

The seaweed *Caulerpa racemosa* on Mediterranean rocky reefs: from passenger to driver of ecological change

FABIO BULLERI,^{1,4} DAVID BALATA,² IACOPO BERTOCCI,^{1,3} LAURA TAMBURELLO,¹ AND LISANDRO BENEDETTI-CECCHI¹

¹Dipartimento di Biologia, Università di Pisa, CoNISMa, Via Derna 1, Pisa 56126 Italy

²School of Biological and Environmental Sciences, Science Building West, University College Dublin, Belfield, Dublin 4 Ireland

³CIIMAR, Centro Interdisciplinar de Investigação Marinha e Ambiental, Rua dos Bragas, 289, 4050-123, Porto, Portugal

Abstract. Disentangling the ecological effects of biological invasions from those of other human disturbances is crucial to understanding the mechanisms underlying ongoing biotic homogenization. We evaluated whether the exotic seaweed, *Caulerpa racemosa*, is the primary cause of degradation (i.e., responsible for the loss of canopy-formers and dominance by algal turfs) on Mediterranean rocky reefs, by experimentally removing the invader alone or the entire invaded assemblage. In addition, we assessed the effects of enhanced sedimentation on the survival and recovery of canopy-forming macroalgae at a relatively pristine location and how their loss affects the ability of *C. racemosa* to conquer space. *C. racemosa* did not invade dense canopy stands or influence their recovery in cleared plots. Competition with *C. racemosa* could not explain the rarity of canopy-forming species at degraded sites. Removing the assemblages invaded by *C. racemosa* and preventing reinvasion did not trigger the transition from algal turfs to canopies, but it enhanced the cover of morphologically complex erect macroalgae under some circumstances. Once established, *C. racemosa*, enhancing sediment accumulation, favors algal turfs over erect algal forms and enables them to monopolize space. Our results show that introduced species that rely on disturbance to establish can subsequently become the main drivers of ecological change.

Key words: algal turfs; alternative states; canopy-forming macroalgae; *Caulerpa racemosa*; habitat degradation; human disturbance; invasive species; Mediterranean; resilience; rocky reefs.

INTRODUCTION

Although the vast majority of introduced species does not succeed in naturalizing in a new region, a number of studies have reported dramatic effects of invaders on the biodiversity and functioning of recipient ecosystems (see Mack et al. 2000). Nonetheless, the general role of biological invasions in driving ecological change has been challenged, arguing that a positive correlation between exotic dominance and decline in native diversity does not provide conclusive evidence of a cause–effect relationship (Gurevitch and Padilla 2004, Didham et al. 2005). Introduced species are, in fact, often successful in becoming established or in stepping up to an invasive status within communities that have been altered by human perturbations (Hobbs and Huenneke 1992).

Assessing if an invader is the main cause of ecological change or an opportunistic species that takes advantage of degraded environmental conditions is key to understanding pathways and impacts of biological invasions. MacDougall and Turkington (2005) have proposed a straightforward rationale to determine whether interactive (e.g., competition, facilitation, predation, diseases/

parasites) or noninteractive processes (e.g., altered physical conditions or regimes of disturbance, habitat fragmentation, demographic constraints) between the invader and native species are the main determinants of altered community structure. Reasonably, whether an introduced species is a driver of change, its removal should result in the recovery of resident assemblages, in terms of species richness and/or relative abundances. In contrast, the effects of the removal of an invader on extant assemblages should be minimal if it is acting more as passenger of change. The two models should not necessarily be viewed as alternatives, but considered as the extremes of a continuum, generated by merging the effects of the invader and those of other human disturbances (Didham et al. 2005).

A limitation of experimental demonstrations of invasive species impacts arises from the impossibility of detecting historical drivers of change in irreversibly degraded systems (Didham et al. 2005). Dominance by invaders can trigger shifts to alternative ecosystem states (Mack and D'Antonio 1998, Suding et al. 2004). In this case, changes caused to native assemblages are likely to persist beyond the removal of the invader. Only a catastrophic event, removing the invader and a critical amount of extant biomass, might be able to promote recovery of native populations. Switches between alternative community states are often triggered when the intensity of disturbance crosses a threshold above

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⁴ E-mail: fbulleri@biologia.unipi.it

which ecological processes such as recruitment, competition, or predation are fundamentally altered (Petratits and Dudgeon 1999).

Therefore, a crucial requirement of experimental tests of the impacts of biological invasions is the removal of assemblages established under the dominance of the invader. In addition, invader removal from surfaces of varying size is important when components of extant assemblages reproduce vegetatively. In marine environments, recolonization of small cleared patches within macroalgal or sessile invertebrate stands mostly occurs through vegetative encroachment from the margins, while supply of propagules or larvae from the water column contributes to the recovery in larger patches (Connell and Keough 1985).

The role played by environmental drivers of change can be further investigated by reproducing experimentally stressful conditions in relatively pristine areas. The advantages of such an approach are twofold; it enables evaluating whether a putative environmental driver of change can actually push assemblages to become more similar to those occurring in degraded areas and whether these changes can, in turn, favor the establishment or spread of the invader.

Although the introduction of exotic seaweeds into shallow coastal habitats is a global phenomenon (Williams and Smith 2007, Thomsen et al. 2009), their effects on native assemblages have been assessed experimentally only for a small proportion of established species (~2%; Thomsen et al. 2009). Here, we report on an experimental study aimed to assess whether the invasive green macroalga, *Caulerpa racemosa* var. *cylindracea*, should be considered more as a passenger or a driver of change on shallow Mediterranean rocky reefs.

As shown elsewhere (Australia [Gorman and Connell 2009]; North Sea [Eriksson et al. 2002]), macroalgal assemblages on Mediterranean rocky reefs are generally dominated by turf- vs. canopy-forming species in urban and pristine areas, respectively (Benedetti-Cecchi et al. 2001, Mangialajo et al. 2008). Although *C. racemosa* can establish in both degraded and pristine environments (Piazzi et al. 2005b), its ability to become a dominant component of macroalgal assemblages seems greater in the former (Piazzi and Ceccherelli 2006, Bulleri et al. 2009; Appendix A). Previous experimental studies on degraded rocky reefs have provided robust evidence for little effects of *C. racemosa* on algal turfs (Piazzi et al. 2005a, Piazzi and Ceccherelli 2006). In contrast, negative effects of this invader on erect algal forms have been documented in some cases (Piazzi et al. 2005a), but not in others (Piazzi and Ceccherelli 2006), preventing a definitive assessment of its role in the switch between alternative habitats.

Predictions from the passenger model were tested by applying disturbance to canopy-forming algal stands on rocky reefs at a relatively pristine site. We predicted that enhanced rates of sedimentation, an important agent of

change in coastal environments (Airoldi 2003), would produce either a degradation of extant assemblages or prevent the recovery of canopy-forming species after disruption from other disturbances (e.g., sea storms), ultimately leading to the domination by algal turfs and *C. racemosa* (Bulleri and Benedetti-Cecchi 2008). In contrast, if *C. racemosa* is the main driver of change, we predicted that its removal would trigger a shift in the dominance from algal turfs to erect or canopy-forming species at degraded sites. If assemblages long colonized by *C. racemosa* represent a stable state, a recovery would be expected following the removal of the entire assemblage, but not that of the invader alone.

MATERIALS AND METHODS

Study sites

This study was done at three different locations along an exposed rocky coast south of Livorno, Italy (Northwest Mediterranean), between July 2006 and August 2008. Predictions from the passenger model were tested on rocky ledges dominated by lush canopy stands mainly formed by *Halopithys incurva* (Antignano, 43°29' N, 10°19' E; hereafter referred to as the pristine site). Stands of canopy-forming algae were not invaded by *C. racemosa* despite this seaweed achieving relatively large covers in nearby habitats (e.g., dead *Posidonia oceanica* rhizomes). Further details of assemblages at this study site are given in Appendix A.

Predictions from the driver model were tested at two sites (hereafter referred to as degraded sites), haphazardly selected 800 m apart, along a sandstone cliff (Calafuria, 43°30' N, 10°20' E) subjected to heavy inputs of fine terrigenous sediments (see Plate 1). Macroalgal assemblages at these sites, characterized by the dominance of turf-forming algae (Airoldi et al. 1996, Bulleri and Benedetti-Cecchi 2006) and by the sparse presence of canopy-forming species, such as *Halopithys incurva* and *Sphaerococcus coronopifolius*, have been invaded by *C. racemosa* since 1996 (Piazzi et al. 2007). Here, this species exhibits large seasonal fluctuations, almost disappearing in winter and peaking in abundance in late summer–early fall (Appendix A).

Experiment 1

Juvenile stages of macroalgae are generally more sensible to sedimentation than adults (Irving et al. 2009). Enhanced sedimentation, by hindering the recovery of canopies after natural events of disturbance (i.e., storms), could promote the dominance of stress-tolerant species such as those that compose algal turfs (Gorman and Connell 2009). Mature canopy stands (~100% in cover and not invaded by *C. racemosa*) and assemblages developing in canopy-cleared plots were therefore exposed to different sedimentation regimes. In September 2006, twenty 20 × 20 cm plots, 2 m apart, were randomly selected within canopy stands, at ~6 m depth. Five plots were randomly assigned to each of the following four treatments: (1) canopy-forming species



PLATE 1. Degraded shallow rocky reefs at Calafuria, Italy. Benthic assemblages are dominated by algal turfs and colonized by (inset) the invasive green macroalga *Caulerpa racemosa*. Photo credits: reef, D. Balata; macroalga, F. Bulleri.

left untouched, natural levels of sedimentation; (2) canopy-forming species left untouched, enhanced levels of sedimentation; (3) removal of canopy-forming species, natural levels of sedimentation; and (4) removal of canopy-forming species, enhanced levels of sedimentation. Where necessary, levels of sedimentation were increased to match those recorded at degraded sites, by adding sediments every fortnight (Appendix B for details).

Percent cover of macroalgae and sessile invertebrates was visually estimated in August 2008, by means of a 20×20 cm frame, subdivided in 25 sub-quadrats. A score from 0 to 4% was given to each taxon in each sub-quadrat, and the percent cover was obtained by summing over the entire set of sub-quadrats. Plants and animals were identified to the species level, except for filamentous and encrusting coralline algae, which were treated as morphological groups. A PERMANOVA (Anderson 2001) including the factors canopy (present vs. removed) and sedimentation (natural vs. enhanced) was used to analyze the response of the whole assemblage to experimental conditions. Bray-Curtis measures of dissimilarities on untransformed data were used to calculate a matrix of distances between pairs of

samples. SIMPER analysis was used to identify taxa contributing most to multivariate differences between experimental assemblages. The percent cover of *C. racemosa* was analyzed with ANOVA using the same design described for PERMANOVA.

Canopy-forming algae were removed from 10 extra quadrats that were maintained free of *C. racemosa*, either under natural or enhanced levels of sedimentation; the comparison between these plots and those that had been treated similarly but that could be invaded by *C. racemosa* (i.e., treatments 3–4) provides an estimate of the effects of the invader on the recovery of algal canopies under different regimes of sedimentation. Variation in the cover of algal canopies across treatments was analyzed with a two-way ANOVA including sedimentation (natural vs. enhanced) and *C. racemosa* (present vs. removed) as fixed, crossed factors.

Experiment 2

In July 2006, 15 20×20 cm quadrats (small plots) and 15 40×40 cm quadrats (large plots) were randomly selected at each of the two degraded sites, at ~ 7 m depth. Small cleared plots are generally recolonized through vegetative encroachment from the margins

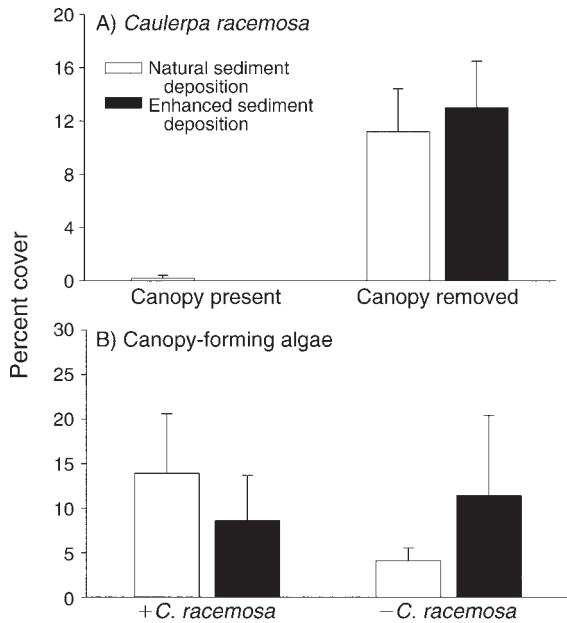


FIG. 1. Pristine site (Antignano): (A) percent cover (mean \pm SE) of the exotic seaweed *Caulerpa racemosa* in plots assigned to canopy (present vs. removed) and sedimentation (natural vs. enhanced) treatment combinations; (B) percent cover (mean \pm SE) of canopy-forming macroalgae in plots that had been cleared within mature stands and assigned to *C. racemosa* (present [+] vs. removed [-]) and sedimentation (natural vs. enhanced) treatment combinations; $n = 5$.

(Bulleri and Benedetti-Cecchi 2006); their size was therefore quadrupled in order to increase the contribution of propagules and spores recruiting from the water column to the process of recovery. Small and large plots were 2–3 m apart and interspersed; five plots for each size were randomly assigned to the following treatments: (1) removal of *C. racemosa* (–*C. racemosa*), (2) removal of the entire assemblage (total removal), and (3) left untouched (control). Removal of the extant assemblages was carried out by means of a paint-scraper and did not include encrusting algal forms, as this type of treatment would not mimic biomass removal due to natural disturbance (i.e., storms) realistically. Where necessary (–*C. racemosa* or total removal plots), *C. racemosa* was removed manually using tweezers, and visits every two weeks were sufficient to prevent reinvasion from the margins of plots (Appendix A). Care was taken not to damage extant assemblages, and generation of artifacts was therefore unlikely (Piazzi and Ceccherelli 2006, Bulleri et al. 2009). Percent cover of macroalgae and sessile invertebrates was estimated visually after two years (July 2008) because previous studies have shown that such a period of time is sufficient to allow full recovery after disturbance (Bulleri and Benedetti-Cecchi 2006).

Macroalgae were grouped into morphological groups for analysis as in Arenas et al. (2006). Their response to manipulative conditions, as well as that of taxa richness

and evenness (calculated as the reciprocal of Simpson's index/number of species) of assemblages, was assessed by means of ANOVAs including the factors site (two levels, random), treatment (three levels, fixed and crossed), and size (two levels, fixed and crossed). Cochran's *C* test was used before each univariate analysis to check for homogeneity of variance and data were transformed when necessary. SNK (Student-Newman-Keuls) tests were used for a posteriori comparisons of means.

RESULTS

Experiment 1

The removal of algal canopies had dramatic effects on understory assemblages, regardless of the sedimentation regime (PERMANOVA, canopy MS = 23874.00; $F_{1,15} = 15.62$; $P < 0.001$; Appendix C). Removing the canopy caused a transition from understory assemblages dominated by *Peyssonnelia* spp., encrusting corallines, *Corallina elongata*, and the foliose *Rhodymenia* spp. to turf-forming assemblages dominated by filamentous forms (SIMPER analysis; Appendix C).

The cover of *C. racemosa* was greatly enhanced by the removal of the canopy (analysis on untransformed data, *C* test: $P > 0.05$; canopy MS = 720.00, residual MS = 28.22, $F_{1,16} = 25.51$, $P < 0.01$; Fig. 1A), while there was no influence of enhanced deposition of sediments, either as a main effect (sediment MS = 3.20, $F_{1,16} = 0.11$, $P > 0.05$), or as an interaction with the factor Canopy (canopy \times sediment MS = 5.00, $F_{1,16} = 0.18$, $P > 0.05$).

The cover of mature canopy-forming macroalgae did not differ between plots in which sedimentation was enhanced ($89.6\% \pm 6.65\%$, mean \pm SE) or left at natural levels ($97.4\% \pm 2.6\%$). The recovery of canopy-forming species in quadrats cleared within intact stands was influenced neither by the removal of *C. racemosa* nor by enhanced levels of sediment deposition (Fig. 1B; analysis on untransformed data, *C* test, $P > 0.05$; *C. racemosa* MS = 61.25, $F_{1,16} = 0.32$, $P > 0.05$; sediment MS = 5.00, $F_{1,16} = 0.03$, $P > 0.05$; *C. racemosa* \times sediment MS = 198.45, $F_{1,16} = 1.03$, $P > 0.05$; residual MS = 192.36).

Experiment 2

After two years from the start of the experiment, the effects of our manipulation on canopy-forming algae varied according to the size of the plot. Removing *C. racemosa* from small plots had weak effects on these algal forms, while removal of the entire assemblage caused a significant reduction in canopy cover (Table 1, Fig. 2A and SNK tests). Removing *C. racemosa* from large plots caused a decrease in the cover of canopy-forming algae, but to a smaller extent in respect to the removal of the entire assemblage (Fig. 2A and SNK tests).

Erect algae, dominated by *Stypocaulon scoparium* that contributed to an average of $93.73\% \pm 2.14\%$ of the total cover of these forms ($n = 39$ plots), exhibited a positive response to manipulative conditions, although

TABLE 1. ANOVAs on the effects of site, plot size, and treatment (control, removal of exotic seaweed *Caulerpa racemosa*, total removal) on the cover of morphological algal groups in northwest Mediterranean rocky reefs.

Source of variability	df	Canopy-forming		Erect algae		Algal turf		Encrusting algae	
		MS	F	MS	F	MS	F	MS	F
Site = St	1	15.73	15.01***	9318.83	36.06***	4.40	0.02	0.89	1.17
Size = Sz	1	6.87	4.29	500.26	768.40*	140.30	0.32	0.01	0.00
Treatment = Tr	2	5.09	3.70	4567.91	4.15	470.55	1.45	2.66	1.29
St × Sz	1	1.60	1.53	0.65	0.00	440.10	1.51	0.89	1.16
St × Tr	2	1.38	1.31	1101.87	4.26*	325.53	1.11	2.06	2.71
Sz × Tr	2	0.78	82.56*	2460.90	0.95	4.11	0.02	0.17	0.13
St × Sz × Tr	2	0.01	0.01	2582.73	9.99***	185.84	0.64	1.24	1.64
Residual	48	1.05		258.53		292.17		0.76	

Notes: Cochran's test showed significance at $P < 0.01$ for algal turf, but no significance for the other algal groups. Data for canopy-forming and encrusting algal groups were $\ln(x + 1)$ -transformed.

* $P < 0.05$; *** $P < 0.001$.

with some variation between sites and according to the size of plots (Fig. 2B, Table 1). At Site 1, the removal of either *C. racemosa* or the entire assemblage from small plots equally resulted in a greater cover of erect algae. In contrast, only removing the entire assemblage enhanced their cover in large plots (SNK tests). Although the SNK test did not show significant differences among treatments at Site 2, the cover of erect algae was fostered by the removal of *C. racemosa* and, to a greater extent, by that of the entire assemblage (Fig. 2B). Turf-forming and encrusting algae (Table 1, Fig. 2C, D), as well as species richness and evenness (Appendix D; Fig. 2E, F), were not affected by our manipulation. The abundance of invertebrates was too small to be analyzed.

DISCUSSION

Our results show that algal canopies can provide a barrier against the invasion of *C. racemosa*. This seaweed rapidly colonized plots cleared within intact stands of the canopy-forming species *H. incurva*, indicating that its establishment relies on the disruption of native assemblages by other types of disturbance. Failure of *C. racemosa* to establish within intact canopy stands is unlikely to be due to light limitation, as this species can thrive at great depths (up to 70 m; Piazzini et al. 2005b). Rather, the sweeping of the substratum by algal fronds could prevent the reattachment of fragments of the seaweed (Irving and Connell 2006).

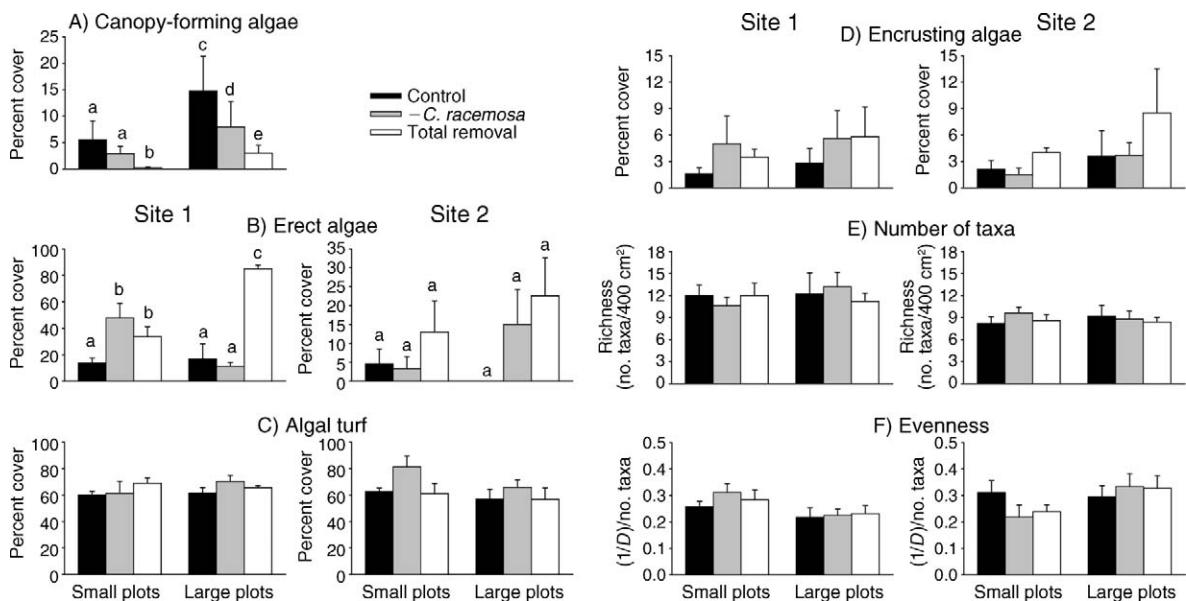


FIG. 2. Degraded study sites (Calafuria): percent cover of morphological groups of algae, number of taxa, and evenness (calculated as the reciprocal of Simpson's index D , divided by the number of taxa) in small and large plots under different treatments: removal of *C. racemosa*, removal of the entire algal assemblage, or left untouched (control). All values are given as mean + SE. In order to enhance interpretation of the analysis, reported values of cover are pooled between study sites for canopy-forming algae, but separately for each site for the other morphological groups ($n = 5$). Letters above columns illustrate the outcome of SNK (Student-Newman-Keuls) tests; different letters indicate significant differences at $P < 0.05$. Note the different y-axis scale between sites for (B) erect algae.

Despite the enhanced cover of turf-forming species and regardless of the presence/absence of *C. racemosa*, canopies recovered, to some extent, in plots experimentally cleared within intact stands. In contrast, neither the removal of *C. racemosa* nor that of algal turfs promoted the recovery of canopies at degraded sites. Noninteractive processes, such as limited dispersal or demographic constraints associated with rarity (i.e., low propagule supply) would therefore prevent not only the expansion of the *H. incurva* population, but also its self-perpetuation at our degraded sites. Seed limitation has been found to hinder the recovery of natives in invaded terrestrial systems (grasslands, Seabloom et al. 2003; oak savanna, MacDougall and Turkington 2005, 2006).

Restriction to optimal habitat can enable declining populations to escape competitive or adverse physical conditions, thus preventing extinction despite limited reproductive potential and substantial degradation and invasion of habitat (MacDougall and Turkington 2006). Here, the removal of *C. racemosa* had negative effects on the cover of *H. incurva*. The seaweed could indirectly facilitate the persistence of adult plants of *H. incurva* by constraining the abundance of other components of the algal assemblage (i.e., erect algae) that, under current environmental conditions, are stronger competitors. Thus, invasions could prevent or delay the collapse of native populations for which competitive ability has been dramatically reduced by habitat degradation. However, maximum values of cover smaller than 3% after two years since plot clearance indicate that this population of *H. incurva* might be at risk of local extinction at degraded sites.

The hypothesis that failed recovery of canopy-formers was due to demographic constraints is supported by the tolerance of both mature and juvenile canopy-forming plants to our experimental enhancement of sedimentation. Neither enhanced sedimentation nor invasion by *C. racemosa*, either in isolation or in combination, is, therefore, able to explain the decline of *H. incurva* at degraded sites. Historical acute events of disturbance, not reproduced by our manipulation (i.e., soil erosion after an extensive deforestation by fire in summer 1990), may have promoted the decline of canopies at our study sites (Airoidi et al. 1996), setting the scenario (i.e., dominance by algal turfs) for the successful establishment of *C. racemosa*. Regardless of the specific cause(s), the relevant question to ask here is if such a shift in dominance would have been temporary without the invader.

Following the removal of *C. racemosa*, there was an increase in the cover of erect algae (mostly *Stypocaulon scoparium*) in small plots at Site 1 and, although not indicated as significant by the analysis, also in large plots at Site 2. These results are consistent with those of previous studies indicating variable effects of *C. racemosa* on these algal forms (Piazzi et al. 2005a, Piazzi and Ceccherelli 2006). The increase in cover of erect algae following the removal of *C. racemosa* was not associated

with a decline in algal turfs (see Fig. 1c). Thus, it was likely generated by qualitative changes in the environment provided by algal turfs. Sediments are an important component of algal turfs, and Piazzi et al. (2007) have demonstrated that *C. racemosa*, by entrapping particles through the complex network of stolons, can result in an up to sevenfold increase in accumulated sediments. Thus, the effects of *C. racemosa* on components of native assemblages on rocky reefs could take place through the alteration of the physical conditions mediated by algal turfs.

Alteration of disturbance regimes by invasive species can maintain ecosystems in alternative stable states (Mack and D'Antonio 1998). For instance, positive feedbacks through the alteration of nutrient dynamics have been identified as important mechanisms enhancing the persistence of exotic terrestrial plants (Allison and Vitousek 2004, Levine et al. 2006). Here, *C. racemosa*, altering the depositional environment, would favor the dominance by stress-tolerant filamentous forms that compose algal turfs (Airoidi 2003, Balata et al. 2008); these, in turn, can facilitate the persistence and spread of *C. racemosa* by providing safe anchoring to its prostrate stolons (Bulleri and Benedetti-Cecchi 2008).

The hypothesis of turf-mediated effects of *C. racemosa* is supported by the marked increase in the cover of erect algae following the removal of the assemblages that had been long colonized by *C. racemosa* and preventing its reinvasion. Previous work at these sites has shown that algal turfs can readily reoccupy space after disturbance, if reinvasion of cleared areas by *C. racemosa* is not controlled (Bulleri and Benedetti-Cecchi 2006). Mean cover values of erect algae >80%, recorded in large total removal plots at Site 1, suggest that, upon the elimination of *C. racemosa* and of related historical legacies, local environmental conditions are not too harsh to prevent the proliferation of erect algal forms.

Likely, the removal of *C. racemosa* alone has limited effects on the depositional environment because accumulated sediments remain entrapped within the tightly packed turf. Competition between *C. racemosa* and erect algae might be thus more intense during recolonization of free space, before environmental conditions are altered to such an extent that the presence of the seaweed is no longer necessary for algal turfs to achieve dominance.

Reinstating the historical regime of disturbance does not guarantee reverting the changes faced by the biotic compartment, due to ecological resilience of the extant community or to demographic constraints of displaced populations (Suding et al. 2004). Under current environmental conditions, the presence of *C. racemosa* enables algal turfs to control the cover of erect algal forms on the reefs we investigated, likely by limiting their recruitment. The dominance by erect forms may represent an alternative to the dichotomy between pristine canopy-dominated and degraded turf-dominated assemblages (Gorman and Connell 2009) or an

intermediate stage of a succession culminating, on a longer term, with the dominance of canopy-formers. Either way, *C. racemosa* can prevent it, ensuring monopolization of space by algal turfs and thus acting as a stabilizer of previous ecological changes.

Our study shows that one single invader acting as a passenger of change (*sensu* MacDougall and Turkington 2005) can subsequently prevent the recovery of native populations by facilitating the persistence of alternative assemblages dominated by stress-tolerant species, likely through the modification of the physical environment. Invasive species have, therefore, the potential to transform transient ecological effects, generated by a temporary deviation from the original regime of disturbance, into permanent changes. In other words, they can erode the resilience of natural communities to acute events of disturbance. These effects can persist beyond the disappearance of the invader. Hence, the removal of the invader alone, a common procedure for assessing the impact of introduced species on native communities, does not guarantee the appreciation of historical legacies of invasion, potentially leading to erroneous identification of primary forces of ecological change. The removal of extant assemblages, the structure of which can be shaped by the dominance of the invader, can be crucial to generate a detectable response of native components. In addition, the extent of the surface over which the removal of the invader or that of the extant assemblage is performed is likely to influence the magnitude of such a response, especially when invaded assemblages are characterized by species that reproduce vegetatively.

The experimental reproduction of degraded environmental conditions in relatively pristine habitats, although generally feasible at scales smaller than those at which they actually operate, can compensate for the inability of experiments to identify historical drivers of ecological change in situations where the system has been irreversibly altered. Unfortunately, that was not the case in our study, stressing the key role of extreme or compounded events of disturbance in structuring natural communities (Thibault and Brown 2008).

Finally, positive effects of removing *C. racemosa* on erect algae emerged despite its relatively low cover and the pseudo-perennial habit (Appendix A), characteristics that have been elsewhere invoked to explain limited effects of invaders on natives (e.g., *Sargassum muticum*; Sánchez and Fernández 2005). In terrestrial environments, manipulative studies have been generally performed in heavily invaded plant communities where covers of invasive species ranged from 60% to 95%, leading to the belief that invasive species need to attain high cover in order to influence community structure (Truscott et al. 2008). This study suggests, in contrast, that exotic seaweeds can alter the structure of native communities even when they are found at relatively low abundances and when characterized by a seasonal resting phase.

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APPENDIX A

Description of macroalgal assemblages at study sites (*Ecological Archives* E091-154-A1).

APPENDIX B

Experimental protocol for enhancing the deposition of sediments at the pristine site (*Ecological Archives* E091-154-A2).

APPENDIX C

Multivariate analyses (PERMANOVA, nMDS, and SIMPER) on the effects of canopy removal and sedimentation on understory assemblages (*Ecological Archives* E091-154-A3).

APPENDIX D

Analysis of the effects of experimental treatments on species richness and evenness at degraded sites (*Ecological Archives* E091-154-A4).