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ARTICLE

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Sedimentation-driven environmental filtering shapes community assembly of cryptic coralline algae

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Abstract

Community assembly of cryptic crustose coralline algae (CCA) underlies the formation of algal reefs across the global ocean, yet the ecological mechanisms shaping these communities remain poorly understood. Sedimentation has been linked to variation in CCA community structure across the Taoyuan Algal Reef (TAR), the world's largest subtropical intertidal algal reef, which occurs in a high-sediment environment. To understand how sedimentation affects CCA community assembly in the TAR, we compared the ecology, geographic distributions, and physiological responses of the CCA from the TAR with those in the New Taipei City Reef (NTCR), a nearby coral reef occurring in a low-sediment environment. By analyzing the benthic cover data and the DNA barcoding data (from 632 CCA specimens) collected in this study and our previous study of the TAR, we found that the high intertidal CCA cover in the TAR was driven by two dominant species (*Harveylithon* sp. and *Sporolithon* sp.), in contrast to the lower CCA cover in the NTCR occupied by a more diverse CCA species pool. Based on these observations, we hypothesized that CCA dominant in the TAR are more tolerant to sediment accumulation than the CCA dominant or common in the NTCR. To test this hypothesis, we conducted sediment burial experiments on *Harveylithon* sp. and *Sporolithon* sp., as well as *Harveylithon catarinense* and *Lithophyllum* sp., which were common in the NTCR but absent in the TAR. These experiments demonstrated that *Harveylithon* sp. and *Sporolithon* sp. exhibited higher physiological tolerance to prolonged sediment burial than *H. catarinense* and *Lithophyllum* sp. In addition, the occurrence data from our previous study (1736 CCA specimens collected around Taiwan and nearby areas) showed that *H. catarinense* and *Lithophyllum* sp. were widely distributed, suggesting that dispersal limitation unlikely explains their absence in the TAR. Together, these results provide strong evidence that heavy sedimentation acts as a powerful environmental filter in the TAR, favoring sediment-tolerant CCA and promoting their ecological dominance. Our findings highlight the role of physiological tolerance in shaping CCA communities and in supporting the formation, resilience, and ecosystem functioning of algal reefs.

KEYWORDS
algal reef, community assembly, environmental filtering, physiological tolerance, sediment burial

INTRODUCTION

A central goal of ecology is to disentangle how environmental filtering, dispersal limitation, and biotic interactions shape community assembly (Keddy & Laughlin, 2021). Environmental filtering influences the species composition of biological communities by excluding taxa that cannot physiologically tolerate local abiotic conditions (Belyea & Lancaster, 1999; Keddy, 1992), consequently impacting ecological patterns (e.g., Thakur & Wright, 2017), resilience of communities to disturbances (e.g., Capdevila et al., 2021), and ecosystem response (e.g., Bagousse-Pinguet et al., 2017). Studies that attribute changes in community structure to environmental filtering often rely on correlation of observed biodiversity data along abiotic gradients (e.g., Zhan et al., 2022); however, these data can be confounded by dispersal limitation and biotic interactions. It has been proposed that robust evidence for environmental filtering requires testing physiological tolerance through experimentation, in isolation from these confounding factors (Kraft et al., 2015).

The widespread use of molecular tools like DNA barcoding to identify species has revealed extensive diversity of cryptic (morphologically indistinguishable) species across ecosystems. Failing to account for this hidden biodiversity can misguide conservation efforts and obscure our understanding of key ecological processes (Bickford et al., 2007; Fišer et al., 2018; Hending, 2025). Ecological studies that take a functional group approach lump cryptic species together, treating them as a single functional group. This approach is appropriate if the species in question have similar ecological and physiological traits or play similar functional roles (e.g., Littler & Littler, 1984; Mauffrey et al., 2020; Steneck & Detheier, 1994). However, different cryptic species can respond differently to environmental changes and make different contributions to ecosystem functioning (e.g., Burgess et al., 2021; Grupstra et al., 2024; Hind et al., 2019; Peña et al., 2021; Schubert et al., 2024).

Reefs formed by crustose coralline algae (CCA), or "algal reefs," are vital marine habitats in the intertidal and subtidal zones occurring around the world's coasts. Their roles as biodiversity hotspots (McCoy & Kamenos, 2015) and in global carbon cycling are increasingly appreciated (Cornwall et al., 2023; Mao et al., 2024; Schubert et al., 2024; van der Heijden & Kamenos, 2015), leading to calls to better understand their ecology as they are threatened by human activities and climate change (Tuya et al., 2023). In the literature, algal reefs are called by miscellaneous names, depending on CCA growth form, reef size, and reef shape (rhodolith bed, algal ridge, algal cup, algal cascade, or coralligenous reef; e.g., Adey, 1978; Ballesteros, 2006; Foster, 2001; Ginsburg & Schroeder, 1973; Richards & O'Leary, 2015; also, for clarification on the terms used to refer to coralline algae-dominated habitats, see Jardim et al., 2025). They often thrive in low-sediment environments characterized by either (1) high light availability and strong waves or (2) low light availability and moderate water movements. Algal reefs may uncommonly occur in high-sediment environments (Steneck et al., 1997). Recent studies using DNA barcoding to detect cryptic CCA species have revealed previously overlooked ecological patterns of variation in CCA community structure in reef ecosystems (e.g., Hind et al., 2019; Peña et al., 2021; Ramos et al., 2025), but the ecological mechanisms behind these patterns are still poorly understood.

Sedimentation is a key driver of disturbance in reefs around the world and is increasingly exacerbated by human activities and climate change (He & Silliman, 2019). Sediment accumulation causes light attenuation and physical smothering (i.e., anoxia and hydrogen sulfide toxication) by burial, creating abiotic conditions unfavorable to the survival and growth of benthic organisms. In extreme cases, intense sedimentation can result in degradation of reef habitats and loss of their ecosystem function (Rogers, 1990). Thus, sedimentation creates a powerful abiotic filter on the communities in reefs.

The Taoyuan Algal Reef (TAR) is the largest subtropical intertidal algal reef in the world, spanning ~27 km along the northwestern coast of Taiwan (Liou et al., 2017; Zhan et al., 2022). Formed by an assemblage of cryptic CCA (Zhan et al., 2022), the TAR is a hotspot for marine biodiversity, but it is under pressure from coastal development and industrial runoff (Chen et al., 2022; Heard et al., 2021; Kuo et al., 2020; Zhan et al., 2022). Remarkably, the TAR withstands extremely heavy sediment accumulation, which coral reefs cannot withstand (Kuo et al., 2020). In contrast, the New Taipei City Reef (NTCR), a nearby intertidal coral reef occupied also by CCA (Kuo et al., 2023), occurs in clear waters due to a much lower level of sediment accumulation. Together, the TAR and the NTCR form a rare "natural laboratory" for investigating how sedimentation affects the community assembly of a key marine ecosystem engineer.

Here, we used this two-reef system to examine the effect of sediment accumulation on the community assembly of CCA. First, we compared the ecological backgrounds of the reefs in terms of the benthic composition of functional groups, sediment accumulation, local water chemistry, and marine climate. Second, we compared the community structures of cryptic CCA in the reefs exposed by DNA barcoding, and we identified four CCA species with markedly different relative abundances between the high-sediment TAR and the low-sediment NTCR. Third, to assess evidence for dispersal limitation, we examined the geographic distributions of these four CCA species around Taiwan and nearby areas. Finally, using sediment burial experiments, we tested whether the four CCA species have different levels of physiological tolerance to prolonged sediment burial. Our findings highlight that a key physiological response to an important environmental filter can underlie the relationship between the community structure and ecological dominance of CCA in reefs.

MATERIALS AND METHODS

Benthic surveys and benthic composition analysis

The TAR and the NTCR are situated ~50 km apart along the northwestern coastline of the main island of Taiwan (Appendix S1: Figure S1). In Zhan et al. (2022), we conducted benthic surveys and extensive biodiversity surveys at various sites in the reefs. In the current study, we used these survey data to compare the benthic composition of the functional groups (this section) and the CCA biodiversity in the reefs (see *Biodiversity surveys and community structure analysis*).

In Zhan et al. (2022), we conducted benthic surveys at the TAR (Datan G2) and the NTCR (Shimen) during three field visits per site between May 2018 and March 2019 (Appendix S1: Figure S1). These benthic surveys were performed in the lower region of the intertidal zone using 10-m permanent line transects, each of which had three sections. We estimated the percent cover of benthic objects per section of each line transect (18 sections in total). Briefly, we used image analysis to classify benthic objects in the photographs taken along the line transects into six categories: CCA, frondose macroalgae, turf macroalgae, articulated coralline algae, Zoantharia, and "others" (which includes rocks, sediments, and water). We estimated the percent cover of each type of benthic object in each photograph based on 40 random points using CPCe v3.3 (Kohler & Gill, 2006). For further details, see Zhan et al. (2022). In Zhan et al. (2022), we presented only the data from the benthic surveys of the TAR, which is the focus of that study. Here, we present new data from the benthic surveys of the NTCR to allow comparison of the benthic compositions of the two reefs.

To test whether there were differences in the benthic compositions of the TAR and the NTCR, we performed a permutational multivariate analysis of variance (PERMANOVA) test, using Bray–Curtis dissimilarity to quantify the dissimilarity between the percent covers of the line transect sections. To control for seasonal effects, we constrained permutations on the percent covers from the same season (in total, 19,999 rounds of permutation). Calculations of Bray–Curtis dissimilarity and the PERMANOVA test were done using the functions *vegdist* and *adonis2* in the R package vegan v2.6-8 (Oksanen et al., 2024), respectively.

Measurements of local environmental factors

We measured the amount of sediment accumulation and several parameters of water chemistry (salinity, pH, total phosphate, and total nitrogen) in the reefs. These measurements were taken once per field visit during our benthic surveys. The data for the TAR (Datan G2) are already published in Zhan et al. (2022), but not the data for the NTCR (Shimen), which are reported in the current study.

To quantify total suspended sediments (in milligrams per liter), we measured the dry mass of total suspended sediments after filtration using 0.7-μm Whatman glass microfiber filters. We measured salinity and pH in situ using a multiparameter Hanna waterproof meter (HI98194, HANNA instruments, Dogger, New Taipei City). For nutrient and sediment quantification, we collected 500 mL of seawater during low tide and divided it equally into two 250-mL subsamples, one for nutrient analysis and the other for total suspended sediment analysis. To determine concentrations (in parts per million) of total phosphate and total nitrogen (ammonia, nitrate, and nitrite), we measured these nutrients using a LaMotte Smart3 colorimeter (Smart3 No. 1910, Smartec Scientific, Taipei), following the manufacturer's protocol.

To quantify the magnitude of difference in the aforementioned environmental factors between the TAR and the NTCR, we calculated Hedges' g_{av}, which is a standardized measure of effect size that allows comparison of variables in different measurement units. This approach standardizes the mean difference by the average of the two SDs and then applies Hedges' correction (Morris & DeShon, 2002). Larger absolute values of this statistic indicate greater differences. We calculated Hedges' g_{av} for each environmental factor using the measurement data. Hedges' g_{av} was calculated using the function *repeated_measures_din* the R package effectsize v1.0.1 (Ben-Shachar et al., 2020).

Marine climate analysis

We compared the year-round marine climatic conditions in the TAR and the NTCR. We took the historical monthly averages of sea surface temperature (SST) and wind speed in the TAR and the NTCR from 2019 to 2023. SST in the TAR and the NTCR was monitored at the Jhuwei tide station (25.12° N, 121.24° E) and the Linshanbi tide station (25.28° N, 121.51° E), respectively. Wind speed in the TAR and the NTCR was monitored at the Xinwu tide station (25.006744° N, 121.047486° E) and the Baishawan tide station (25.283129° N, 121.51906° E), respectively. The data were sourced from the Central Weather Administration, Taiwan (SST: https://opendata.cwa.gov.tw/dataset/climate/C-B0050-001; wind speed: https://codis.cwa.gov.tw/StationData; accessed: December 7, 2024). To compare the magnitude of difference in SST and wind speed between the TAR and the NTCR per month and across the year, we treated the data from each year as independent replicates. Then, we calculated Hedges' g_{av} as described in the previous section.

Biodiversity surveys and community structure analysis

In Zhan et al. (2022), we conducted biodiversity surveys at six sites in the TAR (including Datan G2 and Baiyu, which are ~5 km apart) and two sites in the NTCR (Shimen and Cianshueiwan) (Appendix S1: Figure S1). In that study, we performed DNA barcoding (using the *psb*A marker gene) on specimens collected from three different types of substrates (reefs, cobbles, and snails) across these eight sites. We detected cryptic CCA species in the form of molecular operational taxonomic units (mOTUs), as inferred in a species delimitation analysis. In Zhan et al. (2022), we used these multi-substrate data in an analysis of the CCA biodiversity in the TAR, which is the focus of the study. In the current study, we reused these data (which consist of 632 specimens) to compare the CCA community structures of the TAR and the NTCR. Also, we focused on the CCA found on reef substrates, which are a stable part of the reef communities, in contrast to the CCA found on cobbles and snails, which are likely transient.

To assess saturation in mOTU diversity sampling, we used rarefaction curves. To quantify CCA diversity, we used diversity indices (species richness, Shannon's index, and Simpson's index) and rank abundance curves. To examine similarities and differences in the CCA community structure between the reefs, we performed hierarchical clustering of per-site mOTU compositions, which were calculated as Hellinger-transformed relative abundances (RAs).

The rarefaction analysis and diversity index calculations were done using iNEXT v3.0.2 (Chao et al., 2014). Hierarchical clustering (with complete linkage) was done using the function *hclust* in the R package stats (R Core Team, 2024). Hellinger-transformation was done using the function *decostand* in the R package vegan v2.6-8 (Oksanen et al., 2024).

Collection and DNA barcoding of specimens for sediment burial

We collected bulk specimens from the TAR (Baiyu) and the NTCR (Shimen) between August 2022 and June 2024 (for notes on specimen handling, see Appendix S1: Extended methods). We had originally planned to collect bulk specimens from the TAR at Datan G2 (where we conducted the benthic surveys described in *Benthic surveys and benthic composition analysis*, above), but our access to Datan G2 was restricted due to the ongoing construction of a nearby liquefied natural gas port; therefore, we collected bulk specimens from Baiyu instead. During field collection, we took care to avoid bulk specimens showing nonuniform external morphology, such as overlapping thallus layers and mosaic pigmentation, which indicates the presence of multiple CCA species from our experience (see Zhan et al., 2022). We kept bulk specimens showing a simple, continuous, and non-overlapping thallus layer and uniform pigmentation.

Next, we performed DNA barcoding to determine the mOTUs of the bulk specimens. For each bulk specimen, we arbitrarily sampled two or three tissues and performed DNA barcoding using the *psb*A marker gene on each tissue. DNA was extracted with the All Tissue Extraction Kit (Yeastern Biotech, Shijr, Taiwan). Polymerase chain reaction (PCR) was conducted with coralline-specific primers psbA21-350F and psbA22-350R (Anglès d'Auriac et al., 2019) using the experimental conditions of Zhan et al.

(2022). PCR products were Sanger sequenced (Genomics Biotechnology, Taipei), and the resulting DNA sequences were assigned to mOTUs by matching them using blastn (Camacho et al., 2009) against the *psb*A sequences from Zhan et al. (2022), which have been assigned to the mOTUs defined in Zhan et al. (2022) and linked to taxonomic species.

Sediment burial experiments

To assess the physiological tolerance to sediment burial for four CCA species (mOTU014, mOTU023, mOTU066, and mOTU139; see *Results*: *Selection of mOTUs for sediment burial experiments* for the rationale behind their selection), we carried out months-long sediment burial experiments in a controlled tank environment. Briefly, the experiments were conducted in a 200-L seawater tank with continuous water circulation under controlled conditions (light intensity and temperature), where the control replicates were unburied but the treatment replicates (pieces of bulk specimens) were buried with 25–30 cm of sediments (this burial depth was sufficient to create an anoxic environment; see below). A detailed description of the experimental setup (Appendix S1: Figure S2) and some notes on specimen handling are provided in Appendix S1: Extended methods. To quantify tolerance to sediment burial, we measured the amount of bleaching and recovery of photosynthetic activity after 1 month or 3 months of burial (see *Quantification of bleaching* and *Measurement of photosynthetic activity*).

To bury the treatment replicates, we used sediments from the TAR (Baiyu), which were collected from the surface down to a depth of ~30 cm near the reef. Our grain size analyses showed that the sediments primarily consisted of sand (98.64% sand, 1.25% gravel, and 0.11% mud) and the sand grains were mainly medium-sized (~83%) (Appendix S1: Extended methods and Table S1). It has been shown that medium-sized sand sediments can smother many kinds of reef organisms, including corals, during short-term burial (e.g., Jones et al., 2016; Rogers, 1990). Using an oxygen depletion analysis, we confirmed that the sediments can induce anoxic conditions within just one day of sediment burial (Appendix S1: Extended methods and Table S2).

Quantification of bleaching

Bleaching caused by algal tissue degradation and pigment loss indicates mortality in coralline algae (Krieger et al., 2023; Martone et al., 2010). To quantify bleaching, we measured the amount of whitening on the replicates at two time points (see below) using top-down photography and image analysis (for additional notes, see Appendix S1: Extended methods). For the treatment replicates of mOTU023, mOTU066, and mOTU139, we took photos before burial and on day 14 after excavation. For the treatment replicates of mOTU014, we took photos before burial and on day 5 after excavation. In addition, we took photos on the same days for the corresponding control replicates. For a timeline showing when these photos were taken, see *Results*: *Less bleaching in the CCA from the TAR versus the NTCR*. We define the amount of bleaching ("bleaching proportion") as the proportion of a tracked area on a replicate that lost color. Further, we define an increase in bleaching proportion as the bleaching proportion at a post-excavation time point subtracted by the bleaching proportion at a preburial time point (which was always nearly zero).

To test whether there were differences in the increase in bleaching proportion between the control group and the treatment groups (buried for 1 month or 3 months), we used the two-sided exact Wilcoxon–Mann–Whitney (WMW) test, correcting for multiple tests using the Benjamini–Hochberg method. The WMW tests were done using the function *wilcox_test* in coin v1.4-3 (Hothorn et al., 2008).

Measurement of photosynthetic activity

Fv/Fm measures the maximum quantum efficiency of photosystem II (a physiological condition of chloroplasts), and it is commonly used in experiments to test the physiological tolerance of CCA (e.g., Villas-Bôas et al., 2014). We tracked the recovery of photosynthetic activity in the replicates (which had CCA tissues that were still alive after sediment burial) by measuring Fv/Fm several times over a course of time after excavation (for a timeline of these measurement events, see *Results*: *Photosynthetic activity recovery after months of sediment burial*). Using a MINI-PAM chlorophyll fluorometer (Heinz Walz GmbH, Effeltrich, Germany), we took F_v/F_m measurements (11 in total) on dark-adapted replicates on day 0 (the day of excavation); days 1–7; and days 14, 22, and 28 (for additional notes, see Appendix S1: Extended methods).

To test whether there were differences in the Fv/Fm values between the control group and the treatment groups (buried for 1 month or 3 months), we used the WMW test, correcting for multiple tests using the Benjamini–Hochberg method. We performed the WMW test for each day of measurement. The WMW tests were done using the function *wilcox_test* in coin v1.4-3 (Hothorn et al., 2008).

RESULTS

Ecological backgrounds

Our benthic surveys showed that the benthic composition of functional groups differed between the TAR (Datan G2) and the NTCR (Shimen) across seasonal field visits ($R^2 = 0.537$; $p < 0.001$; PERMANOVA test; Figure 1; Appendix S1: Table S3). The TAR had a higher cover of CCA (34% ± 15%, mean ± SD; range = 21%–65%) and a similar cover of turf macroalgae (14% ± 16%; range, 1%–42%); however, frondose macroalgae, articulated coralline algae, and Zoantharia were not observed. The NTCR had a lower cover of CCA (16% ± 7%; range = 2%–26%); a similar cover of turf macroalgae (11% ± 17%; range = 0%–47%); but higher covers of frondose macroalgae (48% ± 17%; range = 18%–70%), articulated coralline algae (4% ± 8%; range, 0%–24%),

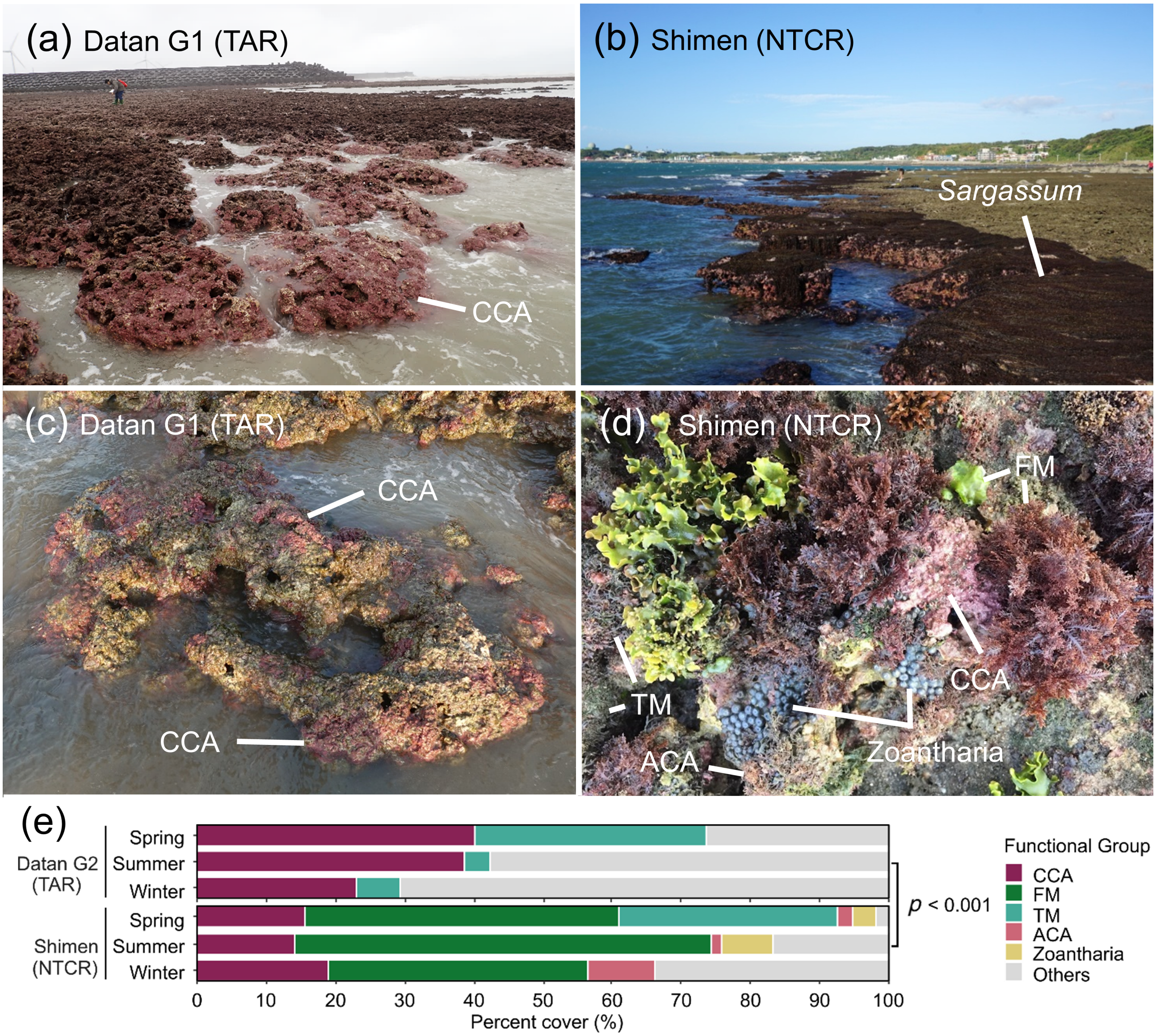

FIGURE 1 Benthic compositions of the Taoyuan Algal Reef (TAR) and the New Taipei City Reef (NTCR). (a, b) The photos show murkier waters in the TAR (Datan G1 and Datan G2) than in the NTCR (Shimen). (c, d) The photos show less diverse benthic organisms in the TAR than in the NTCR. (e) A stacked barplot shows side-by-side comparisons of the compositions of six benthic objects at the TAR (averaged over three replicates per season) and the NTCR (averaged over three replicates per season) observed during each field visit (see *Materials and methods*: *Benthic surveys and benthic composition analysis*). ACA, articulated coralline algae; CCA, crustose coralline algae; FM, frondose macroalgae; TM, turf macroalgae. Photo credits: (a) Ching-Yu Liou and (b-d) Shao-Lun Liu.

and Zoantharia (4% ± 6%; range = 0%–18%). In addition, our inventory of macroalgae showed that the species richness of non-CCA macroalgae (i.e., turf macroalgae, frondose macroalgae, and articulated coralline algae) was higher in the NTCR than in the TAR (35 vs. 14 species; Appendix S1: Extended methods and Table S4).

The TAR and the NTCR were exposed to different levels of sediment accumulation. The TAR had higher amounts of total suspended sediments (annual mean ± SD, 91.92 ± 63.38 mg/L; annual range = 42.4–196.6 mg/L; Appendix S1: Table S5), likely due to sediment discharge from nearby rivers (Appendix S1: Figure S1). In contrast, the NTCR had lower amounts of total suspended sediments (annual mean ± SD, 25.80 ± 4.77 mg/L; annual range = 19.0–32.0 mg/L; Appendix S1: Table S5), which were on average 3.6 times lower than the TAR. Moreover, during our field visits, we observed the presence of sand dunes, which indicate heavy sediment accumulation, and dramatic seasonal fluctuation of sand (or sediment) buildup in the TAR (Appendix S1: Figure S1); however, these disturbances were absent in the NTCR (S.-L. Liu, personal observation).

In addition to sediment accumulation, we considered other local environmental factors that might affect CCA community assembly in the reefs. We found that among the environmental factors measured in this study (Appendix S1: Table S5), total suspended sediments showed the largest difference between the TAR and the NTCR (Hedges' $g_{av} = 2.44$), which is markedly higher than that of the other environmental factors (Hedges' $g_{av} < 1$; Appendix S1: Figure S3). We observed that the wind speeds were higher in the TAR than in the NTCR in the summer months (May–August; Hedges' $g_{av} = 1.65$–3.54) and similar in the other seasons (Hedges' $g_{av} < 1$; Appendix S1: Figure S4), indicating higher wave action that might have contributed to higher sediment accumulation in the TAR. Furthermore, we observed that the seasonal patterns and magnitudes of SST in the TAR and the NTCR were broadly similar (Hedges' $g_{av} < 1$).

Cryptic coralline algal diversity

Next, we compared the CCA community structures of the TAR and the NTCR. We analyzed the mOTUs of CCA from the reefal specimens collected in Zhan et al. (2022): 432 specimens from the TAR (eight sites) and 200 specimens from the NTCR (Shimen and Cianshueiwan). These specimens were assigned to a total of 42 mOTUs, which were defined in Zhan et al. (2022).

Rarefaction curves indicated that mOTU diversity sampling was nearly saturated for the TAR (0.995; 95% CI = 0.989–1.000) but less saturated for the NTCR (0.950; 95% CI = 0.925–0.976) (Figure 2a). Despite this, species richness (the number of mOTUs) was lower in the TAR (22; 95% CI = 19.7–24.3) than in the NTCR (29; 95% CI = 24.6–33.4). Shannon's index was lower in the TAR (2.08; 95% CI = 1.96–2.18) than in the NTCR (2.54; 95% CI = 2.36–2.70), and Simpson's index was higher in the TAR (0.208; 95% CI = 0.184–0.237) than in the NTCR (0.127; 95% CI = 0.107–0.157), indicating lower evenness in the TAR compared to the NTCR due to a few mOTUs with high RA. In addition, we repeated these analyses and calculations using a subset of specimens from Datan G2 (TAR) and Shimen (NTCR), which are the sites where the majority of the specimens were collected, and obtained similar results (also see Appendix S1: Extended results).

Rank abundance curves revealed the mOTUs in the TAR and the NTCR with the highest RA (Figure 2b). In the TAR, *Harveylithon* sp. mOTU023 and *Sporolithon* sp. mOTU139 were the most common CCA (RA = 36.8% and 23.4%, respectively); they were also common in the NTCR (RA = 21.2% and 7.6%, respectively). In the NTCR, *Harveylithon catarinense* mOTU014 and *Harveylithon* sp. mOTU023 were the most common (RA = 24.2% and 21.2%, respectively). Despite being the most common in the NTCR, *H. catarinense* mOTU014 was absent in our specimens from the TAR (Figure 2c).

Furthermore, a clustering analysis showed the per-site mOTU compositions were more similar within each reef than between the reefs (Figure 2d). We found statistical evidence that the mOTU compositions were different between the reefs ($R^2 = 0.395$, $p = 0.035$; PERMANOVA test).

Selection of mOTUs for sediment burial experiments

We selected mOTUs for the experiments based on the results of the community structure analysis (see previous section) and the results of DNA barcoding identification of the bulk specimens (see below). Using the rank abundance curves and the presence–absence data, we identified mOTUs that were either (1) the most common in both the reefs or (2) common in the NTCR but absent in the TAR. Of such mOTUs, we selected four mOTUs for which we could collect enough bulk specimens from the field: mOTU014, mOTU023, mOTU066, and mOTU139.

We hypothesized that the high RA of *Harveylithon* sp. mOTU023 and *Sporolithon* sp. mOTU139 in the high-sediment TAR may be explained by high physiological tolerance to sediment burial. Conversely, we hypothesized that the low RA of *H. catarinense* mOTU014 in the TAR (indicated by a lack of specimens assigned to it), in

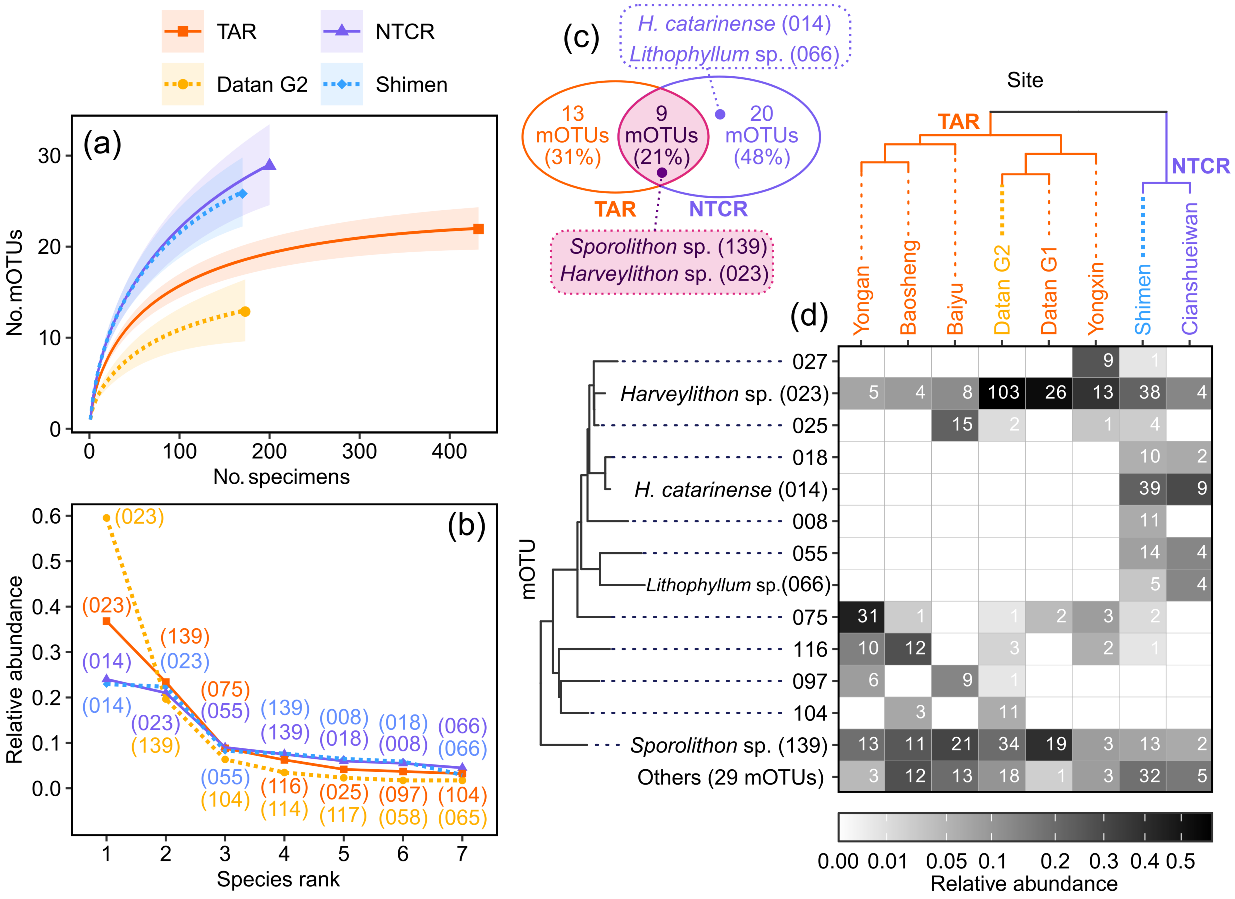

FIGURE 2 Cryptic crustose coralline algae (CCA) species diversity in the Taoyuan Algal Reef (TAR) and the New Taipei City Reef (NTCR). (a) The rarefaction curves show degree of saturation of molecular operational taxonomic unit (mOTU) diversity sampling. (b) The rank abundance curves show the most commonly observed mOTUs. (c) The Venn diagram shows the number of shared and unique mOTUs. (d) The heatmap shows the relative abundances (color-scaled) and the specimen counts of the mOTUs found at each site. The left phylogram is a maximum clade credibility tree from Zhan et al. (2022), except that it was pruned down to the mOTUs examined here. Only the 13 most abundant mOTUs (86% cumulative relative abundance) are displayed, so that mOTU066 (which was selected for the sediment burial experiments) is shown. The top dendrogram shows clustering of the sites by Hellinger-transformed mOTU relative abundances.

contrast to its high RA in the NTCR, may be explained by low sediment burial tolerance. Similarly, we hypothesized that *Lithophyllum* sp. mOTU066, which was common (albeit not the most common) in the NTCR (RA = 4.5%; Figure 2) but had low RA in the TAR (as indicated by a lack of specimens assigned to it), has low sediment burial tolerance. To help readers associate the mOTUs with whether they were common in the TAR and/or the NTCR, we use the following abbreviations for the mOTUs: *Harveylithon* sp. mOTU023, Hs-TAR-NTCR; *Sporolithon* sp. mOTU139, Ss-TAR-NTCR; *H. catarinense* mOTU014, Hc-NTCR; and *Lithophyllum* sp. mOTU066, Ls-NTCR.

We collected 83 bulk specimens from the TAR (Baiyu) and the NTCR (Shimen). These bulk specimens were assigned to 15 mOTUs in total, but only 19 of the bulk specimens were assigned to the four mOTUs selected above (Appendix S1: Table S6). For each of Ss-TAR-NTCR and Hc-NTCR, we prepared 20 replicates (which are pieces of bulk specimens); we subjected 4 replicates to no burial (negative control), 8 replicates to 1-month-long burial, and 8 replicates to 3-month-long burial. For Hs-TAR-NTCR, we prepared 12 replicates (4 for control, 4 for 1-month burial, and 4 for 3-month burial). For Ls-NTCR, we prepared 15 replicates (4 for control, 5 for 1-month burial, and 6 for 3-month burial).

Geographic distributions of the selected mOTUs

To examine the geographic distributions of the four mOTUs above, we mapped their occurrences and RAs based on the multi-substrate CCA biodiversity data from Zhan et al. (2022), which included 1736 specimens collected around Taiwan and nearby islands (and one site in

China). *Harveylithon* sp. (Hs-TAR-NTCR), *Sporolithon* sp. (Ss-TAR-NTCR), and *H. catarinense* (Hc-NTCR) were commonly found in multiple coastal areas of Taiwan and China (Figure 3). In contrast, *Lithophyllum* sp. (Ls-NTCR) was only observed at two coastal areas of Taiwan. Despite broad geographic distribution around Taiwan, neither *H. catarinense* (Hc-NTCR) nor *Lithophyllum* sp. (Ls-NTCR) was detected in the TAR, even though diversity sampling there was nearly saturated (Figure 2a), and the specimen count was much higher than in the other surveyed areas. These four mOTUs were found in broad geographic ranges that span more than the geographic distance between the TAR and the NTCR.

Less bleaching in the CCA from the TAR versus the NTCR

Harveylithon sp. (Hs-TAR-NTCR) and *Sporolithon* sp. (Ss-TAR-NTCR), which were the most common CCA in the TAR, showed no or minimal bleaching (indicating low mortality) after sediment burial (Figure 4; see Appendix S1: Table S7). We found no statistical evidence that the increase in bleaching proportion (see *Material and methods*: *Quantification of bleaching* for the definition) was different between the treatment replicates and the control replicates of these mOTUs after 1 month of burial (Hs-TAR-NTCR, $p = 0.743$; Ss-TAR-NTCR, $p = 0.698$) or after 3 months of burial (Hs-TAR-NTCR,

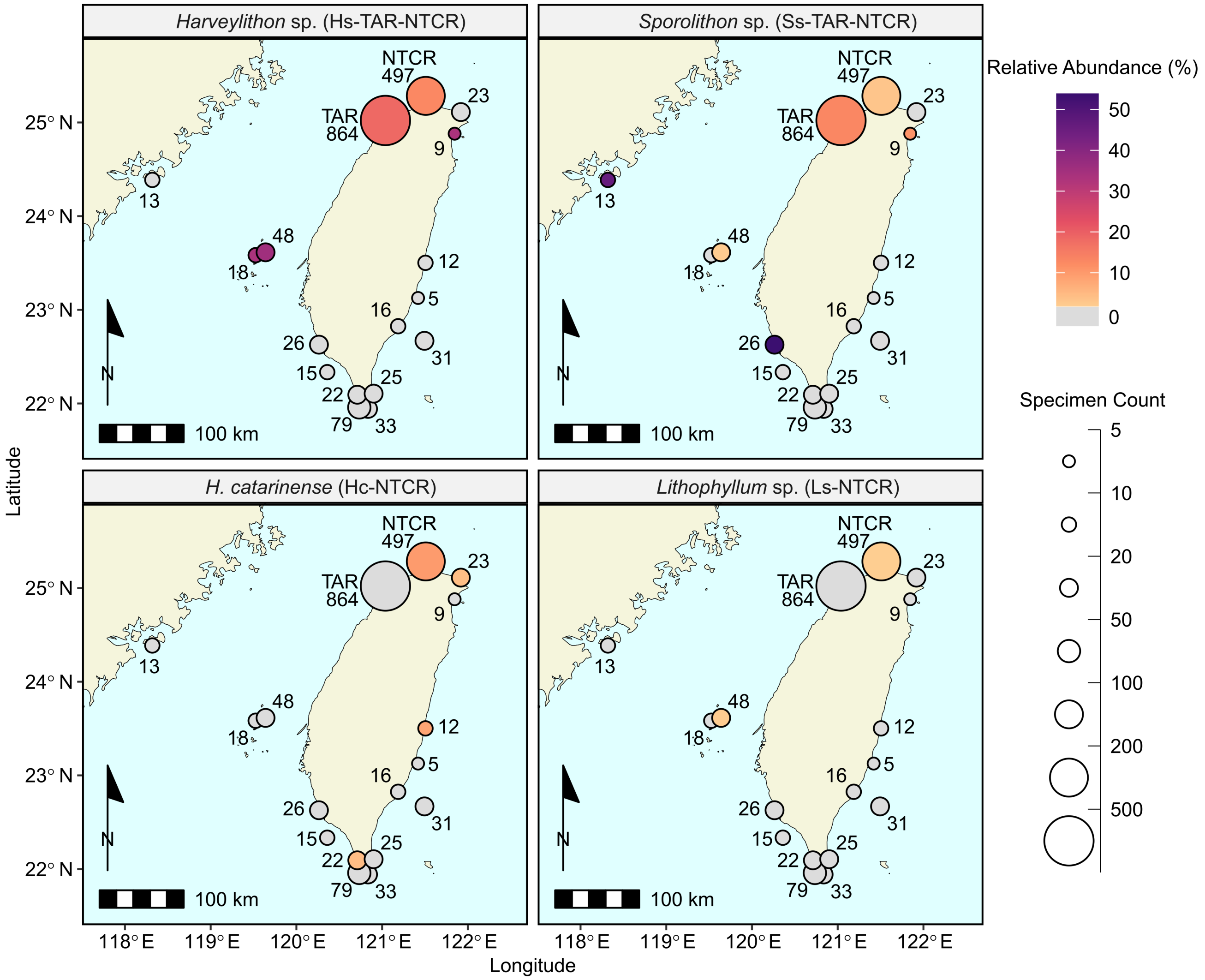

FIGURE 3 Geographic distributions of the four molecular operational taxonomic units (mOTUs) selected for the sediment burial experiments. For visual clarity, 1736 specimens collected across 43 sites (from reef substrates, cobbles, and snails) were grouped by geographic proximity using a 10-km clustering threshold, resulting in 17 geographic groups (circles). The numbers next to the circles indicate specimen counts per group. For each mOTU, its relative abundance within a group was calculated as the proportion of specimens belonging to that mOTU out of the total specimens in that group. The maps were generated using the R package *ggplot2* v3.5.2. NTCR, New Taipei City Reef; TAR, Taoyuan Algal Reef.

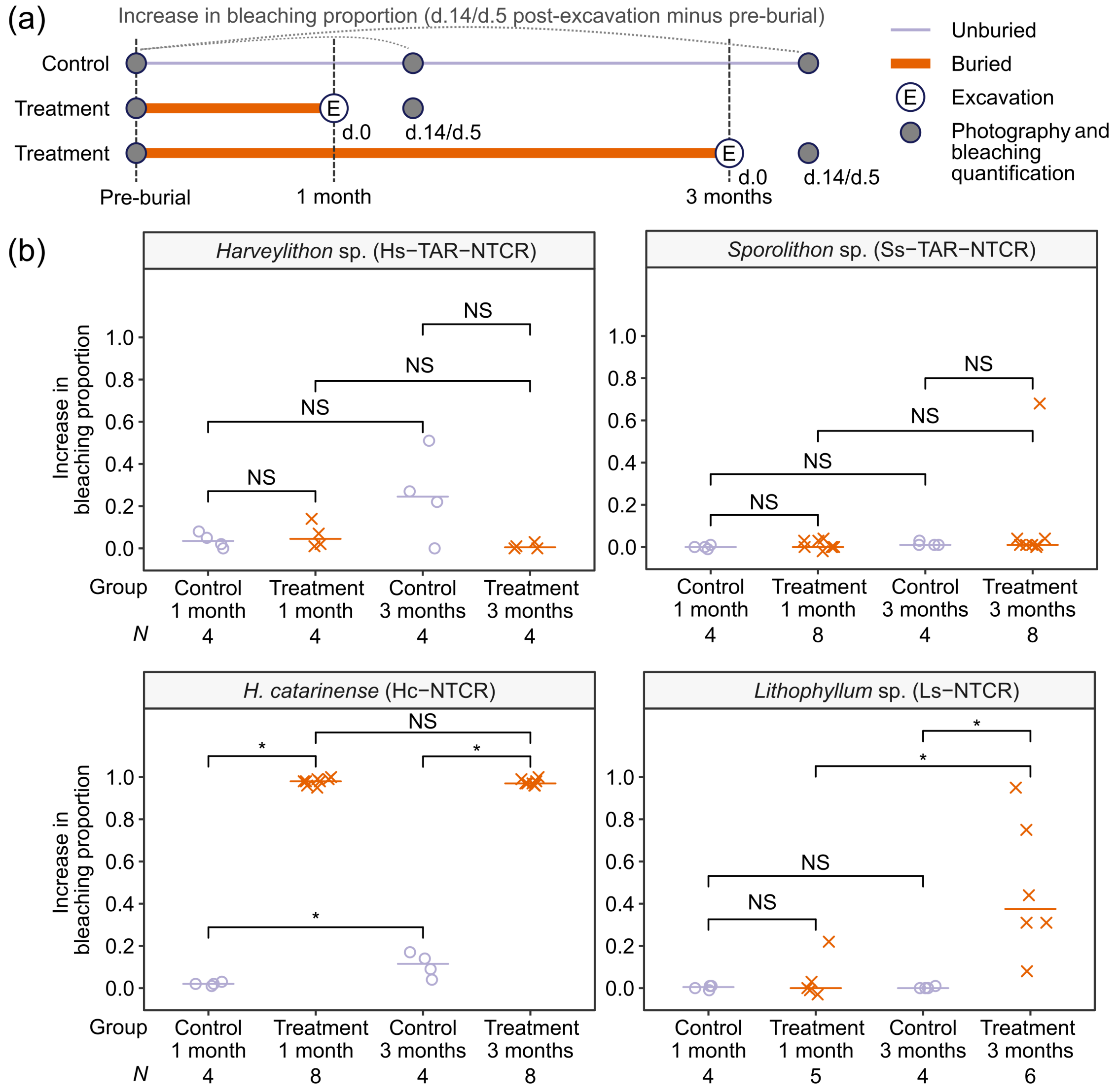

FIGURE 4 Bleaching on the crustose coralline algae (CCA) specimens from the Taoyuan Algal Reef (TAR) and the New Taipei City Reef (NTCR). (a) The timeline shows when different types of events took place during the experiments. (b) Pairwise comparisons of the increase in bleaching proportion were made using the two-sided exact Wilcoxon–Mann–Whitney (WMW) test, with multiple testing correction using the Benjamini–Hochberg method. The horizontal bars represent medians. Significance levels: $^*p < 0.05$; NS, $p \geq 0.05$. *N*, number of replicates.

$p = 0.305$; Ss-TAR-NTCR, $p = 0.731$). For the minimal areas affected, the treatment replicates of these mOTUs displayed gradual color changes or losses, stabilizing over 14 days after excavation, with some patches recovering original coloration while other areas developed irreversible bleaching (for illustrative examples, see Appendix S1: Figure S5).

In contrast, *H. catarinense* (Hc-NTCR) and *Lithophyllum* sp. (Ls-NTCR), which are common in the NTCR but absent in the TAR, showed pronounced bleaching (indicating high mortality), but severity varied by burial duration (Figure 4). For Hc-NTCR, we found a higher increase in bleaching proportion in the treatment replicates than in the control replicates after 1 month of burial ($p = 0.004$) and 3 months of burial ($p = 0.004$). These treatment replicates discolored rapidly and bleached fully by day 5 after excavation (Appendix S1: Figure S5). For Ls-NTCR, we found no statistical evidence that the increase in the bleaching proportion was different between the treatment replicates and the control replicates after 1 month of burial ($p = 1.000$; Figure 4). For the minimal affected areas on these treatment replicates, color change or loss stabilized over 14 days followed by partial recovery in some patches (Appendix S1: Figure S5). However, we found a higher increase in the bleaching proportion in the treatment replicates than in the control replicates after 3 months of burial ($p = 0.013$) (Figure 4). For the affected areas, these treatment replicates showed gradual discoloration and partial recovery in coloration (Appendix S1: Figure S5).

Furthermore, throughout the experiments, most of the control replicates showed low increases in bleaching proportion (median, 1.5%; range, 0%–10%; Figure 4; Appendix S1: Figure S5), indicating that the tank environment overall remained suitable for the growth of CCA. However, we noticed signs of bleaching on seven control replicates, likely due to pathogen infection or epiphyte competition (for additional observations, see Appendix S1: Extended results).

Photosynthetic activity recovery after months of sediment burial

The Fv/Fm values of the control replicates provided a baseline for levels of photosynthetic activity without sediment burial, and remained higher than 0.36 from day 0 to 28 (median = 0.636; range = 0.363–0.754) (Figure 5). After 1 month or 3 months of burial, we found that for all the mOTUs, the treatment replicates had lower Fv/Fm values than the control replicates on day 0 of excavation ($p < 0.01$), indicating that burial had a strong

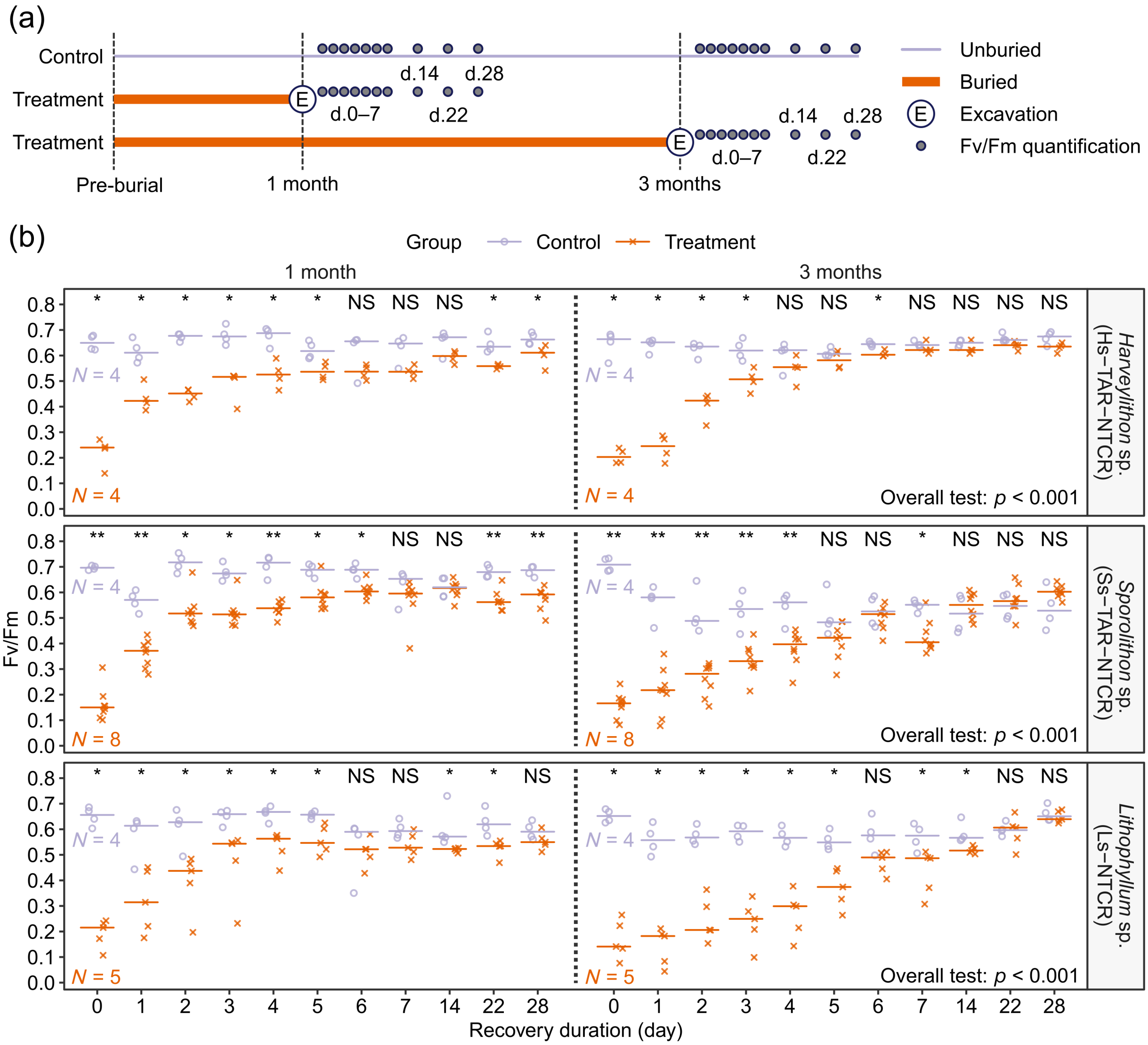

FIGURE 5 Post-sediment burial recovery of photosynthetic activity (Fv/Fm) of the crustose coralline algae (CCA) specimens from the Taoyuan Algal Reef (TAR) and the New Taipei City Reef (NTCR). (a) The timeline shows when different types of events took place during the experiments. (b) Pairwise comparisons of Fv/Fm per time point were made using the two-sided exact Wilcoxon–Mann–Whitney (WMW) test, with multiple testing correction using the Benjamini–Hochberg method. The horizontal bars represent medians. Day 0 is the day of excavation. In the plot for Ss-TAR-NTCR, which shows recovery after 3 months of sediment burial, the drop in Fv/Fm in the control replicates was caused by changes in pigmentation over time (see Appendix S1: Figure S8). Significance levels: $^{*}p < 0.05$; $^{**}p < 0.01$; NS, $p \geq 0.05$. N, number of replicates.

effect on photosynthetic activity. The Fv/Fm measurements are provided in Appendix S1: Table S8.

For *Harveylithon* sp. (Hs-TAR-NTCR), *Sporolithon* sp. (Ss-TAR-NTCR), and *Lithophyllum* sp. (Ls-NTCR), the Fv/Fm values of the treatment replicates recovered within 7 days after day 0, following 1 month and 3 months of burial (Figure 5). That is, the difference in Fv/Fm values between the treatment replicates and the control replicates decreased over time until the Fv/Fm values reached similar levels and then remained relatively stable. Across the mOTUs and the treatment groups, we found no statistical evidence that the Fv/Fm values were different between the treatment replicates and the control replicates by days 4–7.

For all the 1-month and 3-month treatment replicates of *H. catarinense* (Hc-NTCR) and one treatment replicate of Ls-NTCR (voucher ID: 230406CMRe_1-11; 3 months of burial), their Fv/Fm values were nearly zero on days 0 and 1 (data not shown). These low Fv/Fm values (combined with the observation that rapid bleaching occurred within 2 days of excavation) indicated the death of CCA, and no further measurements were taken for these replicates.

DISCUSSION

Here, we use the rare two-reef system of the TAR and the NTCR, which are exposed to contrasting levels of sediment accumulation, to examine the effects of sedimentation on CCA community assembly. Our benthic surveys show that the CCA in the intertidal zone is dominant over other functional groups in the high-sediment TAR but subdominant in the low-sediment NTCR; however, our DNA barcoding surveys expose lower hidden CCA species diversity in the TAR than in the NTCR. Our sediment burial experiments demonstrate that the two CCA species dominant in the TAR can survive prolonged sediment burial better than two other CCA species that were absent in the TAR but common in the NTCR. Our study reveals that heavy sediment accumulation acts as a strong environmental filter on CCA community assembly in the TAR, favoring CCA species with high physiological tolerance to sediment burial and promoting their ecological dominance.

In our previous study (Zhan et al., 2022), we suggest that sedimentation might affect community assembly of CCA in the TAR through a correlation analysis. In this study, we establish evidence for environmental filtering of CCA by sedimentation using the following three criteria proposed by Kraft et al. (2015). First, at the relevant spatial scale and along the gradient of an abiotic factor in question, there exists a regional species pool encompassing the species occurring in a focal site. Second, the species from the regional species pool are able to disperse to the focal site (ruling out dispersal limitation). Third, the species capable of reaching the focal site fail to tolerate the abiotic factor at the focal site in the absence of other species, as shown using laboratory measurements of physiological tolerance (ruling out biotic interactions). We apply these criteria to our study of the TAR as follows. First, our data show that the high-sediment TAR and the nearby low-sediment NTCR occur along a gradient of sediment accumulation (as shown in our comparison of the ecological backgrounds of the reefs) and the CCA from the two reefs form a regional CCA species pool (as shown in our community structure analyses), satisfying the first criterion. Next, our geographic analysis shows that dispersal limitation is an unlikely explanation for the absence of *H. catarinense* (Hc-NTCR) and *Lithophyllum* sp. (Ls-NTCR) in the TAR despite their wide geographic distribution around Taiwan (including the NTCR), satisfying the second criterion. Finally, our experiments confirmed that prolonged sediment burial selects against these two CCA species, in isolation from competition with other benthic organisms or herbivory pressure, satisfying the third criterion. Together, our data provide strong evidence that heavy sedimentation acts as a key environmental filter on CCA in the TAR.

Having established sedimentation as an important environmental filter in the TAR, the next logical avenue for future work is to explore how other abiotic and biotic factors may modulate interactions among sediment--tolerant CCA species. Local spatial and temporal variations in abiotic factors—such as wave action, desiccation, sunlight exposure (i.e., photodamage and heat), salinity, and nutrient availability—can create diverse microhabitats that may shift competitive advantages and promote species coexistence. Also, local biotic interactions—such as competition with turf macroalgae (as observed in our benthic survey), pathogen infection (as observed in our experiments), or herbivory—may suppress common CCA species and, in turn, facilitate the persistence of less common CCA species. Examining the relative importance of these abiotic and biotic factors on CCA community assembly in the TAR (using observational approaches and experimental approaches, e.g., Borer et al., 2007; Grainger et al., 2019) should deepen our understanding of the synergistic or antagonistic interactions between the factors and their effects on the biodiversity and ecosystem functioning of the TAR and potentially other algal reefs around the global ocean.

As a diverse group of species, CCA can tolerate a range of stressors, including low temperature, low light, and sand scour (McCoy & Kamenos, 2015). The ability of CCA to tolerate, survive, and recover from prolonged sediment burial has not been demonstrated until this study. This indicates their resilience to sediment accumulation (as shown by low mortality in nearly no bleaching and rapid recovery in photosynthetic activity within a week of excavation). Many studies report that CCA cannot tolerate or survive prolonged sediment burial (typically, showing signs of bleaching or dying within about 1 or 2 months of burial), with most of them focusing on CCA commonly found in low-sediment habitats, such as coral reefs and rhodolith beds (e.g., Curbelo-Fernandez et al., 2025; Figueiredo et al., 2015; Millar & Gagnon, 2018; Reynier et al., 2015; Riul et al., 2008; Villas-Bôas et al., 2014; Wilson et al., 2004). Our findings raise the possibility that some CCA, such as those found in the TAR analyzed in this study, are adapted to the environmental conditions caused by heavy sediment accumulation (i.e., long periods of time without access to critical resources, such as light and oxygen), facilitating them to build reefs in high-sediment areas, where reefs would not normally be expected to occur. Importantly, their physiological tolerance to sediment burial likely underlies the ecological dominance of CCA in the TAR over other benthic groups, such as frondose macroalgae, which are sensitive to high-sediment conditions. Interesting directions for future work may be to uncover genetic adaptations and nutrient acquisition strategies underlying tolerance of CCA to the hostile conditions of prolonged sediment burial.

Algal reefs, such as the TAR, are currently overlooked in mainstream reef management (Zhan et al., 2022). These marine ecosystems are being threatened by human activities and climate change (e.g., Hicks et al., 2024; Tuya et al., 2023). Conservation efforts to protect these reefs should benefit from strategies informed by knowledge about the key factors impacting CCA biodiversity and the resilience of CCA to stressors. We hope that more studies using integrative approaches, like this study, will improve our mechanistic understanding of these factors to help safeguard algal reefs from disturbances driven by human activities and climate change.

AUTHOR CONTRIBUTIONS

Shing Hei Zhan: Conceptualization; data curation; formal analysis; investigation; visualization; writing—original draft; writing—review and editing. **Yu-Tsen Huang:** Data curation; formal analysis; investigation; methodology; validation; writing—review and editing. **Chen-Pan Liao:** Data curation; formal analysis; investigation; methodology; software; validation; visualization; Writing—review and editing. **Ching-Yu Liou:** Conceptualization; resources; writing—review and editing. **Shao-Lun Liu:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; supervision; validation; visualization; writing—original draft; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Raw data and R scripts to perform the analyses (Zhan & Liao, 2026) are available from Zenodo: https://doi.org/10.5281/zenodo.19548301.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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