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Anthropogenic pressures enhance the deleterious effects of extreme storms on rocky shore communities

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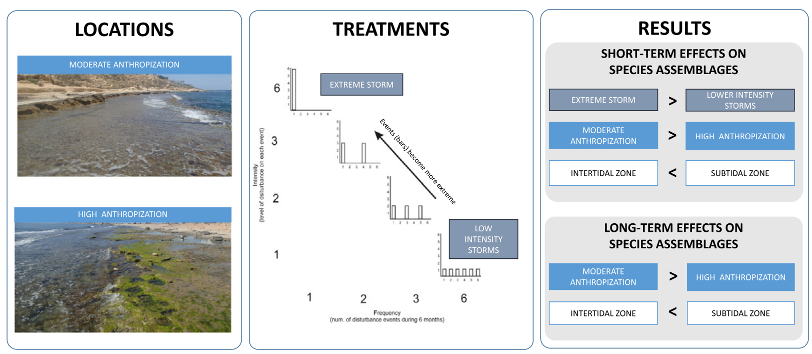
HIGHLIGHTS

- An extreme storm had greater impact on assemblage than other disturbance regimes.
- The assemblage in the area with a high anthropogenic pressure was more affected by the extreme events.
- The assemblages that suffered an extreme storm were generally more affected after the disturbance.
- The effects of extreme events could be strengthened when occurring with anthropogenic pressures.

GRAPHICAL ABSTRACT



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ABSTRACT

Climate change is not only changing the mean values of environmental parameters that modulate ecosystems, but also the regime of disturbances. Among them, extreme events have a key role in structuring biological communities. Ecosystems are frequently suffering multiple anthropogenic pressures which can cause effects that are not additive. Thus, the effects of extreme events need to be studied in combination with other pressures to adequately evaluate their consequences. We performed a manipulative approach in two rocky shores in the Mediterranean with contrasting levels of anthropogenic pressure (mainly eutrophication) simulating storms with different disturbance regimes in the intertidal and subtidal zones. In the short-term, an extreme storm had a greater impact on the species assemblage than other disturbance regimes, being especially notable in the area suffering from a high anthropogenic pressure. In this area, the species assemblages that suffered from an extreme storm took a longer time to recover than the ones affected by other disturbance regimes and were generally more affected after the disturbance. The intertidal zone, having more variable environmental conditions than the subtidal zone, was more resistant and able to recover from extreme storms. Our results suggest that the effects of extreme events on biological communities could be strengthened when co-occurring with anthropogenic pressures, especially ecosystems adapted to less variable environmental conditions. Thus, limiting other anthropogenic pressures that ecosystems are suffering is crucial to maintain the natural resistance and recovery capacity of ecosystems towards extreme events such as storms.

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1. Introduction

Climate change is a major driver of ecological change (Halpern et al., 2008) of increasing concern, altering not only the average levels of environmental parameters, but also the regime of disturbances in ecosystems (Johnstone et al., 2016).

Among disturbances, extreme climate events (hereinafter referred to as extreme events) are disturbances of an enormous intensity and a relatively low frequency of a meteorological origin, such as heat waves or severe storms (Stephenson, 2011). Due to their enormous intensity, extreme events have a key role in structuring ecosystems (Mitchell et al., 2006) and their occurrence is expected to rise due to climate change (Cai et al., 2012; Hannah et al., 1994; IPCC, 2021). Manipulative experiments are an effective approximation to study the effects of disturbance regime shifts, since they allow us to control key parameters such as intensity and frequency, and establish cause-effect linkages (Jentsch et al., 2007). Generally, manipulative works studying the effects of modifications in the regime of disturbances on ecosystems use the intensity and frequency in a full factorial approach, resulting in treatments which are not likely to occur in nature (McCabe and Gotelli, 2000). Additionally, this approach produces treatments with different overall intensity, which limits the comparability of the results (Sanz-Lazaro, 2019).

Ecosystems are commonly affected by several anthropogenic pressures (Vitousek et al., 1997), which can affect biological communities more severely than when the pressures act isolated (Crain et al., 2008). If the effect is severe enough, a shift into an alternative stable state can occur (Scheffer et al., 2001). Extreme events are important drivers of these shifts, for example in rocky shores, cold waves can tip persistent rockweed stands to mussel beds (Petraitis et al., 2009). This shifts are more likely to occur when extreme events are combined with other stressors, such as the case of the shift of kelp forests to algal turfs after a heat wave in 2011 in Australia and a background warming of four decades (Harris et al., 2018).

Despite the recent effort to tackle this issue (Guerrero-Meseguer et al., 2020; Gunderson et al., 2016; Sokolova, 2013), there are few studies that have focused on high levels of biological organization such as communities and ecosystems (Garnier et al., 2017; Tabi et al., 2019) time scale (Garnier et al., 2017) or timing (Smith et al., 2009). Thus, more research effort is need to understand their effects when occurring in combination with other anthropogenic pressures (Wernberg et al., 2012), and several methodologies are available (Álvarez-Yépiz et al., 2018; De Laender, 2018; Sanz-Lazaro, 2019; Smith, 2011). This knowledge is a key to provide environmental managers the scientific basis to design effective adaptation and mitigation strategies against climate change (Cote et al., 2016).

Rocky shores are an ideal habitat to perform manipulative experiments using the whole biological community due the high turnover of the species, the relative high diversity comprising different functional groups and the accessibility (Connell and Slatyer, 1977; Hawkins et al., 2020). Research on rocky shores has widely contributed to the development of ecological theory (Paine, 2010), with a long tradition of studying the ecological consequences of disturbances (Keough and Quinn, 1998; Paine and Levin 1981; Underwood, 1999). These areas can be used as natural labs to create different scenarios of climate change (Bertocci et al., 2005; Kordas et al., 2015; Sanz-Lázaro, 2016), but always considering the disturbance regime associated with a particular shore.

The aim of the work is to study the short- and long-term combined effects of combined pressures (storm and eutrophication) on the biological community. To do so, we performed a manipulative approach in two rocky shores with contrasting levels of anthropogenic pressure (mainly eutrophication) simulating storms with different disturbance regimes. The experiment was performed at the intertidal and upper subtidal zones to embrace communities adapted to more dynamic and stable conditions, respectively, in terms of water immersion and wave exposure. We hypothesized that the effects of extreme storms would be more pronounced in communities suffering from a high anthropogenic pressure and, especially when adapted to more stable environmental conditions.

2. Methods

2.1. Study area

The experiment was performed in two rocky (sandstone) shores located in the Western Mediterranean, in the coast of Spain, in the bay of Alicante, which are 9 km apart and have a contrasting level of disturbance. On this area, the prevailing dominant currents move to the South. One of the sampled shores is in Cape of Huertas (38° 21′ 10″ N, 0° 25′ 07″ W; hereinafter referred to as "Huertas") in the North part of the bay and the other sampled shore Agua Amarga (38° 18′ 06″ N, 0° 31′ 05″ W) is in the middle of the bay. Agua Amarga shore is close to the mouth of a wadi ("Barranco de las Ovejas") that receives effluent of a wastewater treatment plant of the city of Alicante (Megías-Baños, 2019). At the end of this mouth to the North, there is the port of Alicante, which is expected to limit the dispersion and dilution of the wastewater spills in the sea (Fig. S1A). The high levels of nutrients in Agua Amarga compared to Huertas (Terradas-Fernández et al., 2020), resulted in the doubling of chlorophyll *a* values in Agua Amarga compared to Huertas (Fig. S1B). In Agua Amarga, marine litter accumulation is high (Asensio-Montesinos et al., 2019), thus being classified as one of the most polluted beaches in the province of Alicante (Megías-Baños, 2019) (Fig. S2A). In Agua Amarga the predominant algae are the Corallinales, Ulvales and Ectocarpales, while in Huertas, predominate the Dictyotales, *Laurencia* complex, Gigartinales and Fucales (Terradas-Fernández et al., 2020), which indicates a poor and good ecological status, respectively (Ballesteros et al., 2007) (Fig. S2B). Thus, in the present study we consider that Agua Amarga and Huertas are suffering high and moderate anthropogenic pressures, respectively.

In both locations, the shores are dominated by horizontal platforms of vermetid reefs, despite vermetids are only found alive in Huertas in the upper subtidal zone. On each shore, the experiment was performed in two zones within a different height: the intertidal and the upper subtidal zones. The intertidal zone has a reduced length (0.3–0.4 m) typical of enclosed seas, such as the Mediterranean and an average significant wave height of 0.8 m. In the intertidal zone, the sampling was performed between 0 and 0.3 m above the mean low-water level. The upper subtidal zone has a permanent water depth of 0.1–0.4 m and is located in the vermetid platform. In the upper subtidal zone, the sampling was performed between 0.2 and 0.3 m below the mean low-water level. The biological communities that inhabit these areas have a marked seasonality for the community composition (Terradas-Fernández et al., 2020).

2.2. Experimental design

A total of 160 experimental plots (35 × 35 cm) were randomly distributed along the shoreline of each shore at the intertidal and upper subtidal zones and were delimited and numbered with epoxy putty (Subcoat S; Veneziani, Trieste, Italy). To simulate the effect of storms on rocky shores, we eroded the rock of each experimental plot by means of a chisel and a hammer. This kind of disturbance resembles to natural one produced by storms, since waves with a sufficient intensity can break the rocks in the shores producing bare space (Paine and Levin, 1981).The levels of frequency were chosen based on the records of storm surges over the previous decades in this area (0–6 storms per year) (Camuffo et al., 2000). To test the effect of changes of the disturbance regime, we designed a realistic gradient of storms in which frequency and intensity were inversely varied while keeping the overall intensity constant (Sanz-Lazaro, 2019; Sanz-Lázaro, 2016). Accordingly, the following treatments were simulated: one very intense storm that removed 100% of the cover of the community; two intense storms, each of which removed 50% of the cover of the community; three moderate storms, each of which removed 33% of the cover of the community and six mild storms, each of which removed 16% of the cover of the community. The simulation of the storms started at the beginning of the experiment and were performed only once, and every three, two and one months, respectively to the previous mentioned gradient of extremeness (Fig. S4). Additionally, unmanipulated plots were used as the control

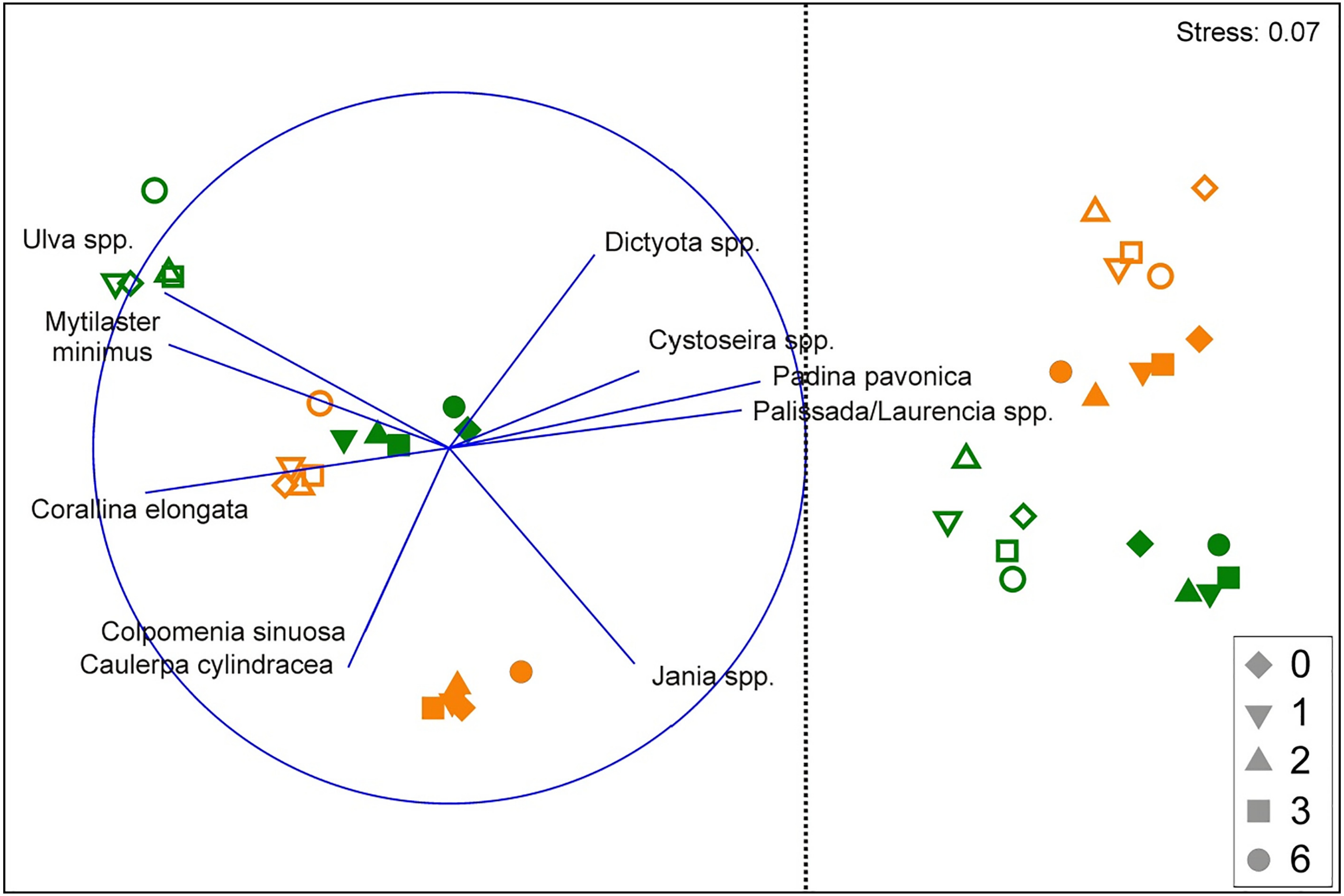
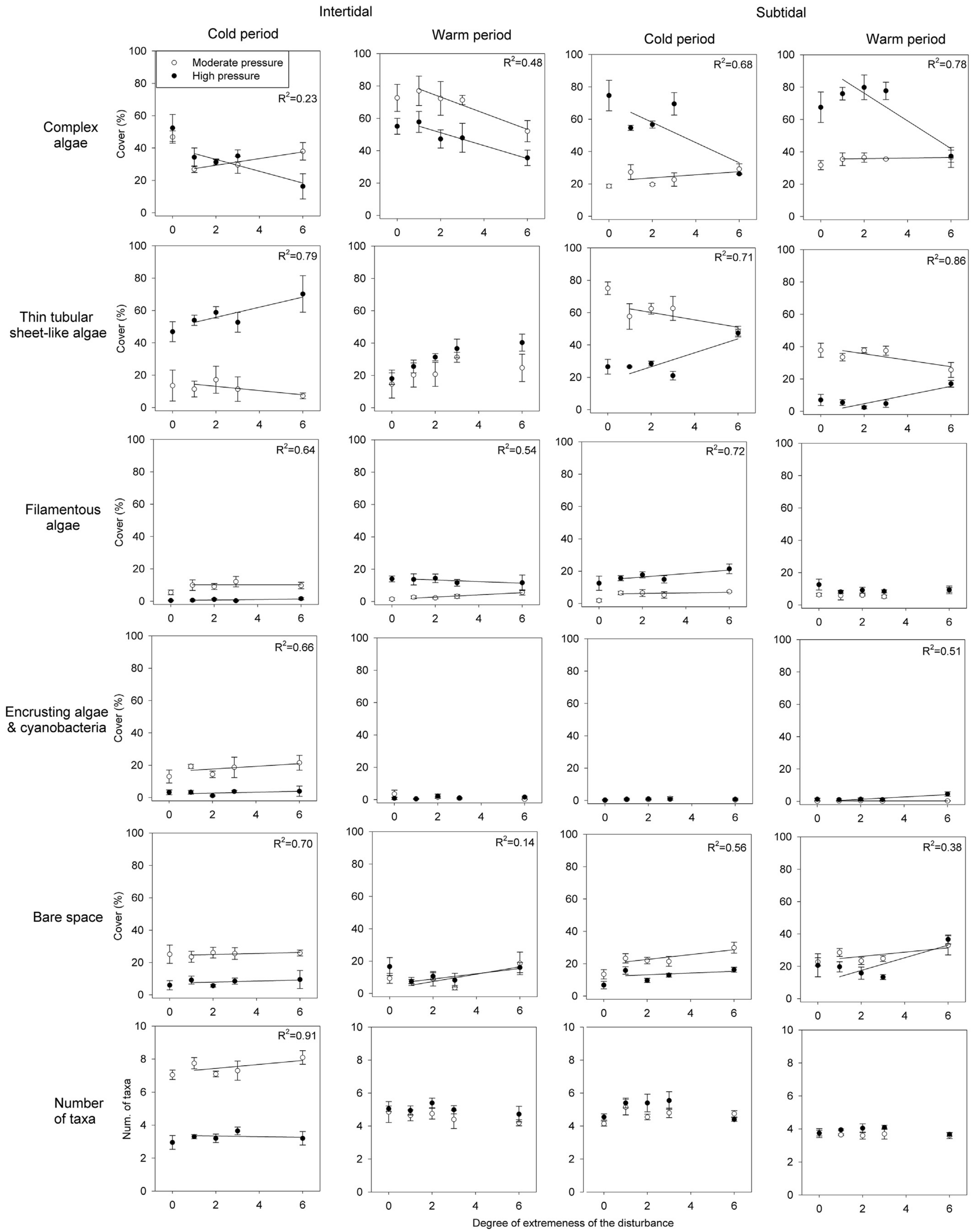


Fig. 1. Non-metric multidimensional scaling (nMDS) of the cover of the sessile taxa based on the pooling of the replicates of treatments of the first five samplings. The different disturbance regimes of simulated storms are indicated by the symbols with the associated numbers that go from several mild storms (1) to a single extreme storm (6) and the control (0), the zone by colours (intertidal: green; subtidal: orange), the time of the year when the storms were simulated by symbols (cold period: empty; warm period: solid) and the dotted line separates the samples from the rocky shore with high (left) and moderate (right) anthropogenic pressures according to the cluster analyses. The solid lines indicate the vectors of the taxa that have a Pearson correlation index with the nMDS axes above 0.5.


Intertidal
Subtidal
Cold period
Warm period
Cold period
Warm period
Moderate pressure
High pressure
Complex algae
Thin tubular sheet-like algae
Filamentous algae
Encrusting algae & cyanobacteria
Bare space
Number of taxa
Cover (%)
Num. of taxa
R2=0.23
R2=0.48
R2=0.68
R2=0.78
R2=0.79
R2=0.71
R2=0.86
R2=0.64
R2=0.54
R2=0.72
R2=0.66
R2=0.51
R2=0.70
R2=0.14
R2=0.56
R2=0.38
R2=0.91
Degree of extremeness of the disturbance

treatment (Table S1). Each treatment was replicated 4 times. In these locations, storms can occur during the whole year. When a natural storm occurred, it was assumed that all the plots where affected similarly.

The experiment was run twice at each of the two zones of the rocky shore of each location to perform the storm simulations during the cold and warm period of the year (hereinafter referred to winter and summer, respectively), since this community assemblage is markedly different in these two times of the year (Pinedo et al., 2015; Terradas-Fernández et al., 2020). For the intertidal and subtidal zones, for the first run of the experiment, disturbances started in November and finished in June, which corresponded with the period of the year when the temperature of the water is low (monthly average during these months: 16.1 °C). For the second run, disturbances started in May and finished in December, which corresponded with the period of the year when the temperature of the water is high (monthly average during these months: 22.9 °C; Table S2). Thus, the experiment consisted of 20 plots for each zone of the shore on each location and each time of the year.

2.3. Sampling

Each plot was sampled ten times. To study the short-term effects of changes in the disturbance regime, 5 sampling 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 (legacy) effects the rest of the five samplings were used, which were performed consecutively every 2–3 months (Fig. S4). To avoid possible border effects, the sampling was carried out in the centre of the experimental plot on a surface of 20 × 20 cm. Out of the total of 1600 samplings planned (160 plots sampled 10 times), only 13 were missed due to the inability to find the corresponding plot due to bad weather conditions and the covering of the epoxy putty used to delimit the plots, despite the organisms attached to them were removed every 1–2 months.

2.4. Data analyses

The experimental design was made of four factors (treatments/levels): *storm* (mild, moderate, intense and very intense storms and an unmanipulated control), *anthropogenic pressure* (moderate and high), z*one of the shore* (intertidal and subtidal) and *time of the year* (warm and cold period) that were considered fixed and orthogonal.

To analyse the short-term effects of the storms in the shore communities, the data of the five first samplings on each experimental plot were averaged. The trends of individual response variables along the gradient of storms becoming extreme were modelled using the treatments of the simulated storms: mild, moderate, intense and very intense as a continuous variable, which corresponded to a level of extremeness of: 1, 2, 3 and 6, respectively (sensu Sanz-Lázaro, 2016). The response variables used were the number of sessile taxa, the bare space (not covered by sessile species) and the cover of the following functional groups of algae based on morphological complexity: complex (including coarsely-branched, articulated corallines and siphonous), thin tubular sheet-like and filamentous as well as encrusting algae and cyanobacteria. By analysing functional groups we could compare communities that were under different anthropogenic pressure despite having a different species composition, while we could have more insights on the effects of disturbance (Littler and Littler, 1984). The models were performed by means of generalized linear models, specifically ANCOVA, that allowed a comparison of the trends of the response variables between the location in the two rocky shores with contrasting levels of anthropogenic pressure. To facilitate comprehension and visualization, each model was done separately for each of the two tidal zones and the time of the year when the storms were simulated. For each response variable, the AICc (corrected Akaike Information Criterion) for the linear and quadratic polynomial regression was calculated and the model with the lowest AICc value was chosen.

Multivariate analyses were employed to analyse the structure of the biological assemblages using the cover of the sessile taxa. Initially, a nonmetric multidimensional scaling (nMDS) along with a cluster routine was performed as an exploratory approach to visualize the spatial ordination of the samples. To facilitate visualization, the average cover values of the replicates of each treatment were used, and the taxa that showed a Pearson correlation index with the nMDS axes above 0.5 were included in the plot as vectors to show which species were the main drivers of the ordination. Then, a four-way permutational multivariate analysis of variance (PERMANOVA) was performed to test significant differences among factors. Prior to PERMANOVA, PERMDISP (Distance-based test for homogeneity of multivariate dispersion) was run at different levels in the design to test for the dispersion of data following the recommendations of Anderson et al. (2008). Then, at the highest significant level of interaction among factors which contained the factor *storm*, a *post-hoc* test was done to find pairwise significant differences between the undisturbed control and each treatment of the simulated disturbance regime.

To analyse the recovey/long-term effects on the shore community after the simulated storms, the structure of the assemblage of the sessile species of the treatments suffering the different disturbance regimes of the simulated storms were compared separately with the control at each sampled time after the last disturbance of each simulated regime by means of a PERMANOVA pairwise test. The results were visually analysed by plotting each *p*-value of the contrast against the time past after suffering the last disturbance. This procedure to analyse long-term effects was chosen because more standard analyses on temporal trends, such as full PERMANOVA analysis including time as a covariate or DISTLM, precluded the comparison among treatments because assemblage composition in these ecosystems is notably driven by season and anthropogenic pressures (Pinedo et al., 2015; Terradas-Fernández et al., 2020).

Univariate analyses were run in the statistical environment R (v. 2.15.0). Multivariate analyses were performed with the software package Primer (v6) and its complementary package PERMANOVA+ (v. 1), and based on the Bray-Curtis dissimilarity index of the square root transformed data. All statistical tests were conducted with a significance level of $\alpha = 0.05$.

3. Results and discussion

The structure of the community clearly differed between the rocky shore with moderate and high anthropogenic pressures, and, also, between tidal zones and the time of the year when the storms were simulated. In many cases, the extreme storms and/or the controls tended to separate from other treatments of simulated storms. *Dictyota* spp., *Cystoseira* spp., *Padina pavonica*, *Laurencia* complex and *Jania* spp., on the one hand, and *Ulva* spp., *Mytilaster minimus*, *Corallina elongata*, *Colpomenia sinuosa* and *Caulerpa cylindracea*, on the other hand were the most important species in the configuration of the structure of the rocky shore with moderate and high anthropogenic pressure, respectively (Fig. 1). These results are in accordance with a previous work that show that many of these species

Fig. 2. Short-term changes in the cover of functional groups, bare space and number of taxa of rocky shore assemblages and their trends along a gradient of disturbance regime of simulated storms with the same overall intensity, ranging from several small storms (degree of extremeness = 1) to a single large one (degree of extremeness = 6; see Fig. S3 for a scheme) (mean ± SE; n = 4) in the intertidal and subtidal zones during the two periods of the year when the experiment was replicated in two rocky shores suffering moderate (empty circles) and high anthropogenic (solid circles) pressures. This analysis refers to the short-term effects, so the values of each replicate correspond to the mean of the five first samplings (during the simulation of the disturbances) from each experimental unit. Treatment 0 corresponds to the control in which no storm was simulated. The lines indicate the best fit trend along the gradient of simulated storms when the model was significant.

are indicative of the corresponding environmental status of rocky shores in this region (Ballesteros et al., 2007).

The analyses of the short-term effects along the disturbance regime for the complex algae under moderate anthropogenic pressure showed contrasting trends along the gradient of disturbances depending on the time of the year when the disturbance was performed and the tidal zone. Under high anthropogenic pressure, the complex algae showed a general trend of decrease as disturbances become more extreme. As regards thin tubular sheet-like algae, the trend along disturbances becoming more extreme were generally opposed depending on the level of anthropogenic pressure, decreasing under moderate levels, while increasing under high levels. Filamentous algae, as well as encrusting algae and cyanobacteria, in general, did not show marked tendencies as disturbances became more extreme, while bare space showed a slight increasing trend (Fig. 2; Table S3).

The present study suggests that under a scenario of high anthropogenic pressure, as disturbances become more extreme, the cover of complex algae, which constitute the latest colonists in the biological succession in rocky shores, is expected to be substituted by thin tubular sheet-like algae, which are earlier colonists than complex algae. This effect does not seem to occur under the moderate anthropogenic pressure scenario. The reduction of late colonists at the expense of early colonists indicates a displacement of the biological assemblage towards early successional stages (Sousa, 1979). These results suggest that areas suffering high anthropogenic pressure could be more sensitive to extreme storms than areas not suffering high anthropogenic pressures, resulting in a less resistant community that is driven to earlier successional stages.

The use of functional groups has been widely used to study the level of disturbances in biological communities (Littler and Littler, 1984). Functional grouping, as any other integrative community metric, such as diversity indices, simplifies information (Phillips et al., 1997) and in some cases the morphological complexity may not predict the function (Ryznar et al., 2021). Nevertheless, it can complement analyses of the whole community (Arenas et al., 2006), being especially helpful when the community has different species composition as in the present study.

The number of taxa of the studied assemblages was generally similar disregarding the level of anthropogenic pressure, being only higher in the intertidal zone in the cold period under moderate anthropogenic pressure conditions. The number of taxa did not show notable changes disregarding disturbance application and no trends along the gradient of disturbance were observed. This observation sides with previous studies that show that in rocky shores the number of species may not fully relate to the stability of the ecosystem (Cusson et al., 2015; Sanz-Lázaro, 2016) (Fig. 1; Table S4).

As regards the analyses of the whole species in the short-term, the PERMANOVA results of the short-term effects showed a highly significant ($P = 0.001$) interaction among the factors: *Anthropogenic pressure* (AP), *Time of the year* (Ti) and *Zone of the shore* (Sh) (Table S4). This is expectable as the assemblage composition is differently influenced by anthropogenic pressures, such as pollution and eutrophication (Ballesteros et al., 2007; Pinedo et al., 2007), and by seasonality(Terradas-Fernández et al., 2020; Titlyanov et al., 2019), as well as by vertical zonation, which constitute a key driver of species distribution (Chappuis et al., 2014). Additionally, there was a marginal significant interaction ($P = 0.059$) among the factors *Storm*, *Anthropogenic pressure* and *Zone of the shore* (Table S4). The pairwise comparisons of the assemblages between the control against the rest of the treatments of the factor storm integrating the two times of the year, showed significant differences in most comparisons of the control versus the extreme storm. Only under moderate anthropogenic pressure in the intertidal zone, the comparison of the control versus the extreme storm was marginally significant, but the P value was the lowest ($P = 0.066$) compared to comparisons of the control versus other disturbance regimes in this category. Assemblages suffering from an extreme event in both rocky shore zones under a high anthropogenic pressure showed more marked differences with their respective control than assemblages suffering from a moderate anthropogenic pressure. Additionally, under moderate anthropogenic pressure, in the subtidal zone also assemblage comparisons of the control with several mild or two high storms were also significantly different, despite the significance values ($P = 0.014$ and $P = 0.037$) were higher than the comparison with the extreme storm ($P = 0.0007$) (Table 1).

These results suggest that a single very intense storm can change more profoundly the structure of the biological assemblage than the other storm regimes that were more frequent but less intense, which is in accordance with previous evidence (Sanz-Lázaro, 2016). These effects are expected to be more pronounced in areas suffering from a high anthropogenic pressure as it has been previously reported (Harris et al., 2018). This outcome agrees with the above commented results using functional groups, suggesting that areas under relevant anthropogenic pressure are expected to be more affected by extreme events, such as an extreme storm. Thus, the resistance of a community towards extreme events such as the one in rocky shores, could be compromised when being under high anthropogenic pressures. Additionally, these results suggest that a community under more stable environmental conditions, such as a subtidal one, could be more affected by a disturbance than a community of a more dynamic ecosystem, such as the intertidal.

The results also show that the subtidal zone was, in general, more sensitive to disturbances and particularly to extreme events than the intertidal zone (Table 1), which could be because the intertidal area is a more dynamic ecosystem naturally subjected to a wider range of changing conditions. This finding could be explained by the fact that ecosystems under more dynamic environmental conditions are expected to be more adapted to environmental changes, conferring them a higher resistance to disturbances than ecosystems that are under more stable environmental conditions as it has been previously reported in rocky shores (Viejo, 2009).

As regards the long-term effects of the simulated storms, when comparing the assemblages of the simulated storms against the control, there was a tendency of all manipulated treatments to resemble the control over time. Assuming that manipulated assemblages were fully recovered when they did not show significant differences with the corresponding control assemblage, recovery took more time in the rocky shore with a high anthropogenic pressure in both intertidal (210 days) and subtidal zones (342 days) than in one with a medium anthropogenic pressure (63 and 247 days in the intertidal and subtidal zones, respectively). When comparing both zones, the intertidal took less time to recover than the subtidal zones regardless of the level of anthropogenic pressure. The assemblages undergoing an extreme storm, were the ones that in more occasions (13) showed a significantly different structure to their respective unmanipulated assemblage after the disturbance, followed by assemblages that simulated three moderate (5 occasions), six mild (4 occasions) and two intense (3 occasions) storms, respectively. In some cases, the assemblages of manipulated treatments that did not simulate an extreme storm showed a fast recovery, but were punctually different from the control (Fig. 3).

The present study suggests that an extreme event could negatively influence recovery, which is likely to take more time in a more stable ecosystem, such as the subtidal than in the intertidal one. In general, more stable

Table 1
Short-term effects of different disturbance regimes on the community structure based on the cover of sessile taxa by means of PERMANOVA pairwise comparisons between the assemblage under control conditions and each one with a different disturbance regime of simulated storms indicated by numbers that go from several mild storms (1) to a single extreme storm (6) (Figs. 1 & S3) in the two rocky shores suffering contrasting levels of anthropogenic pressures and at the two zones of the shore on each location; integrating the two times of the year. Significant comparisons are shown in bold.

	Moderate pressure		High pressure	
	Intertidal	Subtidal	Intertidal	Subtidal
Ctrl vs 1	0.116	**0.014**	0.377	0.212
Ctrl vs 2	0.152	0.07	0.252	0.481
Ctrl vs 3	0.092	**0.037**	0.411	0.619
Ctrl vs 6	0.066	**0.0007**	**0.004**	**0.0002**

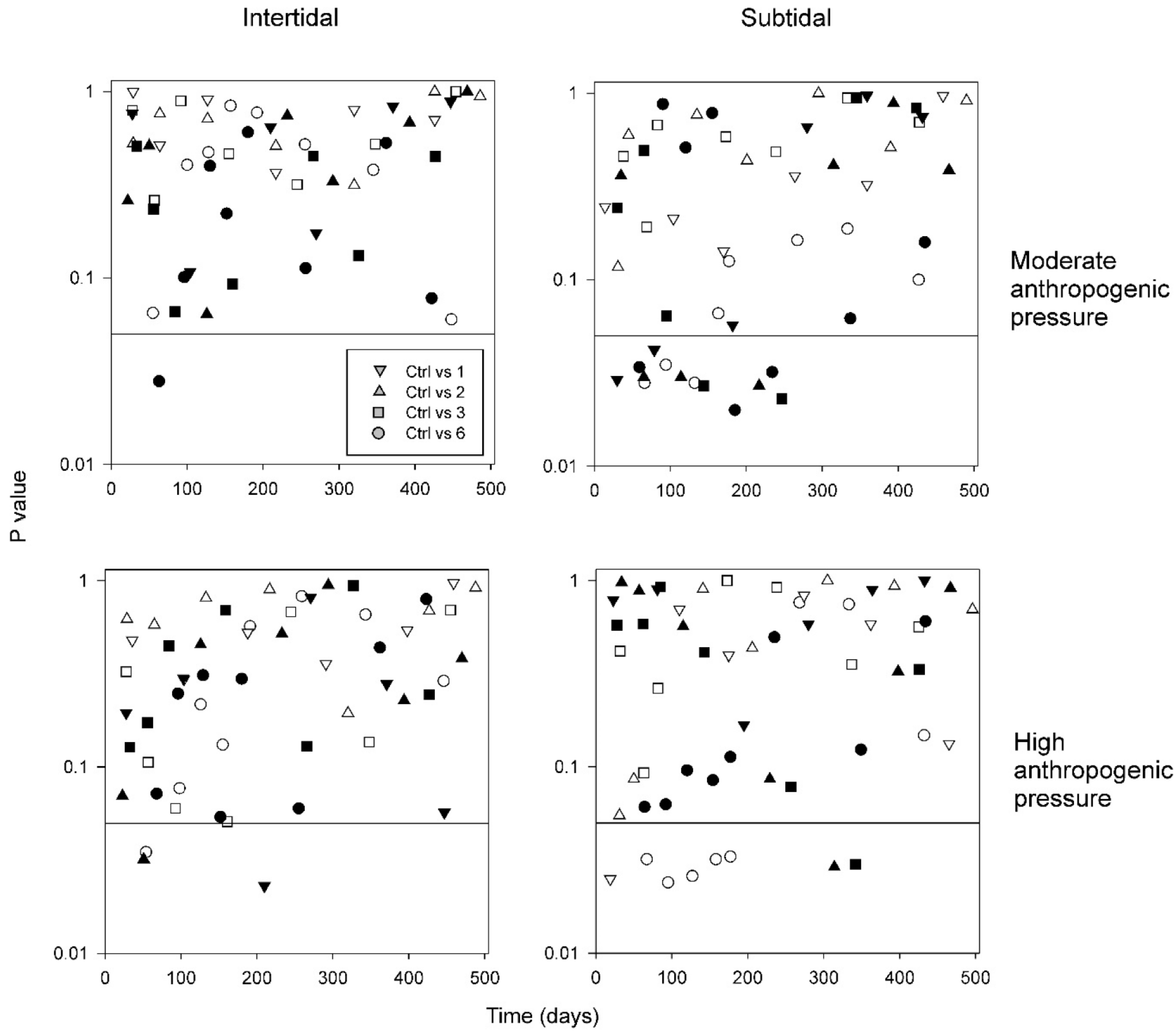


Fig. 3. Recovery/long-term effects of the community based on the cover of sessile taxa from each disturbance regime of simulated storms indicated by numbers that go from several mild storms (1) to a single extreme storm (6; Figs. 1 & S3) by comparing with the control conditions (PERMANOVA pairwise comparison P-value) in the two rocky shores suffering contrasting levels of anthropogenic pressures, at the two zones of the shore on each location at the two times of the year when the storms were simulated [cold (empty) and warm (solid symbols) period] for all the samplings performed after the last simulated disturbance. The solid line indicates the P value of 0.05. The y axis is represented in a logarithmic scale.

ecosystems are expected to recover faster from disturbances (Bertness et al., 2006; Brewer et al., 1997; Crain et al., 2008). This idea is linked to the fact that more stable ecosystems generally have a higher number of species (White et al., 2020; Worm et al., 2006). In the present study, the number of species was not notably different in the intertidal and subtidal areas in the studied rocky shores. Our results agree with previous research, in which recovery has been assessed similarly comparing the similarity of control versus manipulated treatment (Viejo, 2009). This outcome could have two explanations which can be complementary. First, zones that are adapted to high levels of abiotic stress can cope better with additional abiotic stress as far as the stress that the community is suffering does not compromise the performance of the species (Bertness et al., 2006). Second, zones that are adapted to high levels of abiotic stress may remain at an early successional stage compared to communities under low levels of abiotic stress, and thus its recovery could be fast due to a limited succession process to reach its natural successional stage (Hutchinson and Williams, 2003).

In the present study, while the factors *storm*, *zone of the shore* and *time of the year* are all replicated, the factor of *anthropogenic pressure* is mensurative and not replicated, with only one location suffering from a high (Agua Amarga) and another suffering from a moderate (Huertas) anthropogenic pressure. Bearing in mind the associated lack of replication of the experiment for the factor anthropogenic pressure, this was chosen as the best feasible alternative considering the spatial and temporal scale of the work and the inability to fully simulate an anthropogenic pressure of the magnitude found in Agua Amarga (Hurlbert, 2004; Wernberg et al., 2012). The option of in situ manipulations of contaminant addition are not suitable due to their relatively short-term and reduced scale effects (Worm et al., 2000). Not only the experimental units would have needed to be polluted, but also the whole area along which the experimental units were deployed, and within a sufficient time span before the beginning of the experiment, so the rocky shore community of the area was representative of one suffering anthropogenic pressures. Another strategy of finding additional locations with similar high and moderate levels of anthropogenic pressure nor finding a gradient of anthropogenic pressure was not feasible, since the drivers of ecological change co-occur in different intensities and combinations in each area. Replicating the present study in a sufficient number of locations that comprehensively embraced the anthropogenic pressure scenarios in rocky shores would have been unmanageable. Accordingly, we decided to use the mensurative experiment approach, since it provides a unique way of testing hypothesis at sufficiently large spatial and temporal scales to integrate ecosystem processes, which is commonly used to study the effects of climate change, such as ocean acidification (Hall-Spencer et al., 2008), as in other disciplines in Ecology (McGarigal and Cushman, 2002).

The present study suggests that under a scenario of high anthropogenic pressure the recovery of the community can be delayed, especially when suffering from an extreme disturbance. Despite so, no collapse or change towards other stable state (sensu Scheffer et al., 2001) was observed disregarding the degree of extremeness of the simulated storm as it could occur in cases of multiple pressures (Harris et al., 2018; Paine et al., 1998). This finding could be due to the fact that the simulated disturbance affects all the species of the community (it can produce the removal of all of them), but does not bring to extinction any species, as it is the case with other disturbances, such as overfishing, predation or diseases (Estes et al., 1998; Hughes, 1994; Jackson et al., 2001). Storms affect differently the species within an assemblage, for example, the creation of free space in the rocky shore initially favours earlier over late colonists, but as succession advances, late colonists are favoured and the assemblage tends to return to its initial structure (Benedetti-Cecchi, 2000). The high anthropogenic pressure suffering the rocky shore of Agua Amarga is a stronger perturbation than an extreme storm in the modulation of community structure since only by itself can configure an assemblage with remarkably different dominance of species, which could be considered another stable state. The effect could be due to their long-term nature, as well as to the effects of the pressure suffering this area such as eutrophication, which keeps a high level of nutrients that promotes the over competition of some species generating this new stable state. Increased productivity can promote recovery in many ecosystems (Van Ruijven and Berendse, 2005), specifically in the rocky shores, (Guichard et al., 2003). In the present study, the shift towards another stable state, rather than the speed up of recovery was promoted by a more productive system. This could be explained by the fact that the levels of nutrients were artificially increased and could be above natural ones (Kim et al., 2017).

4. Conclusions

The present study suggests that storms can have more deleterious effects on the biological communities from rocky shores as they get more extreme. The resistance and, to some extent the recovery, are expected to be compromised when the community is already under a high anthropogenic pressure and this effect could be more notable in ecosystems with more stable environmental conditions, such as the subtidal compared to the intertidal ecosystem.

The consequences of climate change related to the raise of occurrence of extreme events are expected to inevitably aggravate in the next decades (IPCC, 2021), due to the increasingly growing greenhouse gases emissions and the insufficient compromise at a global level to reduce or at least stabilize them. Accordingly, the present study reinforces the idea of previous works in taking special care to limit other anthropogenic pressures that ecosystems are suffering, as a mitigation measure against climate change, so the natural resistance and recovery of ecosystems towards climate change perturbations in not compromised (Folke et al., 2004; Holling, 1973). Special attention should be paid to ecosystems that are under relatively stable conditions, which are likely to be more affected by extreme events such as an extreme storm.

All these conclusions need to be taken in concordance with the scope of the present study. Further studies dealing with other disturbances derived from climate change, such as the clustering of extreme events, and additional anthropogenic pressures in other regions and ecosystems are necessary to increase our understanding on the effects of multiple pressures, including the ones derived from climate change, in ecosystems.

CRediT authorship contribution statement

Authors' contributions. Ideas and methodology: CS and MT; experimental design: CS; data collection: all authors; data analyses: CS, assisted by NC, AN and MT; writing leadership: CS. All authors contributed to the drafts and gave final approval for publication.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.152917.

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