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The State of Knowledge of CCA Diversity in the Caribbean Coral Reefs

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Crustose coralline algae (CCA) are a diverse and ecologically important species found in most of the world's oceans. The current lack of taxonomic knowledge and relative abundance compromises our ability to predict species diversity numbers and, thus, their ecological roles and impacts on coral reefs. To gather a better understanding of the state of knowledge of crustose coralline algae taxonomy in the Caribbean, 107 different research papers, and other primary and secondary literature were studied; any source with taxonomical information, species identification, or genetic markers for identification was recorded. All Genebank codes were collected and sorted by supposed species marker and then ran through the National Center of Biotechnology Information. The location these genetic markers were gathered from was compared to the natural habitat range of the species, based on the Algaebank habitat description. Of the supposed 83 described species of crustose algae in the Caribbean, based on morphological characteristics, only 24 total were confirmed by DNA markers. This leaves at least 59 species of CCA to be confirmed in the Caribbean Sea with molecular markers. This indicates the importance of DNA barcode survey studies to assess the accurate diversity of this group in the region. With this limited knowledge apparent, it should be seen that a CCAs phylogenetic and taxonomical review must be done. An in-depth assessment should be conducted on CCA collections to identify the Caribbean species correctly and thus know their biodiversity in local habitats.

Keywords: *crutose coralline algae*, *Caribbean*, *coral reefs*, *biodiversity*

Introduction

Crustose Coralline Algae

Crustose coralline algae (CCA) are among the most ecologically important, yet less-known coral reef species (Steneck, 1986). This species has a distribution that expands over most of the ocean floor in all seas, where they can grow even at depths of 268 m (Litter et al. 1985). CCA physiology and morphology allow them to grow in many varied communities; not only in great depths but also in shallow communities, such as kelp forests, temperate intertidal communities, and coral reefs. On coral reefs, CCA's abundance and distribution are variable, but they can contribute significantly to the reef carbonate budget, given their calcification capacity (Kuffner et al., 2007). In situations of high wave action, CCA can create and dominate their own environments, called algae ridges. An example of this can be seen in the St. Croix algae ridges, which grow alongside the coral reef ecosystems and in island atolls. Some species of CCAs are also crucial for coral resilience; the calcium surface that CCAs create allows for coral polyp settlement and recruitment by providing dissolved organic carbon (DOC) to the coral polyp for calcification (Ritson-Williams et al. 2010).

CCA Identification

Identifying CCA is challenging, yet determinant to advance coral reef science in the light of conservation and restoration. The first instances of algae classification were when Carolus Linnaeus, known as an explorer and biologist, invented the taxonomical naming system and placed algae under the class Cryptogamia; plants whose reproductive systems are not visible (Baweja and Sahoo, 2015). Afterward, in 1836, William Henry Harvey attempted to classify algae into different groups based on the color of the thallus. Though this caused more separation in the classification and a better map of algae species, this only helped those macroalgae species with a clear thallus, which crustose coralline algae do not have. After this, 16 more attempts to create a more concise and accurate taxonomical algae classification spanned over 145 years. Robert Edward Lee developed this final attempt at classification in 2008, which divided algae between the domains of Eukaryote and Prokaryote, which further divided algae species based on chloroplasts and membrane structure and developed many more classes to fit additional alga types (Baweja and Sahoo, 2015).

Even with this clarification of their classification, very little is known about CCAs and their diversity and abundance. The Caribbean would be a primary habitat for CCAs, due to its extensive reef systems. However, there are knowledge gaps regarding the quantity of these species and their distribution throughout the ocean. Doing morphological studies on the CCAs are difficult; most of their defining characteristics are internal, such as branching patterns in the thallus, and thus can only be viewed under a microscope. This identification is made more difficult due to plasticity; in which two separate species may have almost the same physical characteristics. The opposite can also be true; two organisms with almost perfectly similar traits can be two separate species. The earliest paper on this was published in 1972, titled *Marine Algae of the Eastern Tropical and Subtropical Coasts of the Americas*. This publication manual was one of the first complete reports of algae along the coast of both North and South America. After that, many documents and manuscripts on the different types of algae in the Caribbean were written, but none reattempted to collect more morphological data on the CCA species there. Since 1972, there have been many more advancements in morphological classification and taxonomical programs that can gather and produce more accurate taxonomical classifications. In 1996, Algaebase, an online database for taxonomical information of algae, was created, and it has some of the most recent information on different taxonomical information, including species that were once thought to be different but now have been found synonyms of one another.

Genetic Identification

There have also been advancements in molecular analysis of algae species. At first, only a few possible plasmid DNA markers could be used to identify red algae species. Using DNA markers from the nucleus, chloroplasts, or mitochondria of an organism has allowed for easier identification based on evolutionary similarities between species (Purty and Chatterjee, 2016). With this new chance to gather markers from different parts of the organism's genetic makeup, red algae now have 18 other genetic features from plastid, mitochondrial, and nuclear parts of their DNA (Maggs et. al, 2007). One of those markers is psbA, which is used for this literature review. PsbA encodes the creation of the D1 protein, which photosynthetic species use to undergo photosystem 2 (Mulo et. al., 2011). This revolutionization of DNA barcoding has facilitated a greater understanding of species grouping and identification, but it has rarely been used for crustose coralline algae due to its calcium carbonate makeup. Fleshy organisms can have DNA removed through a lysis procedure. In the case of CCAs, it is a multi-step process that includes grounding the CCA sample and adding seawater filters to the solution (Webster et al. 2010). This more difficult process has led to less DNA barcoding on these organisms, adding to the discrepancies in what is known about these organisms taxonomically.

Significance

Uncertainty of specific CCA species found in the Caribbean can also lead to incorrect assessments to coral reef health. Some CCAs are beneficial to reefs, but others are harmful to coral settling; knowing the abundance of CCAs can help provide an understanding of the health of a reef and its likelihood to rebound in the face of climate change. Caribbean reefs are being negatively impacted by climate change, and these effects extend to the CCA species that live there; higher water temperatures put these organisms at risk, and ocean acidification can weaken their calcium carbonate skeletons, especially for CCAs, who are known to be sensitive but adaptive to pH changes. Some are known to be naturally tolerant, but instead, it was found that in decreased pH, the calcification rate of CCAs dropped 29% (Johnson et al., 2019). With these climate change effects harming CCAs, there is a high probability that many species may be lost before they can be recorded.

Material and Methods

To understand the full extent of knowledge on CCAs in the Caribbean, 107 different sources were selected (**Table 1**). These sources either came from Web of Science, were published identification books, or were research papers. The keywords used for the Web of Science were Caribbean, Crustose Algae, and Coral Reef, and the search was conducted on August 28th, 2022. Each source was analyzed, and if a CCA species was listed, it was recorded in an Excel document. Along with the scientific name and the paper it was found in, information such as where the CCA was gathered, any morphological characteristics the paper described, and if any Genebank citations were listed, they were also written down on the Excel Sheet. Once the entire list of species was compiled, any repeat species from different sources were removed, as well as species that were listed as CCAs, though they were not. That complete species list was then run through Algaebase [https://www.algaebase.org/] to check whether the species was an accepted taxonomical name. Algaebase also provided information on type localities, or habitats, which were also recorded. The accepted species of CCAs were then inputted into the National Center of Biotechnology Information (NCBI) to search for genetic markers collected from the Caribbean. psbA markers were used due to their gene sequence being a part of Photosystem 2, which means they can be found in CCA. If either NCBI or the literature had a psbA marker gathered from the Caribbean, this marker was saved. Later, all psbA markers were edited to similar lengths in the Bioedit program and then placed in the MEGA program to produce a phylogenetic tree.

Results

Total Number of CCA Species

From the literature search, 255 crustose coralline species were found. This first number was the overall collected CCA species across the 107 different literatures, including repeats and algae species that are not CCAs but were listed as such. These repeats and incorrect identifications were then omitted, which brought the number of listed species down to 127. These 127 species were identified in Algaebase to determine whether they were confirmed taxonomical names or not. In some cases, some species were found to be synonymous, or that "this entity is in some way unresolved or needs further investigation.". There were even some species for which Algaebase had no information; it would not recognize the name, and no taxonomical information would come up. This brought the 127 species found down to 83 total confirmed CCA species.

Type localities of CCA Species

Using Algaebase again, each species type locality, or habitat, was recorded and compared to where the species was supposedly identified from in the literature. Of the 83 gathered species, only 29 were confirmed by Algaebase to have a type locality in the Caribbean (**Table 2**) .

psbA markers of CCA Species

All 83 confirmed CCA species were put into NCBI to check whether any DNA barcodes were determined for these species. Specifically, only DNA barcodes collected from the Caribbean were considered. Only 12 psbA markers were found from all 83 species; some were for a genus and not a specific species. Those 12 species were then placed into a phylogenetic tree (**Figure 1**).

Table 1

List of all sources gathered from Web of Science

Spatiotemporal and species-specific patterns of diseases affecting crustose coralline algae in Curacao. (G. Quèrè, Steneck R. S., Nugues M. M. 2014)
Bioerosion of reef-building crustose coralline algae by endolithic invertebrates in an upwelling-influenced reef. (A.R. Viaña, Diaz-Pulido G., García-Urueña R. 2021)
Histopathology of crustose coralline algae affected by white band and white patch diseases. (G. Quèrè, Meistertzheim A.L., Steneck R.S., Nugues M.M. 2015)
Disease Specific Bacterial Communities in a Coralline Algae of the Northwestern Mediterranean Sea: A Combined Culture Dependent and -Independent Approach. (G. Quèrè, Intertaglia L., Payri C., Galand P.E. 2019)
Trophic cascades result in large-scale coralline algae loss through differential grazer effects. (J.K. O'Leary, McClanahan T.R. 2010)
Patterns of larval settlement preferences and post-settlement survival for seven Caribbean corals. (R. Ritson-Williams, Arnold S.N., Paul V.J. 2016)
SELECTIVE HERBIVORE INCREASES BIOMASS OF ITS PREY - A CHITON-CORALLINE REEF-BUILDING ASSOCIATION. (M.M. Littler, Littler D.S., Taylor P.R. 1995)
Foundational studies of Caribbean crustose coralline algae
Light Absorption in Coralline Algae (Rhodophyta): A Morphological and Functional Approach to Understanding Species Distribution in a Coral Reef Lagoon. (R.M. Vásquez-Elizondo and Enríquez S. 2017)
A classic Caribbean algal ridge, Holandes Cays, Panama: an algal coated storm deposit. (I.G. Macintyre, Willaim P, Steneck R.S. 2001)
Microbial to reef scale interactions between the reef-building coral *Montastraea annularis* and benthic algae. (K.L. Barott, Rodriguez-Muller B., Youle M., Marhaver K.L., Vermeij M.J.A., Smith J.E., Roher F.L. 2012)
Natural history of coral-algae competition across a gradient of human activity in the Line Islands. (K. Barott, Williams G.W., Vermeij M.J.A., Harris J., Smith J.E. 2012)
pH Variability Exacerbates Effects of Ocean Acidification on a Caribbean Crustose Coralline Alga. (M.D. Johnson, Bravo L.M.R., O'conner S.E., Varley N.F., Altieri A.H. 2019)
A centuries-old manmade reef in the Caribbean does not substitute natural reefs in terms of species assemblages and interspecific competition. (C.E.L. Hill, Lymperaki M.M., Hoeksema B.W. 2021)
Larval settlement preferences of *Acropora palmata* and *Montastraea faveolata* in response to diverse red algae. (R. Ritson-Williams, Arnold S.N., Steneck R.S. 2014)
An unusual microbiome characterizes a spatially aggressive crustose alga rapidly overgrowing shallow Caribbean reefs. (B. Wilson, Fan C.M., Edmunds P.J. 2020)
Larval settlement preferences and post-settlement survival of the threatened Caribbean corals *Acropora palmata* and *A. cervicornis*. (R. Ritson-Williams, Paul V.J., Arnold S.N, Steneck R.S. 2010)
40 Years of benthic community change on the Caribbean reefs of Curacao and Bonaire: the rise of slimy cyanobacterial mats. (D.M. Bakker, Duyl F.C., Bak R.P.M, Nugues M.M., Nieuwland G., Meesters E.H. 2017)
The reduction of harmful algae on Caribbean coral reefs through the reintroduction of a keystone herbivore, the long-spined sea urchin *Diadema antillarum*. (S.M. Willaims. 2022)
Steady Decline of Corals and Other Benthic Organisms in the SeaFlower Biosphere Reserve (Southwestern Caribbean). (J.A. Sánchez, Gomez-Crórales M. , Gutierrez-Cala L.,Vergara D.C., Roa P., Gonzáles-Zapata F.L., Gnecco M., Puerto N., Niera L., Sarmiento A. 2019)

Zooxanthellae presence acts as a settlement cue for aposymbiotic planulae of the Caribbean coral *Montastraea faveolate*. (M.J.A Vermeij, Frade P.R., Bak R.P.M. 2013)
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Induction of Staghorn coral settlement and early post-settlement survival in laboratory conditions. (L.A Gómez-Lemos, García-Urueña R. 2022)
Density-dependent settlement and mortality structure the earliest life phases of a coral population. (M.J.A. Vermeij and Sandin S.A. 2008)
Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. (I. Williams and Polunin N. 2014)
The effects of nitrogen and phosphorus enrichment on algal community development: Artificial mini-reefs on the Belize Barrier Reef sedimentary lagoon. (M.M. Littler, Littler D.S., Brooks B.L. 2010)
Resource partitioning along multiple niche axes drives functional diversity in parrotfishes on Caribbean coral reefs. (T.C. Adam, Kelley M. Ruttenberg B.I., Burkepile D.E. 2015)
Coral loss and fish guild stability on a Caribbean coral reef: 1974-2000. (Alevizon W.S. and Porter J.W. 2015)
Biological Responses of the Coral *Montastraea annularis* to the Removal of Filamentous Turf Algae. (N.P. Cetz-Navarro, Espinoza-Avalos J., Hernández-Arana H.A., Carricart-Ganivet J.P. 2013)
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INCREASED ALGAL DOMINANCE DESPITE PRESENCE OF *DIADEMA ANTILLARUM* POPULATIONS ON A CARIBBEAN CORAL REEF. (E.A. Lacey, Fourqurean J.W., Collado-Vides L. 2013)
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Three decades of coral reef community dynamics in St. John, USVI: a contrast of scleractinians and octocorals. (G. Tsounis and Edmunds P.J. 2017)
Coral reef erosion: In situ measurement on different dead coral substrates on a Caribbean reef. (A. Molina-Hernández, Medellín-Maldonado F. Lange I.D., Perry C.T., Ãlvarez-Filip L. 2022)
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A unique algal ridge system in the Exuma Cays, Bahamas. (R. S. Steneck, Macintyre I.G., Reid R.P. 1996)

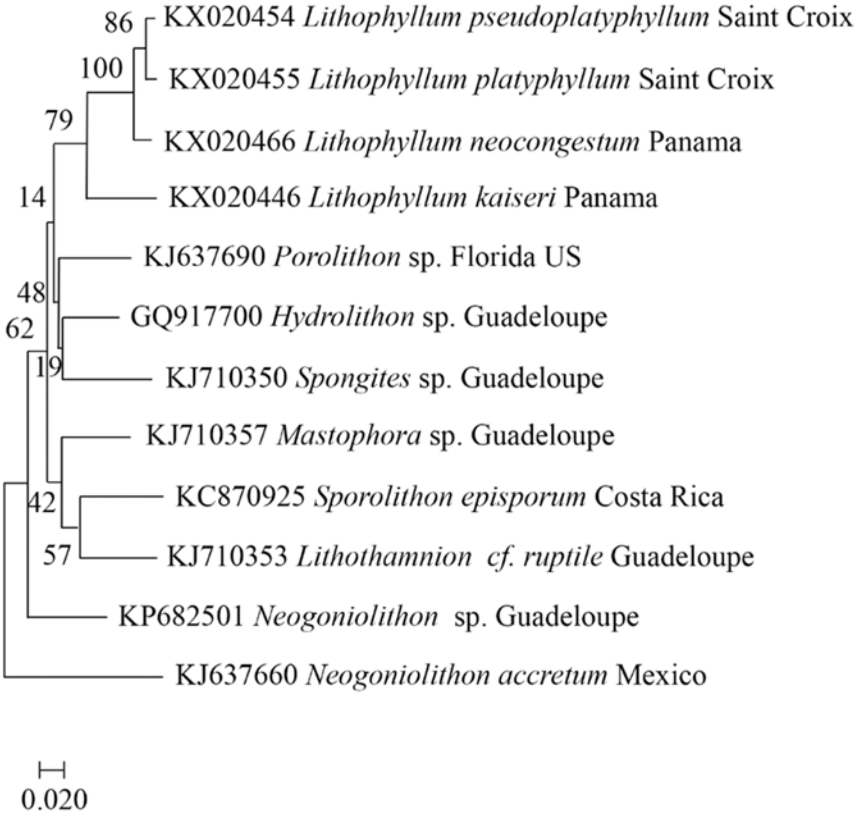
Table 2

Table of the number of algae species found to be confirmed species, how many with the habitat of the Caribbean, and those with direct genetic markers collected in the Caribbean.

Number of Described Species	Number of species with a type locality in the Caribbean	Number of species with a psbA marker
83	29	12

Figure 1

Maximum likelihood tree for psbA marker found in Genbank.



Discussion

There is a considerable discrepancy between the total number of CCA species listed and how many are found in the Caribbean. Of the 255 species found in the literature search conducted, many species were misidentified as CCA species. Other types of calcifying algae were included, but CCAs are specifically encrusting, and the other calcifying algae are filamentous macroalgae. The base knowledge as to what a CCA species is may be incorrect and may lead to researchers improperly identifying CCA species. With these results, it is noted that there is an issue with properly identifying a CCA species, and this leads to greater errors in identifying and distinguishing them properly. Not knowing precisely what a CCA is leads to misinformation on function diversity of these organisms, which can lead to inaccurate assessments of coral reef health and a weakened understanding of how CCAs may impact the health and resilience of Caribbean reef systems.

Only 12 species with DNA sequences have been collected in the Caribbean, therefore, the diversity of species in the area is most likely underestimated, highlighting the need for more genetic-based taxonomic studies in the region. In the case of the first study of Caribbean marl and rhodolith-forming algae using DNA barcoding, eight different species were found, and all were species that had never been barcoded before (Peña et al., 2014). In the collection of the 12 species with genetic barcodes, 6 of them are not specific species; only the genus name could be confirmed, even with genetic information. Consequently, this genetic information could be imprecise and could be connected to a species whose taxonomical information has not been fully resolved or belongs to one of the synonymous taxonomical species. Since the information has not been completed in its entirety, scientists may be classified with limited knowledge. Morphological assessments may not always be beneficial, due to the many specific characteristics of algae that must be studied. The thickness of the algae, the shape and pattern of its thallus and branches, and the structure of its different layers must all be observed. In addition, these characteristics are microscopic, only adding to the difficulty of proper identification. Moreover, those morphological traits can often be absent in the sample collected, adding another obstacle to correct identification. There is also high plasticity in the species, and the opposite is true as well. Often, two species of CCAs will be precisely similar except for one change, such as the branches branching in pairs of two while the other has branched in three parts. This close and almost perfectly similar morphology, known as morphological convergence, means genetic information may be the only way to distinguish species. Without a solid knowledge of how to properly identify species, though, genetic information could be sorted incorrectly or tied to the incorrect species.

A baseline understanding of CCA habitats may also be incorrect, leading to issues in understanding species abundance in the Caribbean. One paper written in 1973 states that CCAs are abundant in arctic and deeper waters, but this has largely been ignored; thus, it may have led to misinformation regarding ecology or paleoecology (Adey and Macintyre, 1973). Scientists have focused their search of CCAs in shallow and tropical waters, leading to a possible misunderstanding of how many species there are and their habitat range. Of the 83 valid CCA species, only 29 had a possible habitat in the Caribbean. It could be possible that these with a type locality in the Caribbean may have a wider habitat range and are not endemic to the Caribbean. In this paper, any genetic markers collected outside the Caribbean were ignored, but oftentimes a species would have psbA markers collected in many different locations as well as the Caribbean. Ignoring these genetic markers may have led to incorrect assumptions about the habitat range of the organism. It could also be possible that a genetic marker collected of a CCA species in the Caribbean and in a different location may be two separate species misidentified as the same species. With so little information, it is difficult to know the exact range of most of the CCA species, leading to possible unknown extinctions or incorrect assumptions about CCA diversity and range.

Climate change is known for its negative impacts on marine environments, and CCAs are also impacted by these negative consequences. As carbon dioxide emission increases, the ocean continues to absorb more of it, lowering the pH of the ocean. This is harmful to CCAs because the calcium carbonate skeleton they produce dissolves in lower pH levels. This raises a new issue; whether the identification of CCA can happen before they possibly disappear. As ocean acidification spikes occur in reef systems, CCAs may become locally extinct in areas where they were usually abundant, giving possible misinformation on habitat distribution or local abundance. Climate change could even cause the extinction of CCA species, leading to the loss of possibly undocumented or incorrectly identified species. CCAs can be both harmful and beneficial to coral reef ecosystems, but in the face of climate change, their impacts may be lessened. Knowing the abundance of these organisms can help determine how a reef system will react to a climate change event and whether restoration and conservation are possible for that ecosystem.

Much of the current experimental work done with CCA is consistently undermined by the uncertainty associated with proper taxonomic identification of CCA. Many experiments have been conducted to determine CCA benefits, but the results are consistently undermined due to limited knowledge. In early 2023, an experiment was conducted in which 15 CCA species from the Great Barrier were collected and identified. Their promotion of coral settlement was then tested against 15 different Pacific coral species (Wahab et. al, 2023) All the CCA species used in this experiment have educated guesses for their taxonomical classification; in which a cf. is placed in the middle of the scientific name to represent uncertainty in the classification. Three species were only identified down to the genus level and not the species level. With this issue, the results they gathered from this experiment will always have the issue of uncertainty, as the CCA species that promote coral settlement may be improperly identified.

There is also continued but uncertain research as to what promotes coral settlement; whether it be the CCA itself or the microbial biofilm that exists on the CCA. The biofilm that is found on a CCA may be what released chemical cues into the surrounding water that then acts as a pheromone for the coral larvae. Tetrabromopyrrole, (TBP) a chemical cue produced by certain bacterial in the genus *Pseudoalteromonas*, has been found to promote coral settlement and the bacteria can often be found as a part of a CCA's biofilm (Tebben et al, 2015.) In comparing settlement rates between CCA with and without the presence of TBP, its effects on settlement were highly dependent on the coral species being tested; *Acropora millepora* larvae had higher settlement, while *Leptastrea purpurea* seemed unaffected by TBP presence. This increases uncertainty on CCA; it could be that the CCA species itself is not what promotes or harms coral larvae settlement, but instead, it could be due to the biofilm composition found on the CCA. This experiment was also much more focused on Pacific corals than Caribbean corals, which means the results of this experiment may not apply to Caribbean CCA or the corals found in Caribbean reefs.

More research must be conducted on CCA species, specifically in Caribbean waters. Collection, morphological identification, and genetic identification must all be undertaken to gather all the possible information about these organisms before they disappear under the effects of climate change. Knowing the species type and abundance may lead to a better understanding of reef health and lead to possible conservation efforts of CCAs, which can help improve coral reef systems globally.

Conclusion

There is little clear understanding of how many CCA species there are in the Caribbean. Lack of proper identification, whether through morphological or genetic studies, has left many discrepancies and possible incorrect identifications of the species that were found. This lack of understanding has led to an overall shortcoming in knowledge of CCA species in the Caribbean and possibly globally. This could lead to incorrect assumptions about reef health due to CCA's impact on coral reef ecosystems. Depending on the abundant CCA species in a reef, it may either promote coral larvae settlement or hinder it, which can lead to the strengthening or collapse of the coral reef ecosystem. Climate change may be only enhancing the lack of information on these species. As the oceans continue to absorb more carbon dioxide, the pH of the water will continue to drop, making it more difficult for both corals and CCA to grow their calcium carbonate structure. This would allow macroalgae to take over, forcing the reef into an alternative, and possibly irreversible, stable state. This also means that there is a high probability that some CCA species may be disappearing from reefs, possibly even going extinct without our knowledge of their existence. More information and species must be gathered to understand better how many species there actually are in the Caribbean Ocean environment and to improve the lack of knowledge.

Future Work

More taxonomical studies must be conducted to clarify these possible incorrect assumptions of CCA diversity and taxonomy. Groups of scientists should collect and analyze CCA species in the Caribbean. Multiple morphological and genetic testing should be conducted to produce a more concise and accurate dataset of the taxonomic information gathered. This will generate a larger data set that can be compared to better identify species. Studies on abundance should also be conducted to better understand what type of CCA is dominating Caribbean reefs to then gain a better understanding of reef health.

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