

Extreme storms can limit the expansion of the invasive species *Caulerpa cylindracea* in the rocky shore.

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Abstract

Invasive species constitute a major environmental concern worldwide and extreme events, favoured by climate change, are expected to enhance their invasibility, however more scientific evidence is needed to better understand this interaction. We tested manipulatively in the rocky shore how the invasibility of the alga *Caulerpa cylindracea*, one of the most deleterious exotic species worldwide, was affected as storms become more extreme. We found that low intensity storms with a high frequency enhanced the invasibility of *C. cylindracea*, while extreme storms, limited the invasibility of this alga. These effects did not only occur on the short-term, but also after several months after the disturbance, suggesting legacy effects. *C. cylindracea* having a low attachment capacity is expected to need other canopy-forming algae to facilitate its attachment to the substrate, while large bare rock patches may leave *C. cylindracea* too exposed to the wave effect on rocky shores hindering its survival in this habitat. This study suggests that extreme events do not necessarily enhance the invasibility of exotic species and can have contrasting effects depending on the habitat. Thus, the effects of extreme events on the invasibility of exotic species needs to be particularly studied in different habitats, so optimized management strategies can be adapted to each habitat in pursuit to mitigate as much as possible the effects of climate change.

Introduction

Invasive species constitute a global environmental threat (Kumschick et al. 2015; Beaury et al. 2020). These species can produce important changes of the structure and functioning of the invaded ecosystems assemblages diminishing their biodiversity (Occhipinti-Ambrogi y Savini 2003; Piazzini y Ceccherelli 2006; Beaury et al. 2020) and the ecological functions they support (Walsh et al. 2016), resulting in ecosystem services and economic loss (Pimentel et al. 2005; Bradshaw et al. 2016). In the current context of global change (Hulme 2009; Katsanevakis et al. 2014), the number of invasive species is continuously growing (Seebens et al. 2017). Thus, the impacts of invasive species and their interactions with other environmental stressors, such as the ones derived from climate change, which are expected to increase their relevance in the coming decades, are necessary to be understood.

Despite the most studied environmental effects related to climate change have focused in the trends of mean climate values, another relevant consequence of climate change is that weather events are becoming more extreme. Extreme climate events (from hereon called extreme events) are climate events of an enormous intensity and a very low frequency. However, climate change is increasing the occurrence of these types of events (Meehl et al. 2000; Stephenson et al. 2008; Cai et al. 2012). Extreme events produce severe changes in the ecosystems due to their catastrophic nature (Wernberg et al. 2013). Thus, climate change is changing the disturbance regime in ecosystems, reducing their resilience (Johnstone et al. 2016), which can favour biological invasions (Walther et al. 2009; Diez et al. 2012).

Extreme events, due to their high disturbance characteristics, are expected to mainly benefit invasive species, that can easily occupy the derived empty space created (Diez et al. 2012; Maxwell et al. 2019), as well as impair the recovery of a community after an extreme event (Vetter et al. 2020). However, more

research effort is needed as extreme events can favour native or exotic species differently depending on the timing of the occurrence and the number of events (Meisner et al. 2013). Thus, it is necessary to fully explore the response of invasive species by testing their invasiveness under scenarios that consider relevant gradients of timing, frequency and intensity (Sanz-Lazaro 2019).

Caulerpa cylindracea (Sonder, 1845) is one of the most deleterious invasive species of the world (Lowe et al. 2000). In the Mediterranean, this species colonizes wide zones between 0 and 50m of depth (Piazzi et al. 2001; Ceccherelli y Campo 2002), modifying benthic assemblages by reducing the diversity of native species, mainly affecting encrusting and erect macrophytes, while promoting turf species (Argyrou et al. 1999; Piazzi et al. 2001; Balata et al. 2004). The high colonization capacity of *C. cylindracea* is due to its vegetative reproduction by fragmentation and stolonization (Ceccherelli y Piazzi 2001). The invasive ability of *C. cylindracea* depends on the canopy of other biological assemblages (Ceccherelli et al. 2014), nutrient levels (Gennaro et al. 2015) and ecosystem status (Terradas-Fernández et al. 2020). Thus, degraded habitats affected by eutrophication with low density canopies have been reported to be more susceptible to the invasion of *C. cylindracea* (Bulleri et al. 2010; Ceccherelli et al. 2014; Terradas-Fernández et al. 2020; Casoli et al. 2021).

Extreme storms are one type of the extreme climatic event which its occurrence is increasing in the last decades in the Mediterranean sea (Amarouche y Akpınar 2021; Martzikos et al. 2021). Storms can physically reduce macrophyte canopy density (Paine y Levin 1981; Thompson et al. 2002; Oprandi et al. 2020) facilitating the colonization by *C. cylindracea* (Bulleri et al. 2010; Ceccherelli et al. 2014; Lisandro et al. 2019; Casoli et al. 2021). Thus, extreme storms are expected to favour the dispersion of invasive species such as *C. cylindracea*. However, to the best of our knowledge, no specific testing has been carrying out on this respect.

The aim of this study is to analyse the invasiveness of *C. cylindracea* under different disturbance regimes of storms. To do so, we performed a manipulative approach in a rocky reef of the Mediterranean, where we simulated a gradient of storms becoming more extreme and we analysed the recovery of the biological assemblage after the disturbance, with special attention to *C. cylindracea*. The experiment was performed twice with a different timing of the disturbances coinciding with the active and lethargy seasons of the invasive species. We hypothesized that the invasibility of *C. cylindracea* will be favoured as disturbances become more extreme, while the recovery of the biological assemblage will be negatively affected.

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Study area

The experiment was performed in the rocky shore of Agua Amarga in Alicante, Spain, (38° 18' 06" N, 0° 31' 05"W) in the Western Mediterranean. The shore is composed by shallow platforms where Corallinales, Ulvales and Ectocarpales are the predominant algae (Terradas-Fernández et al. 2020). This area is

notably anthropized, notably eutrophicated, which favours the abundance of *C. cylindracea* (Martín et al. 2003; Sanz-Lazaro et al. 2022), that peaks in late summer and early autumn, coinciding with the highest temperatures in the water (Terradas-Fernández et al. 2020). The study was carried out at the upper subtidal zone (*ca.* 0.2–0.4 m depth).

Experimental set up

A total of 40 experimental plots (35x35cm) were randomly distributed along the shoreline and were delimited and numbered with epoxy putty (Subcoat S; Veneziani, Trieste, Italy). The effect of storms was simulated eroding the rock of the experimental plots using a chisel and a hammer. We used this kind of disturbance because it is comparable to natural storm which waves can break the rocks in reef producing bare rock (Paine y Levin 1981; Sanz-Lazaro et al. 2022). We chose the level of frequency according to the records of storms waves of the last decades in the Mediterranean sea (0–6 storms per year) (Camuffo et al. 2000; Amarouche y Akpınar 2021; Martzikos et al. 2021). Aiming to create a realistic and comparable gradient of storms becoming more extreme, the frequency and intensity were inversely varied to keep the overall intensity constant (*sensu* Sanz-Lázaro 2016). Accordingly, the treatments comprising the storm extremeness gradient were: one very intense storm, that removed 100% of the cover of the community (level of extremeness 6); two intense storms, each of which removed 50% of the cover of the community (level of extremeness 3); three moderate storms, each of which removed 33% of the cover of the community (level of the extremeness 2) and six mild storms, each of which removed 16% of the cover of the community (level of the extremeness 1; fig. S1). Additionally, untreated plots were used as a control treatment. Each treatment was replicated four times. The study was replicated in time, to test the effect of the timing of the disturbances. As the abundance of *C. cylindracea* in the Mediterranean is markedly seasonal, blooming when the water temperature is high (Ruitton et al. 2005; Terradas-Fernández et al. 2020), we repeated the experiment twice, applying the treatments during the warm (from May to December, average water temperature of 22.9°C) and cold (from November to June, average water temperature of 16.1°C) periods.

Sampling

Each experimental plot was sampled 10 times. To study the short-term effects of changes in the disturbance regime, five samplings were done, starting two months after the first disturbance, and then each following month, until one month after the last disturbance. When disturbances were performed, the sampling was always performed before applying a disturbance, so always, at the time of sampling, all plots had not been disturbed for at least one month. Then, for the long-term effects, five more samplings were performed every 2–3 months (Fig. S2). To avoid possible border effects, the sampling was carried out in the centre of the experimental plot on a surface of 20 × 20 cm.

Data analysis

The experimental design consisted on two factors: *extremeness of the storm* (mild: 1, moderate: 2, intense: 3 and very intense: 6) and *period of the year* when the treatment was applied (cold and warm) that were considered fixed and orthogonal. As the invasibility of *C. cylindracea* is limited by canopy-

forming species, the response variables analysed were the cover of *C. cylindracea*, as well as the cover of canopy-forming species, *Corallina* sp. (being the predominant canopy-forming species; Terradas-Fernández et al. 2020), all sessile species (non- and canopy-forming species) and bare rock. Short-term effects of storms were analysed averaging the data of the five first samplings (Fig. S2), while long-term effects of storms were analysed for rest of the samplings (Fig S2). Regression models of *C. cylindracea* cover along the storm extremeness gradient were made (*sensu* Sanz-Lázaro 2016) to test their effects. Each model was performed separately for each period of the year (cold and warm). To assess differences in the cover of *C. cylindracea* under undisturbed and disturbed conditions, a t-test was applied comparing the control treatment with each of the disturbance treatments. Additionally, to assess the relationship between the cover of *C. cylindracea* and the cover of all sessile species, a regression model was done using all the samplings in which the mean of the overall cover of *C. cylindracea* during a specific sampling period was higher than 5%. In all cases, the best regression model selection was performed by means of the AICc (corrected Akaike Information Criterion). Analysis were made using the statistical platform R (v. 2.15.0). Data were reported as mean $\pm$ standard error (SE) and all statistical tests were conducted with a significance level of $\alpha = 0.05$.

Results

During the warm period, when *C. cylindracea* abundance peaks, the cover of this alga showed a significantly negative trend ($p < 0.05$; $R^2 = 0.77$) as storms became more extreme. Several mild disturbances enhanced *C. cylindracea* cover ($23.1 \pm 0.5\%$), while one extreme storm yielded the lowest cover of *C. cylindracea* cover ($4.4 \pm 0.9\%$); which was notably lower than the cover of *C. cylindracea* under undisturbed conditions ($15.2 \pm 4.3\%$; $p = 0.05$; table S1). The cover of all canopy forming algae and specifically the predominant one in this area, *Corallina* sp. was similar in most of the treatments including the control ranging from 68.1 ± 5.5 to $92.7 \pm 6.0\%$ and from 11.4 ± 0.3 to $32.7 \pm 5.7\%$, respectively. But, the treatment with the most extreme regime showed the lowest cover of all canopy forming algae and of *Corallina* sp., resulting in the treatment with the largest bare rock cover $36.6 \pm 2.8\%$, while the rest of the treatments bare rock ranged from 13.3 ± 1.5 to $20.6 \pm 7.1\%$ (Fig. 1).

During the cold period, the cover of *C. cylindracea* was in general one order of magnitude lower compared to the warm period. The same trend observed during the warm period of decreasing cover of the alga as storms became more extreme was reported in the cold period, albeit the trend being only close to significance ($p = 0.08$; $R^2 = 0.14$; table 1). Similarly, to what happen in the summer period, the cover of all canopy forming algae and of *Corallina* sp. was similar in most of the treatments including the control ranging from 94.8 ± 2.7 to $112.5 \pm 7.2\%$ and from 16.1 ± 10.2 to $61.6 \pm 7.6\%$, respectively. The treatment with the most extreme regime showed the lowest cover of all canopy forming algae and of *Corallina* sp. resulting in the treatment with the largest bare rock cover $16.2 \pm 1.6\%$, while the rest of the treatments bare rock ranged from 6.7 ± 2.3 to $15.8 \pm 2.3\%$ (Fig. 1).

As regards long-term effects, when disturbances were performed during the cold period, the cover of *C. cylindracea* in the next warm period showed a significant decreasing trend as storms become more

extreme ($p < 0,05$; $R^2 = 0.31$). Thus, the trend of decreasing cover of *C. cylindracea* on the short-term was still evident several months after the last disturbance has been performed. As for the short-term effects, several mild disturbances enhanced *C. cylindracea* cover ($30.3 \pm 6.5\%$), while one extreme storm yielded the lowest cover of *C. cylindracea* cover ($10.0 \pm 3.6\%$); which was notably lower than the cover of *C. cylindracea* under undisturbed conditions ($25.7 \pm 12.6\%$). In this case, the cover of all canopy forming algae showed a descending trend as storms became more extreme ranging from $103.7 \pm 8.8\%$, when there were several mild storms, to $68.5 \pm 24.44\%$, when there was a single extreme storm. While the cover of *Corallina sp.* was similar in most of the treatments including the control, ranging from $17.5 \pm 6.8\%$ when several mild storms occurred, to $38.3 \pm 3.3\%$ when three medium storms took place (Fig. 2).

The relationship between the cover of *C. cylindracea* and the cover of all sessile species, in the samplings in which the mean of the overall cover of *C. cylindracea* during a specific sampling period was higher than 5%, showed a significantly positive trend ($p = 0.003$; $R^2 = 0.097$; Fig. 3).

Discussion

In this study, *C. cylindracea* showed the largest cover during the summer and early autumn which coincides with other studies in the Mediterranean (Piazzi et al. 2001; Bulleri et al. 2010; Terradas-Fernández et al. 2020), being the period when the water temperature peaks in the Mediterranean (the temperature of the water is above 24–25 °C), since the natural distribution of *C. cylindracea* is warm-temperate to subtropical (Verlaque et al. 2003).

This experiment, demonstrates that in rocky shores in the upper subtidal zone (less than 50 cm depth) the invasibility of *C. cylindracea* can be favoured by low intensity and recurrent storms, while extreme storms are expected to notably reduce it. This finding apparently contradicts the current paradigm in which extreme events are expected to favour the invasibility of exotic species (Diez et al. 2012). Specifically, previous studies performed in seagrass meadows at deeper zones (5–13 m) than the present study (less than 50 cm), showed that high intensity disturbances can favour the expansion of *C. cylindracea* (Bulleri et al. 2010; Katsanevakis et al. 2010; Ceccherelli et al. 2014).

A plausible explanation is that the effect of extreme events on enhancing invasibility depends if there is an associated resource input from which the exotic species can benefit (Lear et al. 2020), such as empty space (Jiménez et al. 2011). However, in upper subtidal zone, there is no resource input, since empty space does not favour *C. cylindracea* expansion, but limits it, due to the missing protection against wave action in the absence of canopy forming species.

In the case of *C. cylindracea*, at deep subtidal zones, not only empty space, but also light can be a resource that may be limited as light availability decreases with depth. Moreover, in these zones, *Posidonia oceanica* (Linnaeus) Delile, 1813 is the dominant canopy forming species, the height of the canopy produced by this plant is massive (ca. 1m) compared with the height of the canopy of upper subtidal communities (ca. 10 cm). Thus, in these zones, small canopy gaps may not be sufficient for *C.*

cyllindracea to receive enough light (Bernardeau-Esteller et al. 2015), while large gaps of canopy will not only result in more resource of empty space, but also will lead to more light availability, enhancing the expansion of the alga (Ceccherelli et al. 2014).

In the rocky shore, in the shallow subtidal zone, light is not expected to be a limiting resource factor (Bulleri et al. 2010; Marín-Guirao et al. 2015) and empty space maybe the only resource that *C. cyllindracea* can benefit from a storm. However, in the shallow subtidal zone, the eroding effect of waves much more relevant that at deep zones, can hinder the viability of this alga that has a low attachment. Thus, low intensity disturbances that removes a low cover of canopy structure, leaves few, but sufficient gaps of bare rock that allow this species to colonize, while to increase its attachment capacity by using canopy forming species (Piazzi et al. 2003). Large gaps of bare rock produced by high intensity storms may leave *C. cyllindracea* too exposed to the effects of waves in this zone of high hydrodynamism.

This hypothesis is supported by the results of the present study, that find a negative trend on the cover of *C. cyllindracea* as storms become more extreme and the positive relationship of the cover of *C. cyllindracea* with the cover of all sessile species in the rocky shore. Additionally, our results show that the effects of the disturbances of different extremeness can be evident 4 to 9 months after the last disturbance. This period of time is relatively large for rocky shore communities with such a short-life cycle in which the composition of the whole community can totally change among seasons. Thus, in rocky shores, extreme storms can limit the invasibility of *C. cyllindracea* not only on the short-term, but can have a legacy effect in the scale of months.

Conclusions

In the upper subtidal zone, extreme storms can limit the invasibility of one of the most important aquatic exotic species, *C. cyllindracea*. This apparent contradiction with the current paradigm in which extreme events are expected to enhance the invasibility of exotic species can be explained as regards the specific conditions of the habitat. In the upper subtidal zone, large releases of empty space promoted by high intense storms do not favour *C. cyllindracea* expansion, but limits it, due to the missing protection of the alga against wave action in the absence of canopy forming species. This study suggests that extreme events do not necessarily enhance the invasibility of exotic species and can have contrasting effects depending on the habitat. Thus, the effects of extreme events on the invasibility of exotic species needs to be particularly studied in different habitats, so optimized management strategies can be adapted to each habitat in pursuit to mitigate as much as possible the effects of climate change.

Declarations

Author contributions

C.S.-L. contributed with the original idea and analyses presented of the study. C.S.-L., N.C.-C. and M.T.-F. developed the idea and did the field work. C.S.-L. acquired the funding. C.S.-L. and N.C.-C. performed the

proposed analyses and wrote the manuscript. M.T.-F. reviewed the manuscript.

Data availability

Sampling data is available upon request to the corresponding author.

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Table

Table 1 is available in the Supplementary Files section

Figures

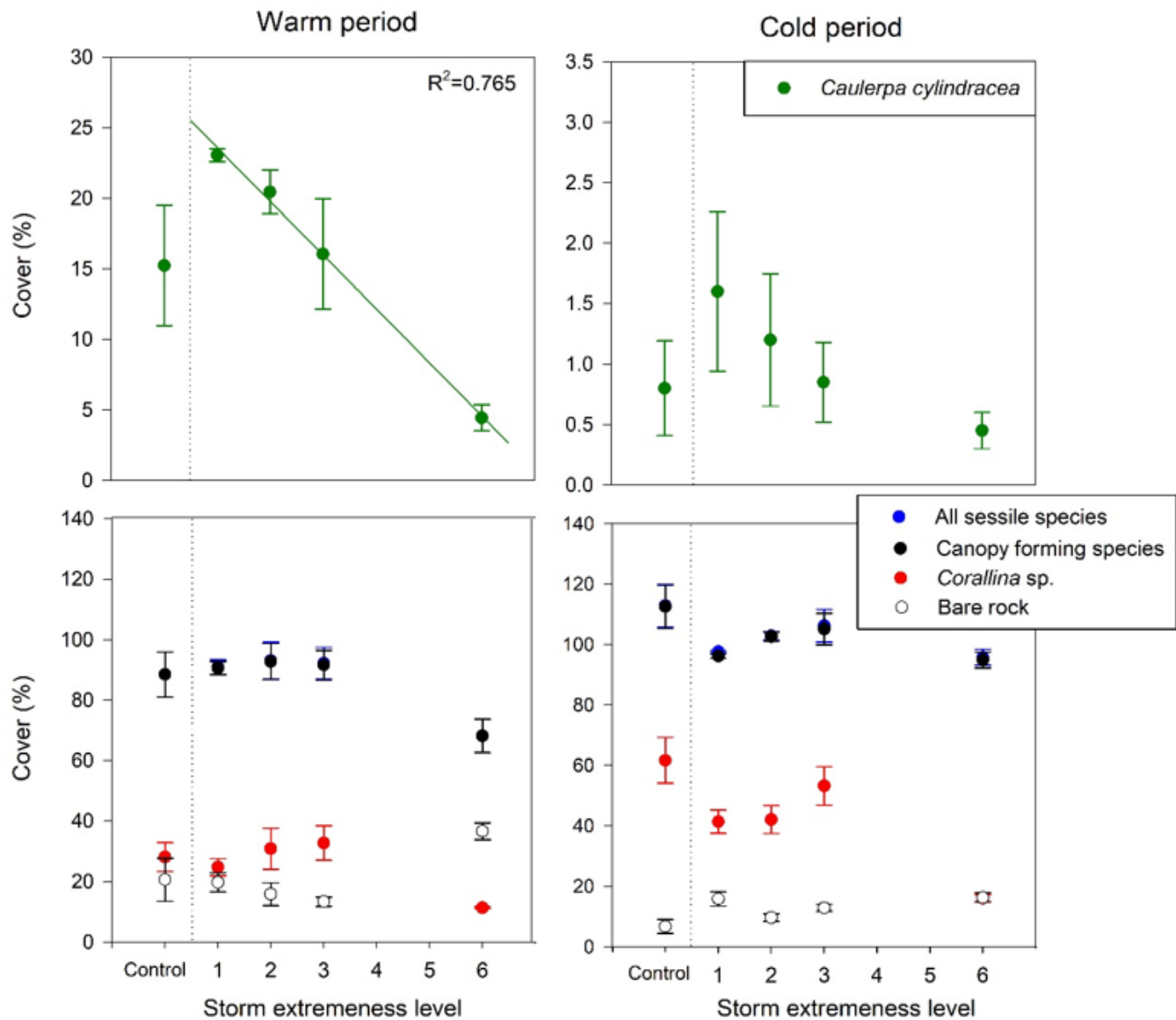


Figure 1

Short-term effects on the trends of a gradient of disturbances becoming more extreme (Fig. S1) in the cover of *Caulerpa cylindracea*, all sessile species, canopy forming species, *Corallina* sp. and bare rock of rocky shore assemblages (mean $\pm$ SE; $n = 4$) during the two periods of the year when the experiment was performed (cold and warm period; Fig. S2). For assessing the short-term effects, the averaged data of the five first samplings (Fig. S2), which were performed during the simulation of the disturbances, was analysed. The control was not included in the extremeness gradient analyses (dotted vertical line separation) since no storm was simulated in this treatment. When there is a significant trend (Table 1), the prototypical trajectory is indicated with a solid line.

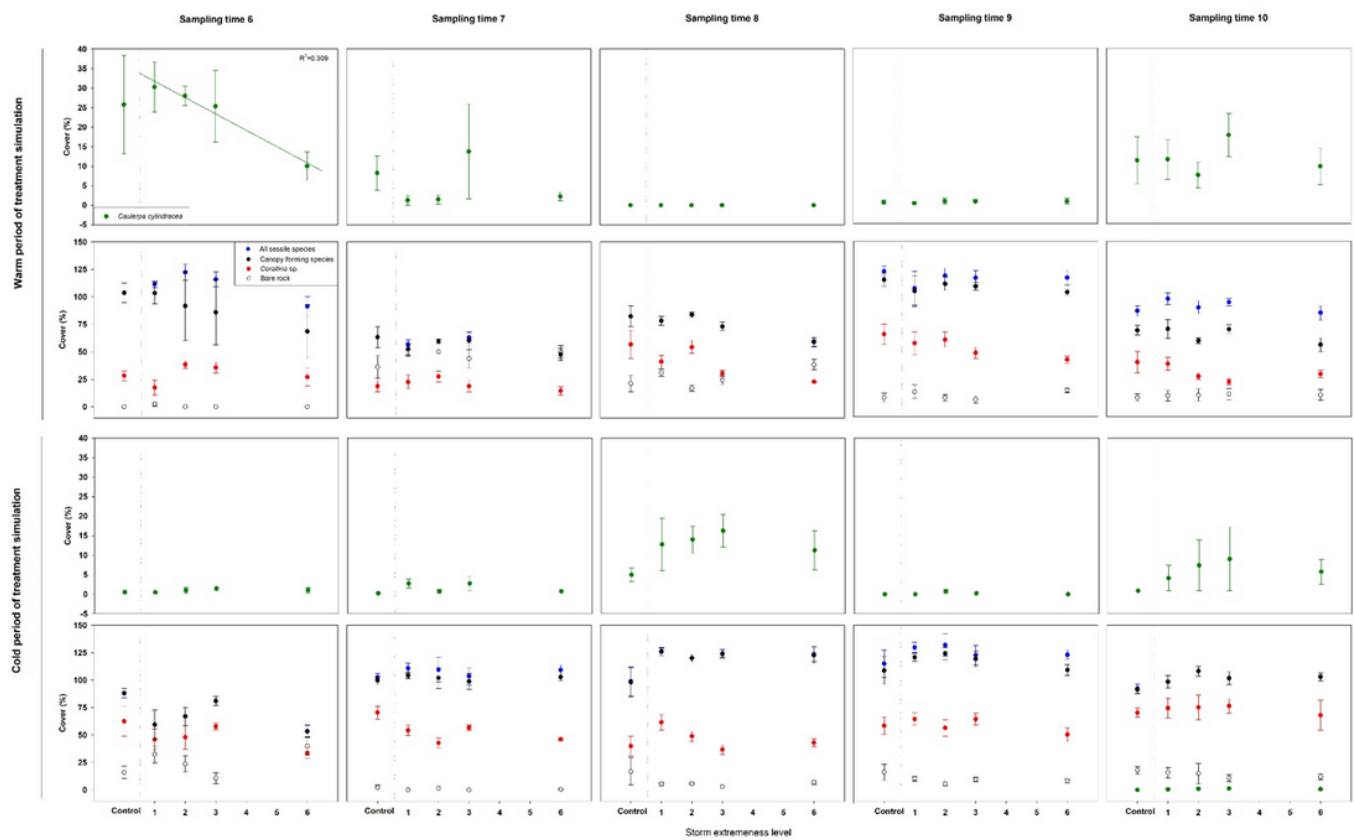


Figure 2

Long-term effects on the trends of a gradient of disturbances becoming more extreme (Fig. S1) in the cover of *Caulerpa cylindracea*, all sessile species, canopy forming species, *Corallina* sp. and bare rock of rocky shore assemblages (mean $\pm$ SE; $n = 4$) during the two periods of the year when the experiment was performed (cold and warm period; Fig. S2). For assessing the long-term effects, the samplings 6 to 10, corresponding to 9 and 21 months after the first disturbance, respectively, were analysed (Fig. S2). The control was not included in the extremeness gradient analyses (dotted vertical line separation) since no storm was simulated in this treatment. When there is a significant trend (Table 1), the prototypical trajectory is indicated with a solid line.

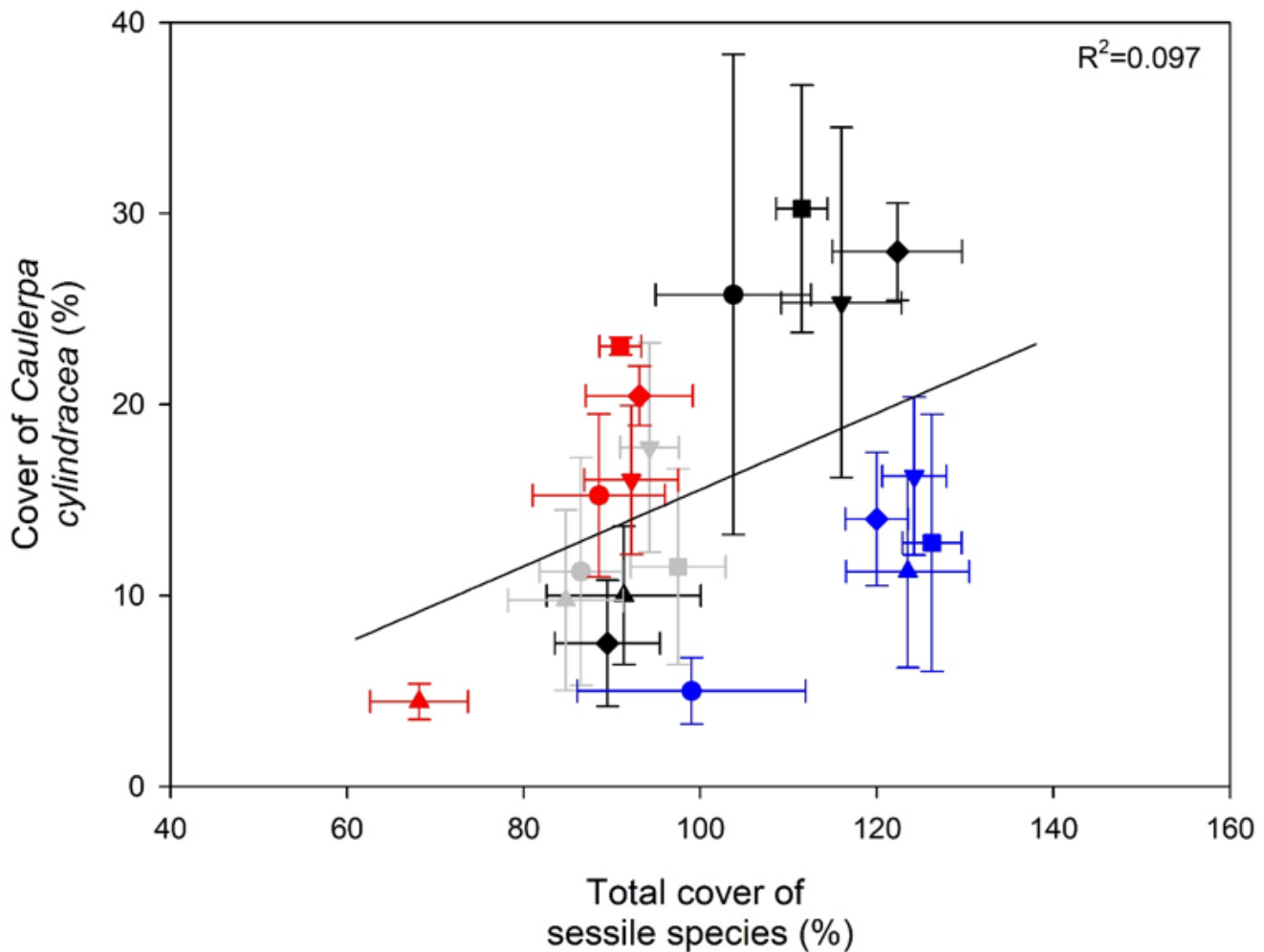


Figure 3. Relationship between the cover of *Caulerpa cylindracea* and the cover of all sessile species in all samplings in which the mean of the overall cover of *C. cylindracea* during a specific sampling period was higher than 5% (mean $\pm$ SE; $n=4$). The line indicates the prototypical trajectory of the regression model regression model is $y=-4.5+0.2x$ (p value=0.003). Solid symbols correspond to treatments that were disturbed during the cold period, while empty symbols correspond to the treatments that were disturbed during the warm period. Black, grey, red and blue symbols represent samplings 6, 10, 1-5 and 8 samplings, corresponding the 6 and 10 samplings to the cold period and 1-5 and 8 samplings to the warm period (Fig. S2). Symbols indicate the treatments: one very intense storm ($\blacktriangle$), two intense storms ($\blacktriangledown$), three moderate storms ($\blacklozenge$), six mild storms ($\blacksquare$) and the undisturbed control ($\bullet$).

Figure 3

See image above for figure legend.

Supplementary Files

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