

# Acknowledging differences: number, characteristics, and distribution of marine benthic communities along Taiwan coast

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**Abstract.** Our knowledge of the ability of coral reefs to face contemporary challenges disregards the wide variety of benthic communities (BCs) that could be associated with contrasted dynamics when facing stressors. Accordingly, this study investigates the number, characteristics, and distribution of BCs responsible for the development of coastal three-dimensional structures in Taiwan. A total of 89 transects among three regions (north, east, and south) and two depths (−10 and −40 m) were characterized using a morpho-functional categorization of benthic organisms. Using an unsupervised learning algorithm, *k*-means cluster, an optimal number of *k* groups were identified among transects in order to minimize total intra-group variance and represent a first level of organization, mirroring the number of BCs. Each BC was then described into prevailing categories and typified by an association with significant indicator groups. Their distributions were further examined and tested among regions and depths. Seven BCs were identified as having different composition and indicator categories. Their distributions suggest that, while sea surface temperature and light regime may be associated with a panel of available BCs, local conditions may have the final say on whether a BC eventually thrives at a given location. Overall, this study proposes an innovative and simple analytical framework for acknowledging differences among BCs. Our results encourage greater consideration of these shades in coral reef ecology studies, as they could conceal a variety of roles and dynamics important for the conservation of these endangered ecosystems.

**Key words:** coral reefs; depth gradient; functionality; high-latitude; marginality; mesophotic; statistical learning.

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## INTRODUCTION

Present-day modifications of our environment alter coral reefs by reconfiguring their biotic assemblages (Hughes et al. 2018b). The changes jeopardize the services they provide to human societies, which contribute up to US\$36 billion to the worldwide economy each year (Spalding et al. 2017). They encourage radical and urgent actions that favor the conservation of these iconic ecosystems, which may be supported by a better understanding of their dynamics when facing stressors.

The degradation has been particularly severe at several locations throughout the Indo-Pacific,

such as recently reported on the Great Barrier Reef in Australia (Hughes et al. 2017b) where multiple and synergistic anthropogenic drivers exist (Hughes et al. 2017a), in addition to an increase in the frequency and intensity of summer heatwaves (Hughes et al. 2017b) that inexorably transform reefs (Hughes et al. 2018a). Nowadays, the loss of reef builder species precipitates the functional collapse of coral reefs and is associated with an overall flattening and simplification of their benthic assemblages (Perry and Alvarez-Filip 2018). An increasing number of reports document either continuous or discontinuous ecological shifts occurring in coral reefs

(Fung et al. 2011), which are usually characterized by a transition from hard coral- to alternative taxa-dominated states (Hughes et al. 2007, Norström et al. 2009, Lesser and Slattery 2011). Those shifts are often considered a monotonic response of the reefs to disturbance and are typically traced by changes in coral cover (Hughes et al. 2010).

The simplification of these regime shifts does not recognize the shades (states) of reefs (Mumby 2017) or their variety of ecological processes. At the global scale, bright spots actually exist in coral reefs (Baird et al. 2018, Moritz et al. 2018) and demonstrate the need to go beyond a one-size-fits-all point of view (Mumby 2017), which heretofore may have led to considerable confusion in our understanding of reef dynamics. Early ecological research in the '70s recognized the presence of different facets in a reef. Those studies identified ecological communities (i.e., a group of interacting organisms that inhabit a particular space and time) based on discontinuous faunal and floral changes (breaks), while describing the species composition and interaction in each of them. For example, van den Hoek et al. (1975, 1978) demonstrated the existence of seven zonal communities in fringing reefs from Curaçao, shaped by variation in light, water movement, and grazing pressure along depth gradient. Similar zonation was later documented in other reefs, such as in Australia (Morrissey 1980, Done 1982) and Chagos (Sheppard 1980). Those studies borrowed and adapted a phytosociological approach defined decades ago by plant ecologists (Braun-Blanquet 1932), while determining associations based on representative organisms. Overall, those studies remained descriptive owing to the computational techniques of that time. Nevertheless, they offered the first detailed depiction of reef communities. Since then, and excepting a few studies such as the recent work of Laverick et al. (2017) which defined the upper boundary of the mesophotic zones based on the composition and structure of coral assemblages, the distinction of these reef communities has otherwise fallen into disuse and remains equivocal. This question is not limited to reef ecology itself, but generally raises a fundamental problem in ecology on the existence and delineation of ecological communities (Ricklefs 1987, Palmer

and White 1994). Instead, most studies have favored spatial and temporal comparisons among self-defined ecological units such as site (Jax 2006), overlooking the subtle facets of reefs within and the variety of responses that they may produce.

Taiwan is located north of the East Indies Triangle and straddles tropical and subtropical latitudes (21.90°–25.30° N) at the confluence of three marine ecoregions (Dai 2014, Spalding et al. 2017). This original geographical setting and the contrasted environmental conditions found around Taiwan confer on the island a high marine species biodiversity (Briggs 2005). Daily average seawater temperature (SST) decreases from southeast to northwest and confounds the effects of latitude and coastal currents. To the northwest, winter SST is too low for reef accretion, so benthic biota develop directly on rocky substrates (Dai et al. 2010). Seawater temperature plays a critical role in the distribution of marine organisms (e.g., scleractinian corals, Chen and Shashank 2009, Denis et al. 2019b) and the biogeography of their functional trait diversity (e.g., reef fish, Denis et al. 2019a). Daily average photosynthetic active radiation (PAR) decreases with increasing latitudes and is highest off the southwest coast of Taiwan because of its clearer skies year round (Syu et al. 2016). The steep topography and great light penetration off east Taiwan offer ideal environmental conditions for reef organisms to extend their depth distribution. In contrast, PAR strongly attenuates with depth to the north where turbidity is high. Consequently, deeper habitats in the north are deprived of most light-dependent species and are dominated by azooxanthellate octocorals (Denis et al. 2019b). Therefore, Taiwan constitutes an excellent location to quantitatively investigate the number, characteristics, and distribution of benthic communities (BCs) responsible for the development of coastal three-dimensional structures. The specific objectives of this study are to (1) identify the number of marine coastal BC across three regions and two depths in Taiwan, (2) describe their composition and outline the association for each BC described, and (3) analyze their distribution and ultimately discuss the possible plurality of reef ecosystems as well as their implications for conservation.

**MATERIALS AND METHODS**

*Study locations*

To select representative habitats with contrasting environmental conditions along the latitudinal gradient of Taiwan, this study focused on three geographical areas (regions): the north (25.15° N), east (22.64° N), and south (21.94° N); and two depths: shallow (−10 m) and deep (−40 m; Fig. 1). To the north, Bitou and Keelung Island were the only two locations selected for this survey because of the low number of zones having depths below −30 m. In the east, we chose three locations around Green Island

(Ludao): Shilang, Guiwan, and Dabaisha. Weather conditions allowed only the west side of this island to be sampled. To the south (Kenting), four locations were targeted: Xiaowan and Mobitou located in Nanwan Bay, Hongchaikeng off the western coast, and Longkeng off the eastern coast.

*Ecological surveys*

Ecological surveys were conducted during 2016–2017 using photo-transects. Each transect consisted of 21 replicate photographs (0.5 × 0.5 m) taken at each meter along a 20-m line within visually homogenous areas totaling a

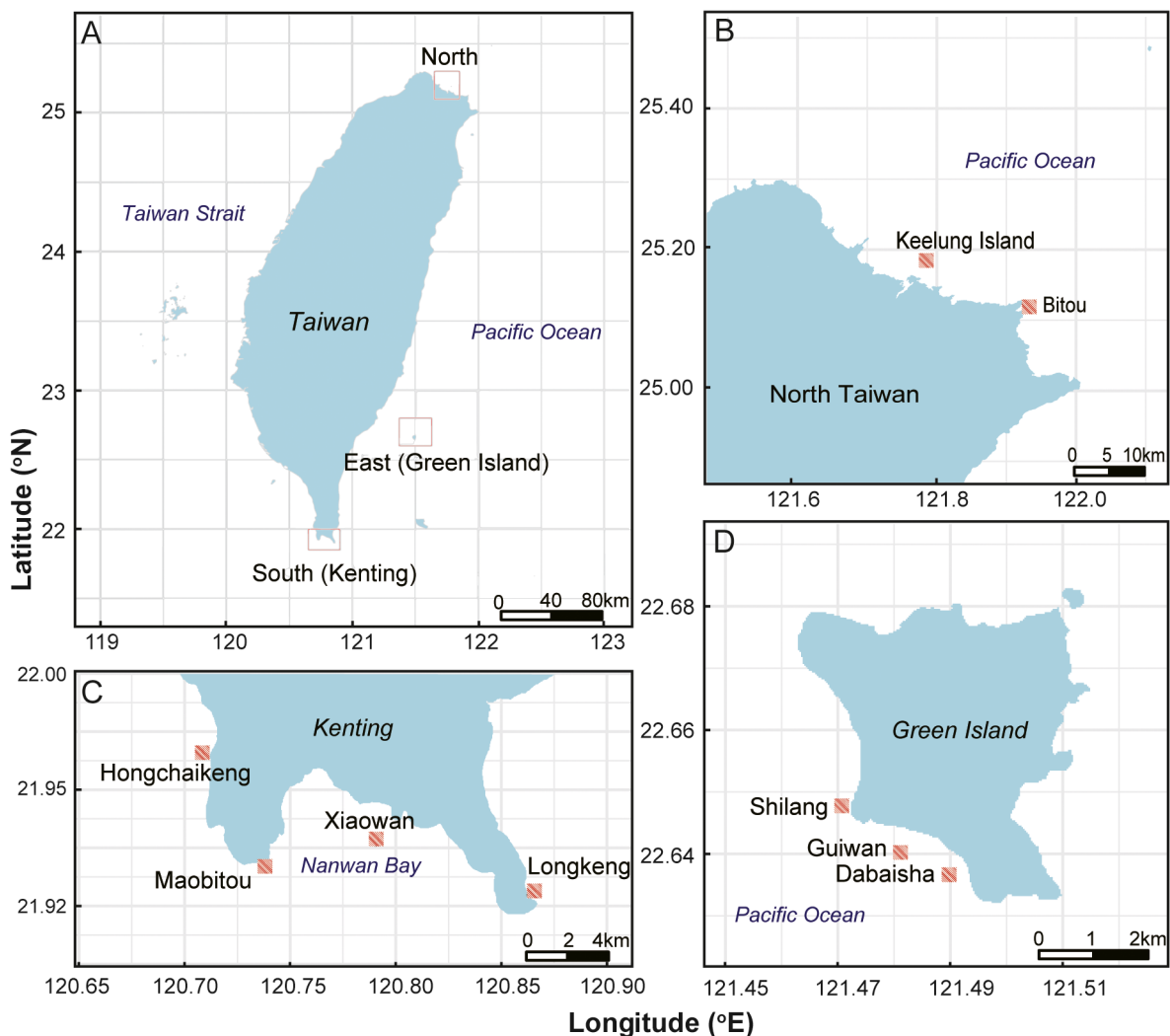


Fig. 1. Study locations. The three study regions around Taiwan (A), with the selected locations to the north (B), south (C), and east (D).

surface area of 5.25 m<sup>2</sup>. This was replicated five times for each location depth while maintaining a minimum distance of 5 m between each pair of transects in order to capture community variation that may change at fine spatial scales.

Overall, the survey encompassed 89 photo-transects (data for one transect were lost during the transfer of photographs from the camera to the computer). Benthic composition was assessed by combining information from the 21 photographs analyzed using Coral Point Count with Excel extensions software (CPCe V4.1, Kohler and Gill 2006). On each photograph, 50 random points were overlaid and organisms or substrates beneath were determined. Organisms were identified to the most reasonable operational taxonomic unit (OTU; considering the limitations of taxonomic identification via photography) possible using literature specific to each taxonomic group (macroalgae, Huang 2000; octocorals, Fabricius and Alderslade 2001, Dai and Horng 2009a; hard corals, Dai and Horng 2009a–c; other benthic organisms, Dai et al. 2010) as well as identifications from a previous diversity assessment (Denis et al. 2019b). The World Register of Marine Species (WoRMS Editorial Board 2019) was used as a reference for taxa name validity. It resulted in a total of 239 OTUs, acknowledging that two taxa may consist of the same organism with different morphologies expressed in contrasted environmental conditions. Eventually, they were summarized into 51 morpho-functional categories (Appendix S1: Table S1).

The contribution of benthic organisms to structural complexity is indeed recognized as among the best predictors of their roles in reefs (Denis et al. 2017). Therefore, the morphology of reef organisms represents a key trait for assessing their involvement in ecological processes (Bellwood et al. 2004). It further depicts the main features of BCs by considering their function as habitat providers. Reef-building species (hard corals) such as scleractinian corals and representatives of Milleporidae, Stylasteridae, Tubiporidae, and Helioporaacea have long been recognized as the primary contributors of biogenic habitats (Risk 1972, Luckhurst and Luckhurst 1978). Their contrasted morphologies attract different species (Brooker et al. 2013, del Mar Palacios and Zapata 2013), and a morphologically diversified coral assemblage

stimulates the overall diversity of a community, especially among mobile invertebrates and fishes (Graham et al. 2006, Graham and Nash 2013). Moreover, morphology has been identified as being among the best predictors of life history strategy in scleractinian corals (Darling et al. 2012). The morphological characteristics of algae also contribute significantly to habitat complexity (Dean and Connell 1987). Their morphologies have been further associated with different levels of primary productivity (Jänes et al. 2017) and, in consequence, also represent a key trait in determining ecological strategies (Steneck and Dethier 1994). Despite local dominance and their ability to form distinctive animal forests (Rossi et al. 2017b), less is known about the role of other reef organisms such as octocorals (OC) and sponges (SP). Octocorals have diverse morphologies (Fabricius and Alderslade 2001), which may partly define their successfulness in a specific habitat (Sánchez 2017, Schubert et al. 2017). Their involvement in reef accretion has also been demonstrated for some species (such as digitate *Sinularia* spp.) that are able to cement sclerites at the base of the colony (Jeng et al. 2011). Morphology varies considerably among SPs (Boury-Esnault and Rützler 1997), and the habitat complexity they produce also represents a good proxy for reef diversity (Bell and Barnes 2001). Some species, such as the common tropical massive barrel sponges, *Xestospongia* spp., can greatly contribute to the three-dimensional structure of a reef by forming large erect structures up to 1.5 m in height (Bell and Smith 2004). Despite hosting a high taxonomic diversity (Farnham and Bell 2018), the positive role of sponges in reef accretion has been largely overlooked (Wulff 2016). Therefore, a consideration of both taxonomic and morphological information about benthic organisms is, to date, the most pragmatic representation of its function in marine communities. It may further constitute an undeniable improvement for assessing the role and dynamics of BCs. Our categorization combining information on taxonomy and morphology is based on specific literature for each group and is available in Table 1. It resulted in a matrix of 89 photo-transects (samples) by 51 morpho-functional groups (variables), which constituted the basis for community delineation.

Table 1. The 51 morpho-functional categories.

Taxonomic group	Morphological type
Hard corals (HC)	8 categories
	Arborescent
	Encrusting
	Tabular
	Bushy
	Foliose
	Unattached
	Columnar
	Massive
	7 categories
Algae (AG)	Articulated calcareous
	Crustose
	Leathery macrophytes
	Corticated foliose
	Filamentous
	Corticated macrophytes
	Foliose
Octocorals (OC)	9 categories
	Arborescent
	Digitate
	Lobate
	Bushy
	Encrusting
	Massive
	Clustered
	Fan
	Whip
Sponges (SP)	9 categories
	Arborescent
	Flabellate
	Papillate
	Branching repent
	Globular
	Pedunculate
	Encrusting
	Massive
	Tubular
Zoantharians (ZO)	3 categories
	Arborescent
	Encrusting
Antipatharians (ANTI)	Massive
	2 categories
Bryozoans (BR)	Arborescent
	Whip
	3 categories
Ascidians (AS)	Arborescent
	Encrusting
	Massive
Ascidians (AS)	3 categories
	Clustered
	Encrusting
	Erect single

(Table 1. Continued.)

Taxonomic group	Morphological type
Hydrozoans (HY)	3 categories
	Arborescent
	Bushy
Corallimorpharians (CO)	Plumose
	1 category
Actinarians (ANE)	Encrusting
	1 category
Cyanobacteria (CY)	Encrusting
	1 category
Other life (OT)	Filamentous
	1 category
	Other

### Data analysis

Several groups did not appear on transects, and their corresponding variables were accordingly removed. Data were then Hellinger-transformed to lower the weights of variables with low counts and many zeros (Legendre and Gallagher 2001). The transformation itself consists of dividing each value in a data matrix by its row sum and taking the square root of the quotient.

An unsupervised learning algorithm (*k*-means clustering, Macqueen 1967) was used in a cascade to determine the optimum number of clusters (*k*) among the 89 transects, thus minimizing variances within groups based on their composition in the 51 morpho-functional groups. The cascade produced various partitions with 1000 iterations, randomly positioning the centroid of the clusters. *k* was decided by maximizing the Simple Structure Index criterion (Dolnicar et al. 1998), which allows a relative uncertainty in the size of the final groups (Milligan and Cooper 1985). Eventually, the significance of *k* clusters in partitioning our dataset was tested under 999 permutations (Biondini et al. 1988). *k* was interpreted as the number of BCs (defined here as a group of interacting benthic organisms that inhabit a particular space and time) occurring among the transects. Resulting clusters were visualized on a *t*-distributed stochastic neighbor embedding (*t*-SNE), which is a dimensional reduction technique that allows the structure of the high-dimensional data from different scales to be displayed in low dimension (van der Maaten and Hinton 2008). Every BC was characterized by the



percentage of its contribution to the different morpho-functional groups. In addition, Dufrière and Legendre (1997) indicator species analyses were further computed to identify the significance of each of the 51 morpho-functional groups in distinguishing each BC. A morpho-functional group became an indicator of a given BC when it occurred on most of the transects composing this BC while being absent from most of the transects constituting other BCs. Its statistical significance was evaluated by the random reallocation procedure of the transects among BCs (Dufrière and Legendre 1997). The association characteristics of each BC were named according to the outputs of this analysis. Eventually, BC distribution was examined across regions and depths. These two factors were tested for their significance in differentiating BCs using Pearson's chi-square tests (Pearson 1992).

All data analyses were conducted with R v 3.5.2 (R Core Team 2018) using the *vegan* (Oksanen et al. 2009), *stats* (R Core Team 2018), and *labdsv* (Roberts 2016) packages. All error terms are given as standard deviation of the mean. All data and script for data analysis are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.p7k5582>.

## RESULTS

The *k*-means cascade detected seven well-supported ( $P < 0.001$ ) clusters (defined as BCs) among the 89 transects (Fig. 2A), which were visualized on the *t*-SNE (Fig. 2B). The Dufrière and Legendre indicator species analyses identified the associations that were representative of each BC (Appendix S2: Table S1), as illustrated in Fig. 3. A detailed description of BC composition is further provided in Table 2.

None of those communities are dominated by hard corals, which average  $20.7\% \pm 11.5\%$  across the seven BCs. In the encrusting and massive hard corals–encrusting and massive zoanthids–encrusting corallimorpharian community (BC1), algae ( $53.4\% \pm 1.2\%$ ), such as crustose, filamentous, and corticated macrophyte algae, dominated together with massive and encrusting hard corals ( $31.6\% \pm 0.8\%$ ). Encrusting and massive zoanthids ( $7.9\% \pm 0.5\%$ ) as well as encrusting corallimorpharians ( $0.8\% \pm 0.1\%$ ) further typified this community. The erect octocorals–

antipatharian–encrusting and tubular sponges–clustered ascidian–arborescent zoanthid–arborescent bryozoan–plumose hydrozoan community (BC2) was composed of abundant other life covered by sediment ( $28.4\% \pm 0.9\%$ ) and sponges ( $23.1\% \pm 2.0\%$ ). Octocorals ( $18.6\% \pm 1.0\%$ ) and antipatharians ( $13.2\% \pm 1.1\%$ ) also prevailed in this community and are represented by a variety of fan, arborescent, and whip-shaped colonies. The presence of bryozoans ( $9.1\% \pm 0.6\%$ ), hydrozoans ( $1.1\% \pm 0.1\%$ ), zoanthids ( $0.6\% \pm 0.1\%$ ), and ascidians ( $0.1\% \pm 0.0\%$ ) also distinguished BC2. In the arborescent, bushy, and tabular hard corals–clustered octocoral–encrusting actinarian community (BC3), octocorals ( $50.7\% \pm 0.6\%$ ) with clustered shape, and hard corals ( $32.3\% \pm 0.8\%$ ) with various morphologies dominated. The low cover of actinarians ( $0.4\% \pm 0.0\%$ ) further represented a characteristic of this community. The unattached hard coral–bushy and encrusting octocorals–massive sponge–encrusting ascidian–filamentous cyanobacteria–bushy hydrozoan community (BC4) was predominantly composed of algae ( $49.2\% \pm 1.0\%$ ), hard corals ( $20.1\% \pm 0.8\%$ ), and octocorals ( $16.8\% \pm 0.9\%$ ). Sponges ( $9.3\% \pm 0.4\%$ ), ascidians ( $0.1\% \pm 0.0\%$ ), hydrozoans ( $0.3\% \pm 0.0\%$ ), and cyanobacteria ( $2.2\% \pm 0.1\%$ ) also featured in BC4. The columnar hard coral corticated macrophyte algae–digitate, lobate, and massive octocorals community (BC5) was outlined by the dominance of algae ( $49.3\% \pm 0.8\%$ ), hard corals ( $23.2\% \pm 0.8\%$ ), and octocorals ( $21.0\% \pm 1.0\%$ ). The articulated calcareous, corticated foliose, and crustose algal community (BC6) was dominated by algae ( $81.3\% \pm 0.6\%$ ), with crustose, articulated calcareous, and filamentous groups differentiating this BC from others. The filamentous algal community (BC7) was distinguished by the high contribution of mostly filamentous algae ( $59.8\% \pm 1.6\%$ ) and some hard corals ( $27.3\% \pm 1.3\%$ ) that were primarily dominated by massive and encrusting colonies.

The distribution of these seven communities is given in Fig. 4. Both regional ( $\chi^2 = 178$ ,  $P < 0.01$ ) and bathymetric ( $\chi^2 = 76.7$ ,  $P < 0.01$ ) factors have a significant role to play in their spatial distribution. With the exception of BC7, each BC could indeed be explained by a combination of these two factors only. BC1 is distributed in

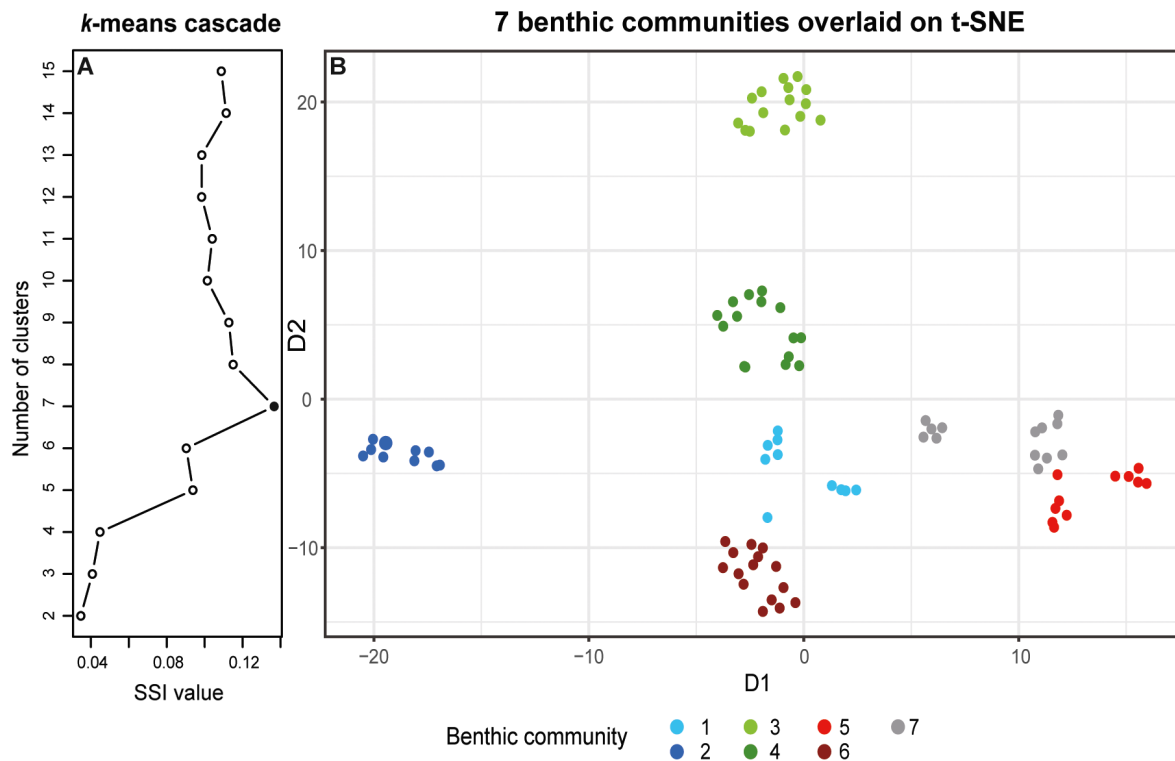


Fig. 2. Benthic communities (BCs). The *k*-means cascade identifying the seven BCs (black dot) (A) and their display on the *t*-distributed stochastic neighbor embedding (B).

shallow waters in north Taiwan. BC2 thrives at  $-40$  m depths in the same area. BC3 and BC4 occur in shallow and deep waters, respectively, at all locations from east Taiwan. BC5 appears at  $-10$  m in the south, while BC6 is restricted there to deeper waters. BC7 occurs across both depths on the west coast of south Taiwan as well as on four of the five transects from shallow waters at Xiaowan (Fig. 4). It further illustrates that communities can vary at small spatial scales.

## DISCUSSION

To our knowledge, this study is the first to attempt the delineation of marine coastal BCs in Taiwan using an unsupervised learning algorithm. It recognizes the existence of seven BCs, pinpoints differences in their composition, and highlights representative associations of these communities. Their distribution indicates that these BCs are partly shaped by the variations in environmental parameters within regions and depths. Nevertheless, while these factors may be

associated with a panel of BCs available, our results suggest that other abiotic and biotic components may have the final say on the presence of a given BC at a given area. These results encourage greater consideration of these shades in coral reef ecology studies, as they could conceal a variety of roles and dynamics.

Seven BCs were identified and characterized across regions and depths. BC1 typifies marginal communities developing in shallow waters in high-latitude locations (Perry and Larcombe 2003), such as those observed in subtropical Australian assemblages (Harriott et al. 1994). They are often dominated by crustose coralline algae (Perry 2003) and commonly portrayed by massive and encrusting hard corals (Celliers and Schleyer 2008, Sommer et al. 2014). BC2 is primarily outlined by the contribution of suspension feeders such as sponges, gorgonians, antipatharians, bryozoans, and hydrozoans. These taxa can be locally abundant and contribute, as do scleractinian corals, to highly three-dimensional structures that stimulate species

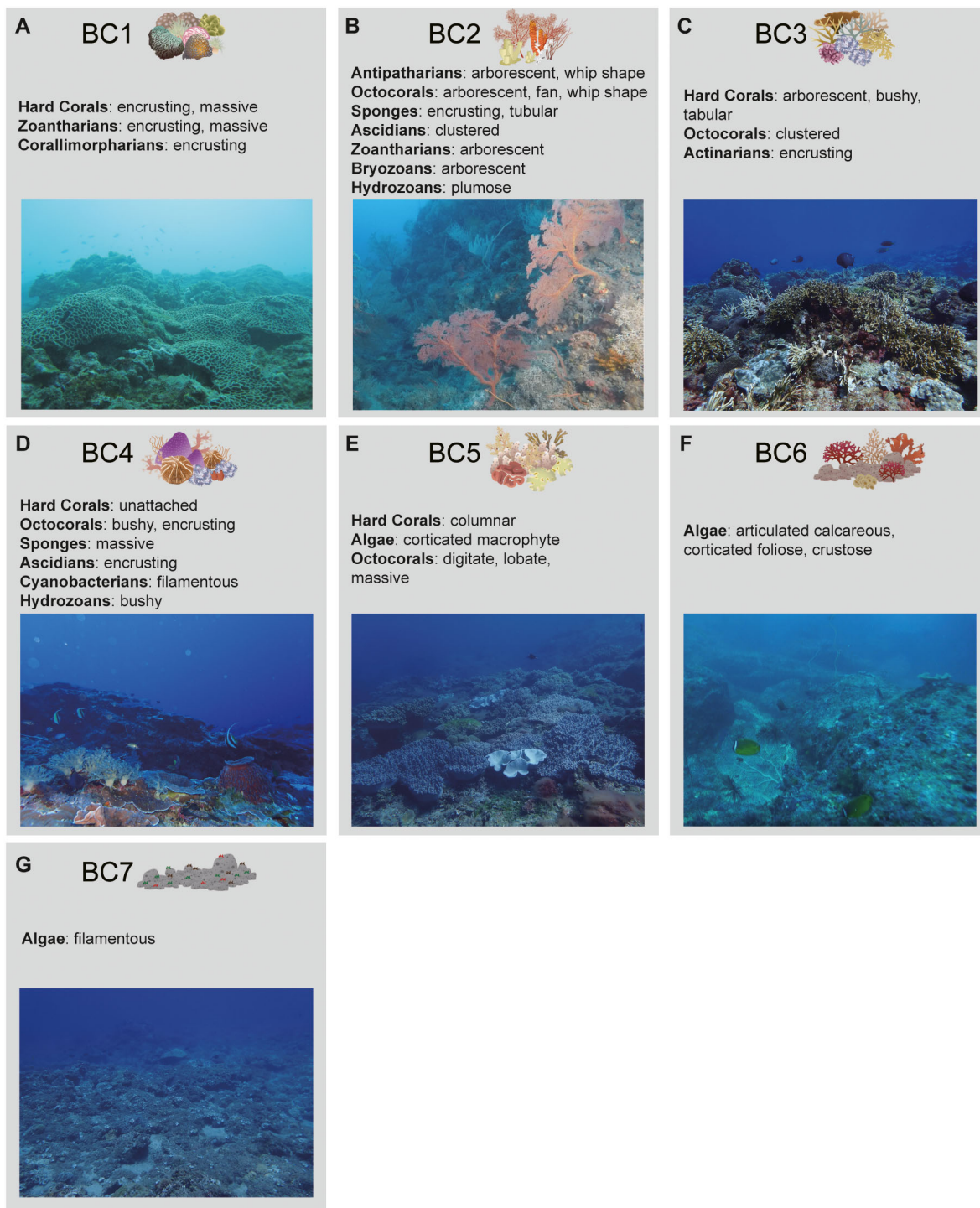


Fig. 3. Photographs and representative associations of the seven benthic communities (BCs). BC1 (photograph credit: YV Lin) (A), BC2 (photograph credit: P Hsieh) (B), BC3 (photograph credit: YV Lin) (C), BC4 (photograph credit: MJ Ho) (D), BC5 (photograph credit: L Ribas-Deulofeu) (E), BC6 (photograph credit: V Denis) (F), and BC7 (photograph credit: L Ribas-Deulofeu) (G).



Table 2. Benthic communities (BCs) and percentage compositions in morpho-functional categories.

BC	1	2	3	4	5	6	7
Number of transects	10	10	15	15	11	15	13
Hard corals (HC)	31.6 (0.8)	3.6 (0.4)	32.3 (0.8)	20.1 (0.8)	23.2 (0.8)	6.7 (0.3)	27.3 (1.3)
Arborescent	0.0 (0.0)	0.0 (0.0)	1.4 (0.1)	0.0 (0.0)	0.1 (0.0)	0.0 (0.0)	0.2 (0.0)
Bushy	1.0 (0.1)	3.2 (0.4)	6.9 (0.5)	4.9 (0.3)	2.6 (0.3)	0.1 (0.0)	2.5 (0.2)
Columnar	0.0 (0.0)	0.0 (0.0)	1.4 (0.1)	0.1 (0.0)	8.3 (0.9)	0.0 (0.0)	1.7 (0.2)
Encrusting	15 (0.6)	0.4 (0.1)	8.6 (0.3)	7.6 (0.6)	4.2 (0.3)	3.3 (0.2)	10.1 (0.4)
Foliose	2.1 (0.4)	0.0 (0.0)	0.1 (0.0)	1.8 (0.2)	0.1 (0.0)	1.2 (0.1)	0.8 (0.1)
Massive	13.4 (0.7)	0.0 (0.0)	8.0 (0.3)	5.6 (0.4)	7.7 (0.4)	2.1 (0.1)	10.8 (0.7)
Tabular	0.1 (0.0)	0.0 (0.0)	5.8 (0.4)	0.1 (0.0)	0.2 (0.0)	0.0 (0.0)	1.0 (0.1)
Unattached	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.1 (0.0)	0.0 (0.0)	0.1 (0.0)	0.0 (0.0)
Algae (AG)	53.4 (1.2)	2.1 (0.4)	13.2 (0.3)	49.2 (1.0)	49.3 (0.8)	81.3 (0.6)	59.8 (1.6)
Articulated calcareous	3.1 (0.3)	0.0 (0.0)	0.0 (0.0)	0.3 (0.0)	10.7 (0.6)	17.2 (0.8)	1.8 (0.1)
Corticated foliose	0.9 (0.1)	0.0 (0.0)	0.0 (0.0)	0.7 (0.1)	0.4 (0.0)	3.1 (0.1)	2.5 (0.2)
Corticated macrophyte	8.0 (1.2)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	4.6 (0.5)	2.7 (0.2)	4.1 (0.3)
Crustose	29.6 (1.0)	2.0 (0.4)	3.3 (0.1)	18.5 (0.5)	9.3 (0.4)	48.3 (0.9)	6.1 (0.3)
Filamentous	11.8 (0.5)	0.1 (0.0)	9.9 (0.3)	29.7 (0.6)	24.2 (0.6)	10 (0.3)	45.3 (1.6)
Octocorals (OC)	0.6 (0.1)	18.6 (1.0)	50.7 (0.6)	16.8 (0.9)	21.0 (1.0)	2.2 (0.1)	4.3 (0.3)
Bushy	0.3 (0.1)	0.5 (0.0)	4.9 (0.2)	10.2 (0.7)	0.8 (0.1)	0.7 (0.0)	1.0 (0.2)
Clustered	0.1 (0.0)	0.0 (0.0)	44.8 (0.5)	5.6 (0.3)	0.1 (0.0)	0.0 (0.0)	0.1 (0.0)
Digitate	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	11.9 (0.6)	0.1 (0.0)	1.8 (0.3)
Encrusting	0.0 (0.0)	0.0 (0.0)	0.2 (0.0)	0.7 (0.1)	0.3 (0.1)	0.0 (0.0)	0.3 (0.1)
Fan shape	0.1 (0.0)	10.5 (1.0)	0.0 (0.0)	0.2 (0.0)	0.3 (0.1)	0.3 (0.0)	0.2 (0.0)
Lobate	0.1 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	5.4 (0.5)	0.5 (0.0)	0.1 (0.0)
Massive	0.0 (0.0)	0.0 (0.0)	0.1 (0.0)	0.0 (0.0)	2.2 (0.1)	0.2 (0.0)	0.5 (0.0)
Whip shape	0.0 (0.0)	1.0 (0.1)	0.0 (0.0)	0.0 (0.0)	0.1 (0.0)	0.1 (0.0)	0.1 (0.0)
Arborescent	0.0 (0.0)	6.6 (0.5)	0.7 (0.1)	0.1 (0.0)	0.0 (0.0)	0.2 (0.0)	0.1 (0.0)
Sponges (SP)	3.7 (0.4)	23.1 (2.0)	0.9 (0.1)	9.3 (0.4)	0.8 (0.1)	2.5 (0.1)	1.5 (0.1)
Branching repent	0.1 (0.0)	0.2 (0.0)	0.0 (0.0)	0.1 (0.0)	0.0 (0.0)	0.0 (0.0)	0.1 (0.0)
Encrusting	0.3 (0.0)	14.4 (1.4)	0.4 (0.0)	1.4 (0.1)	0.5 (0.1)	1.3 (0.0)	0.7 (0.1)
Flabellate	0.1 (0.0)	0.3 (0.0)	0.0 (0.0)	0.2 (0.0)	0.1 (0.0)	0.2 (0.0)	0.3 (0.0)
Globular	0.1 (0.0)	0.0 (0.0)	0.0 (0.0)	0.3 (0.1)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Massive	3.0 (0.4)	1.7 (0.1)	0.3 (0.0)	6.9 (0.4)	0.2 (0.0)	0.6 (0.1)	0.2 (0.0)
Tubular	0.2 (0.0)	6.5 (0.7)	0.1 (0.0)	0.5 (0.0)	0.0 (0.0)	0.5 (0.0)	0.1 (0.0)
Antipatharians (ANTI)	0.1 (0.0)	13.2 (1.1)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Arborescent	0.1 (0.0)	12.0 (1.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Whip shape	0.0 (0.0)	1.2 (0.1)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.1 (0.0)
Ascidians (AS)	0.1 (0.0)	0.1 (0.0)	0.0 (0.0)	0.1 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Clustered	0.0 (0.0)	0.1 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Encrusting	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.1 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Erect single	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Zoantharians (ZO)	7.9 (0.5)	0.6 (0.1)	0.0 (0.0)	0.0 (0.0)	0.2 (0.0)	0.2 (0.0)	0.2 (0.0)
Arborescent	0.2 (0.0)	0.5 (0.1)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.2 (0.0)	0.0 (0.0)
Encrusting	0.1 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Massive	7.6 (0.5)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.2 (0.0)	0.0 (0.0)	0.1 (0.0)
Bryozoans (BR)	0.0 (0.0)	9.1 (0.6)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.2 (0.0)	0.2 (0.0)
Arborescent	0.0 (0.0)	9.1 (0.6)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.2 (0.0)	0.2 (0.0)
Corallimorpharians (CO)	0.8 (0.1)	0.0 (0.0)	0.2 (0.0)	0.1 (0.0)	0.0 (0.0)	0.1 (0.0)	0.0 (0.0)
Encrusting	0.8 (0.1)	0.0 (0.0)	0.2 (0.0)	0.1 (0.0)	0.0 (0.0)	0.1 (0.0)	0.0 (0.0)
Hydrozoans (HY)	1.0 (0.2)	1.1 (0.1)	0.0 (0.0)	0.3 (0.0)	0.0 (0.0)	0.1 (0.0)	0.3 (0.0)
Plumose	1.0 (0.2)	1.1 (0.1)	0.0 (0.0)	0.3 (0.0)	0.0 (0.0)	0.1 (0.0)	0.3 (0.0)
Bushy	0.0 (0.0)	0.0 (0.0)	0.1 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Actinarians (ANE)	0.0 (0.0)	0.0 (0.0)	0.4 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Encrusting	0.0 (0.0)	0.0 (0.0)	0.4 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Cyanobacterians (CY)	0.6 (0.1)	0.0 (0.0)	0.3 (0.0)	2.2 (0.1)	1.5 (0.1)	1.8 (0.1)	1.4 (0.2)
Filamentous	0.6 (0.1)	0.0 (0.0)	0.3 (0.0)	2.2 (0.1)	1.5 (0.1)	1.8 (0.1)	1.4 (0.2)
Other life (OT)	0.2 (0.0)	28.4 (0.9)	1.9 (0.2)	1.6 (0.1)	4.0 (0.1)	4.8 (0.3)	5.1 (0.3)

Note: Standard deviations are in brackets.

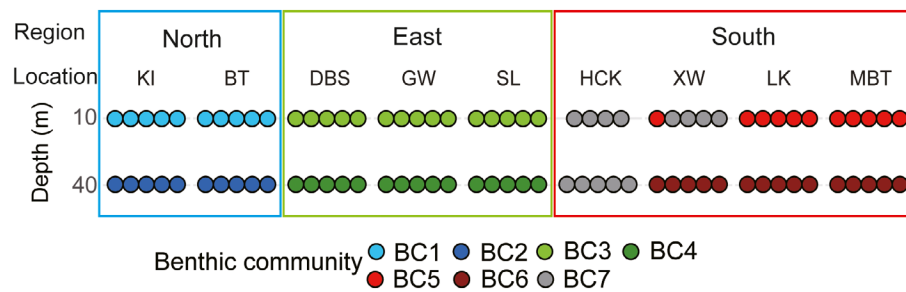


Fig. 4. Distribution of the seven benthic communities (BCs) across depths (–10 and –40 m) and regions (south, east, and north) in Taiwan. Locations are abbreviated as: Keelung Island (KI); Bitou (BT); Dabaisha (DBS); Guiwan (GW); Shilang (SL); Hongchaikeng (HCK); Xiaowan (XW); Longkeng (LK); and Mobitou (MBT).

interactions in animal forests (Rossi et al. 2017a). BC2's features are very similar to communities described for mesophotic habitats such as those observed in the Mediterranean Sea (Bo et al. 2011, Gori et al. 2011). BC3 headlines our conventional vision of pristine shallow-water tropical coral reefs. Those reefs emblemize the high architectural complexity generated by the variety of intricate scleractinian coral morphologies (Bozec et al. 2015). However, abundant clustered octocorals also individualize this community. These resilient corals (Hoang et al. 2015) are often associated with opportunistic behavior (Schleyer and Benayahu 2008) and the ability to rapidly colonize empty spaces after disturbances (Benayahu and Loya 1981). Their occurrence in BC3 could be explained by the recurrent typhoons that affect this region and the mechanical damage suffered afterward by the reefs. BC4 exhibits the co-existence of the light-dependent organisms that are widespread in shallow waters (e.g., hard corals and octocorals) with suspension feeders (e.g., sponges) more common to deeper waters. It typically depicts communities observed in the upper area of mesophotic habitats (Kahng et al. 2010, Baker et al. 2016b), which further recently received a surge of interest for the refuge they might offer for the survival of organisms decimated by bleaching in shallow waters (Baker et al. 2016a). BC5 is composed of abundant filamentous and articulated calcareous algae and may characterize a community experiencing frequent and multiple stressors (Liu et al. 2009, 2012). It is denoted by corticated macroalgae such as *Neurymenia cf. fraxinifolia* and columnar hard corals such as *Heliopora* spp., both of

which have previously demonstrated a high tolerance to turbidity and sedimentation (Chowdhury and Ahmed 2007, Toh et al. 2015). In addition, the resilient digitate, lobate, and massive octocorals further distinguishing BC5 were often considered persistent in earlier studies (Dai 1991, Schleyer and Celliers 2003, Schleyer and Benayahu 2008). These facies portray alcyonacean communities, which have been commonly reported in reefs worldwide (Nagelkerken et al. 2005, Schleyer and Benayahu 2008, Chanthakul et al. 2010) and are often associated with ecological shifting in tropical reef environments (Schubert et al. 2017). BC6 was dominated by crustose algae in the form of rhodolith beds (Foster et al. 2013) that formed a stable substrate for the growth of other organisms such as the distinctive articulated calcareous algae *Dichotomaria* spp. or the pervasive and competitive foliose *Lobophora* spp. macrophytes (Doropoulos 2017). This is a facet commonly observed in macroalgal mesophotic communities (Baker et al. 2016b) such as in Hawaii (–40 m, Spalding 2012), Brazil (–40 to –100 m, Amado-Filho et al. 2012), and the Bahamas (–70 to –90 m, Littler et al. 1991). Filamentous algae dominate and outline BC7. Stress-tolerant encrusting and massive hard corals (sensu Darling et al. 2012) prevail in this community, which further suggests that corals were selected on the basis of their resistance to disturbances. Our understanding of coral reef dynamics disproportionately relies on observations made on a relatively small subset of pristine communities (often considered as the good) shifting toward mediocre states (often considered as the bad). However, a number of other facets

deviating from these idealized reefs could exist (the ugly, not dominated by scleractinian corals) but have often been disregarded. The delineation of these shades, provisionally associated with their roles, needs to be better scrutinized in future ecological studies. These different communities could indeed be associated with contrasted dynamics and trajectories facing contemporary changes.

Both region and depth are paramount in determining the distribution of these seven BCs. Those two factors likely confound the effects of SST and PAR that have long been identified as controlling the latitudinal and bathymetric distribution of reef organisms (Kleypas et al. 1999, Kahng et al. 2010, Guan et al. 2015). In Taiwan, SSTs are responsible for the reduction of species richness along with increasing latitudes (Dai 2014) and preclude reef accretion to the north of the island. By their effects on marine organisms, SSTs are likely the main parameter constraining each BC to a given region. This pattern could be obscured in the scenario of a biotic homogenization caused by anthropogenic activities (Vergés et al. 2016), which has previously been hypothesized for Taiwan (Ribas-Deulofeu et al. 2016). Photosynthetic active radiation is the primary parameter justifying the distinction between shallow and mesophotic depths (Kahng et al. 2010, Baker et al. 2016a). It restrains the vertical distribution of photosynthetic organisms such as scleractinian corals (Muir et al. 2018) upon which relies the hypothesis of deep refuges (Bongaerts et al. 2010). Photosynthetic active radiation could also hold back the poleward migration of some coral taxa, such as *Acropora* (Muir et al. 2015, but see Madin et al. 2016). Here, PAR conditions are likely to be the main explanation for a structuration of the present BCs with depth as admirably exemplified in Laverick et al. (2017) for Honduras with the loss of shallow-water specialists along a depth gradient. This distinction is best represented in our results by the discrimination of a shallow tropical community (BC3) from a mesophotic tropical community (BC4) in the clear-water oceanic conditions of Green Island where we performed our survey. It further adheres to the depth-generalist characteristic of species composing BC4 (Denis et al. 2019b) and contributes to the high overlap in species composition observed among depths (i.e.,

communities). To the north, PAR is tremendously attenuated with depth, which results in two very distinctive marginal communities: BC1 and BC2. Those two communities were characterized by an important turnover (Denis et al. 2019b), which is reflected here by the dominance of autotrophic-photosynthetic organisms in BC1 and the dominance of heterotrophic-particle feeding organisms in BC2. Historically, sedimentation and consequently light availability were identified as strong limitations for the development of extensive mesophotic communities in the tropical waters from southern Taiwan (Dai et al. 1992), as exemplified by BC6. In addition, shallow-water BC5 shows the characteristics of a tropical reef community under stressors. The presence of BC7 across depths suggests the importance of local factors in shaping the communities of this region. Overfishing (Meng et al. 2004), eutrophication, and sedimentation (Meng et al. 2008, Liu et al. 2012) have long been hypothesized to influence the dynamics and the trajectory of Kenting reefs. The local outbreaks of organisms such as sea anemones (Chen and Dai 2004, Tkachenko et al. 2007) and fleshy algae (Dai 1993, Dai et al. 1998) have punctuated the long-term degradation in benthic assemblages reported since the establishment of Kenting National Park in 1984 (Dai et al. 1998, Kuo et al. 2012) and the economic development of the region. Therefore, we hypothesize that while regional and depth factors could have a major role to play in determining the panel of BCs available at a given location, local factors such as those associated with anthropogenic activities could have the last word on the community that eventually thrives. As predicted for the identification of regime shifts (Jouffray et al. 2015), there is a need for a better understanding of the anthropogenic and natural drivers that support and undermine different BCs and their transitions. A focus on parameters triggering fine-scale variations in communities could inform on the processes underpinning them. Here, we hypothesize on the pivotal role of physical (temperature, light, water flow, and sedimentation), chemical (nitrate, phosphate), geological (topography, substrate), and biological (biotic interaction) variables to explain the occurrences of BCs. This contrasts with the relatively poor understanding of the parameters employed to

resolve local benthic variations (Cresswell et al. 2017).

Overall, this study proposes an innovative and simple approach for considering and characterizing differences among benthic marine communities. It identifies seven communities in Taiwan and hypothesizes the abiotic and biotic factors from which they originate. A better understanding of the transitions among those communities and their dynamics could further help to predict their trajectories in the face of stressors. In the present study, the representativeness of each of these BCs could only be achieved by integrating each region and depth, questioning their roles, and the relative importance of considering these shades in a perspective of marine conservation in Taiwan. It further encourages the generalization of the current analytical framework, starting with spatial and temporal expansion of the present work, which was geographically restricted because of limited resources. Currently, advances in automatic annotations constitute an interesting and achievable perspective toward a worldwide characterization of the diversity of these nuances that to date remain disregarded in most ecological studies.

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