Coral Reefs
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RESEARCH

Influence of red gorgonian (*Paramuricea clavata*) forests on coralligenous community structure across different regions, seasons, thermal environment, and water trophic state

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Abstract Habitat-forming species are essential for maintaining biodiversity and ecosystem functioning in marine benthic ecosystems, but their role in modulating community responses to environmental stressors across spatial and temporal scales remains underexplored. In the Mediterranean Sea, the red gorgonian *Paramuricea clavata* forms structurally complex animal forests within coralligenous assemblages, able to enhance habitat heterogeneity. This study assessed the influence of *P. clavata* forests on the structure of coralligenous communities across five Mediterranean regions and two periods (summer and autumn), incorporating thermal (median temperature, temperature range, frequency and duration of heating events) and trophic (chlorophyll, pheophytins, carbohydrates, proteins, organic and inorganic suspended matters) environmental descriptors. Using Generalized Linear Latent Variable Models, we found that environmental variables—particularly temperature, organic matter, and trophic resource availability—strongly shaped coralligenous community structure. Forested sites exhibited a reduced abundance of opportunistic groups (e.g., turf algae, hydroids, perforating sponges) under conditions of elevated temperature and organic matter concentrations, highlighting the buffering role of *P. clavata* forests. However, under intense and prolonged thermal stress combined with high concentrations of carbohydrates and proteins, *P. clavata* itself showed increased necrosis, indicating limits to its resilience. Considering the regional and temporal scales, region emerged as the strongest predictor of community structure (explaining 45% of the variation in group abundance), followed by environmental variables (19%) and period (12%). Further, the presence of *P. clavata* forests significantly increased species richness, Shannon diversity, and evenness. These findings emphasize the importance of *P. clavata* forests in promoting ecological stability and highlight the vulnerability of this foundation species to climate-driven stressors. Understanding these dynamics is pivotal for predicting future changes in biodiversity and for informing conservation strategies targeting Mediterranean coralligenous reefs.

Résumé Le specie fondatrici di habitat sono essenziali per il mantenimento della biodiversità e del funzionamento degli ecosistemi nei sistemi bentonici marini, ma il loro ruolo nel modulare le risposte delle comunità agli stress ambientali su diverse scale spaziali e temporali rimane ancora poco esplorato. Nel Mar Mediterraneo, la gorgonia rossa *Paramuricea* clavata forma foreste animali strutturalmente complesse nel coralligeno, in grado di incrementare l’eterogeneità

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dell'habitat. Questo studio ha valutato l'influenza delle foreste di *P. clavata* sulla struttura delle comunità coralligene in cinque regioni mediterranee e in due periodi (estate e autunno), integrando descrittori ambientali di natura termica (temperatura mediana, range di temperatura, frequenza e durata degli eventi di riscaldamento) e trofica (clorofilla, feopigmenti, carboidrati, proteine, materia sospesa organica e inorganica). Mediante l'utilizzo di Generalized Linear Latent Variable Models, abbiamo riscontrato che le variabili ambientali — in particolare la temperatura, la materia organica e la disponibilità di risorse trofiche — influenzano in modo significativo la struttura delle comunità del coralligeno. Nelle foreste è stata riscontrata una ridotta abbondanza di gruppi opportunisti [ad esempio feltro algale (turf), idroidi e spugne perforanti] in condizioni di temperatura elevata e alte concentrazioni di materia organica, evidenziando il ruolo di mitigazione esercitato dalle foreste di P. clavata. Tuttavia, in presenza di stress termico intenso e prolungato, associato a elevate concentrazioni di carboidrati eproteine, un aumento della necrosi di *P. clavata* è stato evidenziato, indicando limiti alla resilienza della specie. Considerando le scale regionali e temporali, la regione è risultata il principale predittore della struttura delle comunità (spiegando il 45% della variazione nell'abbondanza dei gruppi), seguita dalle variabili ambientali (19%) e dal periodo (12%). Inoltre, la presenza delle foreste di *P. clavata* ha determinato un incremento significativo della ricchezza di specie, della diversità di Shannon e della Pielou's evenness. Questi risultati sottolineano l'importanza delle foreste di P. clavata nel promuovere la stabilità ecologica e mettono in evidenza la vulnerabilità di questa specie fondatrice ai disturbi legati ai cambiamenti climatici. La comprensione di tali dinamiche è fondamentale per prevedere i cambiamenti futuri della biodiversità e per orientare strategie di conservazione mirate alle scogliere coralligene mediterranee.

Keywords Temperete reef · Mediterranean Sea · Climate change

Introduction

Habitat-forming species provide structural support for other organisms, offering refuges, breeding grounds, and feeding opportunities. They can also influence ecosystem functioning by regulating the flow of energy and nutrients (Ellison et al. 2005; Cerrano et al. 2010; Baiser et al. 2013;). Further, these species can alleviate abiotic stressors, fostering species coexistence. In marine environments, habitat-forming species are typically sessile and include, among others, mangroves, salt-marsh plants, kelps, seagrasses, macroalgae, bivalves, sponges, and corals (Altieri and van de Koppel, 2014). Their loss may trigger cascading effects, including the decline or local extinction of associated species (Roff et al. 2020; Piazzi et al. 2021a; Gómez-Gras et al. 2022).

In the Mediterranean Sea, coralligenous reefs are recognized as one of the most biologically diverse ecosystems, supported by a variety of habitat-forming species (Ballesteros 2006; Garrabou et al. 2019). The structural foundation of these reefs is primarily due to encrusting calcareous algae, which create hard substrates under conditions of dim light, narrow thermal fluctuations, and low water turbidity at depths ranging from 20 to about 150 m (Vitelletti et al. 2023). These substrates facilitate the settlement of gorgonians, soft corals, sponges, mollusks, and bryozoans (Ballesteros 2006). The dense assemblages formed by these organisms provide essential shelter and feeding grounds for invertebrates, fish, and several other marine species. Moreover, coralligenous reefs deliver critical ecosystem services such as carbon sequestration and coastal protection, serve as nursery grounds for many commercially important fish species, and are regarded as iconic Mediterranean seascapes, attracting significant attention from the scuba diving tourism (Ballesteros 2006; UNEP/MAP - SPA/RAC, 2016; Thierry de Ville d'Avray et al., 2019; Zunino et al. 2020). Given their critical importance, coralligenous reefs are listed as priority habitats under the EU Habitats Directive, included in the Natura 2000 network (92/43/CE), and monitored under the Marine Strategy Framework Directive (MSFD, EC, 2008).

Recent studies emphasize the key role of the iconic gorgonian *Paramuricea clavata* [Risso (1826)—Cnidaria, Anthozoa, Octocorallia] in preserving the structure and functions of coralligenous reefs. Under favorable environmental conditions, *P. clavata* can become a spatially dominant species at depths between 15 and 70 m (Gori et al. 2010; Previati et al. 2010), forming extensive animal forests (Rossi et al., 2013; Orejas et al. 2022). These forests are characterized by high structural complexity and support high levels of biodiversity, enhancing species co-occurrence by mitigating physical stressors (Ponti et al. 2016; Ponti et al. 2018; Piazzi et al. 2021b). Dense *P. clavata* forests may enhance habitat stability and contribute to overall reef status by influencing the settlement of other epibenthic species that rely on this structural framework for survival (Ponti et al. 2016). Furthermore, this gorgonian may promote community diversity by creating a three-dimensional habitat that supports multiple associated species (including sponges, bryozoans, and other gorgonians, Iborra et al., 2022).

P. clavata populations face significant threats from diverse human-induced stressors. Mechanical damage caused by anchoring, scuba diving, and fishing activities can directly harm colonies (Ballesteros 2006; Betti et al. 2020). Climate change may exacerbate these pressures through more frequent and intense marine heatwaves (MHWs), flood events, and prolonged subtidal warming linked to thermocline deepening. Further, changes in thermocline dynamics can limit the food available to suspension feeders, including *P. clavata*, negatively affecting their performance (Coma et al. 2002, 2004). Changes in water stratification and the resulting variation in trophic conditions could be considered a driver of community changes. During the summer months, in fact, the combined effects of highest annual temperature, minimum seston concentrations, and food availability impose considerable stress on benthic communities (Coma and Ribes 2003). Consequently, many species enter into a state of aestivation, characterized by decreased activity levels and reliance on metabolic reserves accumulated during the winter and spring (Rossi et al. 2006). These environmental stressors are particularly detrimental for *P. clavata*, with elevated sea temperatures causing significant energy reserve depletion and reduced feeding capacity (Tignat-Perrier et al. 2022). Reduced food availability has been shown to significantly decrease *P. clavata*'s gonadal volume, impacting reproductive success (Rossi et al. 2006). Further, prolonged exposure to abnormal temperatures can lead to tissue necrosis, exposing the inner skeletal axis to pathogens, fungi, and epibiotic organisms, further increasing colony mortality (Bally & Garrabou 2007; Garrabou et al. 2009; Estaque et al. 2023). These stressors weaken the gorgonians, reducing their resilience ability and slowing down recovery processes following disturbances (Cerrano et al. 2005; Gomez-Gras et al., 2022; Iborra et al., 2022). Further, over time, the reduction or loss of *P. clavata* populations negatively affects recruitment dynamics in coralligenous reefs (Ponti et al. 2014), reducing habitat physical complexity and highlighting its key role in maintaining community structure and stability of these reefs (Garrabou et al. 2009; Mokhtar-Jamaï et al. 2011; Piazzi et al. 2021a; Ponti et al. 2016, 2018; Capdevila et al. 2024).

Despite physical variables (geomorphological features, light, temperature, hydrodynamics, sedimentation, and resources availability) being considered the most significant drivers of abundance patterns within marine communities (Gaston et al. 2008), site-specific biological interactions across biogeographic regions may have uneven importance. In this framework, understanding the role of *P. clavata* forests in structuring coralligenous communities, buffering changes in environmental conditions across a range of scales and ecological conditions, is a priority.

The aim of this study was to investigate how the presence of *P. clavata* forests affects coralligenous communities across the Mediterranean Sea. Specifically, we addressed the

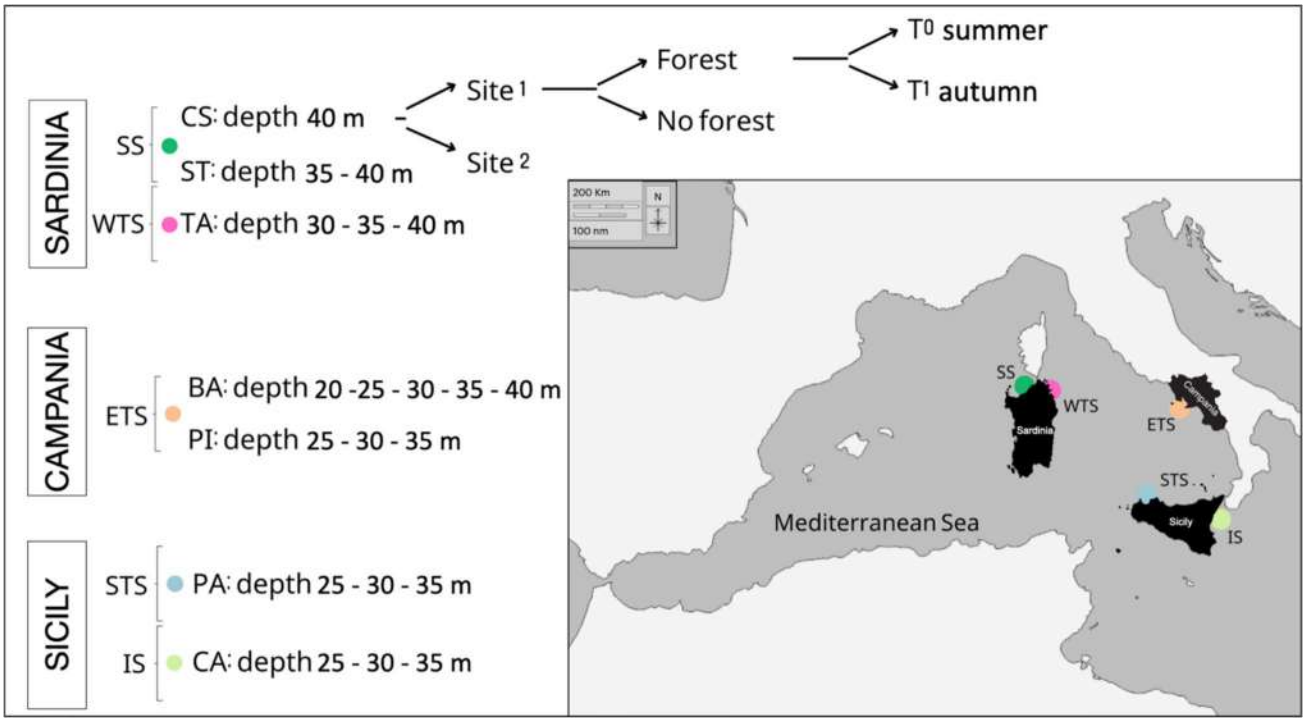

Fig. 1 Study areas and sampling design. Black areas represent the three Italian administrative jurisdictions (Sardinia, Campania, and Sicily). Colored dots represent the five sampled regions belonging to three distinct biogeographic sectors of the Mediterranean Sea: SS (Sardinian Sea), Tyrrhenian Sea (WTS: Western Tyrrhenian Sea; ETS: Eastern Tyrrhenian Sea; STS: Southern Tyrrhenian Sea), IS (Ionian Sea). Localities: CS (Castelsardo), ST (Santa Teresa Gallura), TA (Tavolara Island), BA (Banco Santa Croce), PI (Pizzaco), PA (Isola delle Femmine, Palermo), CA (Catania)

Table 1 Sampling details: regions, localities, depth and periods of biota and environmental data collection

Region	Locality	Lat – Long	Depth (m)	Period (T0)	Period (T1)
Sardinian Sea (SS)	Castelsardo (CS)	40.97575 N 8.66668 E	40	13 June 2023	3 October 2023
	Santa Teresa (ST)	41.25697 N 9.20359 E	34–38	15–21 June 2023	2 October 2023
Western Thyrrenian Sea (WTS)	Tavolara Island (TA)	40.91528 N 8.74775 E	30–35–40	14 June 2023	4 October 2023
Eastern Thyrrenian Sea (ETS)	Pizzaco (PI)	40.75053 N 14.02562 E	25–30–35	29 June 2023	8 November 2023
	Banco Santa Croce (BA)	40.68001 N 14.43213 E	20–25–30–35	3–5 July 2023	20 November 2023
Southern Thyrrenian Sea (STS)	Isola delle Femmine (PA)	38.21347N 13.23257 E	25–30-–35	27 June 2023	11 October 2023
Ionian Sea (IS)	Catania (CA)	37.53317 N 15.12738 E	25–30–35	11 June 2023	4 October 2023

following objectives: (i) to assess whether the presence of *P. clavata* forests influences the structure of coralligenous communities, in terms of morphological group abundance, species richness, Shannon diversity, and evenness, across different regions and seasonal periods; (ii) to determine whether the presence of the forests modulates the relative influence of environmental drivers related to thermal conditions (median daily temperature, temperature range, number and duration of heating events) and water trophic state (suspended organic and inorganic matter, chlorophyll, pheophytin, and concentrations of proteins and carbohydrates) on coralligenous community structure.

Methods

Sampling design

The research took place along the coasts of three Italian administrative jurisdictions (Sardinia, Campania, and Sicily), in five regions belonging to three biogeographic sectors of the Mediterranean Sea (defined as areas with specific combinations of ecological, oceanographic, and historical factors that shape the distribution and composition of biological communities—Bianchi et al. 2012): i) Sardinian Sea (SS); ii) western (WTS), eastern (ETS), and southern Tyrrhenian Sea (STS); iii) and Ionian Sea (IS) (Bianchi et al. 2012). Several localities, more than 10 km apart, were selected within each sampled region: two in the SS [Castelsardo (CS) and Santa Teresa Gallura (ST)]; one in the WTS [Tavolara Island (TA)]; two in the ETS [Pizzaco (PI) and Banco Santa Croce (BA)]; one in the STS [Isola delle Femmine Palermo (PA)] and one in the IS [Catania (CA)]. Within each locality, two sites were identified, separated by several hundreds of meters, and, in each site, the coralligenous assemblage was evaluated at different depths (ranging from 20 to 40 m, depending on the local presence of *P. clavata* forests). At each site and depth (Fig. 1 and Table 1), data were collected in two areas characterized by either the presence (Forest) or the absence (No forest) of *P. clavata* forests. In "No forest" areas, *P. clavata* individuals may be present but at densities insufficient to form a structurally complex forest. Data were collected in two sampling periods (summer = T0 and autumn = T1) to evaluate temporal changes in the community structure (Fig. 1, Table 1).

Temperature data collection and thermal descriptors

Hourly temperature data were collected through the whole period (T0–T1) by deploying temperature loggers (HOBO UA/002) on the coralligenous reef at each site and depths where biota data were also collected (ranging from 20 to 40 m, depending on the site; see Table 1). Two-component epoxy underwater filler or steel nails were used to anchor the loggers to the substratum. From the temperature data, the following thermal descriptors were calculated (following Ceccherelli et al. 2020): i) MEDIAN TEMP: the daily median of the temperature recorded hourly; ii) TEMP RANGE: temperature range as the difference between the maximum and minimum temperatures recorded during the entire period at each site and depth (see Table 1); iii) F90: the number of heating events relative to the 90th percentile calculated from the temperature data collected over the entire period at each site and depth (see Table 1); iv) D90: the duration in days of each heating event recorded during the entire period at each site and depth.

Trophic environment of the water column

Three water samples were collected for each depth (depending on site, ranging from 20 to 40 m) and time (T0 and T1) from each site using a Niskin bottle. Water samples were screened through a 200 µm mesh net to remove large zooplankton and debris. Sub-samples (500 to 2000 mL) were filtered onto pre-washed, pre-combusted (450 °C, 4 h) and pre-weighed Whatman GF/F filters (0.45 µm nominal pore size). Water samples were analyzed to determine phytopigments, including chloroplastic pigments (CHLA-TOT, CHLA-A, µg L^{-1}) and phaeopigments (PHEO), carbohydrates (CHO, mg L^{-1}) and proteins (PRT, mg L^{-1}). Phytopigments were extracted using 3–5 mL of 90% acetone

Table 2 List of morphological groups considered in the analysis

Taxa/morphological groups	Description
Invasive algae	*Caulerpa cylindracea; Asparagopsis* spp.
Turf	Algae smaller than 1 cm
Green algae	Siphonal Chlorophyta (e.g., *Cladophora* spp., *Valonia* spp., *Codium* spp.) *Flabellia petiolata*, *Palmophyllum crassum*, *Halimeda tuna*
Peyssonnelia spp.	*Peyssonnelia* spp.
Corallinaceae	Calcareous encrusting Rhodophyta (e.g., *Mesophyllum* spp., *Lithopyllum* spp.)
Necrotic corallinaceae	Calcareous encrusting Rhodophyta showing sign of necrosis
Red algae	Erect calcareous, cylindrical, and flattened Rhodophyta (e.g., *Amphiroa* spp., *Osmundea pelagosae*)
Brown algae	Dictyotales, encrusting (e.g., *Aglaozonia* spp., *Zanardinia typus*), erect (*Halopteri*s spp.) and flattened Ochrophyta (*Laminaria* spp., *Phyllariopsis* spp.), and Fucales (*Cystoseira* spp., *Sargassum* spp.)
Hydroids	Small and large hydroids: e.g., *Sertularella* spp., *Eudendrium* spp.
Perforating sponges	Sponges: e.g., *Cliona* spp.
Encrusting and prostrate sponges	Sponges: e.g., *Spirastrella cunctatrix*, *Crambe crambe, Ircinia* spp.
Arborescence and massive sponges	Sponges: e.g., *Axinella* spp., *Aplysina* spp.
Encrusting bryozoans	Bryozoans: e.g., *Schizoporella* spp., *Schizomavella* spp.
Ramified bryozoans	Bryozoans: e.g., *Myriapora truncate, Turbicellepora avicularis, Pentapora fascialis, Reteporella grimaldii, Adeonella calveti, Smittina cervicornis*
Zooxanthellate Scleractinia	Solitary and colonial Scleractinia
Anthozoa Zoantharia	Anthozoa: e.g., *Parazoanthus axinellae*, *Savalia savaglia*
Anthozoa Alcyonacea Gorgoniidae	Anthozoa: e.g., *Leptogorgia sarmentosa, Eunicella verrucosa, Eunicella cavolini*, *Eunicella singularis*
Anthozoa other Alcyonacea	Anthozoa: e.g., *Alcyonium acaule*, *Corallium rubrum, Alcyonium coralloides*
Necrotic *Paramuricea clavata*	*Paramuricea clavata* showing sign of necrosis
Serpulids	Serpulids: e.g., *Salmacina-Filogran*a complex
Ascidians	Encrusting and erect ascidians
Vermetidae	Vermetidae: e.g., *Thylacodes arenarius*

(vol/vol) as a solvent, with a 12 h incubation at 4 °C in darkness (Pusceddu et al. 2003; Sarà 2006). Spectrophotometric analysis was performed on these extracts to determine chlorophyll-a concentrations, followed by acidification with 200 µL of 0.1 N HCl to quantify phaeopigments. Protein and carbohydrate contents were measured spectrophotometrically following the protocols outlined by Danovaro (2009). Protein content was determined using the Folin–Ciocalteau reagent in a basic medium and was expressed in equivalents of bovine serum albumin. Carbohydrate content was assessed through the phenol–sulfuric acid reaction with saccharides (Gerchakov and Hatcher 1972), yielding values expressed as D(+) glucose equivalents. Protein and carbohydrate concentrations were converted into carbon equivalents using conversion factors of 0.49 and 0.40 $\mathrm{mgC\ mg^{-1}}$, respectively, based on the carbon content of albumin and glucose standards. Finally, we estimated the total suspended matter (TSM), which was estimated gravimetrically after desiccation (105 °C, 24 h) using a microbalance (± 1 µg accuracy), while its organic fraction (OSM) was estimated by loss on ignition (450 °C, 4 h; Strickland and Parsons 1972).

Coralligenous community structure

The study of the coralligenous community structure was conducted using a non-destructive method based on photographic sampling, collected using underwater cameras (Lumix equipped with two electronic strobes). At each area, ten 0.2 m^2 photographic samples of vertical surface were taken (following Piazzi et al. 2019). From these photographic samples ($N = 1300$), organisms were recorded to the lowest possible taxonomic level (morphological group). The percent cover of each morphological group was estimated for each sampling unit using the software ImageJ. Due to the presence of several inconspicuous morphological groups, percent cover values were pooled into broader categories (Table 2, Fig. SM1). Finally, morphological group richness (the number of different groups found; McIntosh 1967), Shannon index (a metric of species diversity which accounts for both species richness and evenness; Pielou 1966), and Pielou's Evenness index (a measure of how evenly individuals are distributed among the species in a community; Pielou 1966) were calculated using the *R* package vegan (Oksanen et al. 2020).

Statistical analysis

All continuous variables, namely the thermal descriptors (MEDIAN TEMP, TEMP RANGE, F90, D90), the water trophic variables (CHLA-A, CHLA-TOT, PHEO, PRT, CHO, ISM, OSM), and depth were checked for collinearity (Pearson's correlations – Fig. SM2). Regarding the environmental variables, Kruskal–Wallis tests were used to test for differences between regions, and the Mann–Whitney U test was used to test the differences between periods (using the *R* package 'stats4' – R Core Team 2024). A Principal Component Analysis (PCA) was applied to reduce the dimensionality of the environmental data using the prcomp() function of the *R* package 'stats4' (R Core Team 2024), which standardizes and scales the data prior to analysis. Explanatory variables for the following multivariate analysis were selected by retaining the first three principal component axes (those with eigenvalues greater than one—Legendre & Legendre 1998; Table SM1). To assess the robustness of the PCA loadings, we applied a bootstrap approach with 1000 resamplings of the original data. Variables whose 95% confidence intervals did not include zero were considered to contribute significantly to the respective principal component. This approach allows for the evaluation of the reliability of the loadings while maintaining the exploratory nature of PCA (Efron and Tibshirani 1993). Then, Generalized Linear Latent Variable models (GLLVM; Niku et al., 2019) were applied to relate the abundance (expressed as coverage) of the coralligenous morphological groups to the explanatory variables. GLLVMs are designed to handle multivariate abundance data by expanding the standard generalized linear modeling framework to incorporate latent variables, which account for species covariation that is not explained by the explanatory variables (including species interactions and correlations due to unmeasured variables).

In GLLVM we regress the mean of each response $\mu_{ij} = E(Y_{ij})$ against a vector of latent variables and covariates as follows:

$$g(\mu_{ij}) = \eta_{ij} = \alpha_i + \beta_{0i} + x_i{\prime}\beta_i + u_i{\prime}\gamma_i$$

where g() is a known link function, α_i represent the random effect (which account for the site-specific effects in this case), β_{0i} denotes the intercept specific per each group (i), $x_i{\prime}\beta_i$ contains the covariates effect specific to group and $u_i{\prime}\gamma_i$ contains the latent variables and the group-specific loadings. The latent $u_i{\prime}$ can be considered as ordination scores which capture the correlation across groups after accounting for the covariates effect ($x_i{\prime}$). Percent cover data are usually modeled using beta distribution defined for a bounded continuous interval which cannot be exactly equal to zero and

Table 3 Comparisons between Generalized Linear Latent Variable Models (GLLVMs)

Model formula	df	AIC
Null model (LV = 0)	81	– 5291
Null model (LV = 1)	101	– 6015
Null model (LV = 2)	120	– 6157
1) Models to investigate the relationship between coralligenous assemblages and the PCs as proxies of the environmental variables		
Species data ~ PC1	140	– 6256.576
Species data ~ Forest*PC1	180	– 6326.393
Species data ~ PC2	140	– 6316.505
Species data ~ Forest*PC2	180	– 6399.322
Species data ~ PC3	140	– 6185.243
Species data ~ Forest*PC3	180	– 6270.182
Species data ~ Forest*PC1 + Forest*PC2	220	– 6493.141
Species data ~ Forest*PC1 + Forest*PC3	220	– 6415.508
Species data ~ Forest*PC2 + Forest*PC3	220	– 6468.596
Species data ~ Forest*PC1 + Forest*PC2 + Forest*PC3	**260**	**– 6607.320**
2) Models to investigate the relationship between coralligenous and region		
Species data ~ Region	190	– 7093.010
Species data ~ Forest*Region	**285**	**– 7401.715**
3) Models to investigate the relationship between coralligenous and period		
Species data ~ Period	133	– 6468.184
Species data ~ Forest*Period	**171**	**– 6599.582**

"LV" indicates the number of latent variables to be used in the three set of GLLVMs. "*" indicates the interaction with the presence of *P. clavata* forest. In bold the best models based on the AIC values. All models included Site as a random term one. The ordered beta distribution was used here, since it can account for responses belonging to zeros, between zero and one, or ones (Kubinec 2023). Due to the high computational time of GLLVM, data were pooled by area ($N = 130$). Additionally, Scleractinia and Vermetidae were removed from the sample due to their scarce presence, reducing the number of morphological groups to 20.

Three sets of GLLVMs were run: i) models to investigate the relationship between coralligenous assemblages and the principal components (PC1, PC2, PC3) as explanatory variables to investigate the relationship between coralligenous assemblages and the thermal and trophic environment; ii) models to investigate the relationship between coralligenous assemblages and region (a categorical variable with five levels: SS, WTS, ETS, STS, and IS); iii) models to investigate the relationship between coralligenous assemblages and period (a categorical variable with two levels: T0 and T1). All fixed terms in the models were tested both as main effects and in interaction with the presence of *P. clavata* forests (a categorical variable with two levels: Forest, No forest), in order to assess whether the presence of the forest modulated the relationship between the explanatory variables and the coralligenous assemblages (Table 3). Site was included as a random term to account for the likely correlations within coralligenous assemblages due to similar environmental conditions at each site.

A forward selection model approach based on the Akaike information criterion (AIC) was used to first select the optimal number of latent variables and then the best combination of explanatory variables. The R package gllvm (version 1.3.1; Niku et al., 2019) was used to run the models, and residuals were checked using the plot.gllvm function. Further, to assess the proportion of variation in morphological group abundances explained by the explanatory variables, we used the residual covariance matrices obtained from the fitted GLLVMs. Thus, the function "getResidualCov" (from the gllvm *R* package) was used to extract the residual covariance matrix (Σ) for models fitted with and without explanatory variables. The trace of Σ, defined as the sum of its diagonal elements, represents the total residual variance across all morphological groups. By comparing the traces of the residual covariance matrices from the null model (without explanatory variables) and the full model (including explanatory variables), we quantified the proportion of variation explained by the predictors.

The relationship between richness and Shannon and Evenness indices and the explanatory variables previously described was tested using the same three sets of generalized linear mixed models (GLMMs) with Poisson (for richness) and Gaussian distribution (for Shannon and Evenness indices). GLMMs are an extension of generalized linear models that allow for the inclusion of random effects by modeling the covariance structure generated by the grouping of data. A forward selection procedure was applied to select the best models based

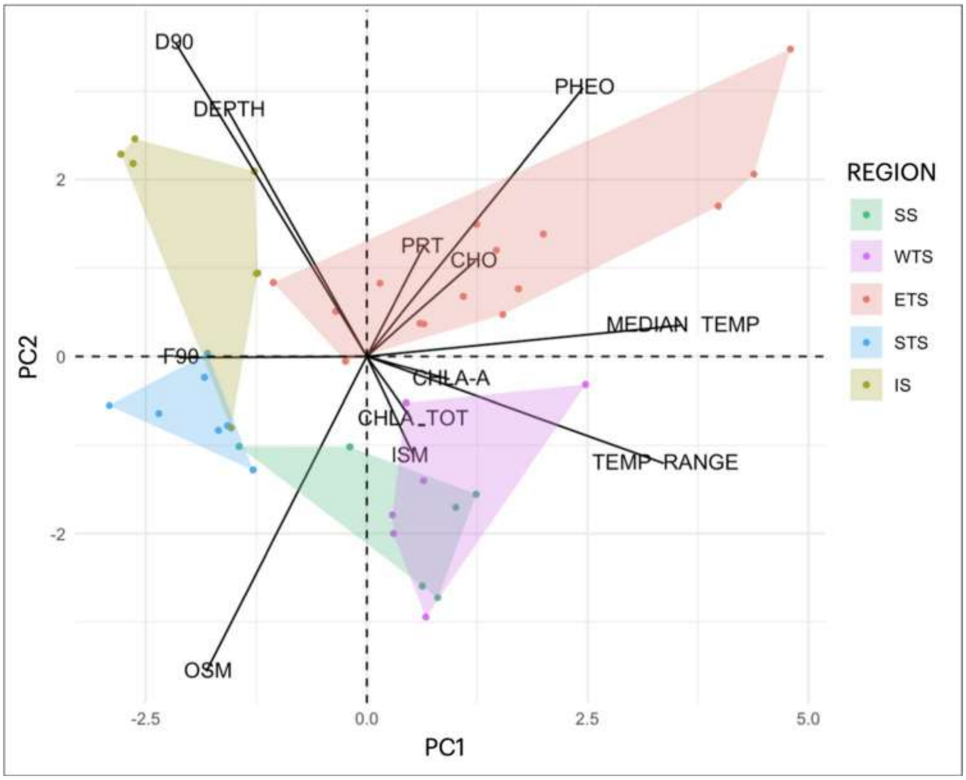

Fig. 2 Biplot for the Principal Component Analysis (PCA) showing the associations between environmental variables and their relationship with the region for the two main principal components (PC1 and PC2). The vectors represent the correlations between PCA scores and the environmental variables. OSM: organic suspended matter; ISM: inorganic suspended matter; CHLA-TOT: total chlorophyll; CHLA-A: chlorophyll-a; TEMP RANGE: temperature range; MEDIAN TEMP: median temperature; PRT: proteins; PHEO: phaeopigments; CHO: carbohydrates; F90: number of eating events; D90: duration of eating event. SS: Sardinian Sea; WTS: Western Tyrrhenian Sea; ETS: Eastern Tyrrhenian Sea; STS: Southern Tyrrhenian Sea; IS: Ionian Sea

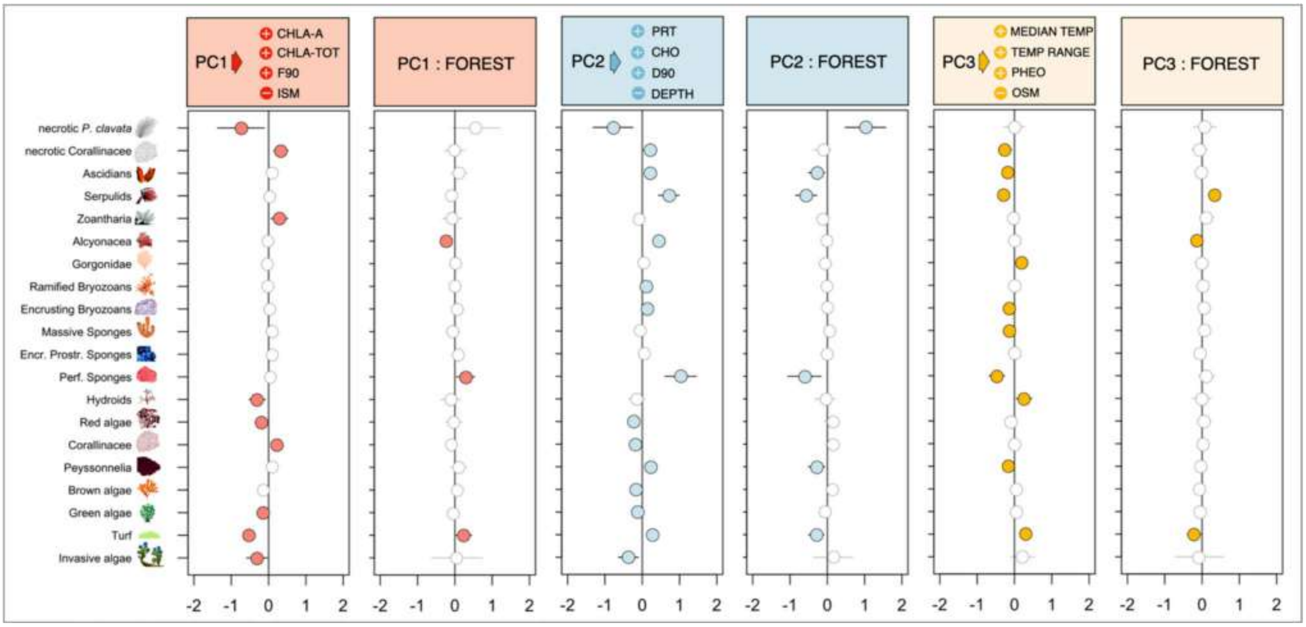

Fig. 3 Effect of the PCs (Principal Components) on group abundance as predicted by the Generalized Linear Latent Variable Model (GLLVM). Coefficient plots show the point estimates (circle) for coefficients of the predictors and their 95% confidence intervals (lines) for the GLLVM. Colored circles located to the right of the zero-crossing show positive coefficients (thus association), while those positioned to the left show negative coefficients. White circle and gray lines denote intervals containing zero and thus not significant for the model

on Akaike's information criterion (AIC). The best model was validated through graphical inspection of residuals (i.e., residuals vs. fitted values to assess homogeneity; and residuals vs. each explanatory variable to check for independence). The GLMMs were performed using the package glmmTMB (Brooks et al. 2017). Pairwise comparisons among the levels of the interactions (presence of *P. clavata* and period; presence of *P. clavata* and region) were performed using the "emmeans" package 5) (Lenth and Piaskowski 2025). Estimated marginal means (EMMs) were computed for each factor combination, and pairwise contrasts were evaluated with Tukey's adjustment for multiple comparisons.

Results

Environmental data

High variability at the scale of regions (hundreds of kilometers) was found for all the environmental variables (Fig. SM3), while temporal variations were only found for ISM and PHEO (Fig. SM4).

The twelve environmental variables were reliably represented by the first three principal components, as indicated by the bootstrap analysis (Table SM1). The first principal component (PC1) explained 26% of the variance and was positively associated with F90, CHLA-A, and CHLA-TOT and negatively associated with ISM. The second principal component (PC2) explained 20% of the variance and was positively associated with D90, CHO, and PRT and negatively associated with DEPTH. The third principal component (PC3) explained 10% of the variance and was positively associated with MEDIAN TEMP, TEMP RANGE, and PHEO and negatively associated with OSM (Fig. 2; Table SM1).

Predictors of coralligenous community structure

A significant relationship between environmental variables, the presence of *P. clavata* forests, and the abundance of most groups (Fig. 3) was found. Higher concentrations of CHLA-A and CHLA-TOT, an increased number of heating events (F90), and lower ISM concentrations (indicated by higher PC1) were associated with a reduced abundance of hydroids, turf, red, green, and invasive algae, and a greater abundance of necrotic and live Corallinaceae and Zoantharia. In the presence of *P. clavata* forest, higher PC1 values were positively associated with an increased abundance of perforating sponges and turfs but negatively associated with the abundance of Alcyonacea (Fig. 3, Table SM2).

Reduced depth, increased duration of heating events (D90), and higher PRT and CHO concentrations (indicated by higher value of PC2) were related to greater abundance

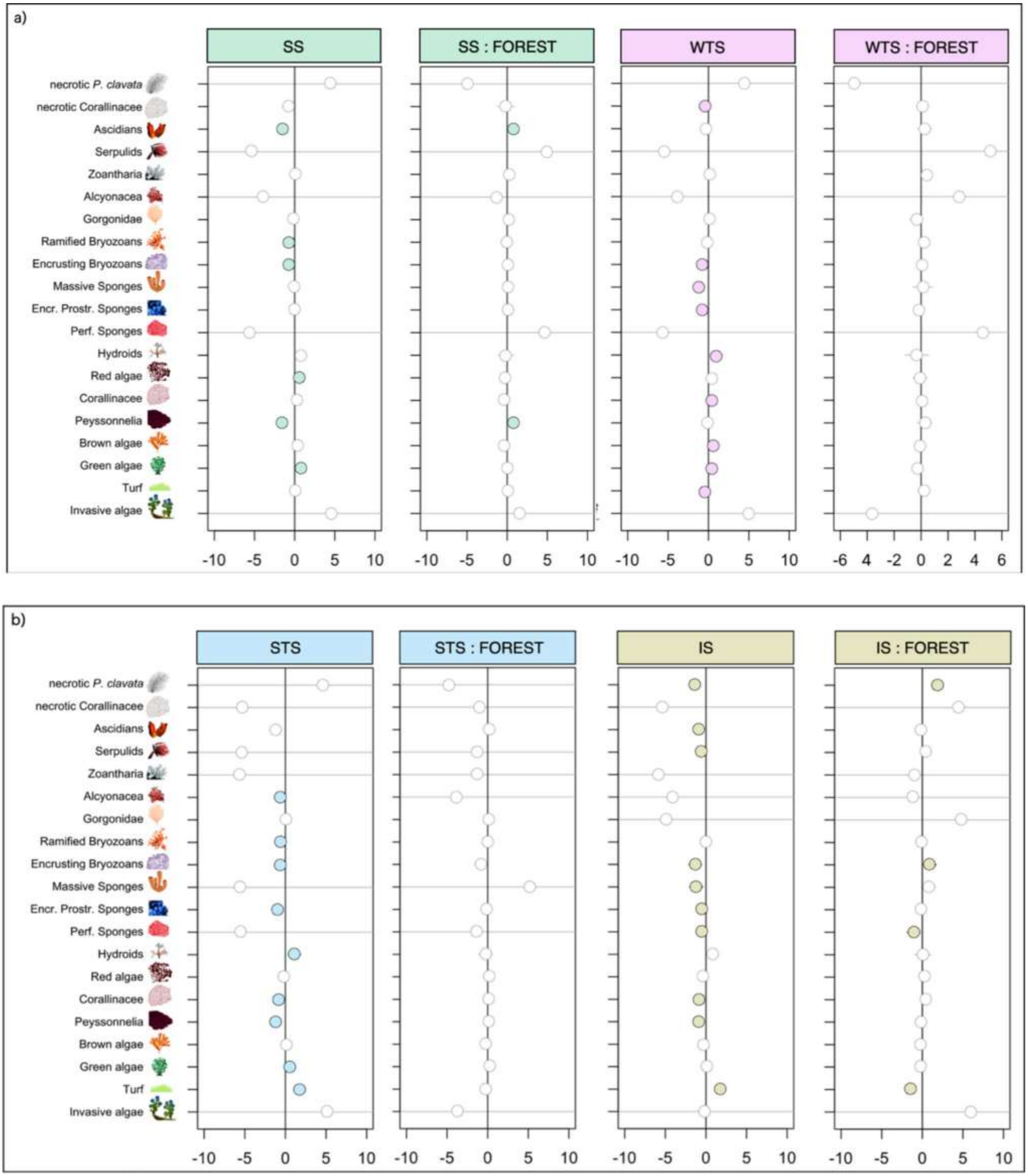

Fig. 4 Effect of region on group abundance as predicted by the Generalized Linear Latent Variable Model (GLLVM). ETS was set as the reference level, as it represents the intermediate region among the five sampled ones distributed along the North–South and West–East axes. Coefficient plots show the point estimates (circle) for coefficients of the predictors and their 95% confidence intervals (lines) for the GLLVM. Colored circles located to the right of the zero-crossing show positive coefficients (thus association), while those positioned to the left show negative coefficients. White circle and gray lines denote intervals containing zero and thus not significant for the model. **a** SS: Sardinian Sea; WTS: Western Tyrrhenian Sea; **b** STS: Southern Tyrrhenian Sea; IS: Ionian Sea

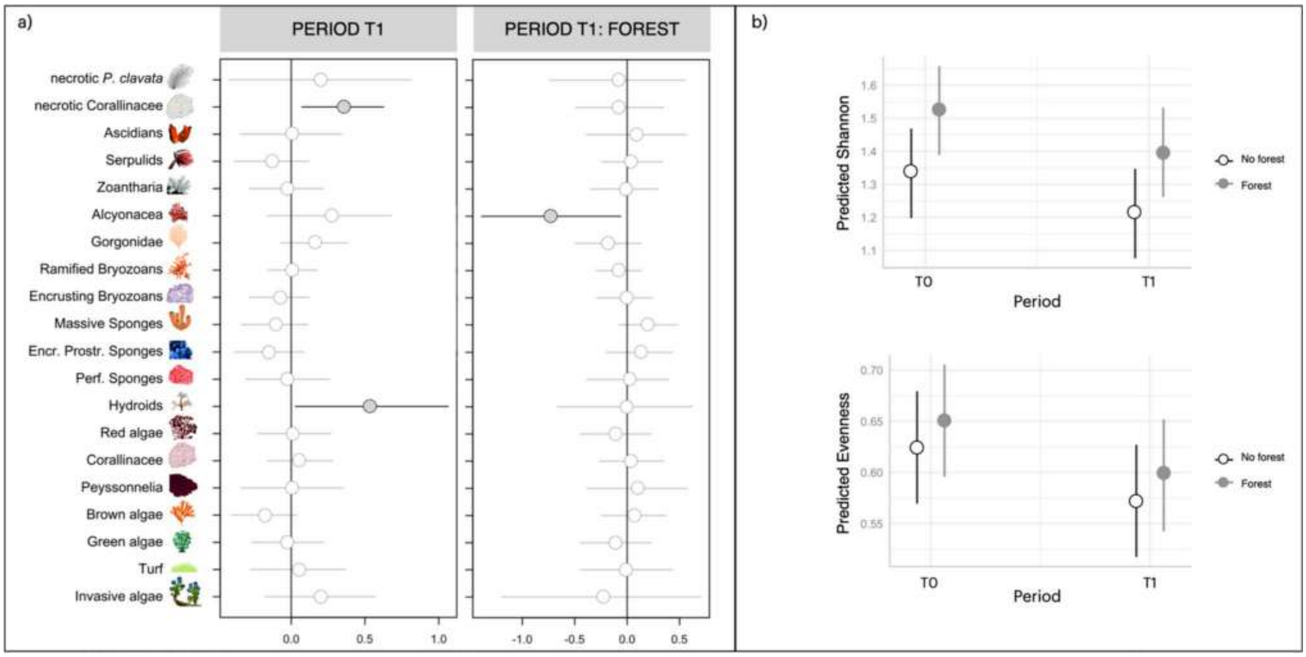

Fig. 5 **a** Effect of period on group abundance as predicted by the Generalized Linear Latent Variable Model (GLLVM). Coefficient plots show the point estimates (circle) for the coefficients of the predictors and their 95% confidence intervals (lines) for the GLLVM. Colored circles located to the right of the zero-crossing show positive coefficients (thus association), while those positioned to the left show negative coefficients. White circle and gray lines denote intervals containing zero and thus not significant for the model. **b** Effect of the interaction between period and forest on Shannon and Evenness indices as predicted by the GLMMs (only significant results are shown)

of necrotic Corallinaceae, ascidians, serpulids, Alcyonacea, ramified and encrusting bryozoans, perforating sponges, *Peyssonnelia*, and turfs, and lower abundance of necrotic *P. clavata*, Corallinaceae, and red, green, brown, and invasive algae. In the presence of *P. clavata* forest, higher PC2 values were associated with a higher abundance of necrotic *P. clavata* and a lower abundance of ascidians, serpulids, perforating sponges, *Peyssonnelia*, and turf algae (Fig. 3, Table SM2).

Reduced OSM concentration, increased PHEO, and higher MEDIAN TEMP and TEMP RANGE (indicated by greater values of PC3) were associated with a higher abundance of Gorgonidae, hydroids, and turfs, but also with a lower abundance of necrotic Corallinaceae, ascidians, serpulids, encrusting bryozoans, massive and perforating sponges, and *Peyssonnelia*. However, in the presence of *P. clavata* forest, PC3 values were positively related to the abundance of serpulids and negatively to the abundance of Alcyonacea and turfs (Fig. 3, Table SM2). The PCs explained 19% of the covariation in group abundance, suggesting that other factors may have also influenced the coralligenous community structure.

Regional differences strongly influenced most groups in the coralligenous community. However, this influence appeared to be limited to a few morphological groups when regions with *P. clavata* forest were compared to regions with no forests (Fig. 4a and b, Table SM3). Region explained 45% of the covariation in group abundance. Finally, the relationship between period and group abundance was limited to a few of them, also when the interaction with *P. clavata* forest was considered (Fig. 5a, Table SM4). Period explained 12% of the covariation in group abundance.

To assess the factors most strongly influencing the abundance of coralligenous groups, the candidate models were compared using Akaike Information Criterion (AIC). The model including the interaction between forest and region exhibited the lowest AIC value (−7401.715), indicating that region is the most important predictor in explaining the abundance of coralligenous groups. The second-best model, which included the interaction between forest and PCs, had a higher AIC value (−6607.320) suggesting that environmental factors represented by the principal components also contributed significantly to the observed patterns, though to a lesser extent than region. The model including the interaction between forest and period with an AIC of −6599.582, was the least supported, suggesting that temporal changes have a relatively minor effect on coralligenous group abundance in comparison to region and environmental.

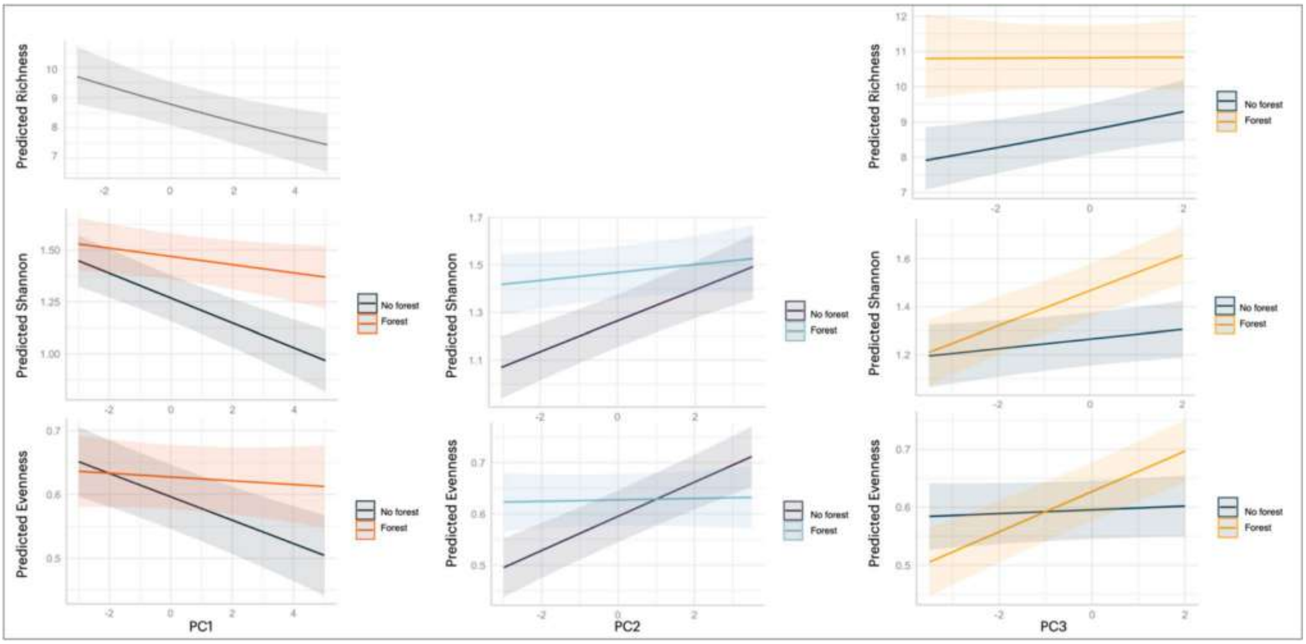

Fig. 6 Effect of the Principal Components (PCs) on richness and the interaction between PCs and forest on Shannon and Evenness indices as predicted by the Generalized Linear Mixed Models (GLMMs). Only significant results of the predictors selected by the best models are shown. PC1 was positively associated to F90, CHLA-A and CHLA-TOT and negatively associated to ISM; PC2 was positively associated to D90, CHO and PRT and negatively associated to depth; PC3 was positively associated to MEDIAN TEMP, TEMP RANGE and PHEO and negatively associated to OSM

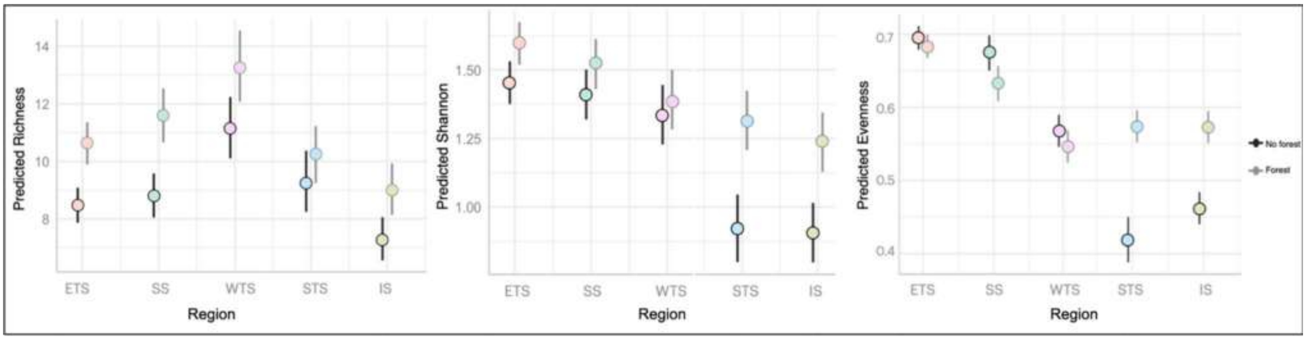

Fig. 7 Effect of the interaction between region and forest on richness, Shannon, and Evenness indices as predicted by the Generalized Linear Mixed Models (GLMMs). ETS: Eastern Tyrrhenian Sea; SS: Sardinian Sea; WTS: Western Tyrrhenian Sea; STS: Southern Tyrrhenian Sea; IS: Ionian Sea

Ecological indices

Based on the AIC comparisons, the models including the interaction between forest and the PCs obtained the lowest AIC value, indicating that the environmental conditions are the most important predictors in explaining the ecological indices, followed by the models including the interaction between forest and regions and those including the interaction between forest and period (Table SM5).

All the ecological indices analyzed (richness, Shannon, and Evenness indices) were negatively influenced by the PC1 and positively influenced by the PC2 and PC3, both as fixed terms and in interaction with the presence of *P. clavata* forest, with the only exception of richness (Fig. 6, Table SM6). Further, all indices were influenced by the regions, both as fixed terms and in interaction with the presence of *P. clavata* forest (Fig. 7, Table SM7). Particularly: i) richness was significantly higher in forested areas across most regions (ETS, WTS, SS, IS), with the exception of the STS; ii) Shannon index was significantly higher in forested areas in the ETS, STS, and IS; iii) Evenness index was higher in forested areas of the STS and IS, but lower in the SS (Fig. 7,

Table SM7). While richness was only influenced by the presence of *P. clavata* forest, both Shannon and Evenness indices were lower at T1 compared to T0, both in the presence and absence of *P. clavata* forest (Fig. 5b, Table SM8).

Discussion

In this study, the complex array of factors shaping the structure of coralligenous communities — including the thermal environment, depth, and the availability of trophic resources across different regions and periods — was examined, with particular attention to how the presence of *P. clavata* forests modulates their effects.

Environments characterized by high productivity and transparency—represented by higher concentrations of chlorophyll (CHLA-A and CHLA-TOT), greater frequency of heating events (F90), and lower concentrations of inorganic suspended matter (ISM) (PC1)—were linked to a decrease in the abundance of several groups, such as hydroids, red and green algae, turf algae, and a reduced presence of necrotic *P. clavata*. Environments indicative of apparent trophic enrichment — represented by longer heating events (D90), higher concentrations of proteins (PRT) and carbohydrates (CHO), and shallower depths (PC2) — were correlated with an increase in the abundance of several groups, including Alcyonacea, perforating sponges, serpulids, various bryozoans, turf algae, and necrotic Corallinaceae, along with a decrease in invasive algae. However, in forested areas, an increase in *P. clavata* necrosis was observed despite the apparent trophic enrichment found in shallow waters under prolonged thermal stress. Although higher CHO and PRT concentrations might suggest greater food availability, prolonged thermal stress can stimulate the microbial loop, altering substrate quality and increasing metabolic stress. Indeed, thermal stress elevates organism metabolic demands (by increasing baseline respiration), degrades substrate conditions (e.g., through greater organic loading and microbial activity), and can induce shifts in symbiotic or microbiome communities, intensifying physiological damage. *Paramuricea clavata* colonies have been shown to face microbiome shifts under thermal stress, with increases in opportunistic or potentially pathogenic taxa associated with higher susceptibility and disease (Bonacolta et al. 2023). This, in turn, can exacerbate colony necrosis (Chimienti et al. 2021; Gómez-Gras et al., 2022; Rubio-Portillo et al. 2021). Lastly, in degraded trophic environments—represented by higher temperature (both median and range), organic suspended matter (OSM), and pheophytin concentrations (PC3)—organic matter is largely senescent, and the availability of "fresh" trophic resources is likely limited. Under these conditions, opportunistic groups such as hydroids and turf algae tend to increase in abundance, whereas more sensitive filter-feeding and encrusting organisms (e.g., sponges, *Peyssonnelia*, and bryozoans) decline (Coma et al. 2002; Torrents et al. 2008; Previati et al. 2010).

Interestingly, the presence of *P. clavata* forests influenced the relationship between environmental factors and the abundance of morphological groups and ecological indices, highlighting their key role in shaping community structure and dynamics. For example, the positive association between PC2, PC3, and the abundance of turf and perforating sponges becomes negative in forested areas, suggesting the capacity of gorgonian forests to limit the spread of opportunistic species (Ponti et al. 2014; Piazzi et al. 2021a, b). Similarly, the positive association between PC1, PC2, and the abundance of necrotic Corallinaceae was also reversed by the presence of *P. clavata* forests, likely indicating their potential ability to buffer the impact of heating events and trophic enrichment on these encrusting red algae. However, these results should be interpreted with caution, as the PCs used in the analysis do not represent individual environmental gradients exactly, but rather combinations of multiple gradients, each associated with its own degree of error inherent to the PCA method.

Regional variation is a key driver of coralligenous community structure (Piazzi et al. 2021b), likely due to evolutionary forces (Silva et al. 2021), biotic interactions, dispersal, and connectivity (the latter influenced by large-scale hydrodynamic structures; García-Girón et al. 2020; Bandelj et al. 2020). In fact, the model comparisons revealed that regional effects were the most significant predictor of morphological group abundance, as indicated by the lowest AIC value. Furthermore, 45% of the observed covariation in group abundance was attributable to regional effects. Clear regional differences were also observed in the ecological indices, emphasizing that the scale of hundreds of kilometers represents a meaningful scale of variation. Spatial patterns in coralligenous communities have previously been linked primarily to biotic factors, owing to the relatively stable environmental conditions that characterize this deep ecosystem (Ballesteros 2006). Instead, short-term temporal changes, although present, had a relatively minor influence compared to the effects of region and environmental variables, in agreement with other studies in the Mediterranean Sea (Garrabou et al. 2002; Teixidó et al. 2011, 2013; Casas-Güell et al. 2015). The observed negligible influence of period on coralligenous community structure is consistent with the life traits of the main morphological groups that contribute to the structure and abundance of these sciaphilous communities, which are long-lived organisms with low dynamics (Coma et al. 2003). However, Shannon and Evenness indices were lower in T1 compared to T0, regardless of the presence of *P. clavata* forests, suggesting a slight temporal shift in biodiversity and community evenness after summer.

The patterns described here reinforce the role of gorgonian forests in buffering the effects of environmental modifications compared to surrounding 'unforested' areas (for example, through structural stability, shading effects, or filtration activities), further supporting the diversity, distribution, and abundance of many organisms (Cerrano et al. 2010; Ponti et al. 2018; Piazzi et al. 2021a). Additionally, regional effects on group abundance were less pronounced in the presence of *P. clavata* forests, supporting the hypothesis that coralligenous reefs dominated by gorgonian forests display similar community structures, even at regional scales (Casas Guell et al. 2015). Further, greater values of richness, diversity, and evenness were observed within the forests across all regions (with few exceptions), supporting the hypothesis that the increased three-dimensional complexity (and the related available space and microhabitats) created by *P. clavata* forest is positively associated with species diversity (Ponti et al. 2018). The relevant role of *P. clavata* forest in influencing diversity and richness of the community here found is in accordance with other studies evaluating the significance of gorgonian forests on the understory species (Scinto et al. 2009; Ponti et al. 2014, 2016, 2018; Valisano et al. 2016; Gatti et al. 2017), but also with the same finding on other habitat-forming species in different ecosystems (Wernberg et al. 2008; Gorman & Connell 2009).

Even though disentangling the factors influencing highly biodiverse communities—and the contribution of habitat-forming species—remains particularly challenging, the current findings provide insight into the complex role of *P. clavata* forests in shaping coralligenous communities across varying regional, temporal, and environmental contexts. However, our models only accounted for a portion of the covariation observed among the different morphological groups, highlighting the need for future research to include additional drivers such as hydrodynamics and connectivity. Furthermore, extending the temporal scale of studies will be crucial to capture long-term ecological processes that may not be evident within the short timeframe considered in this study, especially in the context of climate change (Ramirez-Calero et al. 2024). For example, under severe enrichment and higher thermal stress (PC2), higher evenness values were found in areas without *P. clavata*. This pattern might indicate a subtle enrichment that promotes the inclusion of new species without species turnover, possibly due to a delayed response of the benthic community to stress that may become evident in the long term.

Extensive gorgonian mortality events that have already occurred in the Mediterranean Sea (Garrabou et al., 2009, 2019; Coma et al. 2004; Cerrano et al. 2005) lead to the fragmentation and loss of gorgonian forests. Such events could significantly reduce habitat complexity, species diversity, and ecosystem functioning, while weakening the resilience of affected communities, and thereby diminishing the buffering role of *P. clavata* under increasingly variable environmental conditions.

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Author Contribution GC, SF, GS, OM, GLM conceived and planned the experiments. GLM, FB, MBB, AC, CDM, YF, LL, FPM, OM, GM, SMSM, BMP, AP, LP, FP, MP, AP, PS, MFT collected and analyzed data. GLM, MBB, GC, SF, GS, OM wrote the main manuscript text. All authors reviewed the manuscript.

Data Availability Data have been provided as supplementary material.

Declarations

Conflict of interests The authors declare no competing interests.

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