Spatial and cross-seasonal patterns of coral diseases in reefs of Taiwan: high prevalence and regional variation

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ABSTRACT: Although research on coral diseases is increasing worldwide, it remains limited in Taiwan. Taiwan is located at the Tropic of Cancer and contains both tropical and subtropical reefs. We conducted spatial and cross-seasonal surveys in Taiwan in 2018 and identified 7 types of disease and nondisease lesions and 6 potential factors influencing coral health. The overall mean prevalence of disease and nondisease lesions varied considerably across the reef regions, and host susceptibility differed among the coral taxa. The overall mean prevalence of disease and nondisease lesions was highest in Kenting (mean ± SEM: 8.58 ± 1.81%) and lowest on the Southern Islands (2.12 ± 0.73%). Although the prevalence of diseases did not differ significantly between the seasons, cyanobacteria-related diseases — including black band disease (BBD), BBD-like syndrome, and other cyanobacterial syndromes — were slightly more prevalent in autumn than in spring. Furthermore, 3 of the potential factors influencing coral health (i.e. turf algae, bioeroding sponges, and coral bleaching) were strong predictors of disease and nondisease lesion prevalence. These results advance our understanding of coral disease ecology in Taiwan and highlight the need for further research on the correlations between diseases, hosts, and environment.

KEY WORDS: Coral disease · Taiwan · Distribution pattern · Host susceptibility

1. INTRODUCTION

Coral diseases are a developing crisis that threaten the viability, structure, and function of coral reef ecosystems. These diseases contribute to coral mortality and engender substantial losses in living coral cover and reef biodiversity (Hughes 1994, Porter & Tougas 2001, Lafferty et al. 2004). Caribbean reefs have been subject to repeated disease outbreaks over the past 3 decades, and the dominant reef-building coral populations have

decreased considerably (Aronson & Precht 2001, Miller et al. 2009, Weil & Cróquer 2009). Reefs in the Indo-Pacific region are less disturbed than those in the Caribbean region; however, a number of studies have reported that diseases are highly prevalent in this region (Willis et al. 2004, Raymundo et al. 2005, Myers & Raymundo 2009, Sato et al. 2009, Weil et al. 2012) and have the potential to severely affect certain diverse ecosystems.

The prevalence of coral diseases is a crucial indicator of coral reef health, and the disease distribution

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patterns have been linked to both global and local factors. On the global scale, seasonal fluctuations (e.g. sea surface temperature and light intensity) and climate change-associated thermal stress are correlated with tissue-loss diseases (Boyett et al. 2007, Bruno et al. 2007, Brodnicke et al. 2019). In addition, localized human effects (e.g. eutrophication and sedimentation) appear to promote disease transmission by compromising host resistance or enhancing the virulence of infectious pathogens (Haapkylä et al. 2011, Kaczmarsky & Richardson 2011).

Despite global research efforts, studies on the prevalence of coral diseases in the Indo-Pacific region remain limited, especially in the context of marginal reefs. Taiwan is a continental island located in the middle of the Philippines–Japan island arc, which is near the northern limit of coral reef development (Beger et al. 2014) and includes both tropical and subtropical reefs (Chen & Shashank 2009). To the west and north of Taiwan, the differences in sea surface temperatures between seasons can exceed 10°C because of monsoons and China Coastal Waters (Jan et al. 2002). To the east and south, the Kuroshio Current brings warm water and stabilizes sea surface temperatures. The high variability in hydrology creates a wide range of habitats, making coral reefs diverse and productive throughout Taiwan (Dai & Horng 2009a,b, Ribas-Deulofeu et al. 2016).

However, the dense population of Taiwan and its highly developed industries threaten these reefs. Taiwan's reefs are among the most threatened ecosystems in Southeast Asia, due in part to unsustainable fishing, coastal development, and watershed pollution (Burke et al. 2011). The extent to which these factors affect coral diseases remains unclear. A study integrating information on coral communities and disease prevalence in all regions of Taiwan is required to assess the effects of coral diseases.

Accordingly, the present study (1) quantified the prevalence of coral diseases affecting coral taxa across reefs in Taiwan and (2) investigated the potential factors contributing to these diseases. Scleractinian coral reefs have been identified in 7 major regions in Taiwan: the northeast coast, the east coast, and Kenting on the main island, in addition to the nearby Green Island, Orchid Island, Penghu Islands, and

Liuqiu Island (Chen & Shashank 2009, Dai & Horng 2009a). We investigated all of these reef regions except for Liuqiu Island. Moreover, cross-seasonal investigations were conducted in 3 of the reef regions to determine the spatial and seasonal variabilities of disease prevalence. The correlation between disease prevalence and potential contributing factors was also examined.

2. MATERIALS AND METHODS

2.1. Survey sites and periods

To examine the spatial variability in the prevalence of coral diseases, surveys were conducted in 6 reef regions along the coast of Taiwan: the northeast coast, the east coast, Kenting, Green Island, Orchid Island, and the Southern Islands (located at the southernmost margin of the Penghu Islands). A spatial survey was conducted in the spring and summer (i.e. from April to August) of 2018 by aggregating information from 3 to 5 sites in each reef region, resulting in a total of 22 sites (Fig. 1). To investigate the cross-seasonal variability in the prevalence of coral diseases, additional surveys were conducted in the autumn (October to November) of 2018 in 3 of the reef regions — the northeast coast, Kenting, and Green Island — by aggregating information from 3 sites in each reef region, resulting in a total of 9 sites.
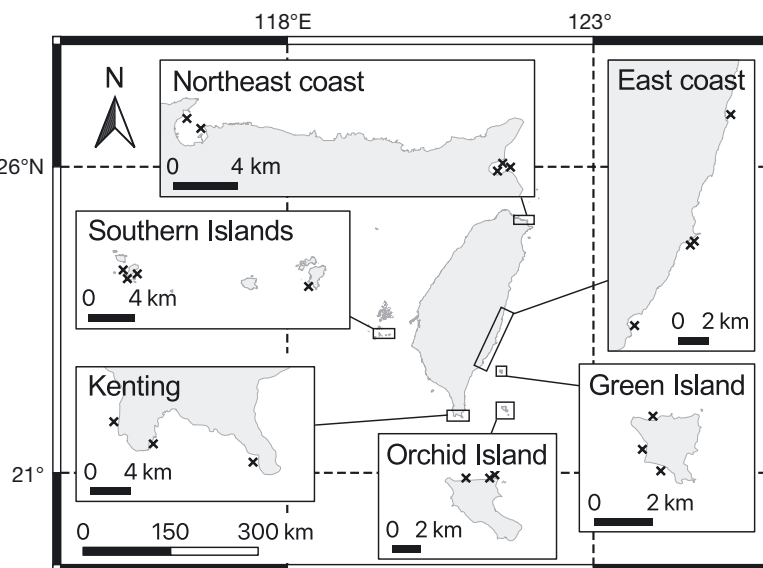

Fig. 1. Survey sites (crosses; n = 22) in 6 reef regions across Taiwan. Map data from the National Land Surveying and Mapping Center, Taiwan (http://maps.nlsc.gov.tw/EN/)

2.2. Survey method

At each site, depending on the reef configurations, a 75–100 m long belt transect was set up parallel to the depth contour at a depth of 5 m and divided into 3 to 4 sampling units. All coral colonies within 1 m on either side of the transect were investigated. Each sampling unit covered an area of 20×2 m^2, and the units were 5 m apart. The survey was conducted using standard protocols (Raymundo et al. 2008). Every coral colony within each sampling unit was counted, identified to the genus level, and inspected for disease and nondisease lesions and factors that could affect coral health. Colonies on the belt margin were counted only when 50% or more of the colony lay within the belt.

Coral coverage was estimated using the point intercept method, and the substrate type was recorded at 50 cm intervals along the transect. The prevalence of disease and nondisease lesions was calculated by dividing the number of affected coral colonies by the total number of colonies. Moreover, taxon-specific prevalence was calculated for a subset of coral hosts in cases that involved a particularly high prevalence of disease and nondisease lesions among specific coral taxa. The influence of each potential factor was also estimated by dividing the number of affected coral colonies by the total number of colonies. The mean value and standard error of the mean (SEM) were calculated for each condition. The frequency of occurrence (percentage of transects surveyed with at least 1 lesion) was calculated for each lesion type to estimate whether it was widespread in Taiwan's reefs.

2.3. Statistical analysis

Statistical analyses were conducted using the 'vegan' community ecology package (Oksanan et al. 2019) in R version 3.5.1 (R Core Team 2018). Permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) with 999 random permutations was conducted to determine the degree of spatial and cross-seasonal variance in the prevalence of assemblages of disease and nondisease lesions. The factor 'reef region' was used for the spatial survey data, and the factor 'reef region × season' was used for the cross-seasonal survey data. For the cross-seasonal survey, only the data obtained from the cross-seasonally surveyed sites were extracted for analysis. The data on disease and nondisease lesion prevalence were transformed using $y' = \sqrt{y + 0.5}$, and resemblance matrices of Bray-Curtis dissimilarity were calculated between every pair of observations. A nonparametric multidimensional scaling (NMDS) analysis (Agarwal et al. 2007) was conducted to visualize the disease assemblage distribution patterns, based on the mean prevalence of lesions related to disease processes, in multivariate space across reef regions. A canonical correspondence analysis (CCA; Legendre & Legendre 2012) was performed to examine the covariances between the prevalence of disease and nondisease lesions and the potential factors affecting coral health.

3. RESULTS

A total of 31 belt-transects were laid in the 6 reef regions in 2018; an area of 3840 m^2 was covered, and 20 709 coral colonies were observed. During the survey, 7 types of disease and nondisease lesions were identified: black band disease (BBD; Raymundo & Weil 2016), black band disease-like syndrome (BBD-like), other cyanobacteria syndrome (CY; Willis et al. 2004), *Porites* ulcerative white spots (Bourne et al. 2016) or multifocal white spots in other coral genera (PUWS/multifocal white spots), white syndrome (WS; Bourne et al. 2016), *Waminoa* flatworm infestation (FL; Biondi et al. 2019), and pigmentation response (PR; Bongiorni & Rinkevich 2005, Palmer et al. 2008, Ravindran et al. 2016). Photos of each type of lesion are presented in Fig. 2, and detailed lesion descriptions are provided in Table 1. Furthermore, 6 types of potential factors influencing coral health were characterized: bleaching (BLE), turf algae overgrowth (turfAL), fleshy macroalgae competition (fleshAL), mixed turf and macroalgae competition (mixAL), *Terpios* or *Cliona* sponge overgrowth (SP), and corallivorous gastropod predation scars (GPS). Descriptions of each factor are provided in Table 2.

3.1. Lesion distribution patterns across spatial and seasonal scales

In the spatial survey, coral disease and nondisease lesions were inspected at all survey sites. The results revealed a significant difference in the distribution patterns of the disease and nondisease lesions across the reef regions (PERMANOVA, df = 5, pseudo-F = 8.3852, R^2 = 0.39958, p = 0.001). The factor reef region alone contributed up to 40% of the observed differences. Among the reef regions, the Southern
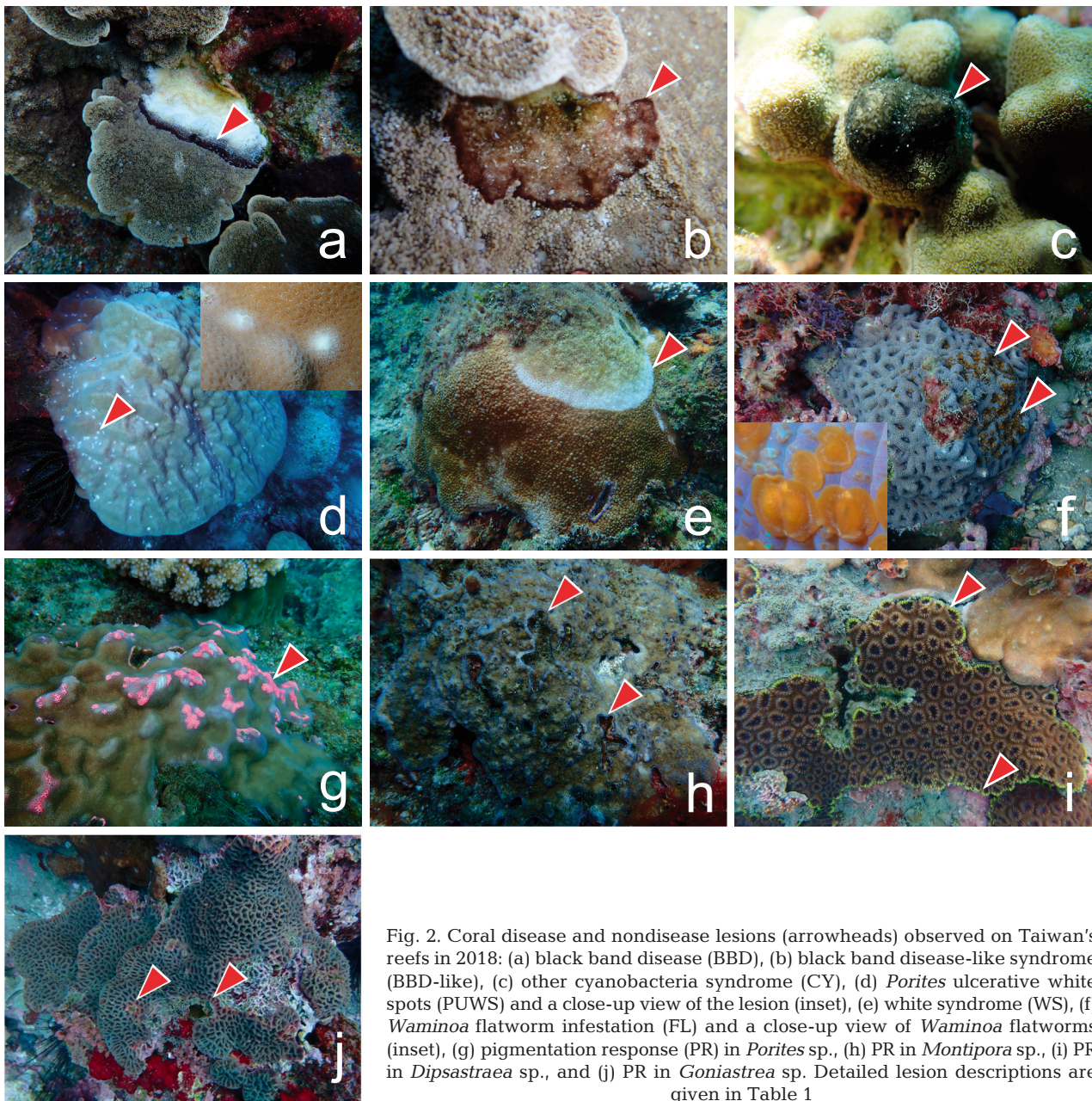
Fig. 2. Coral disease and nondisease lesions (arrowheads) observed on Taiwan's reefs in 2018: (a) black band disease (BBD), (b) black band disease-like syndrome (BBD-like), (c) other cyanobacteria syndrome (CY), (d) *Porites* ulcerative white spots (PUWS) and a close-up view of the lesion (inset), (e) white syndrome (WS), (f) *Waminoa* flatworm infestation (FL) and a close-up view of *Waminoa* flatworms (inset), (g) pigmentation response (PR) in *Porites* sp., (h) PR in *Montipora* sp., (i) PR in *Dipsastraea* sp., and (j) PR in *Goniastrea* sp. Detailed lesion descriptions are given in Table 1

Islands presented the lowest overall mean prevalence of disease and nondisease lesions; the east coast had an intermediate prevalence, and the other reef regions had relatively high prevalence (Table 3, Fig. 3a).

Of the different types of disease and nondisease lesions, the frequency of occurrence was different (Table 3). PR had the highest frequency of occurrence (100%) and the highest prevalence among all reef regions, except for the Southern Islands (Fig. 3a). Specifically, the Southern Islands had the lowest overall mean prevalence and the lowest

prevalence of PR but had the highest prevalence of BBD. By contrast, Kenting presented the highest prevalence of PR and a low prevalence of BBD. Green Island also had a low prevalence of BBD, but notably, it contained other diseases related to cyanobacteria (BBD-like and CY). For Orchid Island, which is near Green Island, of the cyanobacteria-related diseases observed, only CY was recorded. However, compared with other reef regions, Orchid Island had a higher prevalence of PUWS/multifocal white spots. FL was mostly recorded on the northeast coast, and only 1 case was identified on the east coast. Of the

Table 1. Detailed descriptions of disease and non-disease lesions

Lesion	Abbreviation	Description
Black band disease	BBD	Dark band composed of filamentous cyanobacteria, adjacent to clinically healthy coral tissue and a zone of recently exposed white skeleton
Black band disease-like syndrome	BBD-like	Lesions are similar to BBD, with cyanobacteria infections actively spreading, No exposed white skeleton
Other cyanobacteria syndrome	CY	Other cyanobacterial infections that cannot be classified into BBD or BBD-like
Porites ulcerative white spots/ multifocal white spots in other coral genera	PUWS/ multifocal white spots	Multifocal tissue necrosis that exposes small circular areas of bare white skeleton
White syndrome	WS	White lesion that presents as a linear (or annular) band or an irregular patch on the coral colony and is comprised of recently exposed coral skeleton adjacent to apparently healthy tissue
Flatworm infestation	FL	Surface of coral covered by high density of ovoid, brown flatworms, notably in the genus *Waminoa*
Pigmentation response	PR	Non-normally pigmented tissues in corals. The color can change depending on the coral species, and is typically pink, purple, or blue

Table 2. Descriptions of potential factors influencing coral health

Factor	Abbreviation	Description
Bleaching	BLE	Coral tissue discoloration
Turf algae overgrow	turfAL	Colonization and overgrowth of living coral tissue by turf algae (height <2 cm)
Fleshy macroalgae competition	fleshAL	Macroalgae growing within 2 cm range of a coral colony and able to generate an abrasion effect
Mixed turf and macroalgae competition	mixAL	Coral colony is affected by both turf algae overgrowth and fleshy macroalgae competition
Sponge overgrowth	SP	*Terpios* or *Cliona* sponge overgrowth on living coral tissue
Gastropod predation scars	GPS	Feeding scars generated by the corallivorous *Drupella* spp.

Table 3. Means ± SEM of coral coverage (%), Shannon diversity (calculated based on genus level), overall mean prevalence (%), and the prevalence (%) of each type of disease and nondisease lesion in different reef regions and its frequency of occurrence (% of transects surveyed with at least 1 lesion). Abbreviations as in Table 1

|	Northeast coast	East coast	Kenting	Green Island	Orchid Island	Southern Islands	Frequency of occurrence
Coral community							
Coral coverage	24.84 ± 4.14	31.45 ± 4.33	31.67 ± 2.04	37.50 ± 6.33	54.72 ± 2.99	52.50 ± 7.24	
Shannon diversity	2.16 ± 0.08	2.40 ± 0.09	2.44 ± 0.06	1.76 ± 0.16	1.93 ± 0.11	1.30 ± 0.09	
Prevalence of disease/non-disease lesions							
Overall mean prevalence	7.28 ± 0.80	5.25 ± 0.99	8.58 ± 1.81	8.03 ± 1.28	7.76 ± 0.94	2.12 ± 0.73	
BBD	0	0	0.09 ± 0.06	0.14 ± 0.07	0	1.55 ± 0.51	27.3
BBD-like	0	0	0	0.41 ± 0.21	0	0.04 ± 0.04	13.6
CY	0	0	0	1.21 ± 0.61	0.15 ± 0.10	0	13.6
PUWS/multifocal white spots	0.08 ± 0.04	0.13 ± 0.13	0	0	1.48 ± 0.57	0	22.7
WS	0.07 ± 0.05	0.04 ± 0.04	0.04 ± 0.04	0.44 ± 0.19	0.47 ± 0.16	0.08 ± 0.06	45.5
FL	1.13 ± 0.30	0.05 ± 0.05	0	0	0	0	22.7
PR	6.00 ± 0.86	5.03 ± 0.99	8.41 ± 1.84	5.78 ± 1.33	5.59 ± 1.02	0.44 ± 0.25	100.0
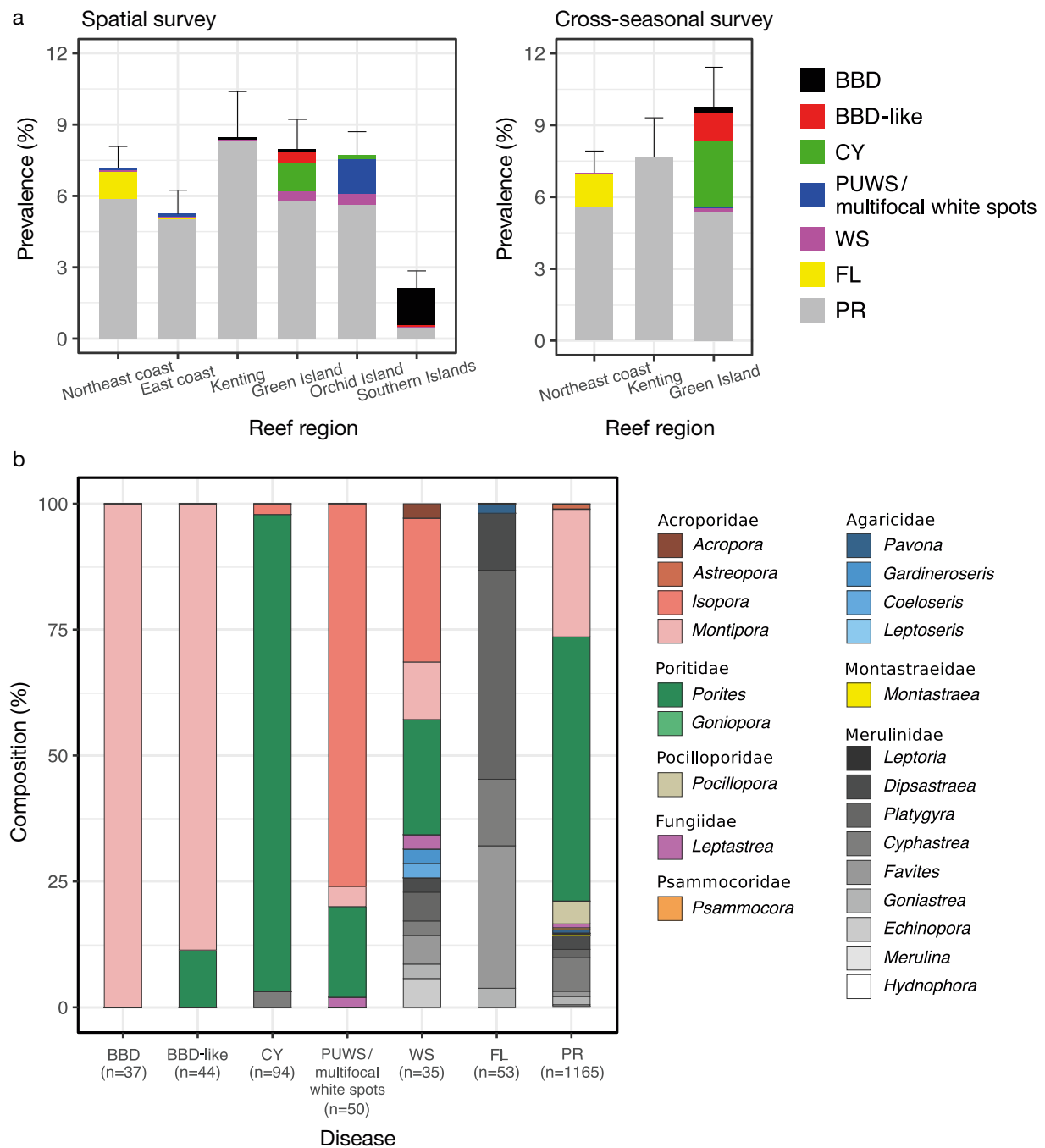
Fig. 3. (a) Mean (± SEM) prevalence of disease and nondisease lesions on the 6 reef regions in the spatial survey and the cross-seasonal survey. The relative abundances of each type of lesion are shown (different colors). (b) Relative contribution of each type of disease on coral host genera (n = total number of colonies that presented lesions recorded in the spatial and the cross-seasonal surveys). Abbreviations as in Fig. 2

lesions that could be related to disease processes (i.e. BBD, BBD-like, CY, PUWS/multifocal white spots, WS, and FL), WS had the highest frequency of occurrence (45.5%), but its prevalence remained low (<0.5%; Table 3).

Disease assemblages, which were based on the mean prevalence of BBD, BBD-like, CY, PUWS/multifocal white spots, WS, and FL, were ordinated in an NMDS space to visualize the differences in disease distribution among the reef regions (Fig. 4). Accord-
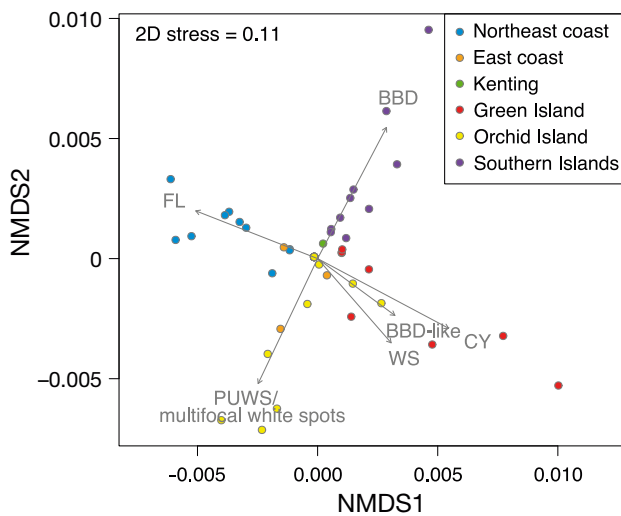
Fig. 4. Non-parametric multidimensional scaling (NMDS) model for disease assemblages (based on the average prevalence of BBD, BBD-like, CY, PUWS/multifocal white spots, WS, and FL across replicate sampling units; abbreviations as in Fig. 2) in the 6 reef regions (different colors) in the spatial survey. Vector overlays indicate the lesion type exerting strong influences on the patterns in multivariate space

ing to the derived NMDS plot, the assemblages from the Southern Islands were predominately driven by BBD, those from the northeast coast were driven by FL, those from Orchid Island were driven by PUWS/multifocal white spots, and those from Green Island were driven by BBD-like, CY, and WS.

The seasonal survey revealed no significant seasonal differences in the prevalence of disease and nondisease lesion assemblages (Fig. 3a, Table 4). The distribution patterns of disease and nondisease lesions differed by reef region (PERMANOVA, df = 2,

pseudo-F = 6.8793, R^2 = 0.21537, p = 0.001), but not by season (PERMANOVA, df = 1, pseudo-F = 0.4670, R^2 = 0.00731, p = 0.645); these disease and nondisease lesion assemblages explained 22 and 0.7% of the variability, respectively. The seasonal patterns were consistent across reef regions (PERMANOVA, df = 2, pseudo-F = 0.3292, R^2 = 0.01031, p = 0.870).

The potential factors influencing coral health predicted up to 25% of the variance in the prevalence of disease and nondisease lesions (CCA, χ^2 = 0.48195, df = 3, F = 6.7912, p = 0.001); these predictors comprised only those with significant marginal effects (Fig. 5). The 2 strongest predictors were turfAL (χ^2 = 0.18894, df = 1, F = 7.9873, p = 0.001) and SP (χ^2 = 0.21006, df = 1, F = 8.8800, p = 0.001); the third most significant predictor was BLE (χ^2 = 0.07100, df = 1, F = 3.0014, p = 0.011).

3.2. Lesion occurrence in different coral taxa

During the survey, 47 coral genera were recorded, 23 of which presented disease and nondisease lesions. The prevalence of disease and nondisease lesions differed among the coral genera (Fisher's exact test, p = 0.0005; Fig. 3b). All the BBD cases occurred in *Montipora* spp. Most BBD-like cases also occurred in *Montipora* spp., but some occurred in *Porites* spp. CY was mostly observed in *Porites* spp., with only a few cases observed in *Isopora* sp. and *Cyphastrea* sp. PUWS was recorded on the northeast and east coasts, whereas multifocal white spots were mainly recorded in *Isopora* sp. on Orchid Island. WS had the widest spectrum of hosts, affecting 13 coral genera in 5 families. FL mostly affected the corals in

Table 4. Mean ± SEM coral coverage (%), Shannon diversity (calculated based on genus level), overall mean prevalence (%), and the prevalence (%) of each type of disease and nondisease lesion in the spring and autumn on the 3 reef regions from the cross-seasonal survey. Abbreviations as in Table 1

|	——— Spring (April to June) ———			——— Autumn (October to November) ———		
	Northeast coast	Kenting	Green Island	Northeast coast	Kenting	Green Island
Coral community						
Coral coverage	17.25 ± 3.87	31.67 ± 2.04	37.50 ± 6.33	17.22 ± 2.55	31.39 ± 4.15	37.22 ± 4.52
Shannon diversity	2.04 ± 0.07	2.44 ± 0.06	1.76 ± 0.16	2.15 ± 0.08	2.42 ± 0.04	2.00 ± 0.15
Prevalence of disease/non-disease lesions						
Overall mean prevalence	7.01 ± 0.83	8.58 ± 1.81	8.03 ± 1.28	7.01 ± 0.91	7.67 ± 1.64	9.75 ± 1.67
BBD	0	0.09 ± 0.06	0.14 ± 0.07	0	0	0.27 ± 0.09
BBD-like	0	0	0.41 ± 0.21	0	0	1.12 ± 0.36
CY	0	0	1.21 ± 0.61	0	0	2.78 ± 1.12
PUWS/multifocal white spots	0	0	0	0	0	0.06 ± 0.04
WS	0	0.04 ± 0.04	0.44 ± 0.19	0.06 ± 0.06	0	0.13 ± 0.07
FL	1.21 ± 0.41	0	0	1.34 ± 0.50	0	0
PR	5.80 ± 0.94	8.41 ± 1.84	5.78 ± 1.33	5.62 ± 0.77	7.67 ± 1.64	5.39 ± 1.22
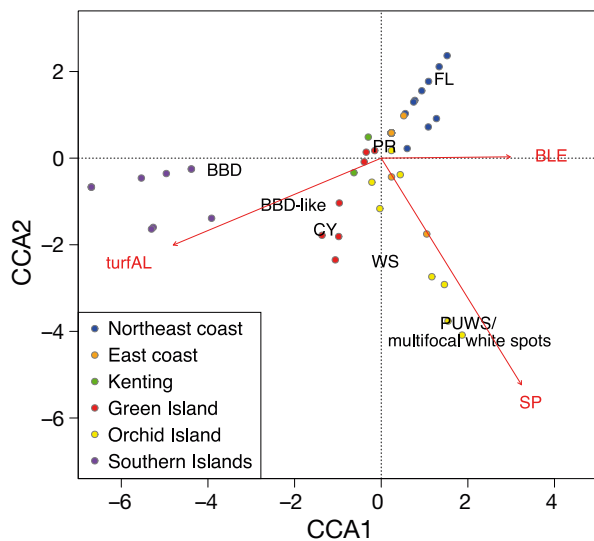
Fig. 5. Canonical correspondence analysis (CCA) for prevalence assemblages of disease and nondisease lesions across the 6 reef regions (different colors) in the spatial survey, using the proportion of potential factors as predictors for the prevalence data. The abbreviation for each lesion type (black text) is on the centroid of its prevalence data. Vectors overlayed (in red) indicate the potential factors exerting strong influences on the patterns in multivariate space; only the potential factors with significant marginal effects are shown. BLE: bleaching; turfAL: turf algae overgrowth; SP: *Terpios* or *Cliona* sponge overgrowth; other abbreviations as in Fig. 2

the family Merulinidae, and only 1 case occurred in *Pavona* sp., which belongs to the family Agaricidae. PR was the most common condition among the reef regions (1165 cases in total). More than 50% of the cases occurred in *Porites* spp., 25% occurred in *Montipora* spp., and another 10% occurred in the family Merulinidae.

4. DISCUSSION

This is the first comprehensive and quantitative study to document the spatial and cross-seasonal variations in coral diseases and coral health across reefs in Taiwan. Taiwan has been described as a 'stepping-stone' connecting the tropical reefs in the Philippines and the subtropical reefs in Japan (Chen & Shashank 2009). This study revealed that the overall mean prevalence of disease and nondisease lesions in Taiwan's reef regions was high (2.12–8.58%) and close to that in regions near Okinawa (3.6–9.7%; Weil et al. 2012) and the Philippines (5.09–11.6%; Raymundo et al. 2005). Despite the similarity in the overall mean prevalence of disease and nondisease lesions between the 3 regions, corals in Taiwan were

mainly affected by chronic and subacute lesion types (e.g. PR) rather than acute tissue loss diseases (e.g. BBD and WS).

4.1. Distribution patterns of lesion prevalence and host susceptibility to diseases

The prevalence of disease and nondisease lesions varied considerably across the reef regions. This finding is consistent with studies on corals in other Indo-Pacific regions (Myers & Raymundo 2009, Haapkylä et al. 2010, Couch et al. 2014). In addition to the NMDS results, this finding suggests that the prevalence of specific disease lesion types predominantly influences coral health in different reef regions. This may be explained by host susceptibility to diseases (Weil et al. 2006, Bruckner 2016) and abundance (Myers & Raymundo 2009). Moreover, host abundance is related to coral coverage (Bruno et al. 2007) and coral diversity (Aeby et al. 2011); therefore, in regions with higher coral coverage and lower coral diversity, colonies of susceptible coral species may be closer to each other, thus potentially increasing the risk of pathogen transmission and infection (Caldwell et al. 2018). This phenomenon was observed for BBD on the Southern Islands, which exhibited the highest coral coverage and the lowest Shannon diversity among the reef regions examined in this study (Table 3). In addition, the coral community was dominated by *Acropora* sp. and *Montipora aequituberculata*. All BBD cases were recorded in *Montipora* spp., and the Southern Islands presented the highest BBD prevalence (Fig. 3a). Orchid Island and Green Island had high coral coverage and medium Shannon diversity. The coral community on Orchid Island was dominated by *Isopora* corals, which are susceptible to multifocal white spots and WS; the prevalence of both lesion types on Orchid Island was higher than that in other reef regions. Green Island had a relatively high relative abundance of *Montipora* and *Porites* corals and relatively higher prevalence of BBD-like, CY, and WS (Table 3, Fig. 3).

Regarding the cross-seasonal survey data for Green Island, no significant difference in prevalence of disease and nondisease lesions was observed between the seasons; nevertheless, the prevalence of BBD, BBD-like, and CY still increased slightly in autumn (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/d146p145_supp.pdf). In addition, the prevalence increased by 2-fold at certain sites compared with other sites. Several seasonal

monitoring programs have revealed the seasonality of BBD (Rodríguez & Cróquer 2008, Sato et al. 2009, Zvuloni et al. 2009). Furthermore, BBD cases have often been found to be clustered during warmer seasons (Page & Willis 2006, Zvuloni et al. 2009). Boyett et al. (2007) and Sato et al. (2009) revealed that seasonally warmer water temperatures and increased light intensity can enhance both disease transmission between colonies and rates of progress within colonies, suggesting an increase in pathogen virulence or host susceptibility (Sato et al. 2009). The latest Intergovernmental Panel on Climate Change (IPCC) model predicts that climate change will continue to increase the temperature of the oceans (The Core Writing Team IPCC 2014) and that the warmer seawater will likely exacerbate the impacts of BBD on Taiwan's reefs by increasing the mortality rates associated with and the duration of coral diseases. Further research should be conducted on the seasonality of BBD and other cyanobacteria-related diseases (BBD-like and CY) and their effects on reefs in Taiwan.

In the 3 reef regions in which BBD was recorded (Kenting, Green Island, and Southern Islands), the coral hosts were identified to the species level on the basis of their morphologies. The affected species were *M. aequituberculata* on Green Island and the Southern Islands and *M. informis* in Kenting. According to the comprehensive list of species compiled by Raymundo & Weil (2016), at least 40 coral species in 12 genera and 7 families are susceptible to BBD in the Indo-Pacific region. Although BBD appears to have a broad range of hosts on a macro scale, it rarely affects more than 1 species on a given reef, even in the presence of other documented host species (Sussman et al. 2006, Myers & Raymundo 2009, Sato et al. 2009). The present study also determined that BBD-like mostly shared the same host species as BBD on the same reefs. Sato et al. (2010) described a similar lesion to BBD-like as 'cyanobacterial patch(es)' and indicated that it could be an early sign of, or a successional change in, BBD. In the reef regions in which BBD-like was recorded (Green Island and Southern Islands), 89% of the cases were *Montipora* corals.

Of the other lesion types, WS had the highest frequency of occurrence (45.5%) among all types of lesions related to disease processes and the widest spectrum of susceptible coral species (Table 3). This finding is attributable to the numerous types of WS that cause tissue loss (Bourne et al. 2016). Despite its generally low prevalence (<0.5%) in the 6 reef regions, WS occurred in 13 coral genera belonging to 5 families and mainly affected Acroporidae, Poriti-

dae, and Merulinidae corals. WS was recently recorded in numerous reefs throughout the Indo-Pacific region (Bourne et al. 2016), and some local outbreaks have been reported (Berkelmans et al. 2004, Roff et al. 2011, Aeby et al. 2016); therefore, the prevalence of WS in Taiwan's reefs cannot be ignored.

Flatworm infestation cases were mainly recorded on the northeast coast, and nearly all of the affected coral colonies belonged to Merulinidae. *Waminoa* spp. (acoels) live on the surface of anthozoans and are potential coral parasites, especially after reaching a high density on the coral surface. If *Waminoa* spp. cover the surface of corals, the resulting shading may reduce the photosynthetic production of the hosts' own zooxanthellae (Haapkylä et al. 2009, Biondi et al. 2019). In addition, *Waminoa* spp. feed on coral mucus, and the removal of the mucus may reduce coral resistance to environmental stressors and pathogens (Barneah et al. 2007, Naumann et al. 2010). Wijgerde et al. (2013) also observed that *Waminoa* acoels impair the heterotrophic feeding efficiency of their hosts. Although *Waminoa* acoels have not been confirmed to cause severe harm to their hosts, they can weaken their hosts and should be considered a chronic health problem.

PR, which indicates coral tissue inflammation, was abundant across the surveyed sites in this study. *Porites* and *Montipora* were the most frequently affected genera, typically displaying pink and blue-purple discoloration, respectively. Additionally, PR was also observed in *Dipsastraea* and *Goniastrea* corals, presenting green-yellow and reddish discolorations, respectively. PR is associated with a generalized innate immune response of corals to physical or pathogenic challenges (Bongiorni & Rinkevich 2005, Ravindran & Raghukumar 2006, Palmer et al. 2008) and is linked to the production of physicochemical barriers in weakened areas (Palmer et al. 2008). PR leads to compromised health states in scleractinian corals and is often attributed to a variety of localized stressors (Bongiorni & Rinkevich 2005, Ravindran et al. 2016). In the present study, PR was attributed to several mechanisms: (1) actions of coral-boring invertebrates (e.g. barnacles and gastropods), (2) aggressive overgrowth (e.g. algae, sponges, or the competition between different coral colonies), (3) predation (e.g. corallivorous fish and gastropods), (4) sedimentation, (5) mechanical injuries, (6) diseases, and (7) unknown reasons. Although PR occurrence is not necessarily correlated with pathogen infections, these mechanisms produce open wounds on coral surfaces and increase the possibility of corals making contact with pathogens in the water, thus

raising the risk of infection. The prevalence of PR can be an indicator of the stress level of a coral community. Furthermore, community composition requires consideration because the response of a coral to PR is species dependent.

4.2. Potential factors contributing to disease

We conducted a CCA to determine the strength of potential factors predicting the prevalence of disease and nondisease lesions. The 2 strongest predictors were turfAL and SP, indicating that turf algae and bioeroding sponges play a decisive role in coral health. BLE was the third most significant predictor. These potential factors may not directly induce coral diseases but can cause a certain level of stress in coral colonies and thus reduce their resistance to diseases.

The CCA results reveal that turfAL was associated with the prevalence of BBD, BBD-like, and CY. As potential competitors, turf algae seize space or overgrow corals (Barott et al. 2012, Jorissen et al. 2016). Moreover, some filamentous turf algae can produce allelopathic chemicals that cause bleaching and necrosis of coral tissue, facilitating turf overgrowth (Barott et al. 2009, Rasher et al. 2011). Such algae also exude photosynthate, which stimulates microbial activity (Smith et al. 2006), thus potentially increasing pathogen abundances (Barott et al. 2012). Consequently, dissolved oxygen decreases (Smith et al. 2006, Haas et al. 2011), and this engenders hypoxia at night (Jorissen et al. 2016), thereby inducing partial or even complete mortality in the corals and causing further turf overgrowth. This process can easily become a vicious circle that creates a disease-susceptible microenvironment (Jorissen et al. 2016).

SP was linked to the prevalence of WS and PUWS/multifocal white spots. Bioeroding sponges were mainly recorded on Green Island and Orchid Island and overgrew on 3.08 ± 0.90 and 8.49 ± 1.64% of coral colonies, respectively. Among such bioeroding sponges, *Terpios hoshinota* is a very thin, encrusting sponge (Rützler & Muzik 1993) that kills coral colonies by overgrowing them (Plucer-Rosario 1987). *Cliona* spp. not only cover corals but also burrow into corals by dissolving their limestone substratum and extending through their complex network of reticulate galleries and chambers (Rützler & Rieger 1973, Hatch 1980). The relationships between these sponges' overgrowth and the occurrence of coral diseases remain unclear; nevertheless, the sponges themselves can deteriorate coral health through the aforementioned mechanisms, causing extensive coral tissue loss (Rützler & Muzik 1993, Liao et al. 2007, Bautista-Guerrero et al. 2014). Coral susceptibility to diseases may increase under such circumstances.

BLE was not associated with a specific type of lesion. The proportion of bleached colonies in the surveyed reef regions was generally low (0~4%), and most coral colonies that were recorded as BLE were partially bleached. We excluded corals with pale growth margins or tips in the identification of BLE. Coral bleaching is mainly driven by seawater temperature anomalies, but such anomalies were not observed during the survey period; therefore, correlating coral bleaching and coral disease may be inappropriate in this study. However, several studies have described the phenomenon of coral bleaching events followed by disease outbreaks (Selig et al. 2006, Bruno et al. 2007, Miller et al. 2009). Both BBD and WS outbreaks are driven by heat stress (Brandt & McManus 2009, Sato et al. 2009).

5. CONCLUSION

We conducted 1 spatial survey and 1 cross-seasonal survey across reefs in Taiwan to investigate the prevalence of disease and nondisease lesions in corals. The overall mean prevalence of coral disease and nondisease lesions in these reefs are consistent with those reported by similar studies on other Indo-Pacific reefs. In addition, the corals were mainly affected by chronic and subacute lesions rather than acute tissue loss diseases. The mechanisms underlying the coral diseases could be attributed to various factors, including (1) host susceptibility to diseases, (2) host abundance, (3) coral coverage and diversity, and (4) potential factors that may induce certain stresses on the coral communities. These factors are consistent with those observed by Weil & Cróquer (2009), who studied Caribbean reefs. The relative importance of each factor varied across regions, scales, seasons, and species. This study advances the understanding of coral health and its ecology in Taiwan's reefs; highlights the correlation among disease, host, and the inhabited environment; and provides valuable information for future reef management strategies.

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