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Extreme storms could limit the expansion of the invasive species *Caulerpa cylindracea* on rocky shores

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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 invasiveness. However, more scientific evidence is needed to better understand the circumstances under which this assumption holds true. An experimental manipulation was performed to test how storm intensity and frequency affected the re-colonisation of rocky boulders by the non-indigenous species *Caulerpa cylindracea* following mechanical disturbance. Low intensity storms with a high frequency were found to enhance *Caulerpa cylindracea* invasiveness, while extreme storms limited the invasiveness. These effects were not only short-term, they were also observed up to nine months after the disturbance. *Caulerpa cylindracea* presents a low attachment capacity to rocky substrata, and its colonisation capacity may be favoured by the existence of other canopy-forming algae that create structures to which *Caulerpa cylindracea* can attach. *Caulerpa cylindracea* may be excessively affected by uprooting and dislodgement following high-intensity disturbances that produce bare rock. The shear stress driven by wave action on rocky shores can hinder its colonisation of the upper subtidal zone. This study suggests that extreme events do not necessarily enhance the exotic species invasiveness and that their effects may vary depending on the habitat. Thus, the effects of extreme events on exotic species invasiveness needs to be studied across diverse environments. Such research is essential to define site-specific management strategies that optimally mitigate the effects of alien species within current climate change constraints.

Keywords: invasion ecology; climate change; extreme events; coastal ecology; alien species; storm.

Introduction

Invasive species constitute a global ecological threat (Kumschick *et al.*, 2015; Beaury *et al.*, 2020). They produce major changes in the structure and functioning of the invaded ecosystems, modifying their biodiversity (Occhipinti-Ambrogi & Savini, 2003; Piazzi & Ceccherelli, 2006; Beaury *et al.*, 2020) and ecological functions (Walsh *et al.*, 2016). Consequently, these alterations lead to a significant reduction in ecosystem services as well as economic losses (Pimentel *et al.*, 2005; Bradshaw *et al.*, 2016). In the current global change context (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 that deriving from climate change, are expected to increase in the coming decades.

Most studies on climate change-related environmental effects have focused on climate variable trends, yet another relevant climate change consequence is that weather events are becoming more extreme (Meehl *et al.*, 2000). Extreme climatic events (hereafter extreme events) are characterised by their high magnitude and exceptionally low frequency. However, they are actually occurring more often owing to climate change (Meehl *et al.*, 2000; Stephenson *et al.*, 2008; Cai *et al.*, 2012). Extreme events produce severe ecosystem changes due to their catastrophic nature (Wernberg *et al.*, 2013). Thus, climate change is modifying ecosystem disturbance regimes, reducing ecosystem resilience (Johnstone *et al.*, 2016), and driving biological invasions (Walther *et al.*, 2009; Diez *et al.*, 2012).

Due to their significant potential to produce disturbances, extreme events are projected to facilitate the proliferation of invasive species, which can easily occupy the empty space left available by disturbance (Diez *et al.*, 2012; Mulas & Bertocci, 2016; Maxwell *et al.*, 2019).

They can also impair community recovery after an extreme event (Vetter *et al.*, 2020). However, depending on event occurrence timing and frequency, their effect on different species can vary substantially (Meisner *et al.*, 2013). Under the current climate change scenario, it is necessary to understand how invasive species respond to modifying disturbance regimes (Sanz-Lazaro, 2019).

Caulerpa cylindracea (Sonder, 1845) is among the most deleterious invasive species in the world (Lowe *et al.*, 2000). In the Mediterranean, this species colonises extensive areas at depths of 0-50 m (Piazzi *et al.*, 2001; Ceccherelli & Campo, 2002), altering benthic assemblages by reducing native species diversity, affecting encrusting and erect macrophytes, while promoting turf species (Argyrou *et al.*, 1999; Piazzi *et al.*, 2001; Balata *et al.*, 2004). The remarkable colonisation capacity of *C. cylindracea* owes mainly to its capacity for vegetative reproduction through fragmentation and stolonisation (Ceccherelli & Piazzi, 2001). *C. cylindracea* invasiveness 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). Degraded habitats affected by eutrophication with low density canopies have been reported to be more susceptible to invasion by *C. cylindracea* (Bulleri *et al.*, 2010; Ceccherelli *et al.*, 2014; Casoli *et al.*, 2021; Terradas-Fernández *et al.*, 2020).

Over the last few decades, the Mediterranean Sea has experienced a rising frequency of extreme storms (Amarouche & Akpınar, 2021; Martzikos *et al.*, 2021). Storms can physically reduce macrophyte canopy density (Paine & Levin, 1981; Thompson *et al.*, 2002; Oprandi *et al.*, 2020) facilitating *C. cylindracea* colonisation (Bulleri *et al.*, 2010; Ceccherelli *et al.*, 2014; Benedetti-Cecchi *et al.*, 2019; Casoli *et al.*, 2021). However, to the best of our knowledge, this hypothesis has not been tested yet.

The study objective was to evaluate the recovery capacity of *C. cylindracea* when subjected to varying storm-induced disturbance regimes. We adopted a manipulative approach and applied disturbances on a Mediterranean rocky reef to simulate a gradient of storm intensities with varying levels of extremeness. We then assessed how the biological assemblage recovered after the disturbances, focusing on *C. cylindracea*. During the experiment, the disturbances were applied separately, at two contrasting times of the year, i.e., when the water temperature was high and low, coinciding with the active and senescence periods of the invasive species, respectively. The hypothesis was formulated as follows: *C. cylindracea* invasiveness increases as disturbances become more extreme, while biological assemblage recovery is hindered, especially when the disturbances coincide with the warm season.

Material and Methods

Study area

The experiment was conducted on the rocky shore shallow platform (upper subtidal zone; *ca*. 0.2-0.4 m depth) of Agua Amarga in Alicante, Spain (38.30167° N, 0.51806° W) in the Western Mediterranean (Fig. S1). This area is notably subjected to coastal development and water eutrophication, resulting in a typical biological community dominated by the algae Corallinales, Ulvales and Ectocarpales (Terradas-Fernández *et al.*, 2020). Eutrophication favours *C. cylindracea* abundance (Martín *et al.*, 2003; Sanz-Lazaro *et al.*, 2022), peaking in late summer and early autumn, coinciding with highest water temperatures (Terradas-Fernández *et al.*, 2020).

Experimental design

A total of 40 experimental plots (35 × 35 cm) were randomly distributed along the shoreline. They were delimited and numbered using epoxy putty (Subcoat S; Veneziani, Trieste, Italy). Disturbances were performed by eroding the rocks using a chisel and a hammer, which caused the removal of sessile organisms. Such a caused disturbance is comparable to the effect of natural storms in providing empty space on rocks (Paine & Levin, 1981). We chose the frequency level based on heavy storm records of the last decades in the Mediterranean Sea (0-6 heavy storms per year) (Amarouche & Akpınar, 2021; Camuffo *et al.*, 2000; Martzikos *et al.*, 2021).

To establish a realistic gradient of storm extremeness, we inversely manipulated frequency and intensity. This approach ensured that total cumulated disturbance applied during the six-month experimental period remained constant across treatments (sensu Sanz-Lázaro, 2016). Accordingly, the manipulative treatments of the storm extremeness gradient were as follow: one very intense storm that removed 100% of the community cover (extremeness level 6); two intense storms, each of which removed 50% of the community cover (extremeness level 3); three moderate storms, each of which removed 33% of the community cover (extremeness level 2); and six mild storms, each of which removed 16% of the community cover (extremeness level 1; Fig. S2). The numbering of the treatment extremeness levels corresponds to the number of times that the treatment was more extreme than the lowest level. For example, the highest extremeness level (level 6) was 6 times more extreme than the treatment with the lowest extremeness level (level 1). The disturbance was interspersed within each experimental plot, so the cover was homogeneously removed along the whole area of the plot for each disturbance event across all treatments.

In addition, the control treatment was created with plots in which the rocks were not eroded. Each treatment level was replicated four times. Plots were placed randomly and interspersed among treatments to maximise data independence. As *C. cylindracea* abundance in the Mediterranean is markedly seasonal and blooms at high water temperature (Ruitton *et al.*, 2005; Terradas-Fernández *et al.*, 2020), we ran the experiment twice: during the warm (from May to December, average water temperature of 22.9^{o}C) and cold (from November to June, average water temperature of 16.1°C) seasons independently. A total of 20 different plots that included the five treatments over each period were used. We interspersed the plots ensuring that *C. cylindracea* cover was evenly distributed at comparable levels.

To minimise border effects, we estimated the sessile species cover (see Table S4 for the species list) in the centre of the experimental plot on a 20 × 20 cm surface. The samplings were always performed immediately prior to simulating any disturbance; thus, each plot had been left undisturbed for at least one month when sampled. To study the short-term effects, the plots were sampled five times at each period of the year, beginning two months after the first disturbance was applied, and subsequently each following month (Fig. S3). To study the long-term effects of the disturbance regimes over each period of the year, five more samplings were performed every 2 to 3 months after the fifth sampling. The latter corresponded to 9 to 21 months after the first disturbance was applied. Thus, each experimental plot was sampled 10 times (Fig. S3). No extreme storms were observed during the experiment.

Data analysis

The response variables analysed were: *C. cylindracea* cover as well as canopy-forming species, which can limit *C. cylindracea* invasiveness (Ceccherelli *et al.*, 2002); *Ellisolandia elongata* individually because it is the area's most abundant canopy-forming species (Terradas-Fernández *et al.*, 2020); other sessile species; and bare rock. In this study, canopy-forming species were considered as the dominant species that create a three-dimensional structure, acting as a foundation species in their habitat, despite their reduced size of 10-20 cm (sensu Terradas *et al.*, 2018; Catra *et al.*, 2019). Short- and long-term effects were assessed separately. Storm short-term effects were analysed by averaging the values recorded for the five samplings performed during the disturbances period to obtain an overall estimate of the disturbance effect while minimising the unavoidable fact that the timing of disturbance application differed among treatments (Fig. S2; sensu Bertocci *et al.*, 2010). To study the long-term storm effects, samplings 6 to 10 were each analysed individually (Fig. S3). Regression models were used to independently evaluate short- and long-term effects across the storm extremeness gradient (cold and warm: sensu Sanz-Lázaro, 2016). Additionally, to test whether *C. cylindracea* abundance depended on other sessile species, a regression was fitted between *C. cylindracea* cover and that of all other sessile species, using all the samplings in which *C. cylindracea* cover exceeded 5%. The best fitting model between a first- and second-order polynomial regression was consistently chosen using the AICc (corrected Akaike Information Criterion) (Burnham & Anderson, 2004). A t-test was applied to compare the control treatment with each disturbed treatment. Homogeneity of variances and normality were assessed through Cochran and Shapiro-Wilk tests, respectively. Analyses were conducted using the statistical platform R (v. 2.15.0). Data were reported as mean ± standard error (SE) and all statistical tests were performed with a nominal Type I error rate (alpha) fixed at 0.05.

Results

Regarding the short-term effects, when disturbances were applied during the warm period, *C. cylindracea* cover showed a significantly negative trend (R^2= 0.76; p<0.001) as storms became more extreme. Several mild disturbances enhanced *C. cylindracea* cover (23±0.5%), while one extreme storm yielded the lowest *C. cylindracea* cover (4.4±0.9%), which was notably lower than the *C. cylindracea* cover under undisturbed conditions (15±4.3%; p=0.05; Table S1). The cover of all canopy-forming algae and, individually, of *E. elongata* (the predominant canopy-forming species in this area) were similar across most treatment levels, including the control group, ranging from 86±7.5 to 93±6.0% and from 25±2.8 to 33±5.7%, respectively. However, the most extreme regime treatment showed the lowest cover of all canopy-forming algae (68±5.5%; p=0.07; Table S2). This treatment level therefore produced a significant reduction in *E. elongata* cover compared to the control (11±0.3%; p=0.01; Table S2). Similarly, the most extreme regime treatment displayed the largest bare rock cover (37±2.8%; p=0.08; Table S2), while bare rock ranged from 13±1.5 to 21±7.1% in the rest of the treatment levels (Fig. 1).

When disturbances were applied during the cold period, *C. cylindracea* cover was generally one order of magnitude lower compared to the warm period. The same decreasing algae cover trend observed during the warm period as storms became more extreme was also reported in the cold period, the trend being albeit non-significant (R^2=0.14; p=0.08; Table 1). Similarly to warm period treatments, the cover of all canopy-forming algae and of *E. elongata* was similar in most of the treatments including the control, ranging from 95±2.7 to 112±7.2% and from 16±10 to 62±7.6%, respectively. As in the case of the plots disturbed during the summer, the treatment with the most extreme disturbance regime showed the minimum cover of all canopy-forming algae and of *E. elongata*, this treatment producing the largest bare rock cover 16.2±1.6%. However, the bare rock cover was not markedly different across the rest of the treatments, which ranged from 6.7±2.3 to 15.8±2.3% (Fig. 1).

As regards long-term effects, when disturbances were applied during the cold period, *C. cylindracea* cover in the successive warm period (9 months after the first disturbance; sampling 6), when *C. cylindracea* bloomed, followed a significant decline as storms became more extreme (R^2= 0.31; p<0.05). This trend was similar to that observed when applying the disturbances (short-term effects) irrespectively of the period of the year when the disturbances were applied. Thus, the short-term decreasing trend of *C. Cylindracea* cover was still visible several months after the last disturbance. In this sampling (sampling 6 of the disturbance applied during the cold peri-

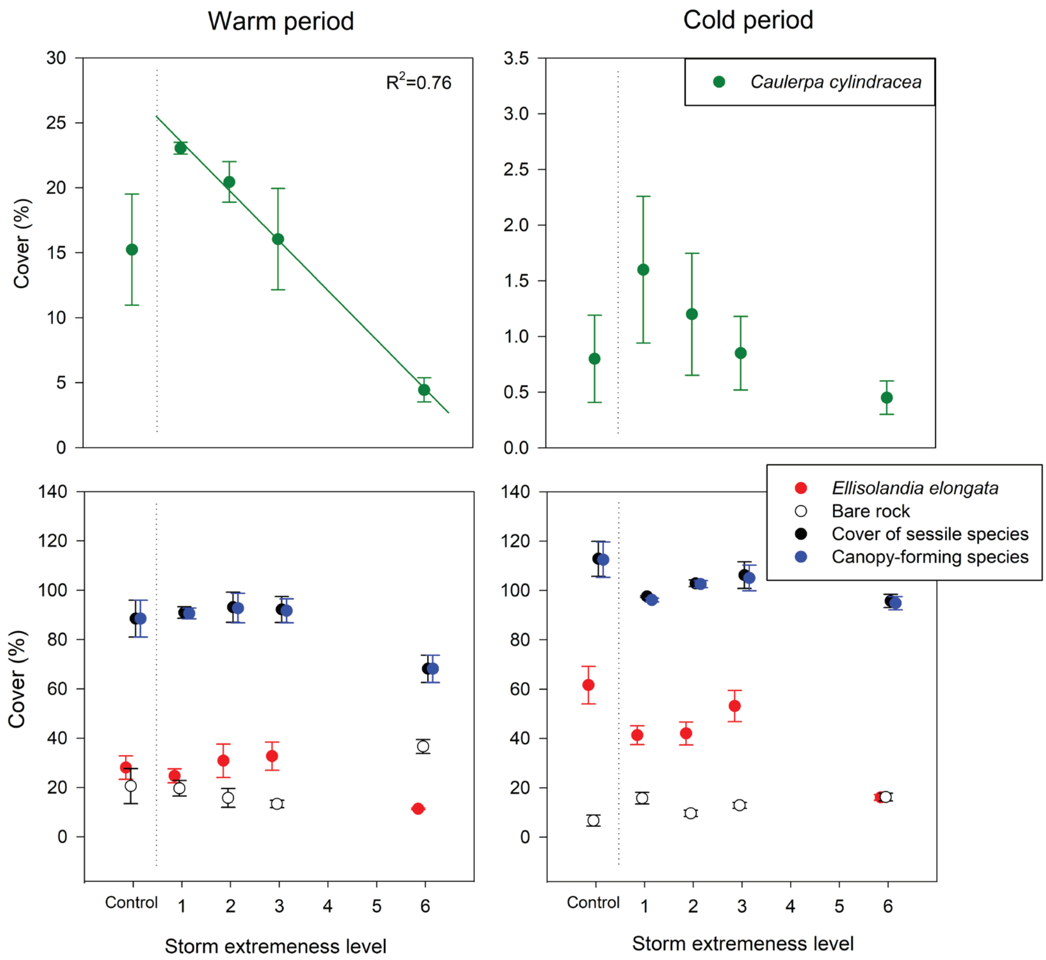

Fig. 1: Trends of *Caulerpa cylindracea* cover, cover of the sessile species, canopy-forming species, *Ellisolandia elongata* and bare rock (mean ± SE; n = 4) across two extremeness gradient scenarios. The disturbances simulating the storms were applied in the warm or cold periods (Fig. S3) on the short-term (averaged data of samplings 1-5 during the application of the disturbances). Although the response variables (the cover of the different taxa and bare rock) were manipulated under the same storm extremeness level, they are slightly displaced from the x axis in the plot to avoid overlapping and to facilitate visualisation. 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.

Table 1. Summary of regression coefficients for *Caulerpa cylindracea* cover across the storm extremeness gradient. Models were analysed separately for disturbances applied during the cold and warm periods, evaluating both short-term effects (averaged data from samplings 1-5) and long-term effects with sampling 6. Included are only those samplings where the regression models yielded a significant or close to significant trend. Significant coefficients are indicated in bold.

Period of the year	***Sampling times (months)***		***Coefficient (SE)***	***P***
Cold	1-5	(Intercept)	**1.68 (0.41)**	**<0.01**
		Extremeness	-0.22 (0.12)	0.08
	6	(Intercept)	**35.9 (5.32)**	**< 0.001**
		Extremeness	**-4.18 (1.51)**	**<0.05**
Warm	1-5	(Intercept)	**27.4 (1.90)**	**<0.001**
		Extremeness	**-3.80 (0.54)**	**<0.001**

od), several mild disturbances enhanced *C. cylindracea* cover (30±6.5%), while one extreme storm yielded the lowest *C. cylindracea* cover (10±3.6%). The latter was notably lower than the *C. cylindracea* cover under undisturbed conditions (26±13%). In this sampling, the cover of all canopy-forming algae showed a decreasing trend as storms became more extreme, ranging from 104±8.8%, when there were several mild storms, to 68±24%, when there was a single extreme storm. For tis part, *E. elongata* cover was similar across most extremeness levels including the control, ranging from 17.5±6.8% – when several mild storms occurred– , to 38.3±3.3% –when three medium storms took place. To assess the long-term effects in the rest of the samplings, no clear decreasing trend of *C. Cylindracea* cover was observed with rising disturbance extremeness (Fig. 2).

In the sampling periods in which the mean of overall *C. cylindracea* cover exceeded 5%, the relationship between *C. cylindracea* cover and the cover of all sessile species showed a significantly positive trend (R^2=0.10; p=0.003; Fig. 3).

Discussion

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

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

The effect of extreme events on enhancing *C. cylindracea* invasiveness can vary depending on the availability of a resource benefitting the exotic species (Lear *et al.*, 2020) –empty space in this case (Jiménez *et al.*, 2011). However, in the upper subtidal zone, empty space may not necessarily favour *C. cylindracea* expansion, but rather limit it. Indeed, the absence of canopy-forming species can reduce their protection against wave action, which is an important driver of natural disturbance

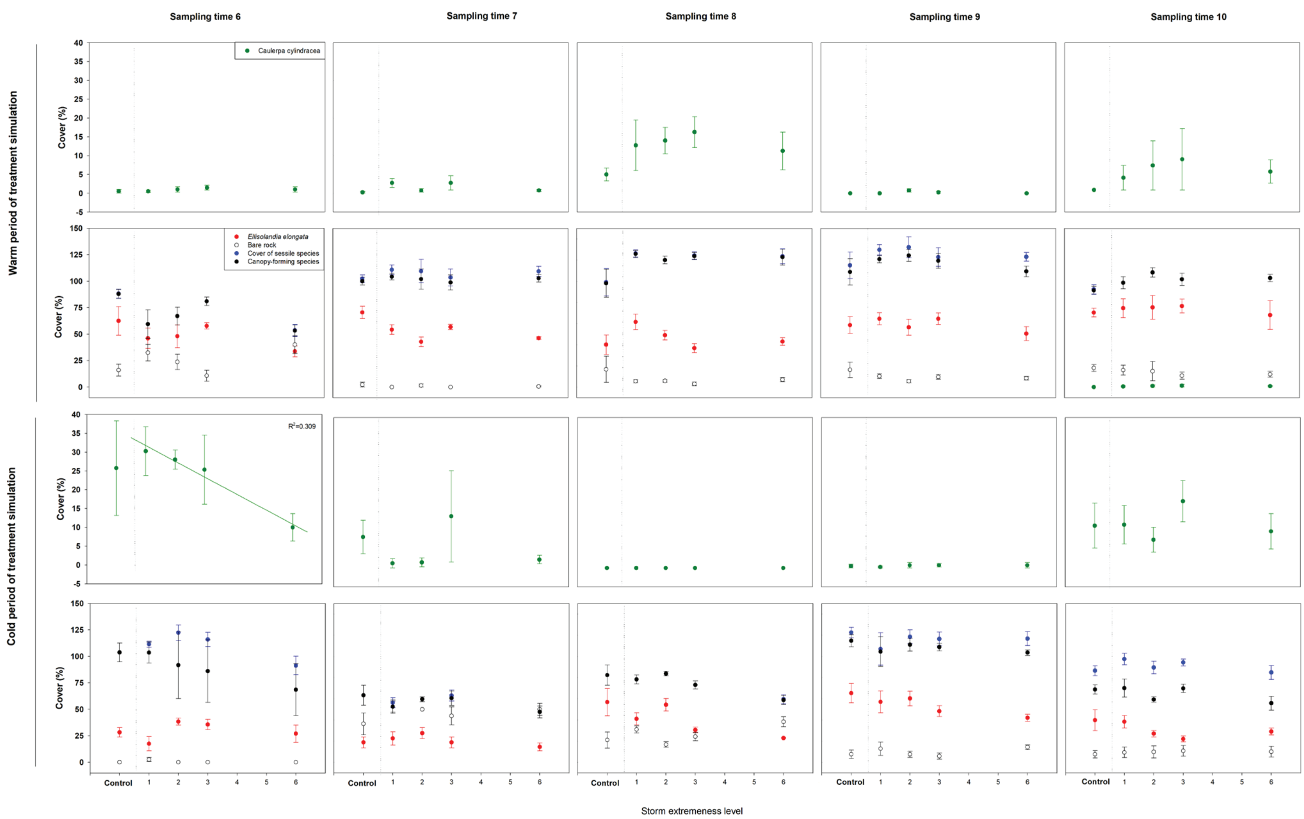

Fig. 2: Trends of the cover of *Caulerpa cylindracea*, cover of sessile species, canopy-forming species, *Ellisolandia elongata* and bare rock (mean ± SE; n = 4) as storms become more extreme when the disturbances simulating the storms were applied in the warm or cold periods were applied in the warm or cold periods; Fig. S3) on the long-term (samplings 6-10, the ones done after the application of the disturbances). 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.

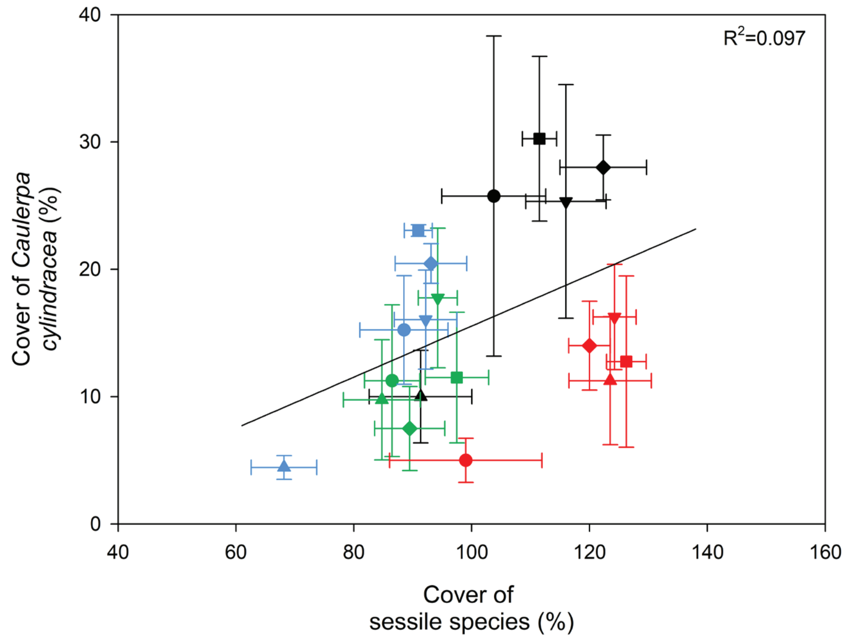

Fig. 3: Relationship between the cover of *Caulerpa cylindracea* and the cover of all sessile species (mean ± SE; n=4) taking the sampling periods in which the mean of the overall cover of *C. cylindracea* was higher than 5%, which were the samplings 1-5 (blue symbols) and 8 (red symbols) in the plots of the experiment where the disturbances simulating storms were applied during the warm period and the samplings 6 (black symbols) and 10 (green symbols) in the plots of the experiment where the disturbances simulating storms were applied during the cold period (Fig. S3). Symbols indicate the treatments: one very intense storm (△), two intense storms (▽), three moderate storms (◇), six mild storms (□) and the undisturbed control (○). The line indicates the prototypical trajectory of the regression model; regression model is y=-4.5+0.2x (p value=0.003).

at this level of the shore (upper subtidal) (Ceccherelli & Cinelli, 1999). This hypothesis is supported by previous evidence gathered on rock pools, where negative effects on *C. cylindracea* cover were found at high disturbance intensities (Incera *et al.*, 2010), especially under nutrient enrichment conditions (Bertocci *et al.*, 2015).

In deep subtidal Mediterranean zones, light, not only empty space, can represent a limiting resource for *C. cylindracea*. Moreover, in these zones, *Posidonia oceanica* (Linnaeus) Delile, 1813 is the dominant canopy-forming species (Marbà *et al.*, 2014), creating a massive canopy in terms of height (*ca.* 1 m) compared to the canopy height of upper subtidal communities (*ca.* 10 cm). Thus, in these zones, small canopy gaps may not be sufficient for *C. cylindracea* to receive enough light (Bernardeau-Esteller *et al.*, 2015), while large canopy gaps will not only result in more empty space resources, but also more light availability, enhancing alga expansion (Ceccherelli *et al.*, 2014).

Along rocky shores, in the shallow subtidal zone, light is not expected to be a limiting factor (Bulleri *et al.*, 2010; Marín-Guirao *et al.*, 2015) and empty space may be the only resource that *C. cylindracea* can draw from a storm. However, in the shallow subtidal zone, the eroding effect of waves, which is much more relevant that at deep zones, can limit the expansion of this alga as its attachment capacity to bare rock is low. Thus, low intensity disturbances that remove a low canopy structure cover may leave few, yet sufficient bare rock gaps to allow this species to expand, while preserving enough cover of canopy-forming species to form the structures to which *C. cylindracea* can attach (Piazzi *et al.*, 2003). Large gaps of bare rock produced by high intensity storms may leave *C. cylindracea* too intensely affected by the effects of waves in this highly hydrodynamic zone, and a reduced number of gaps presenting structures to attach to.

This hypothesis is supported by the results of the present study, which revealed a negative trend in *C.cylindracea* cover as storm extremeness increases. This decline coincides with a notable reduction in canopy-forming species, especially the dominant *E. elongata*, and a notable increase in bare rock coverage. Additionally, the positive relationship of the *C. cylindracea* cover with the cover of all sessile species in the rocky shore also supports the hypothesis. Our results demonstrate that disturbance effects across the extremeness gradient remain evident up to 4 to 9 months after the last disturbance. This period is relatively long for rocky shore communities with such a short-life cycle in which the composition of the whole community can change entirely across the seasons. Thus, in rocky shores, not only can extreme storms limit *C. cylindracea* invasiveness on the short-term, they can also have a legacy effect on the months-long scale. Further studies need to be performed, however, in diverse locations to confirm this hypothesis.

Conclusions

In the upper subtidal zone (< 0.5 m depth), extreme storms can limit the invasiveness of a major aquatic exotic species: *C. cylindracea*. This apparent contradiction with the current paradigm in which extreme events are expected to enhance exotic species invasiveness can be explained by the specific conditions of this habitat. In the upper subtidal zone, large releases of empty space promoted by highly intense storms may not favour *C. cylindracea* expansion, but rather limit its recolonisation ability, due to the lack of wave action protection in the absence of canopy-forming species. This study suggests that extreme events do not necessarily enhance exotic species invasiveness and that their effects can depend on the habitat. Thus, the actual effects of extreme events on the invasiveness capacity of exotic species need to be assessed across various environments. Optimised management strategies should then be adapted to each context to mitigate the effects of climate change.

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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Supplementary Data

The following supplementary information is available online for the article:

Table S1. Summary of the t-test results of *Caulerpa cylindracea* cover comparing the control and each treatment of the storm extremeness gradient for the two periods of the year (cold and warm) when the disturbances were applied, and the corresponding samplings that showed a significant or close to significant gradients (see Fig. 1 & 2).

Table S2. Summary of the t-test results of *Ellisolandia elongata* and canopy-forming species cover, and bare rock comparing the control and each treatment of the storm extremeness gradient for the warm period of the year, when the disturbances were applied and there was a significant gradient in the cover of *Caulerpa cylindracea* as disturbances become more extreme (see Fig. 1).

Table S3. Summary of the Akaike information criterion (AICc) of the regression models. Lower values (in bold) determine the most parsimonious model.

Table S4. List of all the species found in the samplings (in bold if they have been considered as canopy forming species in the analyses).

Fig. S1: Map of the location of the study area.