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A global synthesis of the current knowledge on the taxonomic and geographic distribution of major coral diseases

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ABSTRACT

Although knowledge on the diseases affecting corals has been accumulating exponentially since the 2000s, even more effort is required to summarize and guide further investigation. Here, we used the Web of Science database to review 226 studies published, between 2000 and 2020, to identify the major geographic and taxonomic gaps in the literature, and propose future directions for the study of coral diseases. We classified the studies according to the ocean, ecoregion, coral species, disease types, approach (e.g., observational or experimental), and depth. In total, 22 types of diseases were reported for 165 coral species. *Acropora* spp. was the most studied taxa with 12 types of diseases and 8.2% of the records. Black band, white plague, white syndromes, skeletal eroding, dark spot, and yellow band were the six most common diseases, accounting together for 76.8% of the records. As expected, most studies were conducted in the Caribbean and Indo-Pacific (34.0% and 28.7%, respectively), but only in 44 of the 141 global ecoregions that harbour corals. Observational approaches were the most frequent (75.6% of the records), while experimental approaches accounted for 19.9% and were mainly done on *Acropora*. The vast majority of studies (~98%) were performed in shallow waters (<30 m depth). We conclude that over the past two decades, coral diseases have been assessed on a very small fraction of coral species, in very few locations around the globe, and at a limited range of their depth distribution. While monitoring bleaching is mandatory for reef ecology and conservation, the ecoepidemiology of coral diseases deserves more space in the research agenda of reef ecosystems.

1. Introduction

Coral reefs are one of the most productive and diverse ecosystems on the planet (Pandolfi, 2003; Wilkinson, 2008). However, they are facing unprecedented, widespread mortality caused by coral bleaching events (Dietzel et al., 2020; Hughes et al., 2017; Morais et al., 2021), which often lead to disease outbreaks. For example, the second major wave of coral mortality in the form of stony coral tissue loss in the Western Atlantic (Croquer et al., 2021). Bleaching-induced coral mortality has led to drastic changes in coral biodiversity, productivity, structure, and functioning (Cornwall et al., 2021; Darling et al., 2017; Graham et al., 2015; Hughes et al., 2018; McWilliam et al., 2018). Important hotspots, such as the Caribbean and Indo-Pacific, are decreasing in coral cover by an average of 80% and 50% respectively over the last 40 years (Bruno

and Selig, 2007; De'ath et al., 2012; Gardner, 2003; Schutte et al., 2010). There are studies showing that the transmission and prevalence of coral diseases are strongly associated with ocean warming (Aeby et al., 2020; Howells et al., 2020; Jones et al., 2004; Wall et al., 2018), high ultra violet radiation (Boyett et al., 2007; Coles and Brown, 2003), pollution, and low water quality (Nalley et al., 2021; Redding et al., 2013; Zhao et al., 2021). In this sense, diseases may exacerbate the negative effects of bleaching associated with acidification, global warming, overfishing, pollution, and non-regulated tourism on coral reef ecosystems (McWilliam et al., 2018; Miller et al., 2009; Morais et al., 2018; Moriarty et al., 2020). Nonetheless, coral diseases have received little attention on the reef ecology and conservation research agenda compared to coral bleaching.

Coral diseases are found globally (Dalton and Smith, 2006; Woodley

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et al., 2015). Twenty-two diseases have been identified in the Atlantic ocean (including the Caribbean) (Raymundo et al., 2008; Woodley et al., 2015), nine in the Indo-Pacific (Willis et al., 2004), and nine in the other oceans, totalling 40 coral diseases described thus far. These diseases affect roughly 200 species of reef-building corals (Riegl et al., 2009; Woodley et al., 2015). Despite the extensive literature documenting the impact of infectious diseases on corals, including several valuable reviews (Montilla et al., 2019; Pollock et al., 2011; Richardson, 1998; Sharma and Ravindran, 2020; Sutherland et al., 2004; C. M. Woodley et al., 2015; C. Woodley et al., 2015; Work and Meteyer, 2014), some fundamental issues are still in their infancy. For example, we know little about the causative agents of coral diseases (Pollock et al., 2011), transmission dynamics (Shore and Caldwell, 2019), and how to prevent, control, or mitigate disease impacts (Beeden et al., 2012). However, the investments for this type of research are limited and should be applied wisely to obtain the best results to fill these knowledge gaps. Therefore, we need to first understand both the geographic and taxonomic scope of the current coral disease narrative to apply these limited resources effectively.

In this review, we summarize the most recent information on coral disease ecology to (i) identify major geographic and taxonomic gaps and (ii) propose future directions for scientific investigation. We used the Web of Science database to retrieve studies published between 2000 and 2020 using the word 'coral disease*' in the title. This procedure resulted in 226 articles and 888 records of diseases affecting corals. All records were carefully classified according to the ocean, ecoregion, coral species, disease, study approach (e.g., observational or experimental), and depth. First, we summarize the coral diseases to identify those diseases that have been most studied. Then, we use the results of our analyses to identify the current geographic and taxonomic gaps in the field and make inferences about the bleaching-disease association. Finally, we

suggest future directions to fill current knowledge gaps and guide future research to address the steady growth of disease incidence in corals worldwide.

2. Diseases

Our synthesis revealed that, between 2000 and 2020, 22 diseases were reported to affect 165 coral species (Fig. S2). The six most common diseases are black band, white plague, white syndromes, skeletal eroding, dark spot, and yellow band, accounting together for 76.8% of the 888 records. Black band was the most common disease with 27.1% of the records affecting at least 72 coral species, followed by white plague with 19.4% and 50 coral species, and white syndrome with 15.2% and 52 coral species (Fig. 1). Below, we summarize the main aspects of these major diseases, including their symptoms, geographic distribution, and potential etiology (Table 1).

2.1. Black band

The most common coral disease, Black Band Disease (BBD), was one of the first coral diseases to be described. It was identified in the early 1970s in Belize, Bermuda, and Florida (Antonius, 1973; Garrett and Ducklow, 1975). Considered the most studied coral disease due to its widespread occurrence on reefs around the world (Bourne et al., 2011), BBD is also one of the most virulent diseases affecting corals (Richardson, 2004). There are cases reported in multiple geographic locations, including the wider Caribbean, Indo-Pacific, India, South Africa, Red Sea, Philippines, Maldives, Okinawa and more recently in the Hawaiian archipelago (Aeby et al., 2015, 2021; Antonius, 1985; Sato et al., 2010; Weil, 2004). Forty two Caribbean and 57 Indo-Pacific coral species are highly susceptible to BBD infections (Kaczmarzsky, 2006; Page and

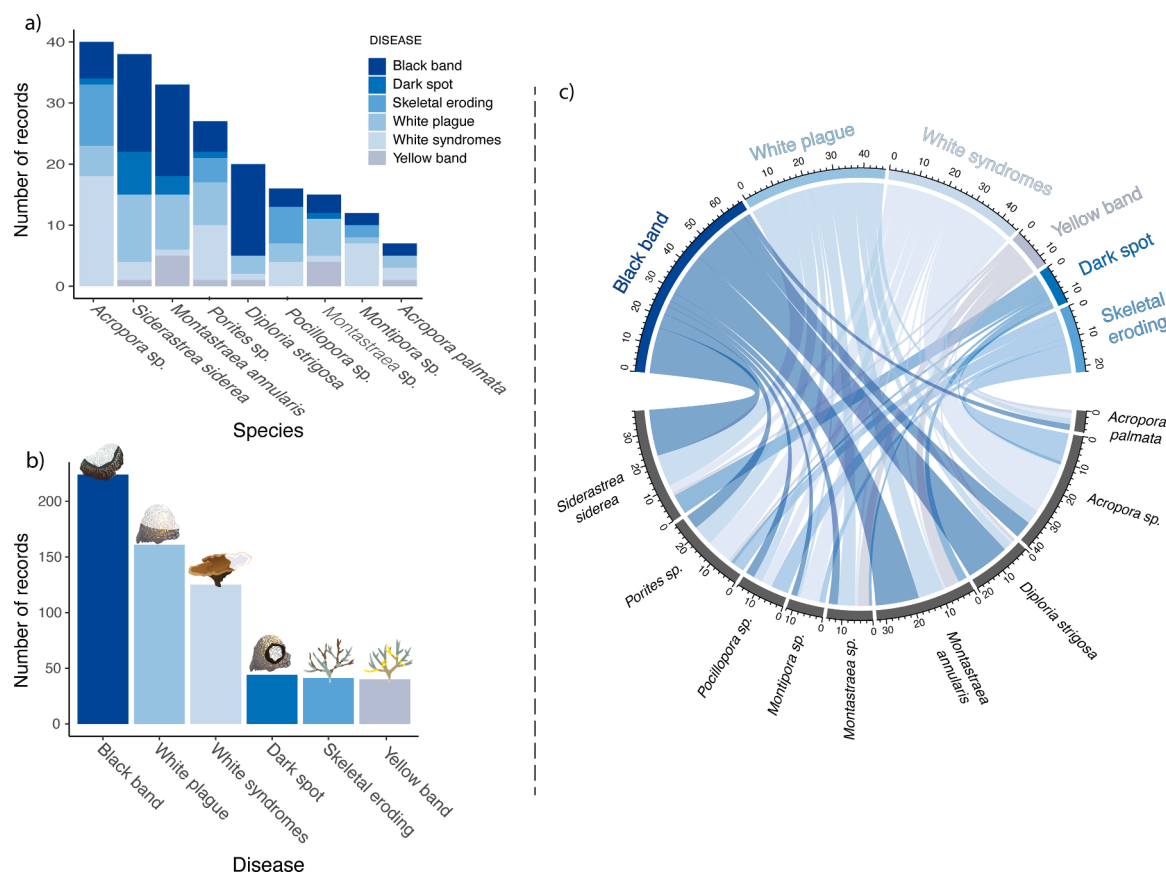


Figure 1. (a) Number of records of the six most cited diseases affecting the nine most cited coral species based on 226 studies published between 2000 and 2020. (b) Number of records by disease based on the same studies. (c) Chord diagram showing coral-disease interactions described in (a).

Table 1

Description, geographic distribution and potential etiology of the six most frequent coral diseases listed in 226 studies published between 2000 and 2020.

Disease name & abbreviation	Disease Description	Distribution	Potential etiology	Key references
Black Band Disease (BBD)	Black microbial band exposing the white skeleton. The BBD is approximately 0.5-1 cm thick and can create a carpet on the surface of the coral	Global	Microbial consortium; cyanobacteria in association with sulfate reducing bacterium <i>Desulfovibrio</i> spp. and sulfide oxidizing bacterium <i>Beggiatoa</i>	Antonius 1985; Miller 1996
White Plague (WP): Type 1: WPI Type 2: WPII Type 3: WPIII	Bright white stripe showing the clean skeleton due to the loss of tissue. Usually starting at the base or sides of the colony	Global	Pathogen “golden-coloured coral killer”, a cyanobacteria from the order <i>Rhizobiales</i> named <i>Aurantimonas corallicida</i>	Antonius, 1985; Dustan, 1977; Richardson, 1998; Richardson et al., 2001; Weil and Cróquer, 2009;
White Syndrome (WS)	Substantial partial mortality that was not recovered in years, causing the fragmentation of larger colonies into smaller size classes	Global	There are several forms of WS with distinct and distinguishable etiologies. However, <i>Rhodobacteraceae</i> may play a role in the pathogenesis of WS	Willis et al. 2004; Pollock et al. 2016; Antonius 1981b
Dark Spots Disease (DSD)	Round, dark areas that apparently grow in size over time, some of which can be associated with a depression of the coral surface and others expand into a dark ring surrounding dead coral	Global	No pathogens confirmed	Gil-Agudelo and Garzón-Ferreira 2001; Gochfeld et al. 2006; Weil 2004 Solano et al. 1993
Skeletal Eroding Band (SEB)	Similar to BBD with a black ciliate mass separating diseased tissue and healthy tissue leaving behind exposed skeleton	Global	Folliculinid ciliate, <i>Halofolliculina covallasia</i>	Antonius and Lipscomb 2001; Page and Willis 2008
Yellow Band Disease (YBD)	Bright-yellow band of tissue at the lesion interface. The band migrates horizontally, producing a margin of decaying tissue; dead skeleton retains yellow pigmentation	Global	<i>Vibrios</i> sp., <i>Vibrio alginolyticus</i>	Korrubel and Riegl 1998

Willis, 2008), yet susceptibility of further species have been reported (Lewis et al., 2017).

BBD is a complex polymicrobial disease dominated by non-heterocystous filamentous cyanobacteria, and includes populations of sulfate-reducing bacteria as necessary secondary pathogens, sulfide-oxidizing bacteria, and a range of other heterotrophic microbes (Brownell and Richardson, 2014; Buerger et al., 2016; Gantar et al., 2011; Ramos-Flores, 1983; Richardson and Kuta, 2003). This disease forms a distinctive dark microbial mat that lies at the interface between live coral tissue and the newly exposed skeleton matrix (Prieto-Barajas et al., 2018; Sato et al., 2016) (Fig. 2). As this mat progresses horizontally across healthy coral colonies with an average spread between 3 mm to 1 cm a day (Miller et al., 2012), it causes loss of tissue and coral death in a short period of time.

Environmental and anthropogenic parameters, such as ocean warming, water depth, solar irradiance, pollution, and even tourism are strongly associated with the occurrence and outbreaks of BBD (Kuta and Richardson, 2002; Lamb et al., 2018; Lamb and Willis, 2011; Page and Willis, 2008). For instance, Lamb and Willis (2011) found the BBD to be on average 4.5 times more prevalent in reefs with tourism than those that are not frequently visited. Nevertheless, the strongest driver to BBD is thought to be ocean warming (Zvuloni et al., 2009), as elevated temperatures may promote high virulence, increase pathogen transmission and survival, and reduce coral immunity (Bhedi et al., 2017; Harvell et al., 2002; Jones et al., 2011; Lewis et al., 2017).

2.2. White Plague

The White Plague (WP), the second most frequent disease in our survey, was described in 1975 shortly after BBD (Dustan, 1977). It is one of the most destructive and widespread coral diseases worldwide, which has caused major reef declines especially in the Caribbean (Antonius, 1985; Dustan, 1977; Navas-Camacho et al., 2010; Weil and Cróquer, 2009). The WP affects more than 35 species of Caribbean scleractinian corals (Sutherland et al., 2004). As other white syndromes, WP provokes rapid tissue loss with lesions that have linear shape and diffuse border, usually starting at the base or margins of the colony (Bourne et al.,

2015). Corals affected by WP are characterized by a distinctively bright line of white tissue between the living parts and the exposed and rapidly algal-colonized skeleton (Miller et al., 2006; Weil et al., 2006) (Fig. 2). In the Caribbean, three different types of WP that potentially differ on causative agents, rates of progression and host species have been proposed (Richardson, 1998; Richardson et al., 2001; Sutherland et al., 2004). WP Type I displays a slow progress of few mm/day; Type II reaches a maximum rate of 2 cm/day; Type III, the most aggressive one, progresses up to 42 cm/day (Dustan, 1977; Richardson, 1998; Richardson et al., 2001).

The complex etiology of this disease is highlighted by studies with culture-independent approaches that revealed a diverse microbial consortium in coral colonies affected with WP, and indicated multiple potential causes (Bourne et al., 2015; Pantos et al., 2003; Roder et al., 2014; Soffer et al., 2014; Sunagawa et al., 2009; Vega Thurber et al., 2020). The three types of Caribbean WP diseases are not likely etiologically related to the ones affecting the Indo-Pacific reefs, therefore the latter are often referred to as White Plague-Like (WP-L) diseases (Sutherland et al., 2004). Among the proposed pathogens of WP and WP-L diseases are: Bacterial Strain BA-3, Nucleocytoplasmic large DNA virus, *Thalassomonas loyana*, and *Vibrio* species (Barash et al., 2005; Soffer et al., 2014; Thompson et al., 2006; Tonon et al., 2017). Although studies suggest that WP II is caused by *Aurantimonas corallicida*, a cyanobacteria from the order *Rhizobiales* (Denner et al., 2003; Richardson, 1998; Richardson et al., 2001), further studies on corals presenting similar signs did not detect the same agent (Pantos et al., 2003; Sunagawa et al., 2009).

As many other coral diseases, WP is strongly related to thermal stress and has shown a tendency to increase with elevated water temperature (Bruno et al., 2007; Chaves-Fonnegrá et al., 2021; Maynard et al., 2015). The Caribbean thermal anomaly of 2005, for instance, was immediately followed by outbreaks of WP (Miller et al., 2006). WP is predicted to double in epidemic magnitude in a scenario with a slight increase of 0.5% in sea surface temperature (Zvuloni et al., 2015). Furthermore, Muller and Van Woesit (2009) demonstrated from field experiments that reducing irradiance on corals affected by WP led to significantly slower disease progression rates. Such knowledge is relevant for assessing and

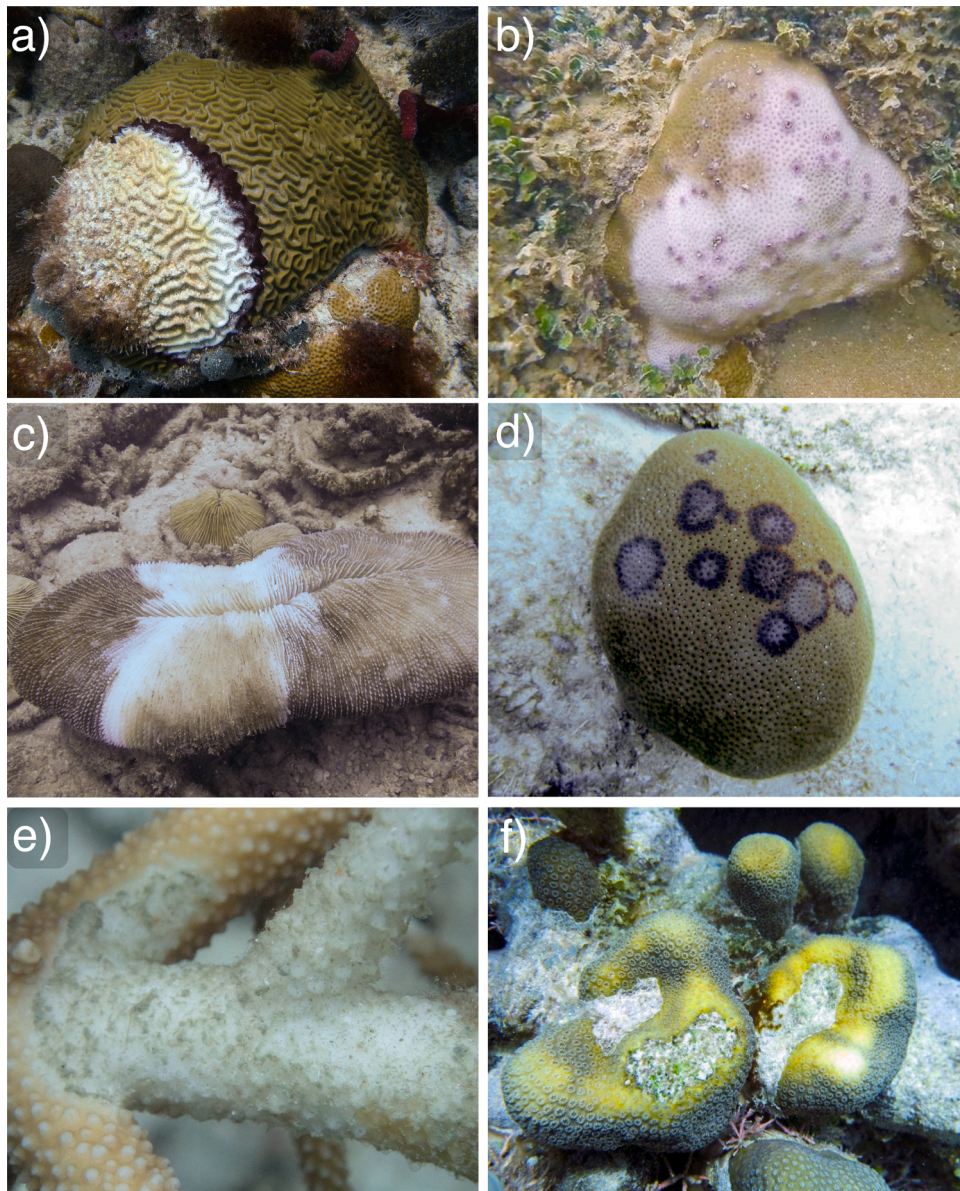


Figure 2. Photographs showing examples of the six most frequent coral diseases in the literature: a) Black band, b) White plague, c) White Syndromes, d) Dark spot, e) Skeletal eroding, and f) Yellow band. Photograph credit: Sara Williams (d, e), Aiara P.L.R Cardoso (c, f), Juliano Morais (b), and Christina Kellogg (a).

predicting future trends of coral diseases through climate change.

2.3. White syndromes

White syndrome (WS) is a collective term for coral tissue loss diseases that display a distinct marked lesion interface between the asymptomatic coral tissue and the white exposed skeleton (Willis et al., 2004). The first reports of “white diseases” on the Indo-Pacific pointed to White Band Disease (WBD) and the conditions observed were similar to the WBD and White Plague (WP) observed in western-Atlantic Ocean (Antonius, 1985). This group of diseases is of great concern worldwide given their widespread distributions, diversity of potential hosts, and rapid and often permanent damage (Aeby et al., 2021; Calnan et al., 2007; Hobbs et al., 2015; Redding et al., 2013; Roff et al., 2006; Weil et al., 2012; Work et al., 2012).

A definitive confirmation on the causative agent(s) underlying WS remains elusive (Pollock et al., 2016), since bacteria, eukaryotes, and viruses may provoke different tissue loss diseases in different coral species (Correa et al., 2016; Daniels et al., 2015; Luna et al., 2010; Soffer

et al., 2014; Work et al., 2012). However, an increased prevalence of bacteria from the Rhodobacteraceae family has been found in diseased corals, suggesting that this group may play a role in WS etiology and progression (Brown et al., 2021; Pollock et al., 2016; Sunagawa et al., 2009). The rates of tissue loss on colonies affected by WS may vary from 1 to 125 cm² or 5% of tissue loss per day (Roff et al., 2006). In addition, WS can lead to substantial partial mortality over years, causing the fragmentation of larger coral colonies into smaller size classes (Howells et al., 2020).

With the increasing number of coral disease studies, it has been notoriously challenging for the scientific community to agree upon the descriptions and diagnostic criteria of this widespread group of diseases (Bourne et al., 2015; Pollock et al., 2011; Woodley et al., 2008). Several distinct names for macroscopically similar disease signs have been emerging both on Indo-Pacific and Caribbean reefs, hence the importance of establishing systematic, standardized criteria to avoid potential erroneous characterization (Bourne et al., 2015; Work and Aeby, 2006). It has been suggested that WS should be reserved for Indo-Pacific corals presenting unexplained white bands/patterns of tissue loss with

unknown etiologies, and the other white disease names should be used on the Caribbean, such as White Band Disease (WBD) and White Plague (WP) (Bourne et al., 2015; Willis et al., 2004). Bourne et al. (2015) also recommend incorporating the coral genus to the disease name (e.g., Porites WS), an unequivocal piece of information, on the reports until the causation of a particular disease is determined.

Similarly to all temperature-dependent diseases, WS outbreaks tend to increase in frequency and severity in response to thermal stress and bleaching events (Aeby et al., 2020; Howells et al., 2020; T. P. Hughes et al., 2018; Jones et al., 2021). It became the most common coral disease on the Great Barrier Reef with a 20-fold increase in prevalence after the anomalously warm summer in 2002, affecting mainly *Acroporidae*, *Pocilloporida*, *Faviidae* and *Poritidae* (Willis et al., 2004). Recent studies also associate WBD outbreaks with climate change-driven increases in sea surface temperature (Gignoux-Wolfsohn et al., 2020; Randall and Van Woesik, 2015).

In the Caribbean, one of the most destructive tissue loss diseases to date is the WB, which is host-specific and affects *Acropora cervicornis* (staghorn coral) and *A. palmata* (elkhorn coral) (Gladfelter, 1982). The WBD was first reported in 1976, and since then it has caused unprecedented mortality of these critical reef-building species, resulting in both species being listed as critically endangered on the International Union for Conservation of Nature Red list (Aronson and Precht, 2001; Carpenter et al., 2008; Gladfelter et al., 1977). Although the definitive causative agents of WBD remain unclear, studies indicate it is caused by bacteria, either singularly or as a consortium (Gignoux-Wolfsohn and Vollmer, 2015; Sweet et al., 2014). *Flavobacteriales*, *Vibrionales* and *Rickettsiales* are thought to be among the potential pathogens (Gignoux-Wolfsohn and Vollmer, 2015). However, considering the high number of diseases known to produce white band-like symptoms (e.g., WP I and II), the report of WBD must be viewed with caution (Willis et al., 2004).

2.4. Dark spot

Dark Spots Disease (DSD) was first documented as a discolouration of healthy coral tissues in the 1990s in Colombia, and since then it has been found in many localities, mainly throughout the Caribbean (Cervino et al., 2001; Garzón-Ferreira et al., 2001; Gil-Agudelo and Garzón-Ferreira, 2001; Solano et al., 1993) but also in other places around the world such as South Atlantic, Indo-Pacific and Red Sea (Francini-Filho et al., 2008; Work et al., 2008; Work and Weil, 2015). DSD is characterized by circular, ring-shaped or elongate lesions, coloured purple, black, or brown, that are found dispersed across the coral tissue surface in variable densities or covering the coral tissue-algal boundary (Borger, 2003; Goreau et al., 1998) (Fig. 2). It is one of the most common diseases affecting at least 11 species of Caribbean stony corals, especially *Montastraea annularis*, *Siderastrea siderea*, and *Stephanocoenia intersepta* (Borger, 2003; Garzón-Ferreira et al., 2001; Gil-Agudelo, 1998; Goreau et al., 1998; Navas-Camacho et al., 2010; Sutherland et al., 2004). This disease may not always be associated with coral tissue mortality, however it has the potential to cause tissue necrosis at rates of up to 4 cm month⁻¹ (Borger, 2005, 2003; Cervino et al., 2001).

As many other coral diseases, the etiology of DSD remains unclear, nonetheless both fungi and bacteria have been pointed as potential causative agents (Gil-Agudelo et al., 2007; Renegar et al., 2008; Sweet et al., 2013). The incidence of DSD is likely to be exacerbated by increases in water temperature, with the highest occurrence during summer months (Borger, 2005, 2003; Gil-Agudelo and Garzón-Ferreira, 2001; Weil, 2004). Furthermore, Randall and Van Woesik (2017) demonstrate that DSD may be influenced by environmental conditions associated with El Niño Southern Oscillation.

2.5. Skeletal eroding

Skeletal Eroding Band (SEB) was first reported in the late 1980s on

reefs in Papua New Guinea and the Great Barrier Reef (Antonius, 1999; Antonius and Lipscomb, 2001). It is the first known stony coral disease caused by eukaryote, and its putative causative agent was identified as the foliicolinid ciliate, *Halofolliculina covallasia* (Antonius, 1999; Antonius and Lipscomb, 2001). Like other "band" diseases (e.g., BBD and WBD), SEB spreads as a line of pathogens moving across the coral colony and leaving behind exposed skeleton. However, unlike the other diseases, the SEB not only affects the soft tissues, but also the skeleton itself (Antonius and Lipscomb, 2001). The tissue damage happens when the ciliates rupture the tissue while embedding their black lorica into the skeletal matrix (Page and Willis, 2008). As the dark band progresses adjacent to the living tissue, the naked skeleton behind becomes replete with distinctive microscopic back marks, the discarded lorica (Page et al., 2015). The disease progression can be relatively slow, approximately 1 mm per week (Antonius and Lipscomb, 2001; Winkler et al., 2004).

SEB is distributed throughout the Indo-Pacific and Hawaii in the central Pacific Ocean (Akmal and Shahbudin, 2020; Antonius and Lipscomb, 2001; Myers and Raymundo, 2009; Page and Willis, 2008; Palmer and Gates, 2010). It affects at least 24 species throughout the Indo-Pacific, and can reach higher levels of prevalence than most other diseases (Antonius and Lipscomb, 2001; Sutherland et al., 2004). For instance, in the Great Barrier Reef, SEB was reported at over 90% of the survey reefs affecting at least 82 coral species (Page and Willis, 2008); in the Red Sea, SEB showed an overall prevalence of 29% of the colonies surveyed by Winkler et al. (2004). SEB prevalence is highest in *Pocillopora* spp. and *Acropora* spp. (Winkler et al., 2004).

From 2004, infections from foliicolinid ciliates (*Halofolliculina* sp.) have also been reported on Caribbean corals (Cróquer et al., 2006a,b). As the species remains unidentified, the term Caribbean ciliate infections (CCI) has been proposed for *Halofolliculina* infections affecting Caribbean coral species (Rodríguez et al., 2009; Weil and Hooten, 2008). A recent morpho-molecular characterization of *Halofolliculina* infections from the Indo-Pacific and Caribbean revealed strong similarities between the pathogens causing SEB and CCI, thus the distinction of these two coral diseases still require further detailed studies (Montano et al., 2020). As expected for other coral diseases, studies indicate a higher prevalence of foliicolinid infections during summer months (Rodríguez et al., 2009; Willis et al., 2004).

2.6. Yellow band

Yellow Band Disease (YBD) was first reported by Dustan in the 1970s as a "ring bleaching" (Bruckner and Riegl, 2015; Cervino et al., 2001). The term "yellow-band disease" was only used in 1994 to describe a condition that affected *Orbicella faveolata* in Florida (Reeves, 1994), and was subsequently reported in other Caribbean localities and north of Bermuda (Santavy and Peters, 1997; Weil and Cróquer, 2009). Currently, this disease is known to occur worldwide, and it is classified according to the region of occurrence: Caribbean yellow-band disease (CYBD), Pacific yellow-band disease (PYBD) and Arabic yellow-band disease (AYBD) (Cervino et al., 2008; Denner et al., 2003; Korrubel and Riegl, 1998; Raymundo et al., 2008).

YBD appears to primarily affect zooxanthellae and secondarily affect coral tissue. In general, it is characterized by blotches followed by a circular ring pattern with a pale yellow to white margin (Cervino et al., 2001, 2008). Studies reported YBD indicate rates of tissue loss around 1cm per month (Bruckner and Bruckner, 2006; Cervino et al., 2001) that may remain for 10 to 12 years or more, progressing until the colony death (Weil and Cróquer, 2009).

CYBD affects dominant reef-building corals and is considered one of the most severe and lethal coral diseases, as cases of recovery have rarely been observed (Randall et al., 2018). CYBD is characterized by a patch or strip of yellow tissue that slowly moves outward, with the central portions of the patch dying and the outer perimeter forming a circular band (Sutherland et al., 2004; Weil, 2004). In the Indo-Pacific, a similar

condition has been reported affecting *Diploastrea heliopore*, *Fungia* and *Herpolitha* spp. However, the yellow lesions disappear as soon as the degradation corrodes all the tissue. This is due to the degeneration of the zooxanthellae, loss of pigment of chlorophyll, as well as to the total degradation of the tissue with a pink colour becoming evident in the final stages (Cervino et al., 2008; Donà et al., 2008).

AYBD presents different dynamics from diseases with similar names detected elsewhere, and is known to predominantly affect *Acropora* and *Porites*. However, it was first reported affecting the genus *Coscinaraea* in the Persian Gulf (Hazraty-Kari et al., 2021; Korrubel and Riegl, 1998;

Riegl and Purkis, 2012). Microscopic examinations on affected *Porites* from Persian Gulf showed a yellow band overlying bare skeleton, composed of a viscous material with presence of zooxanthellae (Aeby et al., 2020).

The etiology of YBD and the mechanisms underlying the coral tissue mortality remain under debate (Bruckner and Riegl, 2015; Cervino et al., 2004; Cervino et al., 2008; Cróquer et al., 2013), but the same consortium of *Vibrio* species is believed to cause YBD infections in the Caribbean and Indo-Pacific. *Vibrio* spp. may initiate the YBD regardless of thermal stress, though the risk of YBD outbreaks has been shown to

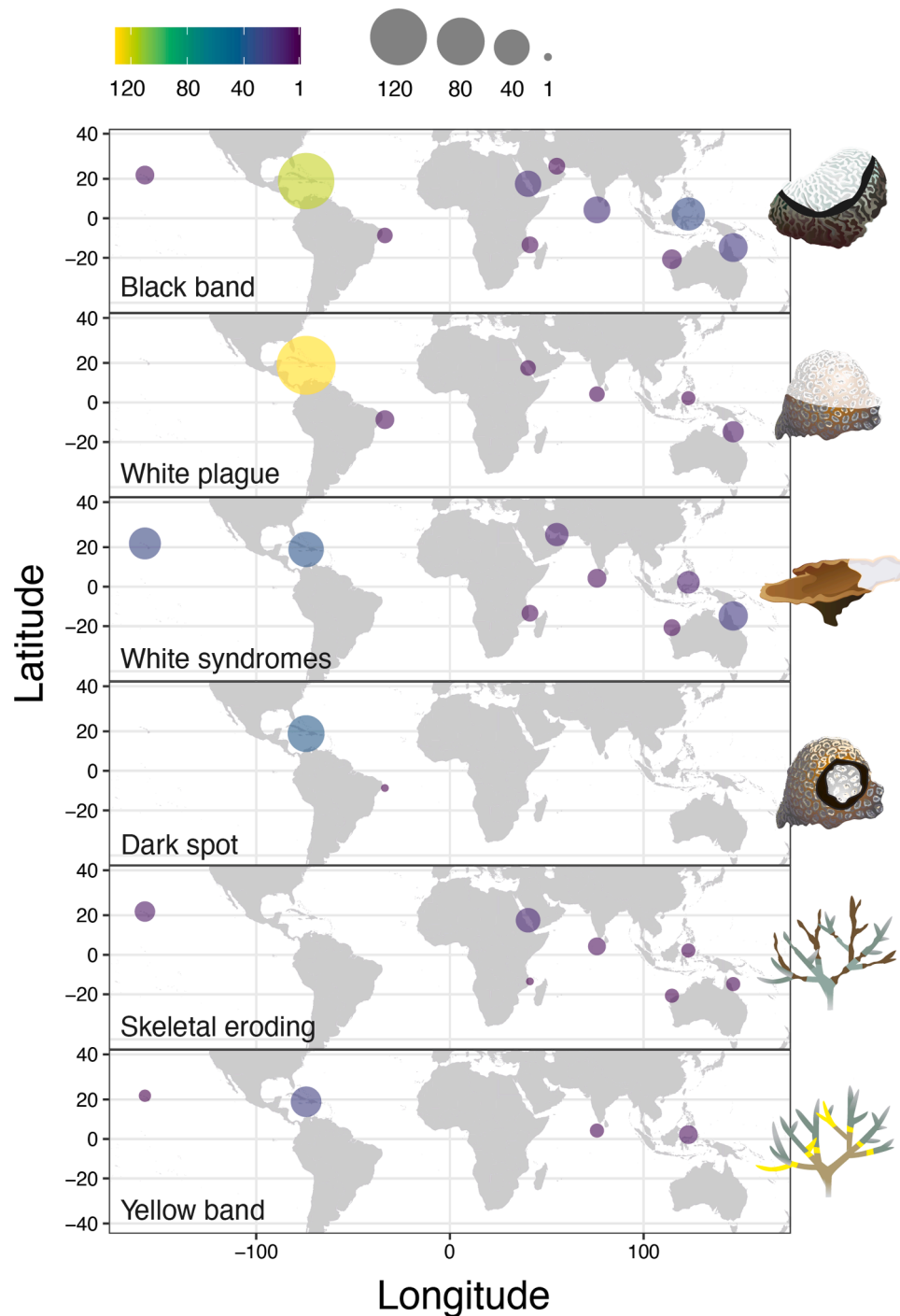


Figure 3. Global distribution of coral disease records based on 226 studies published between 2000 and 2020. Panels represent the six most frequent diseases. Bubbles (size and color) represent the number of records in region: the Caribbean, South Atlantic, East African, Red Sea, Persian Gulf, Indian ocean, Indo-pacific, Western Australia, Great Barrier Reef, and Pacific islands. For visualization purposes, we only show the regions with at least one published record for each category.

increase in regions with warmer-than-average sea-surface temperatures (Aeby et al., 2020; Cervino et al., 2008; Randall et al., 2014; Randall and Van Woesik, 2017, 2015; Van Woesik and Randall, 2017).

3. Geographic gaps

Our analyses revealed some large geographic gaps in coral disease ecology. As expected, most studies were performed in the two most important hotspots of coral diversity: the Caribbean and Indo-Pacific. The Caribbean represented 34% of all studies, while the Indo-Pacific represented 28.7% (Fig. 3). The remainder of the studies were distributed throughout the central Indian Ocean (6.6%), Pacific Islands (5.3%), Red Sea (4.8%), Southwestern Atlantic (1.3%), Africa (1.3%), and the Persian Gulf and Mediterranean (< 1% each). About 16% of the studies did not mention the location or were performed in laboratory conditions. The geographic gaps became even clearer when we analyzed the records by ecoregion: only 44 of the 141 global ecoregions that contain coral reefs (sensu Veron et al., 2009) were studied for coral disease in the last two decades (Fig. S1). This highlights how exceptionally far we are from understanding the global patterns of coral diseases, which are critical to guide future management plans. The most-studied ecoregions were in the Tropical Northwestern Atlantic (i.e., the Greater Antilles and Western Caribbean) and in the Northeast Australian Shelf (i.e., Central and Southern Great Barrier Reef).

Although it is expected that a higher number of studies would coincide in regions with a higher diversity and abundance of coral species, some social and economic factors need to be considered. The Indo-Pacific and Caribbean are located close to countries that have historically supported basic and applied research in the field. For example, in Australia, there are many universities with high capacities to work on many fields of marine ecology in the Great Barrier Reef and are typically funded by the federal government. The same can be seen in the Caribbean, where the United States of America has supported coral reef studies for decades. It is important to note that even in these regions, there are also many less-advantaged countries. However, the presence of developed countries in each of these regions may cover large portions of research investments and result in a high number of publications. For example, a recent study by Ahmadi et al., (2021) reveals that 75% of author contributions in the research conducted throughout East Asian and Pacific reefs are by authors based in Australia, Europe, and the United States, with only about 25% of contributions from authors affiliated in those regions. Contrastingly, while there is a similar volume of research conducted in Australia, the majority of contributing authors are affiliated with Australian institutions, with only approximately 5% from East Asia and the Pacific (Ahmadi et al., 2021).

The fact is, around 64% of the world's coral reefs are located in developing countries that have not prioritized marine scientific research for a myriad of socioeconomic, political, and cultural reasons (Pascal et al., 2016). Together, they home a significant, but poorly known, portion of the evolutionary and functional diversity of corals, which includes defense strategies against pathogenic agents and evolutionary potential for adaptation to environmental changes.

There is no doubt that the main geographic gaps of coral disease ecology are the result of scientists' preferences for species-rich, shallow, and 'traditional' coral reef ecosystems (e.g., the Caribbean or the Indo-Pacific). Coral diseases are spread across the globe and need urgent attention from marine ecologists and conservationists. However, there are also other, often ignored biodiversity hotspots that home endemic coral species (and their defense strategies) that need attention as well. These locations are found in marginal reefs across the globe (Soares et al., 2020). Marginal reefs are ecosystems that offer sub-optimal conditions for most reef biota compared to 'traditional' coral reefs. The sub-optimal conditions include elevated siliciclastic sedimentation rates, turbid waters, mesophotic depths (~30–150 m), high nutrient content (such as phosphorus and nitrogen), extreme pH fluctuations, increased primary productivity (particularly in mesotrophic or

eutrophic waters), and/or highly variable temperatures (see Soares et al., 2020). These ecosystems are important for studies of coral diseases because these sub-optimal conditions can interact and/or act independently to alter coral health in various ways, such as lowering immune defenses or/and increasing the availability of infectious agents in the environment (Howells et al., 2020; Soares et al., 2020; Soares et al., 2022; Wang et al., 2018; Weil, 2019).

We highlight three geographic gaps that combine sub-optimal conditions for corals and low numbers of studies recorded in our result: the South Atlantic, the Red Sea, and the Persian Gulf. The South Atlantic, particularly the Brazilian coast (including its islands and seamounts), is an important geographic gap. Despite harbouring relatively low biodiversity compared to Caribbean reefs (Leão et al., 2003, 2016), the Brazilian reefs sustain high levels of endemism and are predominantly composed of massive forms (Castro and Pires, 2001). For example, Francini-Filho et al. (2008) recorded six diseases impacting 10 coral species, five of which were endemic to Brazil and three were endemic to Eastern Brazil. Most reefs in Brazil are characterized by extreme environmental conditions, such as strong solar radiation, low light levels, and high sediment influx, which have selected stress-tolerant and resistant species (Castro and Pires, 2001; Leão et al., 2016). These environmental conditions paired with the unique diversity found in Brazil demonstrates the work required to understand coral diseases in the South Atlantic.

The Northern section of the Red Sea is another region where coral disease assessments are lacking. Despite the apparent large number of studies on coral reefs in this region, diseases affecting corals throughout the Red Sea are one of the least well explored and documented (Berumen et al., 2013; Mohamed and Sweet, 2019). The Red Sea unique as it homes some of the most productive and richest coral reef ecosystems in the world (Fine et al., 2019; Riegl et al., 2012), with 365 scleractinian coral species, 19 of which are endemic (Dibattista et al., 2016; Rasul and Stewart, 2019; Winkler et al., 2004). Coral reefs in the Red Sea are known for their high species diversity and their ability to persist under extreme environmental conditions, such as high salinity and high temperatures (Osman et al., 2018). However, only 24 coral diseases have been reported for the Red Sea (Berumen et al., 2013). Investing in coral disease research in this area can help fill the gap on (i) why some coral species are more susceptible to certain diseases than others, (ii) why the same species may have different susceptibilities in different locations, and (iii) whether certain areas could act as refuges against disease outbreaks (Mohamed and Sweet, 2019).

The Persian Gulf is the third geographic gap of global relevance. With a relatively low diversity, the species in this region are well adapted to harsh conditions (e.g., *Acropora downingi*, *Acropora clathrata* and *Porites harrisoni*); therefore, the Persian Gulf might reveal pathways towards novel coral reef configurations (Graham et al., 2014). Their species are able to withstand the cold temperatures of the winter and the warm temperatures of the summer more than any other around the world (Coles and Riegl, 2013). As already known, coral disease is strongly related to climate change and increased water temperature (Ferreira et al., 2013; Howells et al., 2020; Miller et al., 2009). This creates an important point of study to understand the influence of coral diseases on coral adaptation to climate change (Burke et al., 2012; Coles and Riegl, 2013).

The geographic gaps reach a global scale when we look at the mesophotic coral reef ecosystems, which are typically found at depths between 30 and 150 m. Our analyses revealed that only 2.2% of all studies were performed in the mesophotic zone. Studies on mesophotic reefs have suggested that the corals in these habitats have specific characteristics in relation to health status when compared to their shallow counterparts (Soares et al., 2020; Tornabene et al., 2016). However, because coral diseases have been recorded below 30 m depth (Bongaerts et al., 2010; Calnan et al., 2007), coral disease ecology in mesophotic zones is a fertile field of scientific investigation (Rogers et al., 2015). Compared with shallow reefs, mesophotic corals live in more stable

environments, especially with regards to temperature fluctuations (Hinderstein et al., 2010). Consequently, even small changes in thermal conditions can trigger bleaching or increase their susceptibility to infectious diseases (Rosenberg and Loya, 2004; Rogers et al., 2015; Smith et al., 2016; Weil, 2019). This might explain why nine of the 28 mesophotic coral species reported for Puerto Rico and the US Virgin Islands were observed with signs of disease (Weil, 2019).

Since Glynn (1996) postulated the notion of thermal refuges for corals, which was further expanded to the deep reef refugia hypothesis (sensu Bongaerts et al., 2010), many studies were performed to describe different aspects of coral biology on mesophotic reefs (e.g., Morais and Santos, 2018; Shlesinger et al., 2017; Soares et al., 2018); however, very few were specifically related to coral disease. The scarcity of studies in this ecosystem is likely related to the logistical and methodological challenges involved in data collection at such depths (Hinderstein et al., 2010; Kahng et al., 2010). The oceanographic technology has been advancing in the last few decades, which has helped researchers estimate the distribution and abundance of coral species in deeper reefs (Kahng et al., 2014). Although recent technological advances, such as Remotely operated vehicles (ROVs) and autonomous underwater vehicles (AUVs), are allowing for deeper surveys, their high cost of operation still makes most research unfeasible (Menza et al., 2007; Wynn et al., 2014). Rebreather diving has also been popularized by researchers, facilitating the data collection in the mesophotic zone, but is met with the same financial barriers as ROVs/AUVs (Rocha et al., 2018).

Regardless of the geographic location, thermal anomalies have been the epicenter of most major coral bleaching events (Hughes et al., 2017; Sully et al., 2019). Over the past 20 years, at least seven mass bleaching events have occurred: three in the Caribbean (2005, 2010/2011, 2015) and four in the Great Barrier Reef (2002, 2016, 2017, 2020). All of these bleaching events (except the 2002 event) were immediately followed by an increase in the number of coral disease studies (Fig. 4). While this reinforces the undeniable correlation between bleaching events and coral disease outbreaks (Howells et al., 2020; Riegl, 2002), it may hide critical aspects of disease ecoepidemiology, including the biology of the pathogenic agents under regular conditions (i.e., between bleaching events) and their relationship with human stressors at local, regional, and global scales (Morais et al., 2018). Fortunately, we also observed three increases in the number of disease studies not related to bleaching events, precisely in the years of 2008–2009, 2013–2014, and 2019–2020

(Fig. 4). Although we agree that bleaching must continue to be monitored globally, we argue that disease monitoring should be part of the same research agenda.

4. Taxonomic gaps

The genus *Acropora*, including their species and subspecies, was the most studied coral taxa. It accounted for 8.16% of the 888 records and was affected by 12 diseases (Fig. 1). The most common diseases recorded for *Acropora* sp. were white syndrome, skeleton eroding, and black band disease (Fig. 1). The Acroporidae is the most speciose family of Scleractinia corals, comprising almost one-third of all reef-building coral species (Madin et al., 2016). However, a recent study with phylogenomic analyses of *Acropora* species demonstrated that the traditional methodology used for taxonomic identification does not reflect the evolutionary relationships between species; consequently, this suggests that the true diversity of the genus is still underestimated (Cowman et al., 2020). Branching corals like *Acropora* are essential for a range of reef fishes and other organisms (Coker et al., 2014), but are particularly vulnerable to bleaching and diseases outbreak (Howells et al., 2020; Loya et al., 2001). Thus, cascading effects on ecosystem functioning are expected if these corals become sick. Similar consequences may arise from disease outbreaks on *Porites* sp. and *Siderastrea siderea*, the second and third most frequent coral taxa in our search with 6.9% and 4.6% of the records, respectively (Fig. S2). However, this does not imply that the 112 coral taxa that had three or fewer records each are more resistant to diseases. Rather, it reflects a profound lack of research across a broad taxonomic scope.

The taxonomy involved in the study of coral diseases is challenging. There are disease-centered studies, in which the whole community of corals in a given area is sampled for its diseases, and species-centered studies, in which the research is based on one or a group of specific coral species and its related diseases. In both cases, a precise identification of corals and pathogens is a hard task to overcome (Ainsworth et al., 2007; Pollock et al., 2011; Work and Meteyer, 2014). We found 165 coral taxa that are affected by one or more diseases, but 44 were identified only to the genus level and 11 were classified at the subspecies level. Even if we consider that the 165 taxa are different species, this implies that only 7.5% of the current, known global diversity of coral species ($n = 2,175$; IUCN, <https://www.iucn.org>) have been surveyed

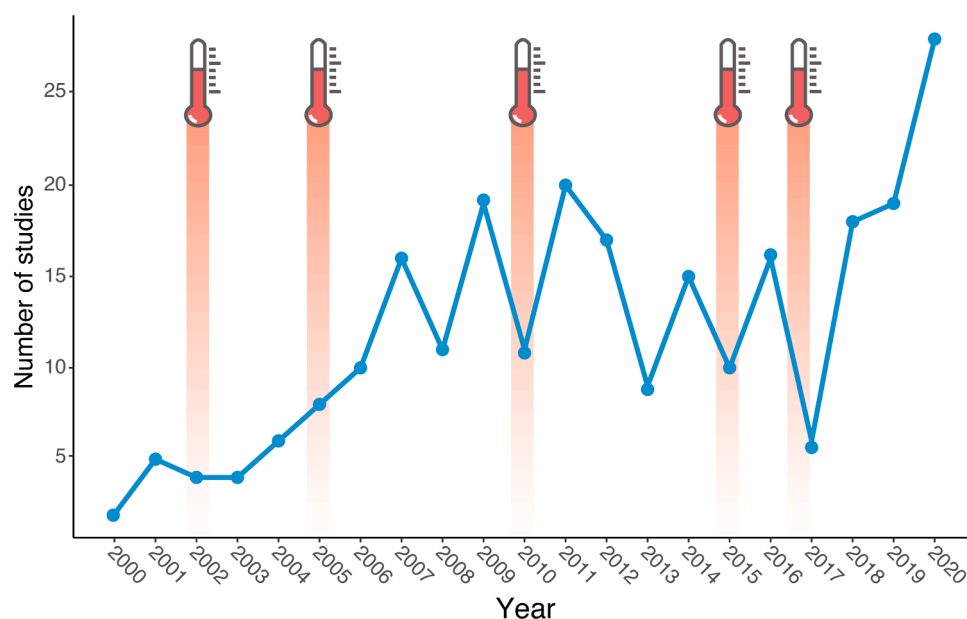


Figure 4. Number of coral disease studies between 2000 and 2020. Red bands represent some examples of bleaching events that have occurred during this time (i.e., Caribbean bleaching events in 2005, 2010/2011, and 2015 and Great Barrier Reef bleaching events in 2002, and back-to-back in 2016 and 2017).

for their diseases in the last 20 years. More than concerning, this finding demonstrates how far we are from drawing general conclusions about the potential emergence of epidemics and pandemics across corals (Mohamed and Sweet, 2019; Weil et al., 2006; Woodley et al., 2015).

Identifying coral colonies at the species level has been a long and arduous task for ecologists (Preobrazhensky, 1977). Due to its high morphological plasticity, the same species may exhibit different colors and shapes depending on the environmental conditions that it is exposed to (Zawada et al., 2019). Some species need to be collected for an accurate identification (Veron, 2002), which typically requires the involvement of taxonomists and large, accurate biological collections. New molecular systematics approaches are emerging (Bonito et al., 2021; Cowman et al., 2020) and helping to identify coral species and their pathogenic agents (Pollock et al., 2011). We encourage the adoption of an integrative taxonomic approach to avoid misidentification, along with microbiological methods (i.e., cellular, molecular, genetic, and genomic), that facilitate the identification of disease vectors and reservoirs (Richardson, 2015; Work and Meteyer, 2014). Such methods may also help to determine the mechanisms of virulence, toxin characteristics, and other eco-epidemiological aspects of the diseases. In fact, the key to better understand the disease dynamics of corals might be the use of a multilayered approach that integrates the interactions between the host-pathogen-environment triad. As the etiology of many diseases do not involve a single pathogen, but rather heterogeneous communities of organisms, it is also important to think beyond standard disease ecology paradigms such as the 'one microbe-one disease' narrative (Thurber et al., 2020).

Solving the taxonomic and etiological issues will be particularly useful for observational and experimental studies. Our analyses revealed that observational approaches were the most common and accounted for 75.6% of the studies, followed by experimental studies (19.9%), and reviews (4.5%). Experimental studies are crucial to isolate variables, causative agents, manipulate conditions, and simulate future scenarios (Pollock et al., 2011). In addition, histological data, which are mostly obtained by experimental studies, are currently the only way to document the relationship between the host, agent, and environment by providing insight into cellular pathology and host responses at the microscopic level (Harvell et al., 2007; Vega Thurber et al., 2020; Work and Meteyer, 2014). Observational studies are critical as well because they allow for the description of patterns at several spatial and temporal scales, and the inference of potential underlying processes driving the observed patterns (Sasano et al., 2016). Whenever possible, we encourage the adoption of both approaches in the same study to produce more conclusive findings; specifically, the correlative evidence provided from observations and the cause-and-effect evidence derived from manipulations (Bartlett, 2013).

5. Future directions

Our review demonstrates that, over the past two decades, the current literature on coral diseases reflects a very small fraction of coral species, very few regions around the globe, and a limited depth distribution. This indicates that the study of coral diseases is still in its infancy, despite substantial advances during this period. Given that corals and the ecosystem services they provide benefit millions of people around the world (Woodhead et al., 2019), moving forward in this field will be essential to achieve the goals of the United Nations Decade of Ocean Science for Sustainable Development (2021-2030). We suggest three priorities for boosting the development of coral disease ecology and its application in conservation actions.

Firstly, we recommend establishing a global research network with standardized protocols to assess the extent of the six major coral diseases described here. This might help practitioners inform society on the diseases that are impacting their local coral reefs, as well as help design eradication plans based on their specific socioeconomic conditions and dominant human stressors. Secondly, we strongly encourage an increase

in survey efforts to describe as many coral and pathogen species as possible, with the specific goals to understand the ecoepidemiology of coral diseases and their interactions with bleaching events. Currently, surveys can be conducted nearly anywhere because even the world's most studied reefs remain understudied in terms of coral diseases. Regions that have currently not been sampled should be prioritized (e.g., Persian Gulf, Red Sea, Southwestern Atlantic), including a variety of marginal reefs distributed across the global ocean (e.g., mesophotic and turbid reefs). Finally, we recommend the enhancement of capacity building to implement effective actions for managing, conserving, and restoring coral reefs with varying levels of diseases. Diseases are a widespread phenomenon and coupling diseases in a fast-changing world requires funding for research, laboratories, biological collections, and training of specialized labor (e.g., taxonomists, ecologists, geneticists, conservationists), along with political will and societal engagement.

CRedit authorship contribution statement

Juliano Morais: Conceptualization, Methodology, Writing – original draft. **Aiara P.L.R. Cardoso:** Conceptualization, Methodology, Writing – review & editing. **Bráulio A. Santos:** Conceptualization, Methodology, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.envadv.2022.100231](https://doi.org/10.1016/j.envadv.2022.100231).

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