

Experimental evidence of spatial signatures of approaching regime shifts in macroalgal canopies

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Abstract. Developing early warning signals to predict regime shifts in ecosystems is a central issue in current ecological research. While there are many studies addressing temporal early warning indicators, research into spatial indicators is far behind, with field experiments even more rare. Here, we tested the performance of spatial early warning signals in an intertidal macroalgal system, where removal of algal canopies pushed the system toward a tipping point (corresponding to approximately 75% of canopy loss), marking the transition between a canopy- to a turf-dominated state. We performed a two-year experiment where spatial early warning indicators were assessed in transects where the canopy was differentially removed (from 0 to 100%). Unlike Moran correlation coefficient at lag-1, spatial variance, skewness, and spatial spectra at low frequency increased along the gradient of canopy degradation and dropped, or did not show any further increase beyond the transition point from a canopy- to a turf-dominated state (100% canopy removal). Our study provides direct evidence of the suitability of spatial early warning signals to anticipate regime shifts in natural ecosystems, emphasizing the importance of field experiments as a powerful tool to establish causal relationships between environmental stressors and early warning indicators.

Key words: *algal turfs; alternative states; canopy–turf transition; early warning signals; macroalgal canopies; regime shift; resilience; spatial ecology; spatial variance.*

INTRODUCTION

The prospect of anticipating regime shifts in ecosystems has called for the development of metrics able to provide advance warnings of unwanted transitions (Lenton et al. 2008, Scheffer et al. 2012). The theoretical foundation of early warning signals (EWS) relies on the expectation of a slower recovery from perturbations close to a catastrophic threshold, due to a phenomenon known as “critical slowing down” (Scheffer et al. 2012). In addition to increasing recovery time after small perturbations, signatures of critical slowing down include enhanced autocorrelation, variance and “reddening” (i.e., higher variance at low frequencies) in the spectral properties of the data (Dakos et al. 2009, 2012, Kefi et al. 2014).

Laboratory-based microbial experiments have successfully probed early warning indicators, providing empirical evidence of critical slowing down (Drake and Griffen 2010, Veraart et al. 2012, Dai et al. 2013, 2015, Chen et al. 2014, Clements and Ozgul 2016). To the best of our knowledge, only four studies have provided experimental tests of critical slowing down in field conditions, including shallow lakes (Carpenter et al. 2011), the aquatic environment developing within a

carnivorous plant (*Sarracenia purpurea*; Sirota et al. 2013), macroalgal canopies (Benedetti-Cecchi et al. 2015), and salt marshes (van Belzen et al. 2017). These studies revealed that (1) variance and autocorrelation are robust indicators of approaching tipping points, (2) high levels of variability may decrease the signal-to-noise ratio in EWS, and (3) spatial EWS are context-dependent and show large site-to-site variability. Although such studies have increased our understanding on EWS, there is still a need for manipulative field experiments to provide rigorous tests of hypotheses about causal relations between environmental degradation and changes in EWS and to narrow the gap between theoretical expectations and the actual performance of early indicators in natural systems (Scheffer et al. 2015).

Most of the research aiming at anticipating regime shifts has so far focused on temporal EWS (Carpenter et al. 2011, Batt et al. 2013, Benedetti-Cecchi et al. 2015, Scheffer et al. 2015, Pace et al. 2017). However, these indicators may fail to provide early warnings of an approaching tipping point in highly variable systems, where external perturbations may muffle the signal of critical slowing down (Dakos et al. 2014). An alternative, but not mutually exclusive approach, involves the development of spatial EWS, which also build on critical slowing down (Guttal and Jayaprakash 2008, Dakos et al. 2009, Kefi et al. 2014). Recent studies have shown that spatial correlation, variance, and skewness can successfully detect an approaching tipping point in continental shelf, grassland, and savannah ecosystems. (Litzow et al. 2008, 2013, Ratajczak et al. 2016, Eby et al. 2017).

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Generic indicators may not perform well in comparison to direct measure of loss of resilience, such as recovery time (van Belzen et al. 2017). The spatial counterpart of recovery time, recovery length, defined as the distance from a pulse perturbation at which a system recovers, has also been proposed as a more direct measure of loss of resilience in space (Dai et al. 2013). The possibility of evaluating resilience in ecosystems from spatial data is important, as it obviates the need for lengthy time series that may be difficult to obtain, especially from experiments (Dakos et al. 2014). Recovery length has been recently probed in a field experiment with macroalgal canopies, showing how the scale of recovery of the system from a perturbation increases before collapse (Rindi et al. 2017). With the exception of this study on recovery length, the experimental evaluation of classical spatial EWS (spatial autocorrelation, variance, and skewness) has lagged behind that of their temporal counterparts (Dakos et al. 2012, Cline et al. 2014, Kefi et al. 2014).

We aimed at filling this gap by experimentally testing the performance of classical spatial EWS in signaling the approach to a tipping point in a rocky mid-shore system in the Mediterranean with two well-characterized alternative states (Benedetti-Cecchi et al. 2015, Rindi et al. 2017): one dominated by the habitat-forming alga *Cystoseira amentacea* Bory var. *stricta* (Montagne) with associated assemblages of understory algae and invertebrates and the other dominated by algal turfs (an intricate mat of small-sized algae that develop on open rocks outside the canopy (Connell et al. 2014). To this end, we carried out a canopy-removal experiment where *C. amentacea* was trimmed to 0% (controls), 25%, 50%, 75%, and 100% (total removal) of initial cover. After 1 and 2 yr following this perturbation, we measured five spatial indicators (standard deviation, coefficient of variation, lag-1 Moran correlation, and spatial discrete Fourier transformation [DFT]) by visually estimating the percentage cover of understory species and related the loss of *C. amentacea* to variation in spatial statistics as indicators of an impending transition between states. We found that spatial variance, skewness, and low-frequency DFT successfully forewarned the approach of the system to the tipping point separating the canopy- from the turf-dominated state.

METHODS

Study system

The experiment was conducted along the rocky shore of Capraia Island (43.048° N, 9.828° E), between 0 and -0.3 m with respect to the mean-low-water-level. At these heights on the shore, the brown canopy-forming alga *Cystoseira amentacea* Bory var. *stricta* (Montagne) forms belts 1–3 m wide that extend alongshore for tens to hundreds of meters. *C. amentacea* is 30–40 cm high and provides habitat and shelter to a diversified understory assemblage of algae and sessile invertebrates (Benedetti-Cecchi et al. 2001, Bulleri et al. 2002; Appendix S1: Fig. S1). Repeated experiments have shown that *C. amentacea* plays a key role for the persistence of the understory assemblage, preventing the invasion of algal turfs—an intricate mat of small-sized algae (Connell et al. 2014)—that quickly outcompete the understory species in the absence of *C. amentacea* (Benedetti-Cecchi et al.

2001, Bulleri et al. 2002, Benedetti-Cecchi et al. 2012, Tamburello et al. 2013). Algal turfs predictably colonize open gaps within the canopy by spreading vegetatively and recruiting as propagules from the water column (Appendix S1: Fig. S1). Once established, algal turfs develop in a dense mat that prevents the settlement of *C. amentacea* (Benedetti-Cecchi and Cinelli 1992, Benedetti-Cecchi et al. 2001, Tamburello et al. 2013). Experiments and models are consistent with the view that beds of *C. amentacea* (the canopy and the associated understory species) and algal turfs are alternative states and the transition from a canopy- to a turf-dominated state follows nonlinear dynamics with a critical threshold at about 75% of *C. amentacea* loss. Beyond this tipping point, *C. amentacea* is no longer able to recover and invading algal turfs drive the understory assemblage to collapse (Benedetti-Cecchi et al. 2015, Rindi et al. 2017).

Experimental design

In July 2013, 16 experimental transects 1.8 m long were established parallel to the shore in areas with 100% cover of *C. amentacea*. Transects were at least 5 m apart to maintain spatial independence. Four replicate transects were randomly allocated to each of the following experimental conditions: 0% (controls), 25%, 50%, and 75% of canopy removal. To achieve the designated level of canopy removal, the canopy was thinned within six contiguous plots of 30 × 30 cm in each transect. Treatments were imposed by removing the fronds and holdfasts of *C. amentacea* haphazardly with hammer and chisel, until canopy cover matched the designated treatment level within each 30 × 30 cm plot. As a consequence of operating on distinct plots within transects, also the amount of canopy removed at the transect scale eventually matched the nominal treatment level. Since holdfasts were removed haphazardly, no predetermined spatial pattern of canopy removal was imposed. When, by accident, more canopy than necessary was removed from a plot, we compensated by clearing less canopy in the adjacent plot. For all transects, observed final values of canopy cover (averages across plots) deviated by <5% from the nominal treatment levels to which transects were assigned.

To better characterize the relationship between the percentage of canopy removed and spatial EWS, in parallel to the main experiment, we established four additional plots of 30 × 30 cm where fronds and holdfasts were completely removed (100% canopy removal treatment). The complete removal of *C. amentacea* was expected to induce the transition from the canopy- to the turf-dominated state, as repeatedly observed in previous studies in this system (Benedetti-Cecchi et al. 2001, Bulleri et al. 2002). As predicted by theory (Scheffer et al. 2015), we expected spatial EWS to show no further increase when the system crossed the tipping point, corresponding to about 75% of canopy loss (Rindi et al. 2017).

New recruits of *C. amentacea* were removed the following summer to maintain canopy cover as close as possible to nominal treatment levels. This was necessary mainly in the 25–50% canopy-removal treatments, whereas canopy recruitment was negligible in the 75–100% removal treatment where algal turfs became dominant (see *Results*).

Sampling

Experimental transects were sampled nondestructively after 1 and 2 yr from set up (July 2014, July 2015). The percentage cover of algal turfs was estimated in a grid of 5×30 small plots of 6×6 cm in each transect. We measured canopy cover in each of six contiguous plots of 30×30 cm and averages were taken to obtain a single value per transect. Percentage cover estimates were obtained with the aid of a plastic frame divided in 25 sub-quadrats; algal cover was scored from 0 (absence) to 4 (full cover) in each sub-quadrat and scores were summed to obtain a final value per plot.

We used 100 minus turf cover (hereafter, understory cover) as the state variable to evaluate how the space occupied by understory species and the holdfasts of *C. ammentacea* themselves changed along the canopy removal gradient (Benedetti-Cecchi et al. 2015). This metric was used as an indirect measure of understory cover in a previous study that focused on temporal indicators (Benedetti-Cecchi et al. 2015) and obviates the need to quantify the space occupied by the holdfasts of *C. ammentacea*, which is difficult to estimate in the presence of a full canopy.

Computation of spatial early warning indicators and statistical analysis

To evaluate if changes in the spatial pattern of understory cover may announce an approaching tipping point, we estimated the classical statistical indicators of impending regime shifts: standard deviation (SD), coefficient of variation (CV), lag-1 Moran correlation, and spatial discrete Fourier transformation (DFT) at low frequency and spatial skewness (Kefi et al. 2014) (Appendix S1).

Spatial indicators were calculated on detrended data; for each experimental transect, detrending was accomplished by fitting a two-dimensional-linear regression to understory cover values and then calculating the residuals from the fitted trend plane. Removing trends in spatial data sets before performing statistical analysis may prevent the occurrence of false positive signals, such as positive spatial correlation (Kefi et al. 2014).

Generalized additive mixed effect models (GAMMs) were used to evaluate the effect of canopy removal on statistical indicators. GAMMs are inferential statistical techniques that allow to flexibly determine the relationship between a response variable and a set of predictors included into the model and to deal with autocorrelated observations and complex variance-covariance structures (Wood 2006). *C. ammentacea* cover was modelled as a cubic regression spline in the fixed part of the model, while replicate transects were included in the random part of the model to account for the lack of temporal independence within observations. Time (the number of months separating the two sampling dates) was used as a covariate in the random part of the model to account for variation in both intercepts and slopes. GAMM were fitted using the gamm function of the package gmv, in R 3.3.2.

Model assumptions were assessed visually using plots of residuals vs. fitted values, box plots of residuals vs. experimental conditions (nominal level of canopy removed and time), and QQ plots of standardized residuals vs. Normal quantiles (Zuur et al. 2010).

RESULTS

Understory cover declined in response to canopy degradation and became nearly completely replaced by algal turfs in the 75% canopy removal treatment (Fig. 1; Appendix S1: Fig. S1). Plots where *C. ammentacea* was fully removed were heavily colonized by algal turfs in both sampling dates (Appendix S1: Fig. S2).

GAMM analysis revealed a significant increase of standard deviation ($F = 17.48$, $P < 0.001$) and coefficient of variation ($F = 184.10$, $P < 0.001$) along the gradient of canopy degradation (Appendix S1: Table S1). Both indicators dropped in the 100% canopy removed treatment (Fig. 1).

Spatial correlation showed a hump-shaped relationship with canopy removal ($F = 16.50$, $P < 0.001$; Fig. 2c; Appendix S1: Table S1). Unlike spatial correlation, spatial DFT at low frequencies linearly increased with increasing canopy degradation and markedly dropped in the 100% canopy removed treatment dominated by algal turfs ($F = 109.30$, $P < 0.001$; Fig. 1d; Appendix S1: Table S1). Sensitivity analysis showed that the observed trend in spatial DFT held for a wide range of frequency cut-offs (Appendix S1: Fig. S4).

Spatial skewness also increased as the system approached the critical threshold ($F = 34.34$, $P < 0.001$; Fig. 1d; Appendix S1: Table S1). However, in contrast to other indicators that decreased in the 100% canopy removal treatment, spatial skewness did not show any further change upon total canopy removal. GAMM analysis of raw data (undretrended) yielded similar results (Appendix S1: Table S2 and Fig. S3).

DISCUSSION

Recent work on early warning signals has mainly focused on the development of indicators as a tool for management and conservation purposes (Clements and Ozgul 2016, Pace et al. 2017). While there are many studies addressing temporal early warning signals, research into spatial indicators is far behind, with field experiments even more rare (Cline et al. 2014, Scheffer et al. 2015). Our experimental findings revealed that spatial variance (measured as standard deviation and coefficient of variation), skewness and low-frequency DFT forewarned the approach of the system to the tipping point separating the canopy- from the turf-dominated state and dropped, or did not show any further change in the 100% canopy removal treatment dominated by algal turfs. Our results are consistent with recent experimental studies on spatial EWS showing that direct (e.g., recovery length) and indirect signatures of ecosystem fragility (classical spatial EWS in our study) may successfully forewarn the approach to a critical threshold (Cline et al. 2014, Butitta et al. 2017, Rindi et al. 2017, van Belzen et al. 2017). The weight of evidence so far indicates that no single indicator performs well in all situations and that the integration of direct and indirect measures of ecosystem fragility provides the best strategy to improve our capacity to anticipate unwanted and possibly irreversible transitions in ecosystems.

In our study system, spatial effects may have originated from a nonlinear, threshold-like relation between turf colonization and canopy gap size. Only clearings larger than 200 cm^2 are effectively colonized by algal turfs and the size of clearings increases with the amount of canopy removed

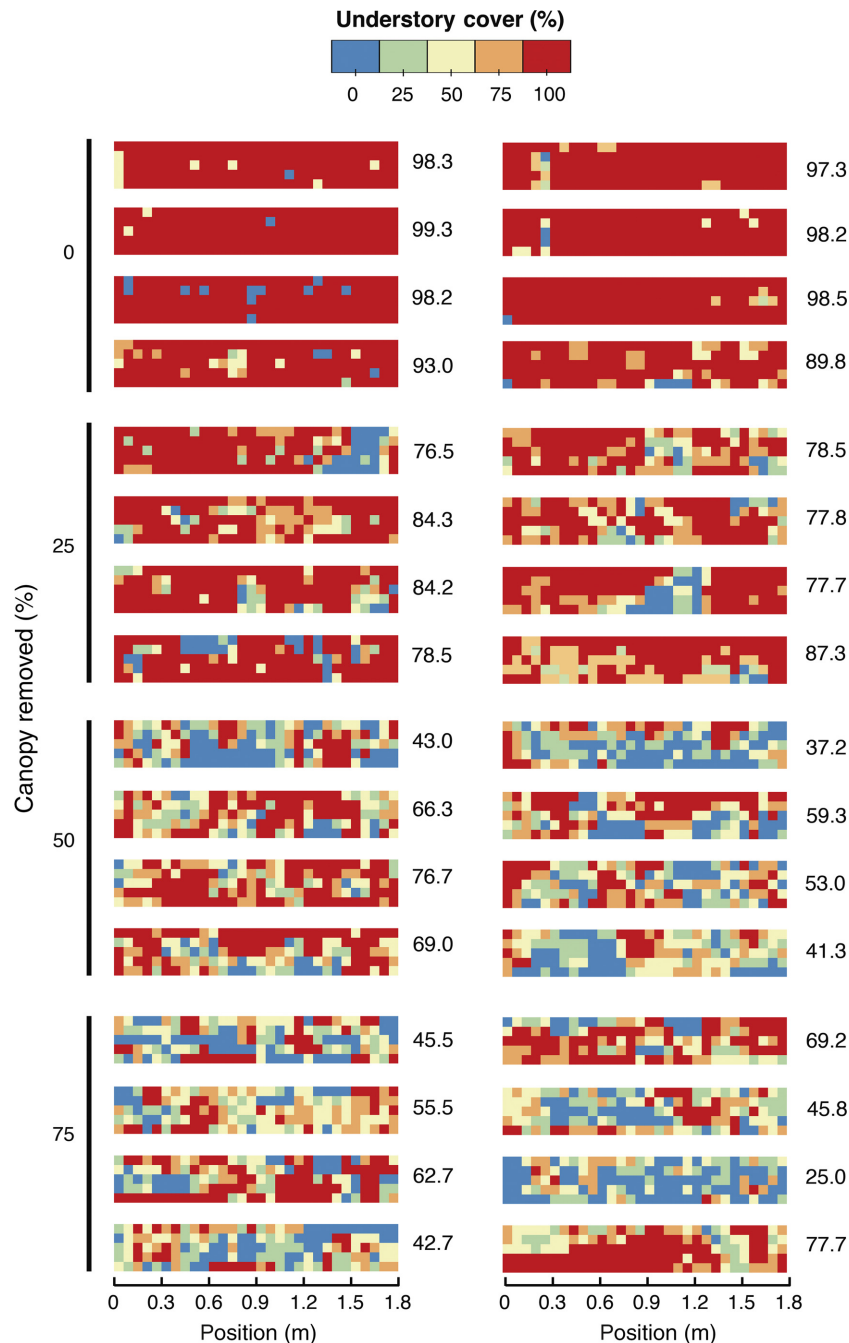


FIG. 1. Heat maps of understory cover as a function of canopy degradation. Experimental transects are shown for each canopy removal treatment (0%, 25%, 50%, and 75%). Mean values of understory cover are indicated for each experimental transect.

(Tamburello et al. 2013). For small clearings, the fronds of the surrounding plants can still form a closed canopy, suppressing the recruitment of algal turfs from the water column. Thus, as the percentage of canopy removed increased, in particular in 50% and 75% canopy removal treatments, larger clearings became more frequent leading to a greater and more heterogeneous colonization of algal turfs (Fig. 1). The emergence of patchiness in turf colonization produced the observed increase in spatial variance, skewness, and DFT at low frequency.

After a regime shift, spatial EWS are expected to show no further change or to undergo an opposite trend to that

occurring before the transition (Dakos et al. 2011). We observed this behavior in DFT at low frequency, standard deviation, and CV, which showed a pronounced drop after the transition to the turf-dominated state. The complete removal of *C. amentacea* (100% canopy removed treatment; Appendix S1: Fig S2) caused the invasion of algal turfs and the collapse of understory cover, with a consequent reduction in spatial heterogeneity. Unlike CV, which increased linearly with canopy degradation, standard deviation showed a nonlinear trend reaching a plateau at approximately 30% of canopy removal. The different response of the two

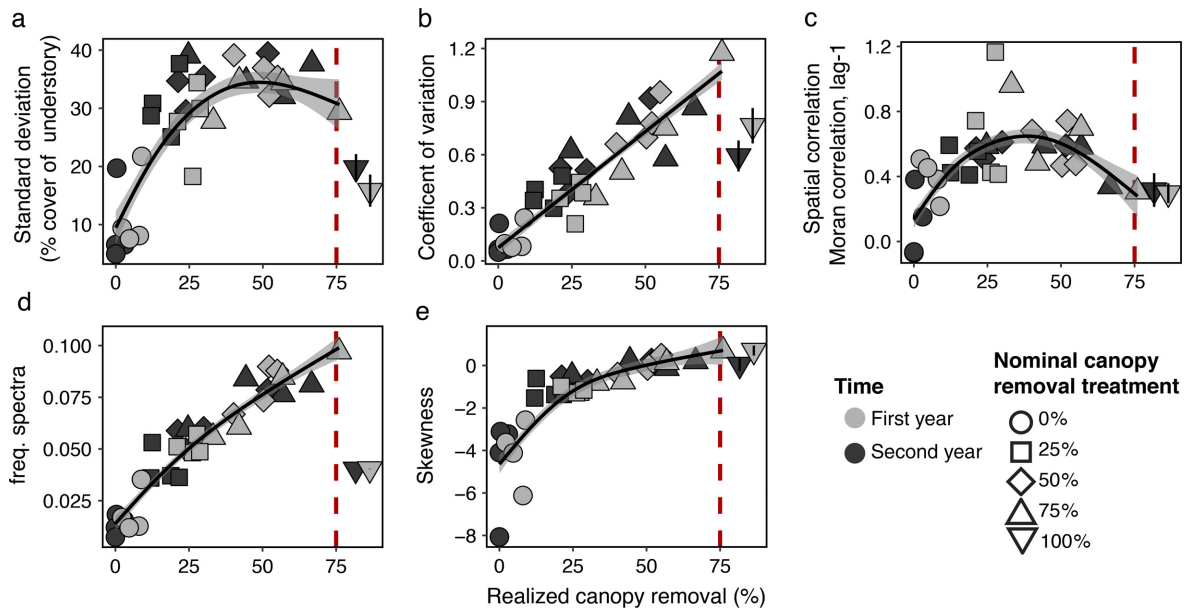


FIG. 2. Spatial early warning signals (EWS) of critical slowing down as a function of canopy degradation. (a) Standard deviation, (b) coefficient of variation, (c) Moran correlation (lag-1), (d) spatial low-frequency spectra, and (e) spatial skewness. Spatial EWS of 100% canopy removal treatment (down-facing triangles) were computed from four plots where *Cystoseira amentacea* was completely removed and are shown as mean \pm SE ($n = 4$). Trends are summarized as generalized additive mixed-effect models (GAMM) regression lines (in black) with standard errors (in light gray).

indicators can be explained in terms of the mean–variance relationship in understory cover. While the increase in standard deviation reflected larger spatial heterogeneity as the system approached the tipping point, the monotonic rise in CV was largely driven by the decline in mean understory cover with canopy loss. Spatial skewness also signaled the approaching tipping point. At low levels of canopy removal, spatial skewness was negative, since the distribution of understory cover was skewed toward large values. As canopy degradation increased, understory cover decreased resulting in a more symmetric distribution with skewness close to zero, reflecting the mix of patches of algal turf and understory cover.

In contrast to the other indicators, spatial correlation (Moran coefficient) showed a muffled response to canopy degradation. High level of diffusion among neighboring spatial units is fundamental to promote spatial correlation (Dakos et al. 2009). Changes in habitat morphology may strongly shape the diffusion among neighboring spatial units and in turn affect spatial correlation. In our experiment, canopy removal, by increasing the availability of suitable patches for algal turfs, should have increased the correlation among neighboring locations. However, the scatter distribution of the remaining clumps of *C. amentacea* in manipulated transects may have created barriers to the vegetative spread of algal turfs, a key process connecting nearby patches (Rindi et al. 2017). This explanation is in line with results of experimental and theoretical studies reporting that the local alteration of the connectivity pattern may strongly affect spatial correlation (Dakos et al. 2009, Cline et al. 2014). The boundary effect created by clumps of *C. amentacea* also explains why recovery length successfully forewarned the approach to the tipping point in this

experimental system (Rindi et al. 2017). Recovery length is expected to perform well in systems where perturbations create boundaries between regions of different quality, but may fail in other circumstances (Dai et al. 2013).

An important requirement to formally test EWS is that data should be stationary, implying that their statistical properties remain constant over the course of the study (Dakos et al. 2011, 2014). Unlike other studies on EWS, where the driving parameter changed over time and statistical metrics were computed using non-stationary data, here early warnings were obtained from a press perturbation experiment where levels of environmental deterioration (canopy removal) were maintained in time, as in laboratory studies of critical slowing down (Dai et al. 2012; Dai et al. 2013). This is important to ensure that the observed patterns in early warning indicators are produced by critical slowing down and not by temporal changes in the driving parameter (Dakos et al. 2014).

Competitive hierarchies among species of primary producers control the distribution of alternative habitats in both terrestrial and marine ecosystems (Didham et al. 2005, Bulteri et al. 2018). In pristine environments, macroalgal canopies exert a strong control on the abundance and distribution of turf-forming species that are usually sparse within intact canopy belts (Benedetti-Cecchi et al. 2001). Regulatory mechanisms include space pre-emption and modifications of environmental conditions, such as light penetration and sediment deposition, which promote the establishment of the understory assemblage and prevent the penetration of algal turfs (Connell 2005). Patches of algal turfs can develop in macroalgal stands only when the competitive dominant, here *C. amentacea*, is dislodged by waves or other disturbances (Tamburello et al. 2013).

Competitive interactions may become less important in driving the structure of these assemblages in less pristine environments. For example, eutrophication or high sediment deposition may cause a shift from macroalgal canopies to turf-forming algae as documented worldwide in urban areas (Benedetti-Cecchi et al. 2001, Steneck et al. 2003, Mangialajo et al. 2008, Filbee-Dexter and Scheibling 2014, Strain et al. 2014). Increasing anthropogenic disturbance and climate change are likely explanations for the decline of macroalgal forests, although their vulnerability to ocean warming may be overestimated (Reed et al. 2016) and overgrazing can also be important locally (Ling et al. 2009, Krumhansl et al. 2016). For example, sea urchins are widely recognized as the main driver of shifts from subtidal macroalgal forests to barren grounds dominated by encrusting coralline algae (Ling et al. 2014, Wernberg et al. 2016). In the Mediterranean, the herbivorous fish *Sarpa salpa* (L.) can have a strong impact on *C. amentacea*, affecting size, biomass and fertility of this furoid alga (Gianni et al. 2017). Although we cannot exclude the possibility that grazing may have occurred during our experiment, we have never observed fish or other grazers such as urchins and gastropods feeding on *C. amentacea* over 20 yr of field work at our study site. Thus, competition remains the most plausible interaction regulating the balance between macroalgal canopies and algal turfs on our pristine shores.

As their temporal counterparts, spatial indicators may also benefit from the implementation of large-scale sampling programs and automated data acquisition. Increasing use of remote-sensing vehicles and aerial drones will make high-resolution data on the distribution of benthic species increasingly available (Ling et al. 2016), paving the way for the wide application of spatial indicators to monitor regime shifts in the marine environment. The possibility to derive cost-effective spatial indicators from remote-sensing data will further strengthen the role of macroalgal canopy cover as an essential ocean variable to employ in global observing networks of the status and trends of coastal ecosystems (Miloslavich et al. 2018).

Experiments can establish causal links between environmental degradation and the approach to a critical threshold in complex systems, which is a crucial step to unambiguously assess the performance of early warning indicators of regime shifts. Recent laboratory experiments have provided direct empirical support to critical slowing down and its indicators, using a multiple perturbation approach that evaluates the proximity of the system to a tipping point along a spatial gradient of environmental degradation (Drake and Griffen 2010, Dai et al. 2013, 2015, Chen et al. 2014). Our study has extended this approach to field conditions, showing how advance warning of critical thresholds can be achieved in spatially noisy and variable environments. Further experimental work is required to assess the generality of our findings in other systems.

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and L. Benedetti-Cecchi performed the experiment. All authors contributed to interpreting the results and commented on the manuscript. The authors declare no competing financial interest.

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