due to the presence of strong

internal feedbacks, transitions between these feedback-stabilized states or ‘attractors’ will occur rapidly because intermediate states are inherently unstable [29]. As a consequence, multimodality in a fitted probability density function (i.e. multiple peaks in occurrence) indicates multiple attractors: maxima in occurrence are identified as attractors, and minima as transition thresholds (or ‘repellers’) between attractors (Supplemental Experimental Procedures, [30-32]). For our analysis, we estimated a probability density function from NDVI data per 0.1-m interval along the drought stress gradient approximated by elevation (i.e. exposure time).

In line with climate and NDVI analyses, potential analysis shows that seagrass degradation was most likely initiated by desiccation in 2011. The analysis also identified two distinct ecosystem states of high and low NDVI, indicating that the collapse was not simply the result of external environmental forcing, but that shifts between the two states were mediated by internal feedbacks (Figure 3). For 2007 and 2009, the analysis identified only high NDVI attractors (i.e. high seagrass cover) at elevations below mean water level (MWL), and low NDVI attractors (i.e. low seagrass cover) above MWL. In contrast, near the end of the drought in 2011, when the system was collapsing, the analysis revealed two distinct attractors at intermediate elevations (-0.4 to 0 m MWL), indicating that areas with a high seagrass cover were propelled into an alternative, degraded state. In 2013, only the lower attractor was stable above -0.4 m MWL, implying that most areas at intermediate elevations had transitioned from a high seagrass cover state to a degraded state.

Field measurements

The intertidal at Banc d’Arguin is dominated by the seagrass *Zostera noltii* that accumulates large amounts of silty, organic matter-rich sediment of up to ~1-m thick [33]. Characteristic for intertidal mudflats in general, the morphology throughout the area is typified by gently sloping

terrain with shallow overlying relief (<10 cm; spatial scale: 10-50 m; Figure S2), resulting from sediment trapping by seagrass in interaction with morphodynamics driven by waves, tidal currents, and low-tide dewatering dynamics [11, 34, 35]. Because the die-off was patchy in nature, we first compared the characteristics of degraded patches with adjacent healthy patches at 8 sites (4 replicates per site) throughout our study area (Supplemental Experimental Procedures, Figure S1). Height measurements demonstrated that degraded patches were on average situated 6.7 cm higher than healthy areas (Figure 4A). Moreover, at low tide, we found that degraded patches were typically dry with only 6% of the patches covered with a thin water film. In contrast, water drainage from higher towards lower patches resulted in the presence of a thin water film on the sediment surface at 88% of the healthy areas (Figure 4B). Apart from height and water, we detected no significant differences in general characteristics as indicated by sediment organic matter content ($11.9 \pm 0.4\%$; mean \pm SE) and median grain size ($70.0 \pm 1.5 \mu\text{m}$).

Detailed investigations of the benthic community revealed that, since the onset of degradation and our survey in 2012, aboveground seagrass biomass in degraded patches had been reduced by 89% (healthy: 124.3 ± 21.0 g dry weight per m^2 ; degraded: 13.9 ± 6.9 g). Densities of the small (~1 cm) dominant lucinid bivalve *Loripes lucinalis* were 9 times lower in degraded patches (Figure 4C), while sulfide concentrations in the sediment pore water were over 4 times higher, and showed an increase with depth (Figure 4D). Finally, a comparison of patches sampled both before (2009) and after the collapse (2013), confirmed that lucinids declined dramatically (4-5x) in degrading patches while remaining stable in healthy patches (Figure S3).

Discussion

Our findings of feedback-mediated seagrass decline, combined with low lucinid numbers and high sulfide levels following the 2011-drought, provide evidence that this climatic event initiated the sudden failure of a facultative mutualism that in turn exacerbated the observed collapse. Local climate data combined with NDVI and potential analyses suggest that seagrass degradation was initially triggered by desiccation induced by high evapotranspiration (evaporation plus plant transpiration) during drought. After the onset, however, the decline **persisted** in the years following the drought, and potential analyses suggest that disruption of internal feedback mechanisms played an important role in the observed collapse.

Clearly, although the potential analysis reveals that the observed collapse was mediated by internal feedbacks, it provides no indication of which feedbacks were involved. A likely contributing feedback was sediment accumulation by seagrass that hampered seagrass itself: variations in shoot densities in interaction with morphodynamics probably resulted in the observed local sedimentation differences [11, 34, 35], making higher patches more vulnerable to drainage and drought stress. Our field measurements, however, also show that the mutualistic seagrass-lucinid feedback was broken by the drought, as both seagrass biomass and lucinid densities declined dramatically, and that associated accumulation of toxic sulfide probably contributed to the collapse. This suggests that decreased seagrass condition caused by desiccation stress led to decreased photosynthesis-driven oxygen release from the roots, stimulating sulfide production. As an apparent consequence, sulfide-oxidation by the lucinid-bacteria diminished, causing sulfide accumulation to levels that are known to seriously hamper growth and survival of seagrass in general [20], and in our case to levels twice as high as those previously reported to decrease *Z. noltii* biomass by 30% [3].

Our study, combined with earlier work, highlights the importance of indirect responses of ecosystems to droughts [10]. Desiccation is a well-known stressor in subtropical to tropical intertidal seagrass beds such as Banc d'Arguin where drought and heat waves can cause severe desiccation events, particularly when coinciding with strong winds and neap tides causing prolonged low-tide exposure [15, 24]. Extreme events such as drought, strong winds and tidal extremes are all predicted to increase in frequency and severity with global warming [36]. Although sea level rise could be expected to mitigate future extreme drought events, expected increases in tidal amplitudes [37] might, depending on local conditions, also further enhance drought stress. Overall, desiccation stress is therefore increasingly considered to become an important threat to intertidal seagrass meadows in warmer regions [15, 16, 24, 38].

Apart from desiccation, there are many other stressors for seagrass beds worldwide that could initiate breakdown of this mutualism, many of which are anthropogenic in origin [13, 39]. For example, eutrophication typically reduces light availability (and thus photosynthesis-driven oxygen release from seagrass roots) due to the higher competitive strength of algae [40], while sulfide levels may increase as a result of enhanced input of easily degradable algal and other organic matter [20, 40]. Other examples are siltation events reducing light levels [39], salt stress hampering photosynthesis by seagrasses [37], and increased temperature driving enhanced sulfide production [41]. Due to global change, mutualism breakdown and sulfide toxicity may therefore become a more common phenomenon in seagrass meadows, and thus potentially an important factor in the worldwide decline of seagrass ecosystems [13, 39].

Our results point at a hidden risk of mutualism-dependency in marine ecosystems that goes beyond the obligate coral symbiosis: environmental change can disrupt facultative mutualistic feedbacks, and this may in turn have important consequences for ecosystem functioning and the provided services (e.g. biodiversity enhancement, carbon and nutrient

storage, food and water supply, and flood protection) [13, 14, 42]. Indeed, many marine ecosystems with mutualisms such as coral reefs, seagrass meadows, kelp forest, salt marshes, and mangroves have declined dramatically due to global change (e.g. global warming, eutrophication, overfishing) over recent decades [13, 42]. Clearly, the importance of mutualisms for ecosystem functioning, as well as their role in ecosystem losses needs a better understanding. As mutualism breakdown is likely to become more common in a future governed by global change [4], we suggest that these mechanisms need to be included in marine conservation and restoration approaches.

Supplemental information

Supplemental Information includes three figures, one table and Supplemental Experimental Procedures and can be found with this article online at [url].

Author contributions

JdF, TvdH, LG, AS, LL designed the study. JdF, TvdH, LG, MSC, MC, KvdR, MvdG, HO, and JvG collected data. JdF, TvdH, JvB, and WD conducted analyses. JdF and TvdH wrote the first draft of the paper and all authors contributed substantially to revisions.

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Figure legends

Figure 1. Number of extreme days in the three warmest months (August to October) – expressed as days over the 95% percentile in that period – for daily averaged temperature, wind speed, dew point depression, and water vapor pressure deficit. This number of days was higher in 2011 compared to other years for all variables. Differences are most pronounced for the two most direct measures of evaporation (and thus low-tide desiccation): dew point depression and water vapor pressure deficit.

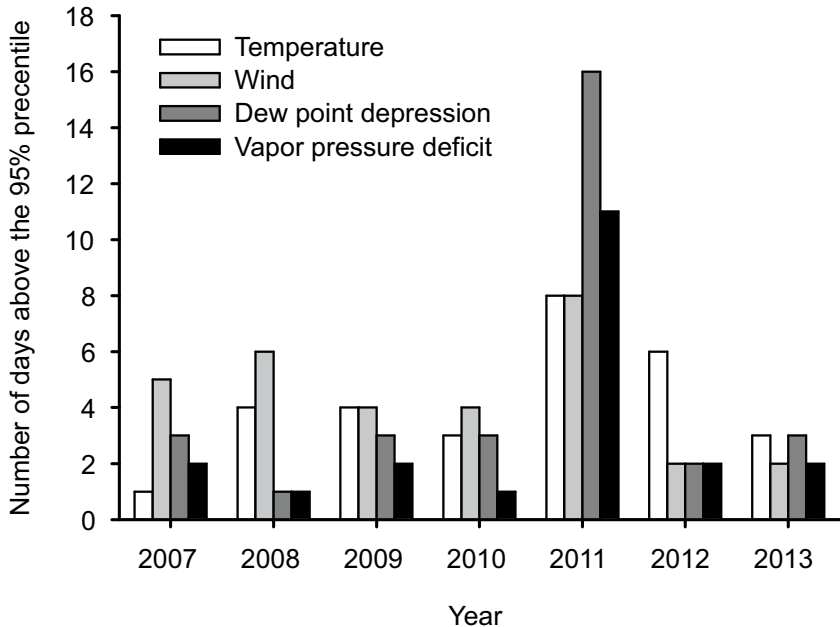
Figure 2. NDVI from 2007 to 2013 as calculated from Landsat imagery (A-E) and corresponding ground observations (F) (see also Figure S1 and Table S1). NDVI remained relatively stable from 2007 to 2011, after which a sharp 44% decrease followed between 2011 and 2013 (E; $F_{3,946} = 131.15$, $P < 0.001$; letters indicate post hoc groups). Ground observations showed a 50% decrease between 2009 and 2013 ($F_{1,429} = 124.94$, $P < 0.001$). Error bars depict standard errors (n=239 and n=213 respectively).

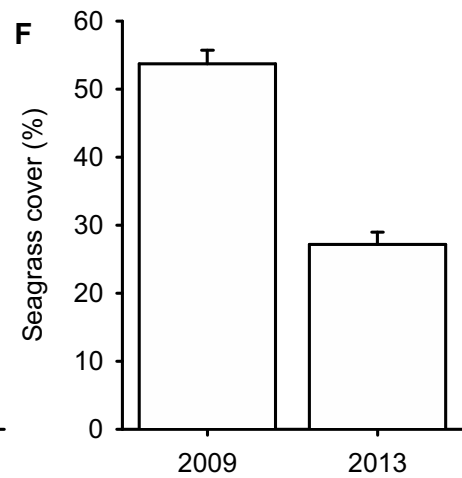
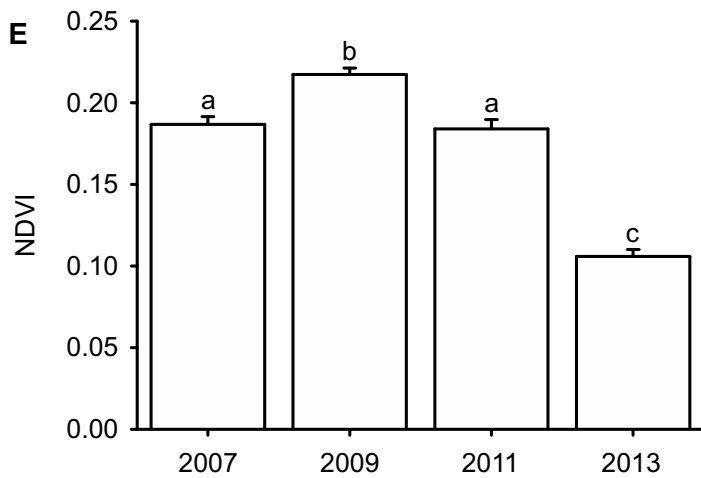
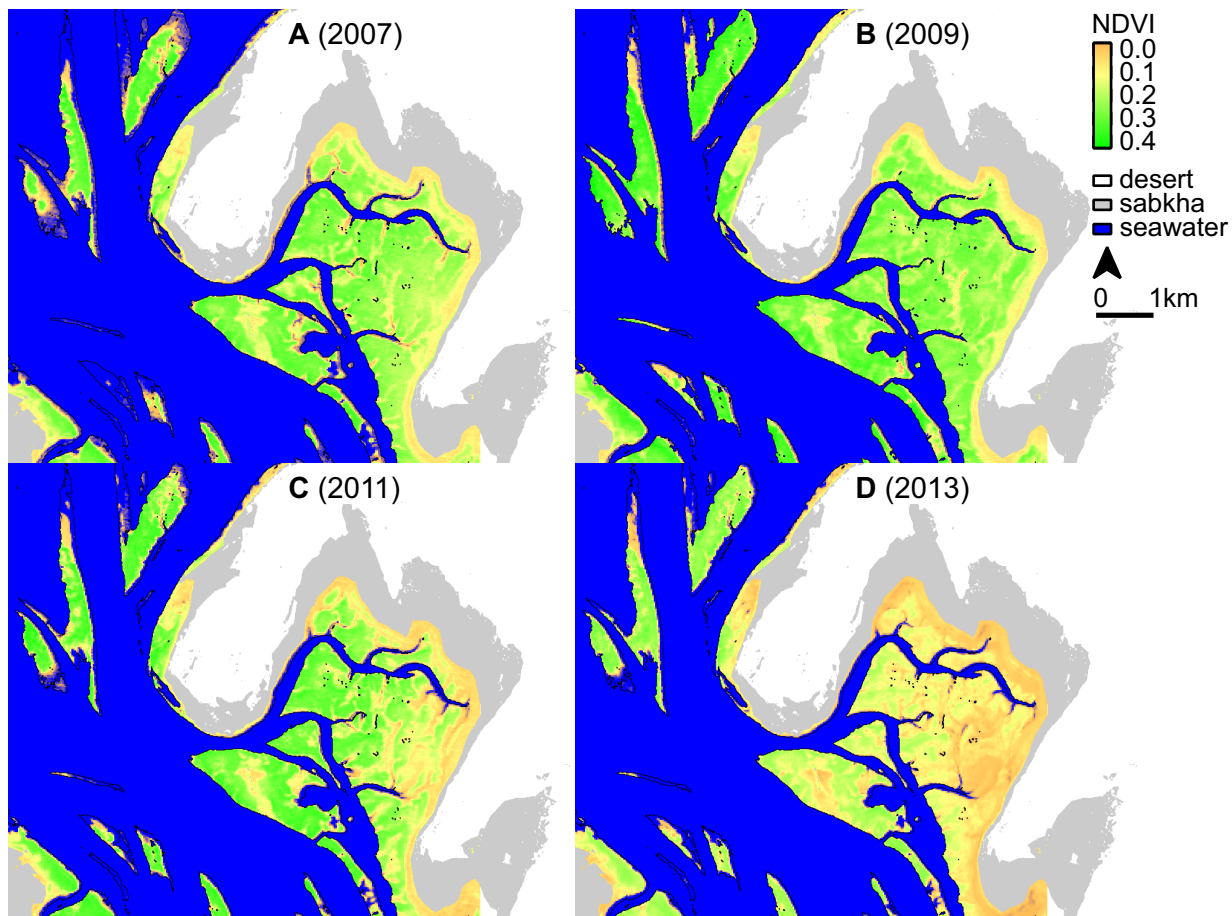
Figure 3. (A-D) Potential analyses on NDVI across elevation from 2007 to 2013. Dark and light shades depict NDVI-ranges of high and low occurrence, respectively; closed and open markers depict ‘attractors’ (peaks in occurrence) and ‘repellers’ (lows in occurrence) that are automatically identified by the analysis per 0.1-m elevation interval. In 2007 and 2009, the analysis identified only a single high NDVI attractor (>0.2) at low elevations, and a low NDVI attractor (~ 0.1) above mean water level (MWL). For 2011, the analysis reveals the existence of two distinct stable attractors at intermediate elevations, with unstable repellers in between. In 2013, only the lower attractor was stable above -0.4 m MWL. Overall, the analyses combined

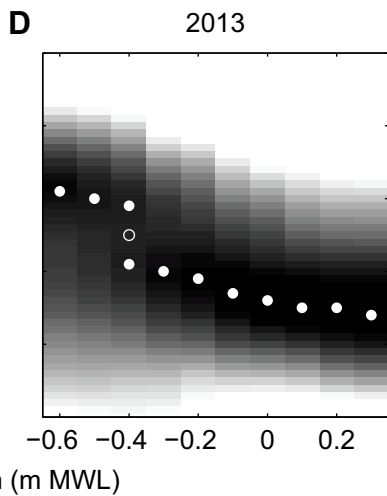
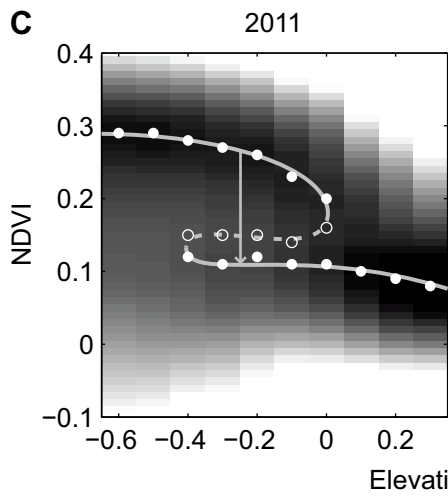
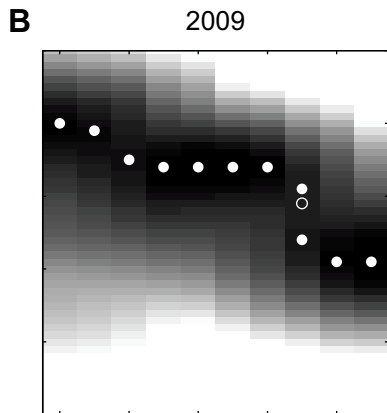
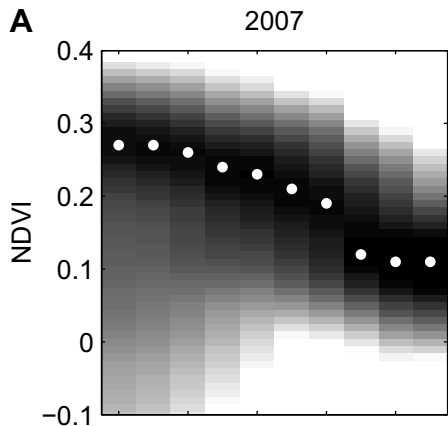
indicate that the 2011-drought triggered a feedback-mediated transition at intermediate elevations from a high seagrass cover state to a degraded state as manually illustrated in panel C. Solid and dashed grey lines depict stable equilibria and transition thresholds, respectively; the grey arrow indicates the direction of the shift.

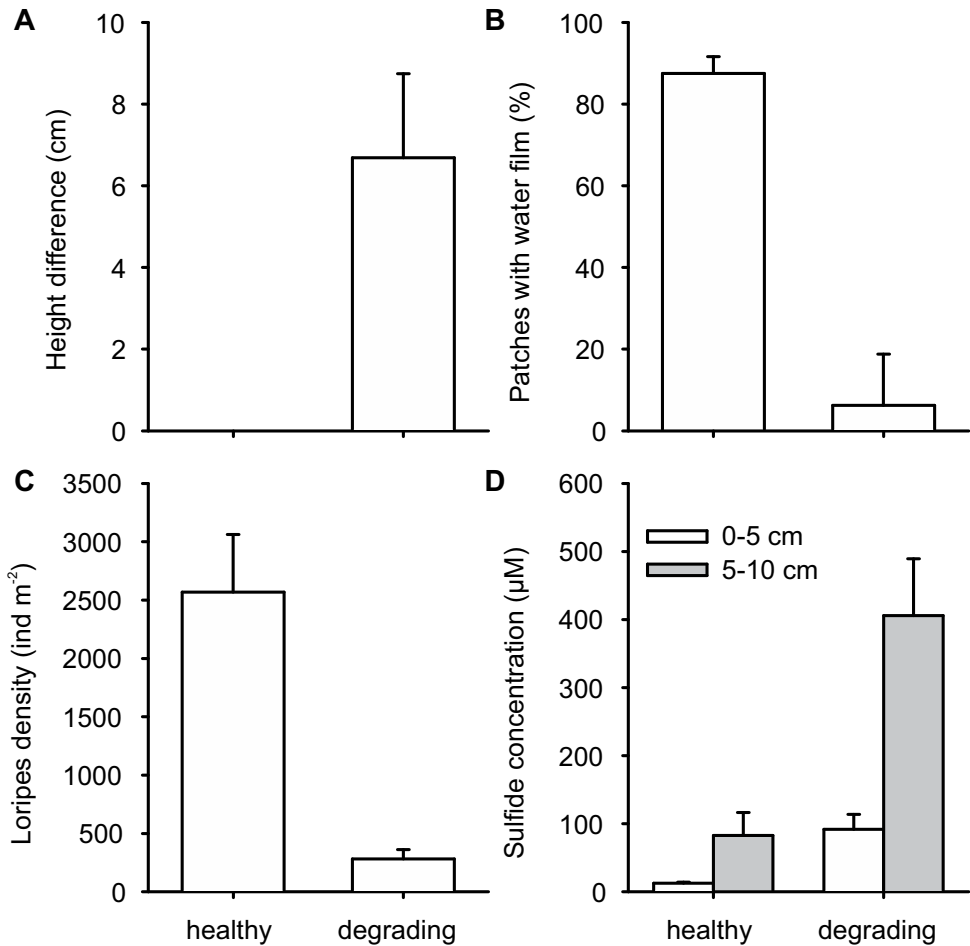
Figure 4. Comparisons of the environmental characteristics of healthy and adjacent degrading seagrass patches (see also Figures S1, S2 and S3). (A) Degrading patches were elevated compared to healthy controls ($F_{1,55}=60.91$, $P<0.001$; $n=32$), and (B) were typically dry whereas healthy patches were characterized by a thin film of water on the sediment surface ($X^2=7.56$, $P=0.006$; $n=32$). (C) Lucinid densities were significantly lower in degrading patches ($X^2=302.69$, $P<0.001$; $n=8$), and (D) sulfide concentrations in the pore water were higher ($F_{1,14}=15.99$, $P=0.001$; $n=8$). Sulfide levels showed a significant increase with depth ($F_{1,14}=21.0$, $P<0.001$; $n=8$) and an interaction between patch condition and depth ($F_{1,14}=8.4$, $P=0.011$; $n=8$). Error bars depict standard errors.

Figure 1









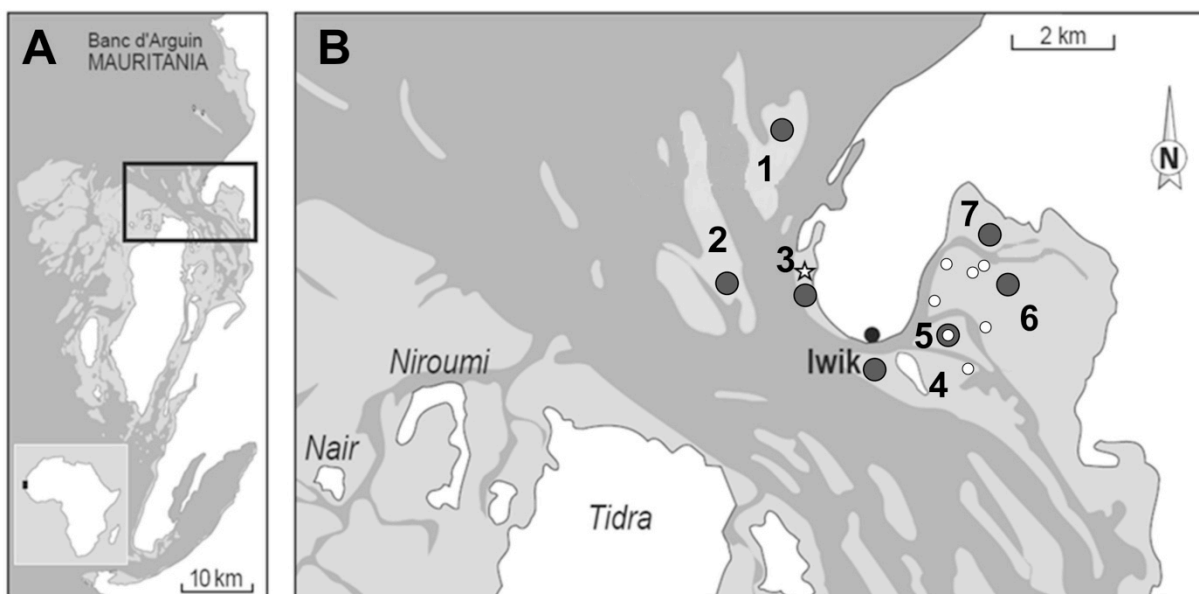


Figure S1. Related to Figures 2 and 4, and the Supplemental Experimental Procedures. (A) Parc National du Banc d'Arguin (PNBA) in Mauritania, West-Africa with intertidal flats (light grey), ocean (dark grey) and desert land (white). (B) Numbers depict mudflat areas used as random factor in our statistical analyses of NDVI. Grey dots depict areas where seagrass cover observations for the ground truthing of remote sensing data were carried out. At each site, we randomly sampled between 29 and 32 points in 2009 within a 200-m radius circle, and resampled these points in 2013 (total number of sampling points: 213). To investigate the potential link between drought, the observed seagrass die-off, and breakdown of the seagrass-lucinid mutualism, we carried out an 8-site field survey (4 replicates per site) across the study area (white dots and star) where we compared general characteristics of degraded and adjacent healthy patches. At one of the sites (star: Abelgh Eiznaya; $19^{\circ}53.54'N$, $16^{\circ}18.85'W$) we carried out a more detailed survey (8 replicates) in which we also examined sediment sulfide levels and the benthic community.

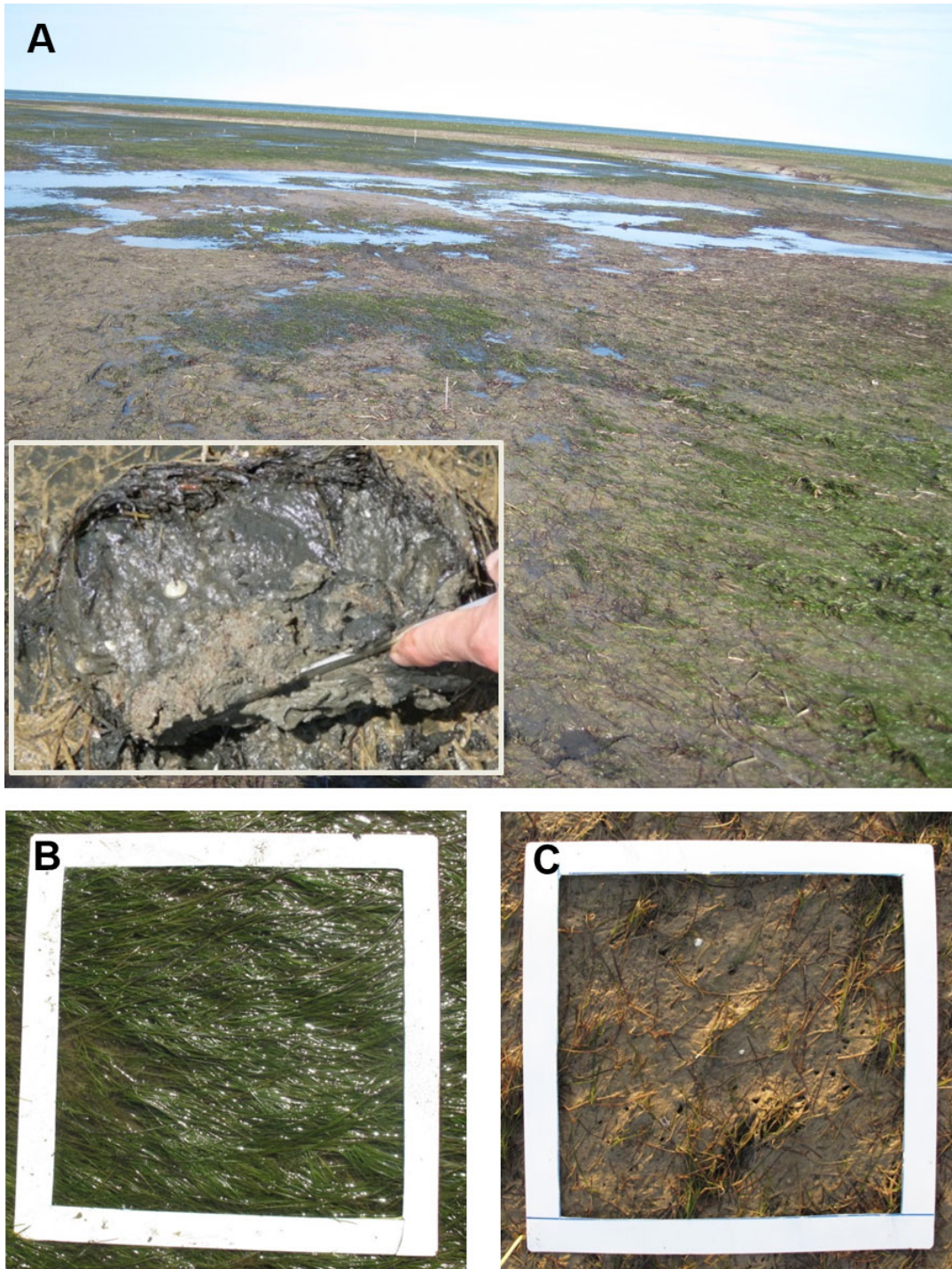


Figure S2. Related to Figure 4. (A) Seagrass die-off patches with anaerobic, sulfide-rich sediment (insert) at Banc d'Arguin. (B) Close-up of a healthy seagrass patch with a water film, (C) a dry, degrading seagrass patch.

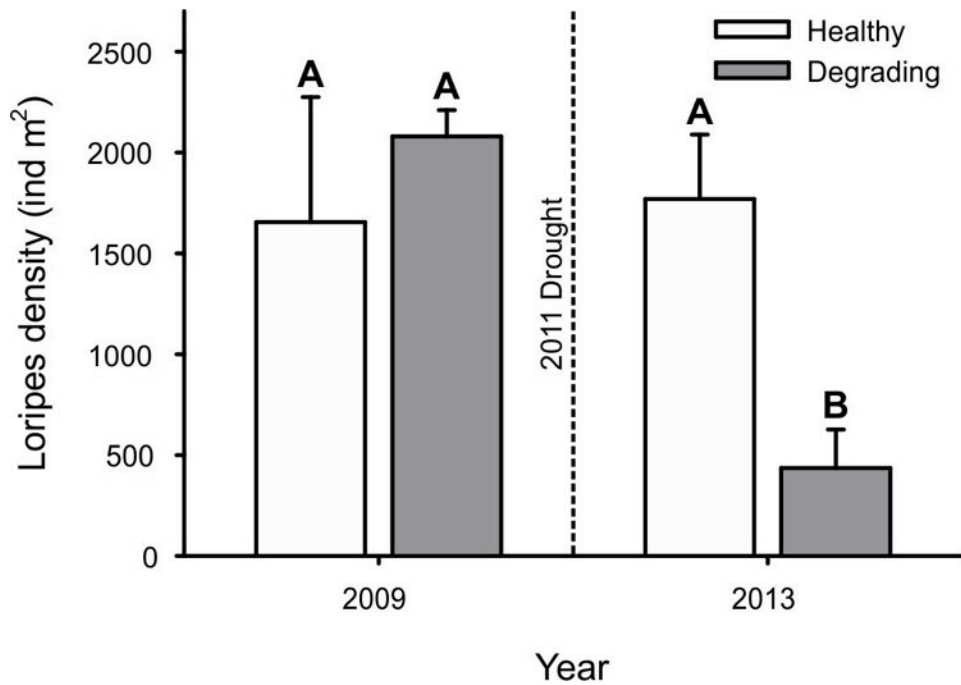


Figure S3. Related to Figure 4. Analysis of 8 healthy sites sampled prior to the collapse of 2009, of which 3 patches had become degraded after the collapse in 2013. Lucinid numbers were high and similar in both years for patches that remained healthy. Lucinid counts in patches that became degraded after the collapse did originally not differ from (other) healthy patches in 2009, but contained 4 to 5 times lower densities after the collapse (GLMM – Year: $\chi^2 = 2311.1$; $P < 0.001$; State 2013 (healthy vs. degrading): $\chi^2 = 1.7$; $P = 0.19$; Year*State: $\chi^2 = 5232.1$; $P < 0.001$).

Table S1. Related to Figure 2 and the Supplemental Experimental Procedures. Suitable (i.e. regarding season, low tide, haziness) Landsat images used for the GIS analyses.

<i>Image</i>	<i>date</i>	<i>time</i>	<i>Mapping</i>
Landsat 5	15-Sep-2007	11:18:58	NDVI
Landsat 5	11-Sep-2009	11:21:45	NDVI (baseline map)
Landsat 5	17-Sep-2011	11:20:31	NDVI
Landsat 8	24-Oct-2013	11:33:49	NDVI

Supplemental experimental procedures

Study system

Our study was carried out in the tropical intertidal seagrass meadows of Parc National du Banc d'Arguin (PNBA) in Mauritania (19°52.42' N, 16°18.50'W; Figure S1). The intertidal area covers about 500 km² of mudflat dominated by mixed meadows of *Zostera noltii*, *Halodule wrightii* and *Cymodocea nodosa* [S1] that retain consistent aboveground biomass throughout the year [S2] which is typical for seagrasses around the equator [S3]. Characteristic for intertidal mudflats in general, morphology is typified by a gently sloping terrain with a shallow overlying relief (< 10 cm) with depression and elevations alternating at a scale of roughly 10 to 50 meters (Figure S2). This subtle morphology primarily results from sediment trapping by seagrass in interaction with morphodynamics driven by waves, tidal currents, and low-tide dewatering dynamics [S4-6]. In our system, seagrass meadows accumulate large amounts of silty, organic matter-rich sediment of up to ~1-m thick. The sediment layer between the seagrass roots is inhabited by high densities (up to 3700 ind. m⁻²) of the small (~1 cm) lucinid bivalve *Loripes lucinalis* [S7, S8], which obtains 71% of its carbon nutrition from the obligate mutualism with its gill-inhabiting sulfide-oxidizing bacteria [S9]. Temperature loggers show that mudflat surface temperatures can peak well above 40°C during tidal exposure in this desert climate, causing desiccation that is considered stressful for intertidal seagrass in this system and in general [S10-S13].

Local climate analyses

We obtained daily averaged temperature, dew point temperature, and wind speed data from the coastal weather station in Nouadhibou, which is nearest to our study area (located ~140 km northwards). Dew point depression and water vapor pressure deficit – two direct measures of atmospheric water moisture deficit and thus suitable proxies of atmospheric moisture extraction from land surfaces [S14] – were calculated from the temperature and dew point temperature data. Next, we determined the number of extreme days – defined as days over the 95% percentile – for temperature, wind, dew point depression and vapor pressure deficit for the three warmest months (August to November) over the period 2007-2013. These three months are not only the most stressful for the intertidal seagrass beds with respect to low-tide solar radiation and temperature, but also regarding strain on detoxification by the mutualism as sulfide production is temperature-dependent [S8].

Remote sensing and potential analyses

To investigate seagrass cover changes over time, we used GIS analyses combined with ground observations. We were able to select Landsat 5 and 8 images taken in the warmest months (August-October), at low tide, and with sufficiently low haziness for 2007, 2009, 2011 and 2013 (Table S1). To be able to compare them, we first standardized the images against each other to correct for atmospheric effects, and potential sensor differences. We converted the digital numbers of the spectral bands to top-of-atmosphere reflectance and empirically cross-calibrated reflectance (2009 Landsat image served as baseline), using a linear model fitted to random common ground targets with low and high reflectance (ocean and desert sites, respectively) [S15, 16]. Next, we calculated the Normalized Difference Vegetation Index (NDVI) for each image as a proxy for seagrass cover in the intertidal zone. NDVI (or red NDVI) was calculated from the near-infrared (NIR) and red (RED) spectral bands: (NIR-RED)/(NIR+RED). Analysis of the spatial autocorrelation in each NDVI image using autoregressive AR(p) model estimation revealed that the correlation length (L_c ; calculated using $1/e$ as a correlation threshold) was highest in 2007 with a distance of 112.2 m. To avoid any correlation (and thus potential dependency) between data points, we therefore sampled 239 points from a 250x250 m grid (i.e. at least $2 \times L_c$) for further statistical analysis. Finally, supporting ground observations were carried out by photographing and scoring seagrass cover in 0.5x0.5-m quadrats in two repetitive field surveys in 2009 and 2013 (213 sampling points, Figure S1).

To examine possible feedback-mediated dynamics in our study system, we used potential analysis, a novel statistical method to detect alternative states or 'basins of attraction' along an environmental stress gradient [S17-S19]. Potential analysis assumes that variation in NDVI is the result of feedbacks and stochasticity approximated by:

$$dz = -U'(z)dt + \sigma dW \quad (\text{eq. 1})$$

where the potential function $U(z)$ describes deterministic processes (i.e. feedback), and dW is a Gaussian noise term with intensity σ . If distinct ecosystem states exist due to the presence of strong internal feedbacks, transitions between two 'attractors' (or stable states) occur rapidly as intermediate states are inherently unstable. The analysis therefore estimates a probability density function P_d for the variable of interest z (NDVI in our case) per interval class of an environmental gradient (elevation in our case). Multimodality in the potential function $U = -\log(P_d)$ in an interval class is an indication of multiple stable attractors: local minima and maxima of U correspond to stable and unstable attractors, respectively [S19, S20]. Graphically, a system with bimodality would be typically represented by

a ‘folded sigmoid response’ along the environmental gradient, with two stable attractors separated by an unstable repeller per interval class [S19, S20].

For our analyses, we first binned all 17672 NDVI values of each map in 0.1-m height classes from -0.6 to 0.3 m relative to mean sea level based on a digital elevation map. This map was derived from Landsat images taken at varying tidal levels. Contour lines of the water edge were manually derived from false color images composite using Landsat SWIR, NIR and Green bands and combined into a new map. To assign an absolute elevation to the contour lines, we determined the elevation of each contour line relative to mean sea level using real-time kinematic differential GPS, resulting in a vertical accuracy of approximately two centimeters. Finally, the map was created with in ArcGIS 10 using 3D analyst. For each elevation class we estimated P_d using a standard Gaussian kernel estimator, smoothed with a moving window (size: 0.025). Local maxima and minima of U were identified by an automated peak search function.

Field measurements

To investigate the potential link between desiccation stress, seagrass die-off, and mutualism breakdown we compared degraded patches (as die-offs were patchy in nature) with adjacent healthy patches at 8 sites (4 replicates per site) across the study area in October 2012 (Figure S1). At each sampling location, we randomly selected 4 die-off patches – i.e. typified by low cover (<20%), dying seagrass with browning leaves (average cover: $9.4 \pm 1.0\%$; mean \pm SE; $n=32$). Next, we compared their general habitat characteristics with adjacent (<10 m) high cover (>60%) healthy areas (average cover: $77.4 \pm 2.0\%$), thus resulting in a pairwise approach. To test whether subtle elevation differences on the mudflats (see “Study system”) affected local water run-off and desiccation stress, we first compared relative elevation differences between degrading and healthy patches with a laser to the nearest 1 mm (Spectra Precision Laser LL500) and visually scored the presence or absence (cutoff at 50% cover) of a water film on the sediment surface at low tide (Figures S2B and C). In addition, we measured sediment median grain size and organic matter as indicators of general sediment characteristics. Sediment samples were taken with a small core (ϕ 1.5 cm) to a depth of 5 cm, weighed immediately after collection and frozen (-10°C). Samples were freeze-dried in the laboratory, after which we determined median grain size using a particle size analyzer with auto sampler (Coulter LS 13 320) and organic matter as loss on ignition (LOI; 5 hrs at 560°C).

Next, we carried out an in-depth investigation at the site of Abelgh Eiznaya (Figure S1) that was selected because it exhibited a level of degradation representative for the study system (Figure 2) and was readily accessible from the research station. In addition to the above variables, we compared lucinid bivalve densities (*L. lucinalis*), seagrass biomass (*Z. noltii*), and pore water sulfide concentrations ($n=8$) between degraded and adjacent healthy areas. Lucinids and seagrass were sampled following a standard procedure [S21]: sediment cores (ϕ : 15 cm) were taken to a depth of 20 cm and then sieved over a 1-mm mesh. Lucinids in the sample were counted in the laboratory and total dry weight (above + belowground) of the seagrass inside the cores was determined after drying (48 hours at 60°C). Sulfide was measured by anaerobically collecting sediment pore water samples in 60-ml vacuumed syringes connected to 5-cm rhizon samplers (Eijkelpamp Agrisearch Equipment, Giesbeek, the Netherlands), which had been placed in the root zone at two depths (0-5 cm; 5-10 cm). Total dissolved sulfide concentration in the pore water was measured immediately after sampling, in a mixture of 50% sample and 50% Sulfide Anti-Oxidation Buffer (SAOB) using an ion-specific silver-sulfide electrode calibrated against a set of 5 standards (1, 10, 100, 1000, 10000 $\mu\text{mol l}^{-1}$) prepared from $\text{Na}_2\text{S}\cdot 9\text{H}_2\text{O}$ (98% pure) and nitrogen-flushed Milli-Q water [S8, S21]. Finally, to investigate the possibility that degraded sites already contained lower lucinid numbers before the 2011 drought, we resampled 8 patches at Abelgh Eiznaya in 2013 that were healthy (>60% seagrass cover) prior to the collapse and had been sampled in 2009. Of these patches, 5 were still healthy in 2013 and 3 had become degraded (<20% seagrass cover).

Statistical analyses

All statistical analyses were conducted using the software program R [S22]. NDVI was analyzed using Generalized Linear Mixed Models (*glmm*) with a Gaussian distribution with year as a fixed factor, mudflat area (Figure S1) as random factor with Satterthwaite approximation of the degrees of freedom, and Tukey HSD for post-hoc comparisons. Ground observation data were analyzed using the same type of Gaussian *glmm* with year as a fixed factor and sampling site as random factor (Figure S1).

Differences in sediment height, grain size distribution and organic matter content were tested using one-way ANOVA (*aov*) with location as a random factor. Presence/absence of a water film was fitted with binomial regression (*glmm*; location as random factor). Sulfide concentrations in the field survey were log-transformed to meet assumptions of normality of residuals. We used a Gaussian-distributed *glmm* with patch condition (health/degrading) and sediment depth (0-5 and 5-10 cm) as fixed factors, and sampling point as a random factor to link the upper and lower sediment layer. We used a Generalized Linear Model (*glm*) with Poisson distribution to

compare lucinid counts in degraded and healthy patches 2012. Finally, to compare lucinid densities between patches that remained healthy and patches that became degraded between 2009 and 2013, we used a Poisson-distributed *glmm* with year as fixed factor and sampling point as random factor, followed by pairwise post hoc comparisons with Bonferroni correction of significance levels.

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