ECOLOGY

Active restoration of a long-lived octocoral drives rapid functional recovery in a temperate reef

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Whether restoration actions achieve full ecological recovery is still debated. This is particularly controversial in the marine realm, where the success of restoration is mostly evaluated in terms of the short-term survival of transplanted organisms. In view of this, we combined population and trait-based approaches to explore the long-term effectiveness of active restoration of a key Mediterranean octocoral. For this purpose, an assemblage with restored *Corallium rubrum* colonies was monitored over 10 years and compared with a nearby reference site. Our results revealed growth of the transplanted colonies followed by a change in the functional structure (i.e., dominance and diversity of traits) of the restored assemblage. This change was related not only to the development of the coral but also to the arrival and/or increase of species with different traits. Overall, our findings provide an example of how active restoration of long-lived octocorals can be an effective tool for recovering high-diverse coralligenous assemblages at decadal timescales.

INTRODUCTION

In recent decades, restoration initiatives have been promoted globally to halt and reverse the degradation of ecosystems (*1*, *2*). Considering that we have entered the United Nation's (2021–2030) "Decade on Ecosystem Restoration", a further surge of these initiatives is expected. Although there is an urgent demand for restoration, practitioners do not always have direct evidence-based guidelines (*3*), as many initiatives lack success criteria and even fewer perform long-term monitoring to assess success (*4*–*6*). In addition, although some studies indicate that restoration actions increase biodiversity and ecosystem services, it is not guaranteed that they promote full recovery of the characteristics of reference systems [reviewed in (*7*)].

Bridging the gap between community and restoration ecology might be key to overcoming these drawbacks. For example, a functional perspective can help assess whether restoration actions are facilitating the recovery of ecosystem functions and services (*8*). One possible approach is to use trait-based functional diversity (*9*–*11*), as species functional traits can be designed considering their contribution to specific ecological functions (*12*, *13*) and therefore can be used to implement functional restoration goals (*14*). Moreover, an inherent result of a functional perspective is that not all species are functionally equal, as they play different roles in an ecosystem. When assessing the effect a species can have on its surroundings, ecological knowledge has advanced to the point where several kinds of ecologically important species can now be defined (*15*) (e.g., "keystone species," "foundation species," etc.). Linking both concepts suggests that restoration initiatives should first focus on dominant species with relevant functions for the whole ecosystem, as they will increase the benefits of restorative actions (*8*).

A functional perspective is urgently needed in marine restoration science, which is in an earlier phase than terrestrial and freshwater systems (*16*), where trait-based analyses are already frequently used (*17*). In marine systems, most efforts are focused on rebuilding habitat-forming species, those that shape coral reefs, seagrasses, mangroves, saltmarshes, and oyster reefs, which sustain key ecosystem services but are threatened globally (*18*, *19*). While a correct selection of important functional groups is performed, the success of these initiatives is mostly based on the short-term survival of the transplanted habitat-forming species [(*16*), but see (*20*–*22*) for some exceptions]. Unfortunately, these short-term assessments are not sufficient when target species need recovery times that are longer than the monitored time, which tends to be the case in marine restoration because of the long-lived nature of most targeted species (*23*). If used by themselves, then these assessments are also insufficient from an ecological perspective because they do not capture changes that may occur at the community or ecosystem levels, such as the potential recovery of functions and services (*24*, *25*). Consequently, there has been a recent increase in marine studies that test for restoration success while accounting for ecological processes, including direct measures such as carbon sequestration and recovery of marine livestock (*26*–*28*), as well as more indirect measures such as soundscape analysis of a restored coral reef (*29*). Moreover, some coastal restoration actions are starting to implement trait-based approaches in their targeted communities [e.g., macroalgae forests (*30*) and fish communities (*31*, *32*)], further reinforcing their potential in marine restoration.

In trait-based ecology, the functional structure of a community is usually described through two main components: dominance and diversity of functional traits (*11*, *33*). These two components have been linked to two nonexclusive hypotheses that attempt to explain how community composition influences ecosystem processes: the mass-ratio hypothesis and the niche-complementary hypothesis (*34*–*36*). On the one hand, the most dominant traits should be tracked because it is expected that the most dominant species and traits will play a key role in determining the ecological processes occurring within that system. On the other hand, tracking the diversity of functional traits provides information on how different species and their traits fulfill their niche roles. Quantifying niche differentiation indicates how complete the utilization of resources is and therefore also determines the ecological processes that can take

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place. Thus, to assess whether a restoration initiative promotes functional recovery, at least these two components should be considered.

With these concerns in mind, we revisited a red coral *Corallium rubrum* (Linnaeus, 1758) restoration (*23*) via trait-based approaches to assess whether it has facilitated the recovery of ecological functions in a Mediterranean coralligenous habitat. These habitats are biogenic temperate reefs situated in dim light conditions and are composed of a variety of calcareous algae and invertebrates (such as cnidaria, porifera, bryozoan, and tunicate), which act as biodiversity "hot spots" (*37*) and support a large variety of ecosystem services (*38*) (e.g., food provision, natural medicine availability, or recreationally attractive submerged seascapes). The structural complexity of these habitats can be greatly improved by the formation of red coral monospecific "animal forests" (*39*). In coralligenous reefs, octocorals that form these forests play an important role in determining the configuration of their surrounding assemblages (*40*, *41*). As a result, their presence supports highly diverse associated fauna that sustain these ecosystem services (*38*).

Because of this key role, in 2011, approximately 300 colonies of *C. rubrum* were actively restored to provide a second chance for illegally harvested red coral. The colonies were provided by Catalan authorities after confiscation and were transplanted in the Montgrí, Medes Islands, and Baix Ter Natural Park in the northwestern Mediterranean Sea (42°02′51″N; 3°13′22″E). This location was selected for its protection status, convenient access, and environmental conditions that support red coral at shallow depths (<15 m). Specifically, the Medes Islands are exposed to high hydrographic variability (e.g., intrusion of open-sea waters, a stormy rainfall regime, and seasonal wind characterizations) that favors large fluctuations of nutrient concentrations (*42*). Combined with the continental water inputs of the nearby Ter River, these conditions allow for the development of red coral populations at shallow depths (*43*). Given the need for rapid actuation and the logistic constraints of reinstalling 300 colonies, all transplants were installed at a single site. The transplantation was performed in a rocky wall 8-m wide and between 15- and 17-m deep, which presented some sparse red coral colonies (*23*). The lack of a well-developed population within this site is driven by the poaching activity documented in the past in this protected area (*44*). This wall was also chosen because of its proximity to a *C. rubrum*–dominated assemblage, approximately 20 m apart, that had similar characteristics (i.e., both are lightly inclined, calcareous overhangs facing southeast, of comparable extent, and situated at the same depths) and could act as a reference (hereafter referred to as such). Considering that the sites are adjacent and share the same geomorphic features, they should be exposed to similar environmental conditions (such as light conditions or water temperature), thus limiting the effect of any potential confounding variable that could be hidden under a pseudoreplicated design. Although multiple interspersed spatially nested sites would have been ideal, our study still provides a unique opportunity to evaluate the success of a relevant restoration action in terms of the number of transplanted colonies.

From a demographic standpoint, the restoration was deemed successful after 4 years, as the transplants attained natural survival and reproductive rates (*23*), aligning with other initiatives involving Mediterranean octocorals (*45*, *46*). A decade after transplantation, we have assessed the long-term success of this restoration by exploring whether the restored assemblage is recovering the functional structure of *C. rubrum*–dominated communities. We evaluated restoration success by measuring progress over time in achieving structural and functional similarity to the reference assemblage. During the last 10 years, the restored population has flourished from a demographic perspective, while its community composition and functional structure have changed, approaching the reference site in terms of trait range and trait divergence [measured as functional richness and functional divergence (*11*)] and matched it in terms of trait dominance [measured as functional identity (*11*)]. Both the red coral's demographic traits and its community functional traits illustrate how restoring a key habitat-forming species can drive and potentially speed up the recovery of functions in highly diverse communities, such as Mediterranean coralligenous assemblages.

RESULTS AND DISCUSSION

Demographic traits of the reference versus restored *C. rubrum* populations

We found that all the demographic traits of the restored colonies demonstrate a maturing of the population. This maturation is especially apparent in terms of colony size, as its mean maximum height has a significantly positive trend ($P < 0.001$; see table S1), growing from 26.4 ± 0.95 to 38.0 ± 3.73 mm (mean ± SE, Fig. 1C), which, in terms of annual growth rates (1.16 mm/year), falls within the expected range for natural red coral populations [1.78 ± 0.7 mm/year; (*47*)]. As a result of this growth, we detected a significant increase in biomass throughout the study period ($P < 0.05$; table S1), from 132.32 ± 11.13 to 206.37 ± 37.47 g/m^2 (mean ± SE; Fig. 1D). In contrast, density had a negative trend ($P < 0.05$; table S1), with a total decrease from 6.05 ± 0.53 to 4.24 ± 0.62 colonies/400 cm^2 (mean ± SE; Fig. 1A). While initial colony loss could be related to the restoration itself, the continued decrease in density should not be regarded as negative, as it mimics the self-thinning growth previously described for undisturbed Mediterranean octocoral populations, including red coral populations (*48*, *49*). Last, restored population recruitment has increased throughout the years, from 0 to 0.44 ± 0.15 recruits/400 cm^2 (mean ± SE, Fig. 1B), achieving and maintaining natural rates (*47*, *50*). This result supports the future viability of the restored population and aligns with previous results that explored its reproductive potential (*23*). Together, the restored red coral seems to have continued developing successfully at a natural rate.

In contrast to the restored site, we found a stable reference population with no significant trend in any of its demographic traits ($P > 0.05$; see table S1). The observed values could either indicate that the population has reached its local climax or that the occurrence of natural or human-induced disturbances is preventing further growth of the colonies. Regardless of the underlying cause, the stability of the reference population combined with the development of the restored *C. rubrum* colonies resulted in the restored population surpassing the reference population in terms of biomass and size. Comparatively, in 2021, the reference population presented greater density and recruitment (7.41 ± 1.21 colonies and 1.45 ± 0.35 recruits/400 cm^2, respectively, mean ± SE; Fig. 1, A and B) and a lower mean maximum height and biomass (20.5 ± 1.48 mm and 145.52 ± 31.23 g/m^2, respectively, mean ± SE; Fig. 1, C and D). The restored population initially had a greater mean height, which enabled it to overtake the reference population in terms of biomass. This result highlights the value of actively restoring adult colonies, as it allows the bypass of sensitive early stages and low recruitment rates, effectively promoting the rapid development of transplanted populations (*51*).

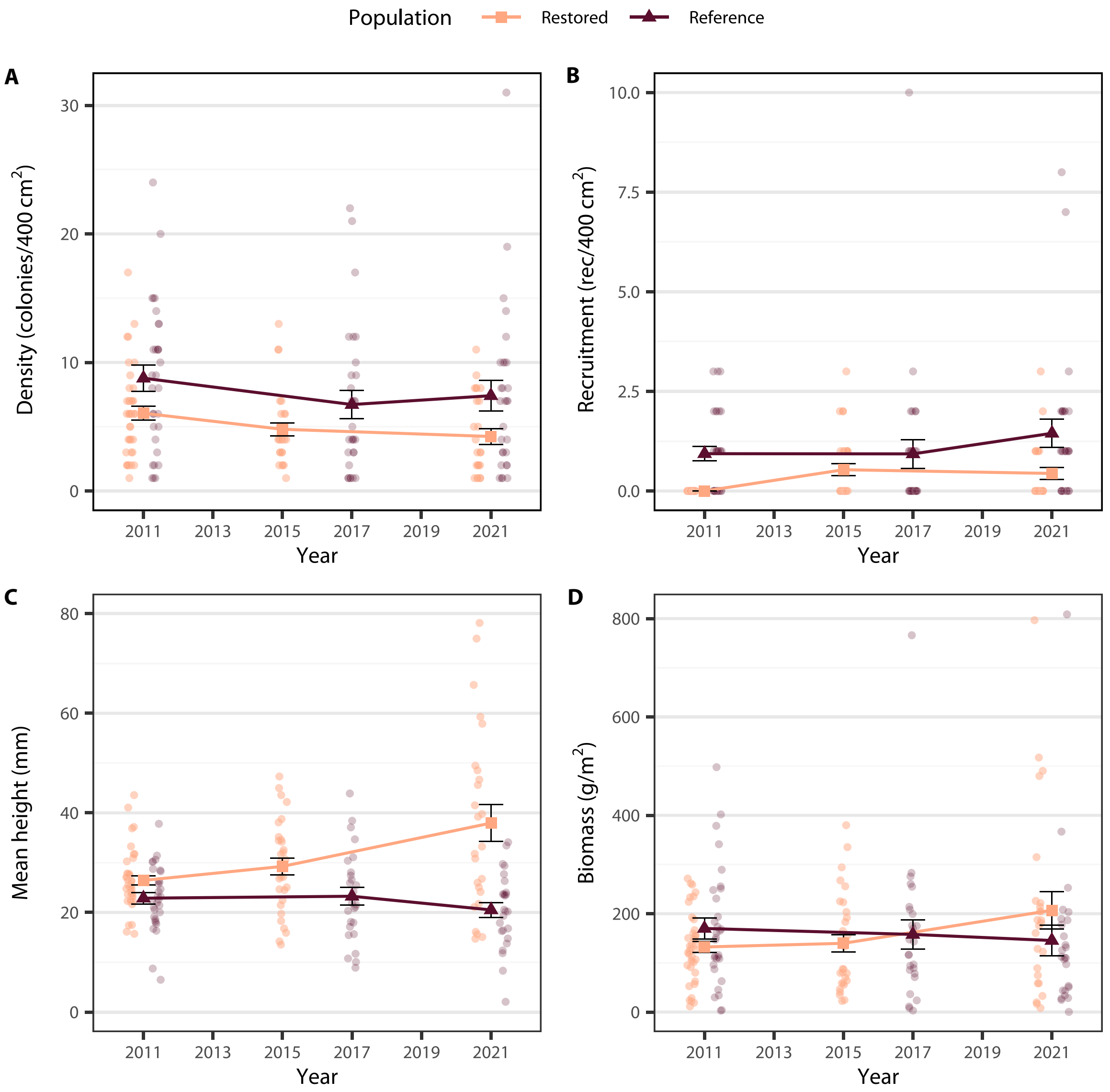

Fig. 1. Demographic traits for the studied red coral *C. rubrum* reference and restored populations. (**A**) Density (colonies/400 cm^2), (**B**) recruitment (recruits/400 cm^2), (**C**) mean maximum height (mm), and (**D**) biomass (g/m^2). The small dots represent the values from each individual quadrat –400 cm^2, while the squares and the triangles represent the mean values of the restored (in orange) and the reference (in brown) population respectively, while errors bars represent the SE.

These results are further reinforced by the high frequency distribution of the red coral colonies (Fig. 2). While the reference population has maintained a negatively skewed distribution throughout the years, the restored population has transitioned from a similar one to a more centered platykurtic one, which is associated with more mature populations (*52*). The development of the restored population is especially clear when considering the decreasing number of small colonies (<30 mm). In 2011, 72% of the restored population was composed of small colonies, which was similar to the value observed at the reference site (which ranged from 73 to 78%), but in 2021, it decreased to 45%. While the progress of the restored population is positive, both populations present values for all demographic traits that are still far from those recorded in other marine protected areas, where well-preserved and nonexploited red coral populations thrive (*52*–*54*). This is extremely evident when accounting for the number of large colonies (>100 mm), as not even one was found within both studied populations, but they are expected to encompass more than 30% of pristine *C. rubrum* populations (*52*). Therefore, the restored colonies are developing successfully but are still far from attaining the characteristics of pristine colonies.

Coverage of the main taxonomic groups in the reference versus restored assemblages

The coverage of the main taxonomic groups shows a reconfiguration of the restored assemblage that brings it closer to the composition observed at the reference site (Fig. 3). This reconfiguration is driven mainly by a reduction in red algae and mixture complex replaced by cnidaria, porifera, and the transplanted *C. rubrum*. Overall, this implies going from a co-dominance of algae and filter feeders, typically associated with shallower coralligenous assemblages, in some cases even referred

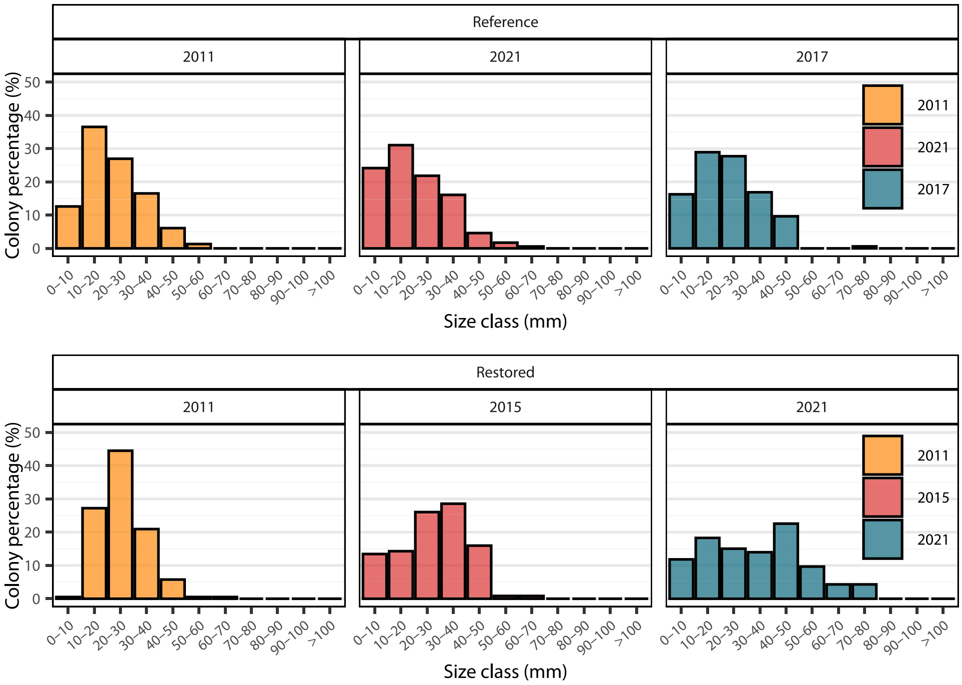

Fig. 2. Size class frequency (%) for the reference and restored *C. rubrum* populations. Obtained from distributing the maximum colony height in 10-mm increments up to the maximum size recorded. The number of colonies analyzed are 230, 213, and 187 for the reference site in 2011, 2017, and 2021 and 191, 163, and 152 for the restored site in 2011, 2015, and 2021, respectively.

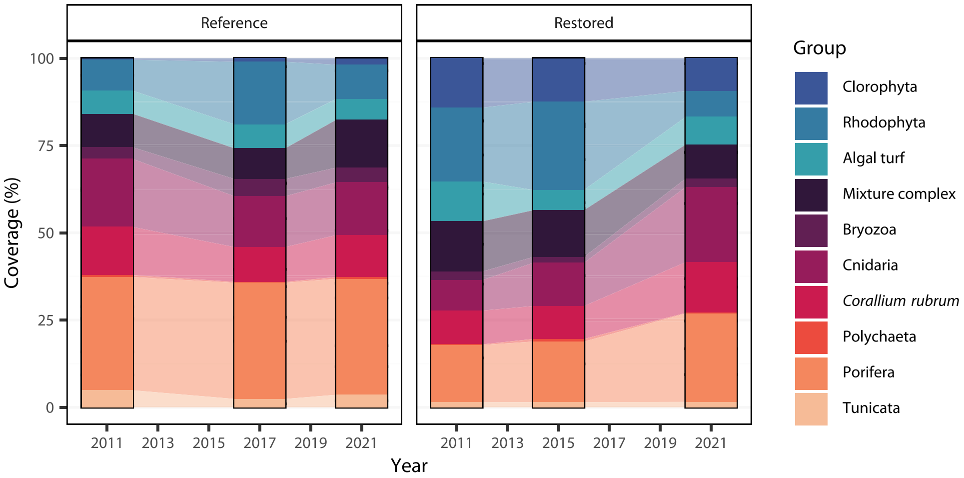

Fig. 3. Coverage (%) of the main taxonomic groups for the assemblages with reference and restored *C. rubrum* populations. The plotted bars mark the benthic coverage filled by each taxonomic group at the monitored time points, while the translucent filled in areas represent a lineal change between time points to facilitate tracking the coverage changes across time. Blue colors represent algae taxonomic groups, while purple to orange colors represent animal taxonomic groups. Algal turf and mixture complex are the basal layer of coexisting species that cannot be identified at a macroscopic level composed by algae and a mixture of algae and invertebrates, respectively.

as "precoralligenous" assemblages (*37*), to a dominance of filter feeders more typically associated withs coralligenous assemblages under dim-light conditions (*37*) and assemblages dominated by *C. rubrum* (*55*). In Mediterranean rocky benthic communities, this transition of algae to animals is usually observed with depth and is attributed to changes in abiotic factors, such as light, water movement, temperature, nutrients, or sedimentation (*56*, *57*). Therefore, considering that the restoration site was chosen for its proximity to the reference site and similarity in environmental conditions, such a dominance change is remarkable. This transition, in contrast to the stable taxonomic composition at the reference site, suggests that the transplanted red coral colonies might have played a role in transforming the surrounding assemblage.

Ideally, a nearby coralligenous assemblage without red coral would have been monitored, but a similar facilitation has been documented in coralligenous assemblages dominated by another habitat-building octocoral (*Paramuricea clavata*, Risso 1827), both in terms of recruitment processes (*40*) and the composition of their understorey community (*41*). Within this system, the abundance and composition of algae are attributed mainly to light conditions, whereas the abundance of suspension feeders is attributed mainly to the availability of food and current intensity (*37*). Hence, this facilitation mechanism has been associated with octocorals, causing a shading effect that reduces light intensity or modifying microscale hydrodynamic conditions and sediment deposition rates (*40*). The observed coverage changes in the specific taxonomic units (see table S2) suggest that the latter might have played a greater role, as the greatest reductions occurred in macroalgae found in both higher- and lower-irradiated coralligenous assemblages [(*37*); i.e. *Peyssonnelia* sp., *Palmophyllum crassum* (Rabenhorst, 1868) and *Mesophyllum alternans* (Cabioch & Mendoza, 1998), from 6 to 1.6%, 10.1 to 5.9%, and 4.1 to 0.4%, respectively], whereas the greatest increases occurred in filter feeders [*C. rubrum* itself, nonidentifiable white sponges, *Leptopsammia pruvoti* (Lacaze-Duthiers, 1897), and *Parazoanthus axinellae* (Schmidt, 1862), from 9.7 to 14.6%, 1.3 to 5.3%, 1.9 to 5.8%, 0.3 to 3.8%, respectively]. The observed reconfiguration has brought the restored assemblage toward a general composition expected in *C. rubrum*–dominated assemblages, but in this case, it remains taxonomically different than the reference site, as it presents a lower portion of sponges, a higher portion of cnidaria, and an overall higher portion of algae. A principate coordinate analysis (PCoA) of the taxonomic unit abundances revealed that in the ending year, the sites still maintained different species compositions (see fig. S1).

Functional trait structure of the reference versus restored assemblages

Accounting for the traits of the detected taxa shows that the observed reconfiguration also translates into a change in the functional structure of the restored assemblage, with likely consequences for its ecosystem functioning. In terms of trait diversity (Fig. 4), tracking the occurrences of the functional entities, that is, the species that share the exact combination of trait values, shows an increase in functional richness (i.e., the portion of the global trait space filled by each community). During this period, the restored assemblage's functional richness approached the values of the reference assemblage, with a 0.17 difference in the first year and a 0.12 difference in the last year. While we can only effectively plot the first two dimensions, which compile a 51% variance, the diversity metrics are computed on a multidimensional trait space. Therefore, plotting the first two dimensions of the restored functional space does not reflect an increase, but visualizing the combination of all the dimensions used to compute it shows that, in most cases, 2021 covers a larger functional range than 2011 does, adding up to the total 0.09 increase (see figs. S2 and S3).

Computing the functional beta diversity of the restored assemblage revealed a 0.33 dissimilarity in the overlap between the multidimensional functional spaces of the first and last years (Fig. 4). From this dissimilarity, more than two-thirds are caused by turnover (0.23), which is dissimilarity caused by replacement of the functional entities (*58*). These results combined with the increase in functional richness indicate that through this reconfiguration, the restored assemblage has mostly transitioned into a distinct and more diverse set of trait values and therefore is now covering a different and wider range of functional strategies. Moreover, the dissimilarity between the restored and reference functional spaces has decreased over time (from 0.41 to 0.32), meaning that in 2011, while not as complete, it covered a functional range that is more similar to that of local red coral-dominated coralligenous assemblages. Part of this transition might not be related to the restoration, as the reference assemblage has also undergone a slight increase in its functional richness (Fig. 4), in this case, through the appearance of species with similar combinations of traits but exhibiting slightly more extreme values [i.e., nestedness (*58*)]. However, it is a small contribution, as its dissimilarity across time only adds up to 0.07. Because of these metrics being based on the volume of the global trait space filled by the present species, they are highly influenced by the most original functional entities (i.e., those with the most extreme combination of trait values), as they compose the vertices of the functional space (*11*, *59*). Bearing this in mind, the transition of the restored assemblages can mostly be pinpointed to a few infrequent and original functional entities that have either disappeared (e.g., erect red macroalgae) or appeared [e.g., *Halocynthia papillosa* (Linnaeus, 1767) and *Clavularia crassa* (Milne Edwards, 1848)] over the monitored time.

The inclusion of the abundances of the functional entities also revealed a change in the functional diversity of the restored assemblage (Fig. 4.), in this case, through a reduction in functional divergence (i.e., the coverage supported by the entities with the most extreme trait values). Specifically, it decreased from 0.93 in 2011 to 0.86 in 2021, close to the values of the reference assemblage, which remained stable across the study period at approximately 0.83. This reduction in trait divergence indicates a lower degree of niche differentiation, as a higher portion of the community presents more intermediate trait values and therefore plays less specialized functional roles (*60*). In community assembly theory, convergence is attributed mainly to abiotic or biotic filtering, which favor certain trait combinations (*61*), further suggesting that a facilitation mechanism is occurring. Overall, after the restoration, the assemblage approached the functional diversity of the reference assemblage not only by covering a more diverse presence of distinct functional strategies, albeit due to changes in rare taxa, but also by promoting the abundance of less specialized functional roles, which were restricted without the presence of red coral.

Exploring trait dominance confirmed that the functional structure of the coralligenous assemblage with restored red coral has undergone a significant transition (Fig. 5). The functional identity (i.e., the functional entities abundance weighted centroid) follows a similar pattern to that of the other results. The reference *C. rubrum* assemblage presented a stable centroid [Fig. 5A; $P > 0.05$, permutational multivariate analysis of variance (PERMANOVA); see table S3], whereas a significant change was recorded for the restored centroid (Fig. 5B; $P < 0.05$, PERMANOVA; see table S3). Notably, while a significant difference was present between the two assemblages in 2011 and 2015–2017 ($P < 0.05$, PERMANOVA; see table S3), the trait dominance of the restored site moved closer to that of the reference site, to the point that no significant difference was present in 2021 ($P = 0.99$). This displacement occurred mainly on the first PCoA axis as a result of a decreased abundance of the functional entities distributed on the right side of the plot and an increased abundance of the majority distributed on the left side. Considering the trait positions within the functional space (Fig. 5, C to G), this displacement implies a

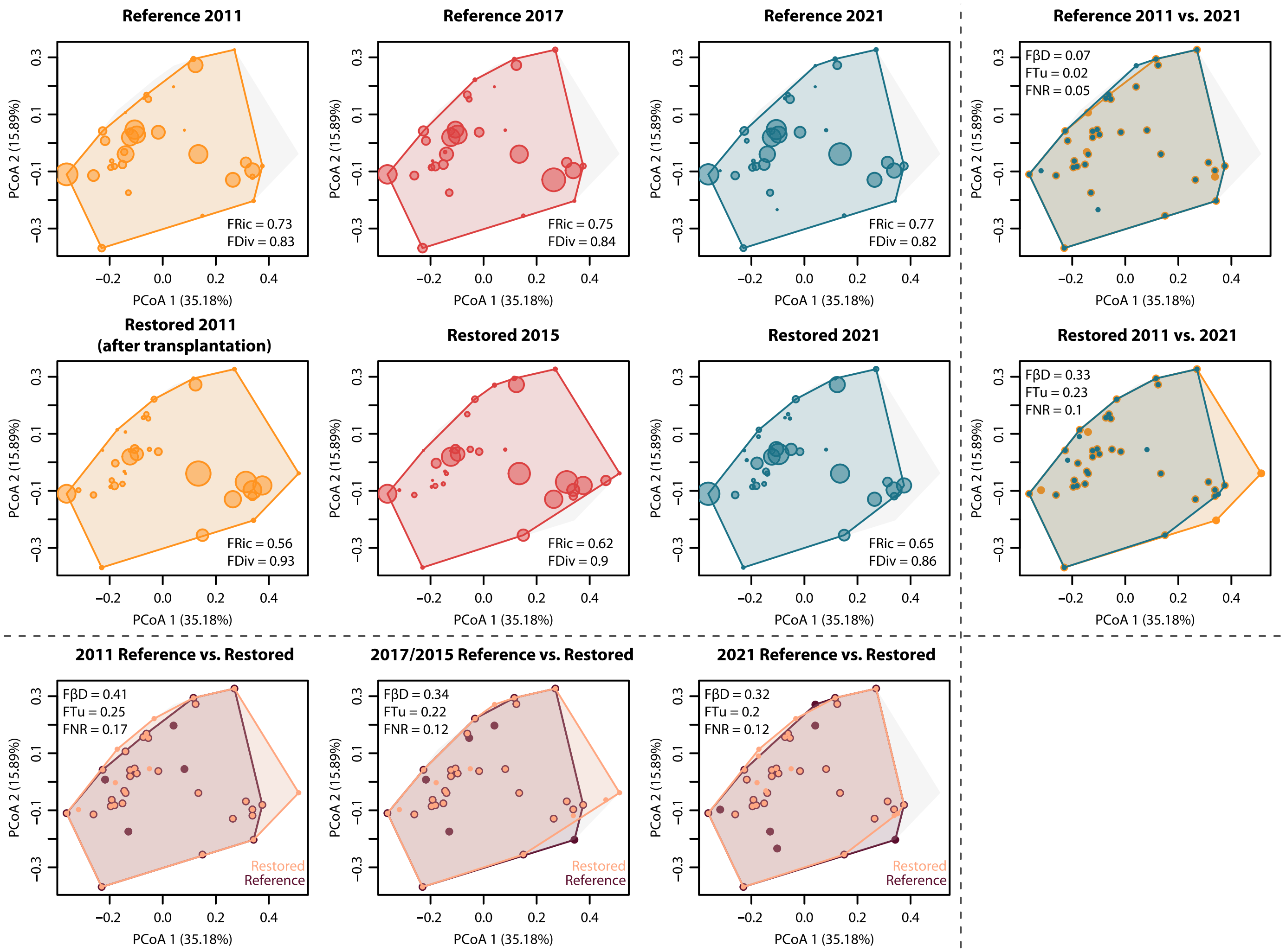

Fig. 4. Functional diversity for the assemblages with reference and restored *C. rubrum* populations. Here, several indices have been used: Functional richness (FRic), computed as the portion of the 6D functional space filled by each community each year; functional divergence (FDiv), computed as the portion of coverage supported by the FEs with the most extreme trait combinations; and functional β diversity (FβD), computed as the nonoverlap between the 6D convex hulls, decomposed into functional turnover (FTu), the dissimilarity caused by replacement of FEs and functional nestedness resultant (FNR), the remaining total dissimilarity not caused by turnover, therefore by nestedness. In the plots, the 2D functional space has been represented, with colored polygons being the community's functional space, while gray polygons represent the global trait space (FRic = 1). PCoA, principate coordinate analysis.

reduction in fast growing, early reproducing, individual, and autotroph taxa with red- and green-type photosynthetic pigments and an increase in heterotroph, slow-growing, late reproducing, and colonial taxa with tree-like, massive, cup, and corymbose morphologies and physical defenses (to assess the precise changes in each of the 12 traits used, see fig. S4).

Bearing in mind the observed taxonomic reconfiguration, this change in trait dominance is not unexpected, as within coralligenous communities, the lost traits can be linked to macroalgae, whereas the increasing traits are more commonly observed in filter feeders. Nonetheless, whether the assemblages would share the exact dominance of functional strategies was not evident, as they still differed in taxonomic composition. In addition, there is also variety in trait combinations among filter feeders, as observed with the distribution of functional entities across the functional space. Consequently, coralligenous assemblages dominated by red coral foster a specific functional structure by increasing a specific set of trait combinations. Notably, the increased traits have been linked to the three-dimensional (3D) structural complexity, nutrient cycling, benthic-pelagic coupling, and resilience (*62*). Hence, the observed reconfiguration of traits is expected to play an important role in the coralligenous functioning, which in turn sustains important ecosystem services (*38*). Even at the trait level, the observed changes are a quantitative example of the critical role that key habitat-building octocorals can play in transforming the functional structure of coralligenous assemblages.

Evidently, some of the displacement can be directly linked to the growth and long-term success of the transplanted red coral colonies, but some functional entities have undergone greater changes than *C. rubrum* has (see fig. S5). Specifically, a greater reduction occurred in red encrusting macroalgae (from 12.1 to 2.3% total coverage), whereas a greater increase occurred in encrusting sponges (from 4.5

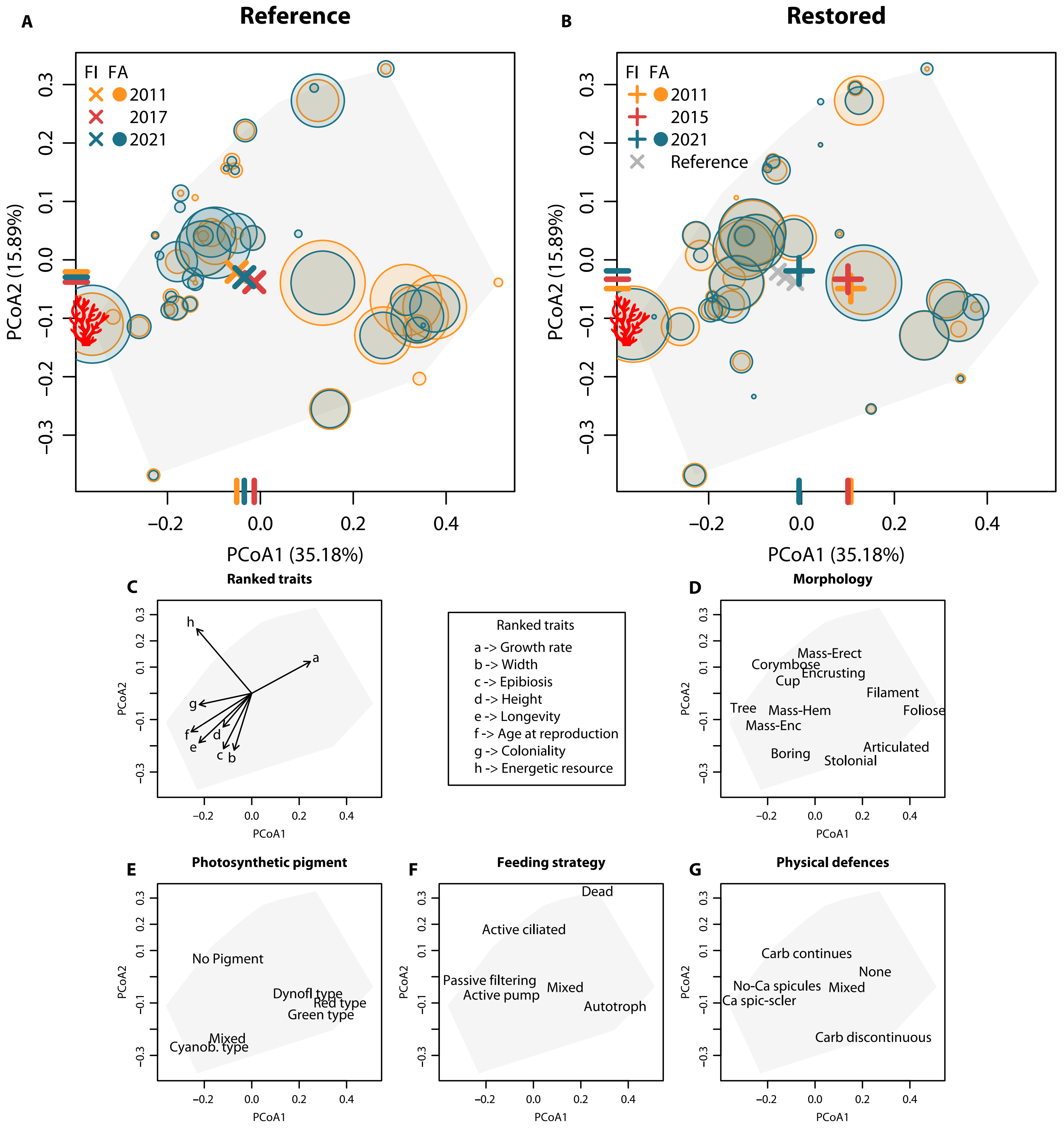

Fig. 5. Functional identity for the assemblages with reference and restored *C. rubrum* populations. Functional identity (FI) of the (**A**) reference and (**B**) restored assemblage. The FEs abundance distribution of the reference and has been represented for the first and last year (orange and green circles, respectively), while the FI has been computed as the weighted abundance centroid and represented for the three time points (orange, red, and green crosses, respectively). (**C**) The direction and importance (i.e., the longitude) of the eight ranked traits within the functional trait space. (**D** to **G**) Position of the four categorical traits within the functional trait space.

to 12.1%). Exploring the functional identity of the assemblages without including *C. rubrum* revealed a transition in the surrounding community (see fig. S6). Thus, red coral not only modifies the coralligenous functioning by improving structural complexity through its own presence but also seems to control the traits, and therefore functional roles, of its underlying community. Considering that the restored assemblage approaches the reference assemblage in terms of trait diversity and matches it in terms of trait dominance, the restoration promoted the successful transition of the community's functional structure closer to that of local *C. rubrum*–dominated coralligenous assemblages.

Lessons learned from long-term restoration of red coral colonies

Together, our demographic and community metrics results indicate that while the height and biomass of the restored red coral population have surpassed those of the reference populations, its assemblage still did not fully recover the reference composition and diversity of traits. This delay is expected, as if the red coral is promoting transformation, it is understandable that the transplanted organism matures first, while the community trails behind it. Nevertheless, in terms of the most dominant traits, the restored assemblage has caught up to the reference assemblage, which reinforces the success of this restoration. The fact that it has done so but has not matched its taxonomic composition supports that setting targets in terms of function might be more attainable for restorative initiatives, especially in the current context of global change (*14*, *63*). Directly quantifying ecosystem functioning to set these targets would be ideal but can be challenging to achieve. Thus, our results reinforce that translating composition data into trait-based methods might be a good compromise to guide restoration efforts, as they are more relevant than taxonomic analysis when trying to reinstate ecological functions (*8*). In our case, adding the functional perspective highlights the foundation role that *C. rubrum* plays within this community, not only through the structural complexity it offers but also by favoring a specific set of functional roles within its understorey that sustain important ecosystem services.

Another interesting observation is that the restored community transition mainly occurs in the second time period. This effect suggests that recovery times for these initiatives are not linear, strengthening the idea that while time is a crucial factor when striving for complexity in restoration (*64*), its development and the consequential emergent properties, such as ecosystem functions, can be nonlinear with time (*65*). Hence, to account for nonlinear dynamics within restoration, long-term field experiments are needed to properly identify system regimes and better predict restoration outcomes. Our results further emphasize this need, as an evaluation based on the recovery of traits could deem the initiative unsuccessful if it is performed only after the first 4 years. Thus, the outcome of restoration can be directly related to the period of observation (*20*). This long-term focus has gained special importance for long-lived species-dominated ecosystems, as marine sessile invertebrates tend to need long recovery times, which can last several decades for the red coral (*23*). Considering the expected recovery times, being able to accelerate the process highlights the value of actively restoring adult colonies. Recently, systematic reviews have shown that active restoration is not associated with a faster or more complete recovery than passively recovering systems, both in terms of taxonomic biodiversity (*6*) and functional diversity (*17*). However, for ecosystems that are stressed beyond certain thresholds, unassisted passive recovery might prove insufficient, as ecosystems can follow alternative successional trajectories (*66*). Therefore, a robust theoretical framework of the studied system is necessary to assess whether an active initiative is appropriate. Here, we argue that for benthic communities with key structural species that have life history traits at the slow end of the fast-slow gradient (*67*) (e.g., low recruitment, low larval dispersion, and slow growth rates), active transplantation of adult colonies can be beneficial.

The role of active restoration as a conservation tool has been widely discussed (*1, 6, 7, 68, 69*). A notion shared over time is that for restoration to be effective, disturbance sources should first be reduced or eliminated. Otherwise, the rate of degradation can outpace restoration efforts. This concern is critical in the current context of climate change, where global impacts, which are difficult to address on a local scale, might reduce the benefits of restoration actions. In our case, restoring red coral populations at shallow depths might not be sustainable in the long term, as they are currently threatened by Mediterranean-wide marine heatwaves with lethal (*70*) and sublethal effects [e.g., lowering reproductive success (*71*) or reducing colony size (*72*)]. To date, no temperature driven mortality has been recorded for *C. rubrum* within our study sites (*73*), which is likely driven by the positive effect of nutrients discharged by the Ter River, favoring the resistance of this species in this area. However, in the last decade, there has been an accelerated warming rate in the area (*74*, *75*), increasing the severity of temperature anomalies, as they have already caused critical mass mortalities in other octocorals (*76*, *77*). While the composition of the assemblage might have been influenced by these marine heatwaves, the reference site suggests it has not been enough to modify its functional structure, contrary to the observations of other *C. rubrum*–dominated assemblages under severe temperature conditions (*62*). This effect might have been partially reduced by the presence of healthy red coral colonies, as habitat-building octocorallia have been documented to mitigate warming effects on coralligenous assemblages (*78*). Nonetheless, the success of this restoration is likely temporary, as even under the most optimistic climate scenarios, marine heatwaves are predicted to worsen in the Mediterranean (*79*). Its duration might be even shorter than expected, as our dataset does not include 2022, the worst year to date in terms of temperature anomalies within our locality (*77*). Therefore, future initiatives aimed at restoring red coral colonies should perform the transplantation at depths where temperature impacts are less intense. Even if restoring at greater depths comes with methodological constraints and increased costs, deeper transplantations have been performed successfully [e.g., at 70 m (*45*)] and should be further encouraged by the positive results provided from our study case.

The overexploitation of red coral has depleted many populations and even caused local extinction events, resulting in the remaining populations rarely being dominated by large colonies and, as a result, virtually losing their ecological role as key habitat-forming species (*53*, *80*, *81*). The fact that *C. rubrum* transplantation can facilitate the development of the functional structure of its surrounding community offers a glimmer of hope from a conservation perspective. This case is particularly remarkable, considering that the restored population is quite underdeveloped compared with well-preserved coral populations (*52*). Evidently, using the reference community as a benchmark is not ideal, as it further promotes the shifting-baseline syndrome affecting this species (*53*). If a pristine assemblage had been available onsite, then it would have been expected that it would have shown a much larger gap between its functional structure and the restored assemblage's one. Moreover, we acknowledge that this study cannot be used as a direct formula for how to sustainably restore red coral populations, as the colonies used were derived from an intercepted poaching event. This handicap is especially relevant considering that scaling up restoration efforts is essential for them to be effective conservation tools. Nevertheless, this study quantitatively demonstrated that it is possible to transition coralligenous assemblages to more functionally diverse and structurally complex stages through the active restoration of key octocorals. Considering that the functioning of red coral–dominated coralligenous assemblages is still threatened by a lack of enforcement of *C. rubrum* harvesting regulations, which are worsened by poaching events (*44*) and by marine heat waves (*49*), this study provides managers with evidence of effective tools to reverse current dire trends at local scales if these threats can be overcome.

MATERIALS AND METHODS

To assess the state of the transplanted colonies and the community functional structure, from 2011 to 2021, we monitored the restored and reference assemblages three times, with the in-between surveys being performed in 2015 and 2017 for the restored and reference sites, respectively. To assess the demographic traits of *C. rubrum,* four permanent transects covering a total are of 1.6 m^2 were established within each site (*23*). The monitoring of the colonies consisted of sequentially positioning and photographing a 20 cm–by–20 cm plastic quadrat along the length of each transect (2 m). Three photographs were taken from each quadrat from different perspectives (left, center, and right). Using photogrammetry techniques, this sampling allowed us to count the colonies and measure their maximum colony height [for a detailed description, see (*82*)]. For each set of pictures, we estimated the following descriptors: density, which was the number of colonies in each quadrat (colonies/400 cm^2); recruitment, which was estimated as the number of recruits (i.e., colonies smaller than 10 mm) appearing within each quadrat (recruits/400 cm^2); mean maximum height, which was quantified for each quadrat; and biomass, which was the cumulative biomass in each quadrat obtained through a relationship relating colony height (cm) and biomass (dry weight in grams) ($B = 0.1535H^{1,9732}$) (*53*). To assess whether each population has undergone a significant trend over time, we fitted a linear regression model for each demographic trait using the traits as response variables and time as the explanatory variable. For density, biomass and mean height a parametric linear regression was fitted, whereas for recruitment, owing to the non-normality of the residuals and the count nature of this variable, we fitted a generalized linear regression model via a negative binomial family. Last, by grouping the height of the colonies in 10-mm increments, we estimated the size structure and frequency of the restored and reference populations. We also computed the percentage of small (3 mm) and large (>100 mm) colonies because the latter has been proposed as an indicator of red coral population conservation status (*52*). All analyses were performed via R software (v. 4.3.0) (*83*).

To explore the temporal trends of the coralligenous assemblage, we also used a photographic sampling method. Specifically, we analyzed 24 photos (3 × 8 replicates of the 20 cm–by–20 cm quadrat) situated within the permanent transects for each condition (year and station). We chose the number of replicates following previously defined guidelines for the optimal sampling effort needed to assess biodiversity patterns in *C. rubrum*–dominated assemblages (*84*). In all the pictures, we analyzed the coverage (%) of macrobenthic sessile species by distributing 100 points within the quadrat in a random stratified pattern and determining the lowest possible taxonomic level of the marked species. This identification process was performed with the Photoquad photoquadrat software (*85*).

Once the taxonomic data were collected, we first explored the community over time by plotting the coverage of major taxonomic groups at each time point. To do so, all the taxonomic units were classified into the groups Chlorophyta, Rhodophyta, Algal turf, mixture complex, Bryozoa, Cnidaria, Polychaeta, Porifera, and Tunicata while also differentiating *C. rubrum* to observe the changes in its surrounding community. Algal turf and mixture complex are defined as the basal layer of coexisting species that cannot be identified at the macroscopic level and are composed of algae and a mixture of algae and invertebrates, respectively. After the taxonomic exploration, we computed a multidimensional functional space for the monitored coralligenous communities. Considering that gathering trait data at the individual level can be costly and difficult, especially in the marine realm, we computed the functional structure of the communities based on trait values at the species level [see (*86*) for a detailed workflow].

To construct this space, we focused on 12 traits that are related to different ecosystem functions and that have been previously used to characterize the functional structure of *C. rubrum* assemblages [see table S4, for a description of the traits and their ecological relevance adapted from (*62*)]. Specifically, we included eight ranked traits (growth rate, maximum width, maximum height, epibiotic preference, maximum longevity, age at reproduction, coloniality, and energetic resources) and four categoric traits (morphology, major photosynthetic pigment, feeding strategy, and physical defenses). The trait values of most identified taxonomic units were previously coded in (*87*) and/or (*62*). Nevertheless, we coded any units not previously identified following the same fuzzy coding procedure on the basis of coarse ranked and nominal categories (*88*). As in the aforementioned works, these coded trait values represent the best available descriptions of species-specific traits and were selected on the basis of the expertise of team members, identification guides, online databases, and previous scientific publications (see data S1). From the 78 identified taxonomic units, we constructed 45 functional entities (FEs). Each *FE* is composed of species that have the same combination of trait values across all 12 traits (*62*, *87*). To construct the multidimensional trait space, we used a multidimensional functional diversity (mFD) R package (*86*). First, we computed a Gower dissimilarity matrix from the functional trait-based distances between the obtained FEs. With the obtained matrix, we performed a PCoA to build the functional space. Following the package's authors guidelines, we assessed the quality of the PCoA-based multidimensional spaces according to the deviation between trait-based distances and distances in the functional spaces (*86*, *89*). Based on this evaluation, we chose the functional space with six dimensions, which accounts for 81% of the variance, as the best space in terms of quality (see fig. S7).

With the functional space constructed, we calculated a set of functional indices for each condition (site and year), enabling us to assess whether functional recovery is occurring within the restored assemblage by comparing it to a reference system. To explore the changes in functional diversity, we quantified functional richness

(FRic), which measures the total functional range (i.e., range of functional traits) covered by a community, and functional divergence (FDiv), which measures niche differentiation within a community (i.e., specialization of functional traits). We calculated FRic as the portion of the 6D convex hull volume (the global functional space) filled by the multidimensional space resulting from the FEs at each assemblage (*11*), whereas we computed FDiv as the portion of the community supported by species with extreme trait combinations (*11*). We chose these two metrics, as the first provides us information on the presence of species that have the most unique trait combinations, whereas the second provides information on whether the most abundant species and their traits fulfill niche roles. Here, we avoided the third component of functional diversity, functional evenness, as it has been recently reported to not capture this property well (*90*, *91*). Both FRic and FDiv combined allowed us to assess whether the restored assemblage covered the same diversity of ecosystem functions as the reference assemblage. To better track the sites' functional dissimilarity throughout time and between them at each time point, we computed the functional β diversity (FβD) by accounting for the overlap between the convex hulls of the first and last monitored years (*58*). FβD can then be decomposed into: functional turnover (FTu), which is the dissimilarity due to FE replacement between communities, and functional nestedness-resultant (FNR), which is the remaining total dissimilarity not caused by turnover, therefore by nestedness (*58*, *92*). These indices allowed us to explore whether the restored assemblage is shifting into a different set of functional strategies (FTu) or is expanding/decreasing its functional range by becoming a superset/subset of its functional structure (FNR). Last, we complementarily computed the assemblages' functional identity (FIde), which is the community weighted mean value of functional traits and includes the abundance changes in all FEs. Specifically, we estimated FIde by weighting the FEs position by their abundance and calculating the resulting centroid (*11*). Tracking the most dominant traits in both assemblages can help us test whether functional recovery is occurring, as for similar ecosystem functions, a similar distribution of functional traits presence is expected. Last, to test whether the obtained FIde values varied significantly over time within a site and whether a significant difference was present between the restored and reference site at the different stages of the monitoring, we performed multiple comparisons of nonparametric analysis of variance PERMANOVA for all combinations of time and sites as fixed factors (*62*). To do so, we computed the abundance-weighted centroid for the 24 quadrats of each condition (time and site) and then performed multiple comparison PERMANOVA using the coordinate values of the centroids as variables.

Supplementary Materials

The PDF file includes:

Figs. S1 to S7
Tables S1 to S4
Legend for data S1
References

Other Supplementary Material for this manuscript includes the following:

Data S1

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