UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS DEL MAR Y LIMNOLOGÍA

Evaluación del impacto de los huracanes del 2020 en parches someros de *Acropora palmata* en ortomosaicos generados a partir de vuelos de dron comercial

TESIS

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MAESTRA EN CIENCIAS

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MÉXICO, QUINTANA ROO, PUERTO MORELOS. AGOSTO, 2024

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(Graduación con trabajo escrito)

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Evaluación del impacto de los huracanes del 2020 en parches someros de *Acropora palmata* en ortomosaicos generados a partir de vuelos de dron comercial

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RESUMEN

Acropora palmata es la especie que más contribuye a la complejidad estructural de los arrecifes del Caribe. La información sobre la complejidad de sus poblaciones a nivel de paisaje es relevante para determinar cómo responde el sistema arrecifal a eventos de perturbación, entre otros, eventos ciclónicos. Este estudio examina las repercusiones de los huracanes Gamma y Delta (2020) en los parches de *A. palmata* en el arrecife Limones, uno de los arrecifes mejor conservados del Caribe con amplia presencia de esta especie. Se generaron dos ortomosaicos utilizando vuelos programados de drones, uno antes y otro después del paso de los huracanes. En estos ortomosaicos se delinearon archivos vectoriales dibujados a mano que representan los parches de *A. palmata*. El área de la cobertura total de esta especie afectada por los huracanes fue aproximadamente del 25%. Se utilizaron modelos de regresión para analizar la influencia de los atributos del paisaje en la probabilidad de permanencia de los parches y el área restante de estos. Los parches que son más compactos, con una forma más compleja y ubicados a menor profundidad tienen mayor probabilidad de persistir después del impacto de los huracanes. Sin embargo, las métricas del paisaje utilizadas no fueron decisivas para explicar el daño sufrido por los parches restantes. La zonación del arrecife tiene efecto en ambas variables, siendo la zona más protegida (el arrecife posterior) la que presenta menos pérdidas y menor daño a los parches que permanecen. Esta aparente contradicción puede explicarse por la plasticidad fenotípica de las colonias de *A. palmata* en zonas de mayor energía, que tienen características de crecimiento que les permiten soportar mejor el impacto de condiciones de alta energía.

A. INTRODUCCIÓN

A.1. *Ecología del paisaje y su aplicación al paisaje marino.*

La ecología del paisaje es la disciplina que estudia la conexión entre los patrones espaciales de los elementos del paisaje y los procesos ecológicos que ocurren es este (Turner, 2005; Wu, 2013). Esta disciplina permite entender los cambios en el paisaje, tales como eventos de perturbación, sucesión y uso de suelo (Riitters et al., 2002). Además, esta disciplina se ha convertido en una herramienta para determinar criterios de zonificación, catalogación y conservación de elementos estructurales de los ecosistemas (Grober-Dunsmore et al., 2009; Muñoz-Criado, 2012; Kool et al., 2013; Pittman et al., 2014). La información generada con métodos de ecología del paisaje proporciona un marco para responder preguntas relacionadas con la influencia de los patrones espaciales en los procesos ecológicos a múltiples escalas, que también son aplicables en los entornos costeros, especialmente los ecosistemas bentónicos (Grober-Dunsmore et al., 2009; Pittman et al., 2011; Wedding et al., 2011; Santos et al., 2016).

La ecología del paisaje marino se ha enfocado poco en los arrecifes y la mayoría de los estudios referentes a esto se han realizado mediante técnicas de monitoreo con esnórquel y buceo. Estas técnicas de muestreo clásicas han demostrado ser eficientes a escalas finas (Lirman, 2000; Mayor et al., 2006; Álvarez-Filip et al., 2009; McMahon et al., 2012; Richardson et al., 2017; Böstrom et al., 2014; González-Barrios & Álvarez-Filip, 2018). Sin embargo, actualmente se están desarrollando nuevas técnicas de estudio a mayor escala para evitar la sobre o subestimación de los datos, además de reducir los altos costos de los métodos tradicionales. Además, se siguen desarrollando métodos de muestreo con base en imágenes aéreas y satelitales para obtener información espacial (Ventura et al., 2016; Casella et al., 2017; Castellano-Galindo et al., 2019).

A.2. *Modelos e índices de ecología del paisaje*

Se han propuesto varios modelos de paisajes para medir la heterogeneidad espacial de estos (Levin, 1970; Turner, 1989; Mandelbrot, 1983; Forman & Godron, 1986; Noss, 1991; Taylor et al., 1993; Turner & Gardner, 2015). Dentro de este contexto, un paisaje puede definirse como la representación de áreas espacialmente heterogéneas que comprenden un mosaico de diferentes tipos de cobertura de suelo (McGarigal y Marks, 1995; Wu, 2013; Boyce, 2017). Los tipos de cobertura se representan como unidades de área de diferentes formas y tamaños, denominados parches, que luego se agrupan por características compartidas llamadas clases (Wu, 2013; Boyce, 2017). Existen dos categorías generales en las que se agrupan estos modelos: los modelos de gradiente en los que se asume una transición gradual entre clases y los de mosaico de parches en los que se presentan clases discretas con características homogéneas (Boyce, 2017). Los arrecifes de coral están compuestos por parches dentro de una matriz que varían en disposición, tamaño y forma, lo que permite su estudio considerando un modelo de paisaje de tipo mosaico de parches (Huntington et al., 2010).

El patrón del paisaje se cuantifica utilizando índices de ecología del paisaje y métodos estadísticos espaciales (Wu, 2013). Los índices sirven para cuantificar la composición y configuración de las características de un paisaje (McGarigal y Marks, 1995). Los índices de composición evalúan los elementos del paisaje y sus cambios como ganancias y pérdidas de área. Mientras que los índices de configuración documentan la forma en que los elementos se distribuyen en el espacio mediante descripción de la fragmentación y conectividad (McMahon et al., 2012; Santos et al., 2016). Se ha desarrollado una variedad de índices para evaluar la composición y configuración a diferentes escalas espaciales, a nivel de paisaje, clase y parche (McGarigal y Marks, 1995; Uuemaa et al., 2009). El estudio a escala de parche, en contraste con los análisis a nivel de clase y paisaje, enfatiza los rasgos de parches como unidades individuales y descubre información que podría pasarse por alto en categorizaciones espaciales más amplias.

A.3. *Acropora palmata y su complejidad estructural.*

Acropora palmata es la especie de coral que más contribuye a la complejidad estructural de los sistemas arrecifales en aguas poco profundas del Caribe (Aronson y Precht, 2001; González-Barrios y Álvarez-Filip, 2018). Es una especie susceptible a la fragmentación causada por huracanes lo que se puede considerar como una especie de estrategia de reproducción asexual debido a la supervivencia de fragmentos desprendidos; sin embargo, se sabe también que la fragmentación reduce su potencial de reproducción sexual limitando la producción de gametos (Lirman, 2000).

Sus poblaciones generalmente se distribuyen en forma de parches, formados por agregaciones de colonias, a lo largo de los sistemas arrecifales del Caribe (Miller et al., 2008; Rodríguez-Martínez et al., 2014; García-Urueña y Garzón-Machado, 2020). Investigar las características espaciales de los parches de *A. palmata* es relevante para evaluar la salud del ecosistema, ya que es una especie fundamental en la construcción de arrecifes en el Caribe y, por lo tanto, su salud y distribución tienen un impacto profundo en el estado general de los ecosistemas arrecifales (González-Barrios & Álvarez-Filip, 2018). También proporciona información sobre los mecanismos que las hacen resistentes a las perturbaciones, como son los impactos de huracanes, lo que puede informar estrategias para la restauración y conservación de arrecifes después de este tipo de eventos, guiando intervenciones como la restauración de corales y la gestión de áreas protegidas (Rodríguez-Martínez et al., 2014).

A.4. *La plasticidad fenotípica de A. palmata y la zonación del arrecife.*

Además de la disposición espacial y estructura de los parches, la plasticidad fenotípica a nivel de las colonias de *A. palmata* es otro factor que proporciona información sobre su respuesta a eventos de perturbación severos. como por ejemplo después de un huracán (referencia). La zonación arrecifal está definida por la construcción de la estructura del arrecife, así como por otras características geológicas como la profundidad y la pendiente del fondo (Storr, 1964). Las características oceanográficas, como la energía del oleaje, son cambiantes a lo largo de la zonificación y se sabe que influyen en las morfologías de las colonias de coral residentes (Storr, 1964; Bottjer, 1980; Storlazzi et al., 2004; Lohr, 2020). Así, las colonias de *A. palmata* que crecen en las diferentes zonas del arrecife varían en patrones de crecimiento, como adaptación a diferentes regímenes de energía. Esta plasticidad fenotípica está relacionada con la energía de las olas recibidas y las corrientes oceánicas experimentadas durante el crecimiento de la colonia (Storr, 1964; Graus et al., 1977). Las variaciones morfológicas estudiadas en *Acropora* van desde rasgos estructurales de la colonia, como el tamaño de esta, los ángulos de crecimiento y la orientación horizontal de las ramas (Graus et al., 1977; Bottjer, 1980), hasta características de pólipos individuales como son la expresión génica y la variabilidad epigenética (Durante et al., 2019; Wyatt et al., 2022). La plasticidad fenotípica puede influir en la resistencia de esta especie de coral a los huracanes ya que se ha descrito que, en los Cayos de Florida y para otras especies de *Acropora*, está asociada con una mejor aclimatación en el espacio y el tiempo (Wyatt et al., 2022).

A.5. *Efectos de los huracanes en los arrecifes de coral y particularmente en corales ramificados como Acropora.*

Aunque los arrecifes coralinos son ecosistemas adaptados a los impactos de los huracanes (Nyström et al., 2000), hay muchos factores a considerar antes de hacer esta afirmación, como las condiciones cada vez más desfavorables a las que están sujetos estos ecosistemas, mayormente asociadas con el desarrollo costero y el cambio climático, que disminuyen su resistencia a las perturbaciones naturales (Rogers et al., 1983; Lirman, 2000; Nyström et al., 2000). Particularmente en especies como *A. palmata*, que forma estructuras ramificadas extensas, los impactos de los huracanes, y de las fuertes olas y lluvias intensas producto de estos, conducen a daños físicos como ruptura, fragmentación y desplazamiento de colonias completas de coral (Harmelin-Vivien, 1994; Zimmerman et al., 2020). La fuerza de los huracanes no solo daña directamente las estructuras de los corales, sino que también contribuye al aumento de la sedimentación y turbidez en el agua, reduciendo la disponibilidad de luz (Harmelin-Vivien, 1994; Edmunds et al., 2019). Además, las características físicas de la zona del arrecife, como la profundidad y la exposición a las olas, donde se encuentran las colonias, son factores que influyen también en la forma en que estos daños se distribuyen (Woodley et al., 1981).

A.6. *Justificación y objetivos*

Aunque, debido a su gran importancia ecología, existe una investigación sustancial sobre *A. palmata*, aún hay lagunas en nuestra comprensión de los rasgos espaciales de sus poblaciones, especialmente en el contexto de la resistencia a perturbaciones de alta intensidad como son los huracanes. Abordar estas lagunas es esencial para avanzar en el conocimiento científico y desarrollar estrategias de conservación más efectivas. En este trabajo, el objetivo fue obtener información sobre los factores que influyen en la vulnerabilidad y resiliencia de los parches de *A. palmata* a los impactos de huracanes. Específicamente, se busca entender cómo la complejidad de los parches de *A. palmata* así como su distribución espacial contribuyeron a las modificaciones observadas en el área después de los eventos ciclónicos del año 2020, y posteriormente relacionarlas con procesos a menor escala espacial que determinan la forma en que las poblaciones de esta especie responden a eventos de disturbio naturales, como la plasticidad fenotípica a nivel de colonia a lo largo de la zonificación del arrecife, que es determinante de la forma en que las poblaciones de *A. palmata* responden a eventos de perturbación naturales.

B. The spatial distribution and arrangement of the colonies of *Acropora palmata* determines its resistance to hurricane impacts

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B. 1. ABSTRACT

Acropora palmata is the species that contributes the most to the structural complexity of Caribbean reefs. Information concerning the complexity of its populations at the seascape level is relevant to determine how the reef system responds to disturbance events, amongst others, hurricanes. This study examines the repercussions of hurricanes Gamma and Delta in the year 2020, on the patches of *A. palmata* in the Limones reef, one of the best-preserved reefs in the Caribbean. Two orthomosaics were generated using programed drone flights, one prior and the other after passage of the hurricanes. Hand-drawn vector files representing the patches of *A. palmata* were delineated on these orthomosaics. The area affected by the hurricanes was approximately 25%. Regression models (a Binomial GLM and a Linear regression model) were used to analyze the influence of seascape ecology patterns on patches permanence probability and remaining area. Patches that are more compact, with a more complex shape, at shallower depths have higher probability of persisting after the impact of hurricanes ($p<0.01$). However, the metrics used are not decisive in explaining the damage suffered by the remaining patches. The spatial location of the patches (proximity and size of its neighbors) did not have a significant effect ($p>0.05$) on the permanence rate. This could be explained by the phenotypic plasticity of *A. palmata* colonies in higher energy zones having growth characteristics that allow them to better withstand the impact of high-energy conditions.

Keywords: seascape ecology indices, *Acropora palmata*, hurricane.

B. 2. INTRODUCTION

The spatial distribution and structure of ecosystems is determined by environmental conditions and the occurrence of disturbances. For example, fires or plagues impact species composition as well as growth and survival of the tree community in forest ecosystems (Sturtevant & Fortin, 2021), which modify the spatial traits in the system, and result in an alteration of the entire systems functioning (Pickett and White, 1985; Lindenmayer et al., 2017). A commonly used approach to understand the landscape effects of disturbance, is to explore changes in spatial units classified according to aggregated and homogeneous characteristics, commonly referred as patches (Boyce et al., 2017; Turner, 2010). The use of these units is particularly relevant for systems such as coral reefs, that are composed of patches within a matrix that vary in arrangement, size, and shape (Shedrawi et al., 2017; Folkard, 2019), as this seascape perspective allows a detailed representation of the structure and dynamics of the system, avoiding extrapolation of sample data and therefore allowing better understanding of spatial traits of the components of patchy systems (e.g., Grober-Dunsmore, et al., 2009; Pittman et al.,2011; Wedding et al., 2011; Santos et al., 2016).

However, most studies on coral reefs, and particularly those on the impacts of disturbances have focused on the fine scale detail, for example evaluating changes in the total amount of coral cover measured within linear transects or photo quadrats (Shedrawi et al., 2017; Vercelloni et al., 2020). This level of information has proven to be efficient to portray changes in the composition of benthic components (Álvarez-Filip et al., 2009; Boström et al., 2011; Lirman, 2000), and allows for the generalization of these trends across larger ecological scales (e.g., Contreras-Silva et al., 2020; Melo-Merino et al. 2020; Gonzalez-Barrios et al 2023). Yet, fine measurement along transects or photo quadrats do not have the capacity to portray the landscape properties of the systems, for example, the modification of coral patches and their consequences for the overall ecosystem functioning. The use of relative novel technologies such as Unmanned Aerial Vehicles (UAVs),) used in photogrammetry, have rapidly emerge in recent years allowing for development of techniques that represent the structure and composition of reefs in two or three dimension and facilitation of the analysis of reef systems from a seascape perspective. Recent seascape ecology studies show that remote perception techniques are a powerful tool for the study of coral reef systems, from satellite imagery used in large scale spatial assessment, to aerial photography used in 3D modeling of coral colonies (Hattori & Shibuno, 2015; Hedley et al., 2016). UAV images are efficient in the perception and spatial modeling of coral populations (Casella et al., 2017; Wyatt, 2022). Information provided by orthomosaics of this nature is being used to assess coral populations changes and dynamics, such as carbonate production rates (Husband et al., 2022), as well as management strategies for these ecosystems (Hedley et al., 2016; Peterson et al., 2023).

Hurricanes or tropical cyclones are one significant force that can modify the structure and composition of reef patches within short temporal scales (i.e., days; Hughes and Connell, 1999). These modifications probably have an impact on the seascape structure of the reef, which in turn potentially affects some of their properties, including the structural connectivity across patches, the hydrodynamics of the systems, and even the ecological and biological connectivity across the mesoscale (Meurice, 2019; Odériz et al., 2020). The effects of hurricanes are particularly relevant on branching coral species such as *Acropora palmata*, as the strong waves, powerful storm surges, and heavy rainfall associated with these phenomena led to physical damage such as breakage, fragmentation, and dislodgment of coral colonies (Harmelin-Vivien, 1994; Zimmerman et al. 2020). The force of hurricanes not only directly damages the coral structures but also contributes to increased sedimentation and turbidity in the water, reducing light availability (Harmelin-Vivien, 1994; Edmunds et al. 2019). Also, the reef zone physical characteristics, such as depth and exposure to waves, on which colonies are located influence the way these damages are distributed (Woodley et al., 1981). *A. palmata* is the species that contributes the most to the structural complexity of reef systems in shallow waters of the Caribbean (Aronson & Precht 2001; González-Barrios and Álvarez-Filip, 2018). It is also a rare species nowadays, however extensive patches were common in the Caribbean before its population decline in the 1980 decade (Aronson & Precht, 2001). It is a species susceptible to fragmentation caused by hurricanes, which results in the asexual reproduction of the species due to the survival rate of fragments; however, this phenomenon reduces its reproductive potential (Lirman, 2000). The populations of *A. palmata* are generally distributed in patches, formed by colony aggregations, along the Caribbean reef systems (García-Urueña & Garzón-Machado, 2020; Miller et al., 2008; Rodríguez-Martínez et al., 2014). Investigating *A. palmata* patches spatial traits is relevant for evaluating ecosystem health since it is a foundational reef-building species in the Caribbean and therefore its health and distribution have a profound impact on the overall health of coral reef systems (Gonzales-Barrios & Alvarez-Filip, 2018). It also provides information about the mechanisms that make them resistant to hurricane impacts, which can inform strategies for reef management after disturbances, guiding interventions such as coral restoration, protected area management, and land-use planning (Rodríguez-Martínez et al., 2014).

In addition to spatial arrangement and structure of the patches, phenotypic plasticity also provides insights into the response of corals to strong disturbance events. Individual morphological plasticity is likely strongly linked to reef zonation, in the same way other oceanographic characteristics such as wave energy, that are variable along the reef zoning (Storr, 1964; Graus et al., 1977; Bottjer, 1980; Storlazzi et al., 2005; Lohr et al., 2020). In the reef crest zone, there is a shallow environment and wave energy is high, in contrast to the backreef where water is usually deeper and calm, due to the reef crest protection from wave impacts. Colonies of *A. palmata* occurring under different energy regimes are therefore likely to reflect different growth patterns as adaptation to these conditions. Indeed, *Acropora* has a wide range of morphological variations that can be modulated by the environment, from colony structural traits such as colony size, branch growth angles and horizontal branch orientation (Graus et al. 1977; Bottjer 1980), to the gene expression and epigenetic variability of individual polyps occurring under different conditions (Durante et al., 2019; Wyatt et al. 2022). Given this variation in colony morphology, it may be expected that coral colonies inhabiting under high energy regimes are better adapted to resist the impact of strong currents and waves associated, for example, with hurricanes, in contrast to colonies in low-energy environments that have not developed any phenotypic adaptation to these environments (Wyatt et al. 2022).

While there is substantial research on *A. palmata* ecological relevance as a habitat producer due to its structural complexity, and its geological importance as a reef formation element, there are still gaps in our understanding of how the spatial traits of *Acropora* patches, such as spatial arrangement and distribution along the reef, are modulated by disturbances. Here we aim to investigate the factors that influence the vulnerability and resistance of *A. palmata* patches to hurricane impacts. We use as a study case Limones reef, in Puerto Morelos, Mexico that was impacted in 2020 by three consecutive hurricanes. Using two UAV derived orthomosaics from before and after the impact of two of these hurricanes, we quantified how patch complexity, spatial distribution, and shape characteristics determine changes in patch structure after disturbances. Then we explore how the morphological plasticity of *A. palmata* along the reef zonation relates to the magnitude of the damage.

B. 3. METHODS

B. 3. 1. *Study area and hurricane impacts*

Limones reef is in the northern of the Mexican Caribbean, centered at coordinates 20.988452 N, -86.79719 W. This reef holds particular significance as it hosts one of the world's largest populations of *Acropora palmata* (Rodríguez-Martínez et al., 2014). The reef is within the Puerto Morelos Reef National Park (PNAPM) and given its ecological value, it is open only for scientific research (i.e., fishing and tourist activities are prohibited). *Acropora palmata* patches from a few colonies to hundreds of m^2 are distributed along the reef within 1 to 3 m depth. The area was affected by hurricanes Gamma, Delta, and Zeta during October of 2020. In this study we assessed the consequences of the first two events to evaluate the effect of hurricanes on *A. palamata* dominated reefs from a seascape ecology perspective. Hurricane Gamma (category 1 on Saffir-Simpson scale) hit land on October 3rd 2020 with winds up to 120 km/h and quickly diminished its intensity during its pass through Quintana Roo region; Hurricane Delta (category 2 on Saffir-Simpson scale) hit land on October 7th presenting winds of 166 km/h adding its effects to the previous hurricane ones (Bravo-Lujano, 2020 a,b).

B. 3. 2. *Orthomosaics*

Two orthomosaics were generated, one before hurricane impacts (August 4th, 2020) and one after the occurrence of hurricanes Gamma and Delta (October 16th, 2020). Mavic Pro UAV flights were performed at altitudes of 100 m, 50 m, and 25 m. Images were then processed with PIX4D Mapper software using maximum resolution, with a minimum of two photos per matching point and an optimal point density to generate the orthomosaics. For the creation of the first orthomosaics 1048 Images were used, and 1022 for the second one.

Georeferencing and alignment of the two orthomosaics was performed in ArcMap 10.4 software. For both processes 16 large colonies of *Pseudodiploria strigosa* were used as visual reference since they are colonies that withstand hurricane impacts. UTM/WGS 84 Zone 16 projected coordinate system was employed so the units were expressed in meters. To co-register both orthomosaics we used pre-hurricane one as the base, while the post-hurricane was divided into four segments. This division aimed to mitigate the object position errors associated with the UAVs GPS (~1.5 meters). The spatial resolution of both orthomosaics was 2 cm, however object size errors (~10 cm^2) may be found in the orthomosaics because of the different flight heights at which images composing the mosaics were captured.

B. 3. 3. *Identification of Acropora palmata patches*

The sampling units implemented in this study were *A. palmata* patches, defined as bidimensional area units (> 2 m^2) with continuous borders and no contact with other colonies of *A. palmata*. Patches are the vectorial representation of the area covered by alive colonies, or groups of colonies of *A. palmata* observed in the orthomosaics. To delineate patches and emphasize the contrast between *A. palmata* and other structures or dead colonies, we adjust the RGB bands of the orthomosaics, from natural color (1-2-3) to false color (1-3-2) using the semi-automatic classification plugin in QGIS 3.22. *Acropora palmata* patches were outlined manually with the add polygon tool in QGIS 3.22. We used a visual identification of the patches because it increases the accuracy of patch determination when performed by a trained eye, and because the moderate size of the studied area and the good image resolution allowed us to make a clear delineation of the borders of each patch. Through this procedure a vector file corresponding to the pre-hurricane orthophoto (August 4th, 2020) was generated. For the post-hurricane one (October 16th, 2020) we created a second vector file modifying the vertexes of the pre-hurricane one according to the change observed on the patches. Each patch was assigned an ID number, and their areas were calculated using field calculator feature in QGIS 3.22.

We computed the difference between both vector files by overlapping them using QGIS 3.22 geoprocessing tools and the field calculator feature to quantify area modification. Changes in patch area were attributed to the impact of hurricanes. We observed two types of change, the loss of some portions of the patch, and the appearance of new section of patches (195 out of 576, representing 3.8 % of the initial area). The latter category was attributed to *A. palmata* dislodgements from their original locations; therefore, they represent a redistribution of loss within the mosaic. We reported it but do not include the dislodgements into our analysis, given the small spatial area they represent, and because we were unsure whether these portions of the original patch survived.

B. 3. 4. *Modeling spatial traits in relation to area loss.*

To explore the influence of spatial traits of *A. palmata* patches on their resistance to hurricanes we measured attributes related to patch complexity, location, and size. These attributes are potential predictors of the extent of loss associated with the catastrophic event. We first calculated remaining area in % (RA) for every patch as follows:

$$\mathbf{RA = 1-((A1-A2)/A1)}$$

Where RA is the remaining area of patches, and it is the loss rate subtracted from 1 (100% of the initial area). A1 is the initial area of each patch, A2 the final area only considering loss (ignoring dislodgement).

Then we calculate four landscape indices to describe landscape modifications in the *Acropora* patches resulting from hurricane impacts. (1) Perimeter-area ratio (PARA) that is related to patch compactness, (2) shape index (SHAPE) that measures patch complexity, (3) related circumscribing circle (CIRCLE) that measures patch elongation, and (4) proximity index (PROX) that relates to distance and size of neighbor patches within a range (Fig. 1). All indices were computed with VecLI 2.0.0 software (Yao et al. 2022). Size and reef zonation were also considered as spatial traits influencing patch permanence. We expected that more compact patches, that were less complex, elongated, and with more and bigger neighbors would have greater remaining area. We also expected that larger patches and located in the most protected reef zone (backreef) would have greater remaining area.

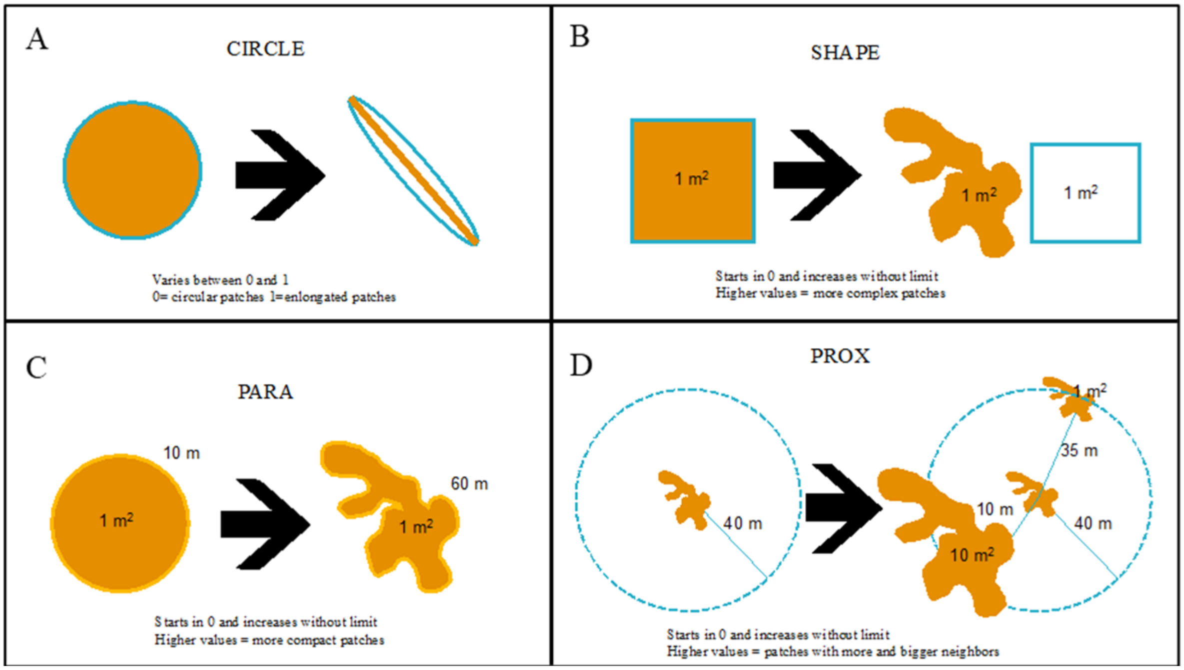

Figure 1. Graphic representation of the seascape metrics. Index values increase in the direction indicated by the arrow, all indices base is 0. Orange figures represent *Acropora palmata* patches. Blue full lines represent hypothetical perimeters used for calculation of the A) related circumscribing circle (CIRCLE) and B) shape index (SHAPE). Yellow lines represent the actual patch perimeter in the C) perimeter-area ratio (PARA). Blue dashed lines represent a hypothetic range within which patches are considered to calculate the D) proximity index (PROX).

B. 3. 5. *Modelling patch remaining area and permanence probability*

A large number of patches were totally lost after the impact of both hurricanes; therefore, we conducted two separate models to test the effect of localization, morphology and distance within *A. palmata* patches. First, to explore the permanence probability of the patches, we performed a binomial generalized linear model (GLM), relating the selected spatial traits and landscape indices with the total loss or permanence of the patches as the model's binomial response variable. Second, to analyze the influence of the predictor variables in the remaining area of the prevailing patches we performed linear regression model (for the spatial traits and landscape indices) in relation to the remaining area as a continuous variable excluding patches that were totally lost. Arcsine transformation was applied to the remaining area to improve the models fit. A linear regression model considering all the patches (including those that were completely lost) was also performed and results were similar to the GLM confirming total loss influence on the data (Figure S1).

For all our models we proved the absence of significant spatial autocorrelation, through Moran I index and Monte Carlo, in the residuals of the models performed as well as in the response variables, indicating the suitability of regression models to our data simulation approach (Table S1).

B. 3. 6. *Assessing phenotypic plasticity across reef zones*

We explored the phenotypic plasticity of *A. palmata* colonies along the reef zones to gain insights into finer scale characteristics influencing the permanence probability and the remaining area of patches. For this, we developed field methods based on Bottjer's (1980) methodology, created to assess morphological metrics in *A. cervicornis*.

Four transects of 200 x 2 m, were placed based on observations of patch distribution in the orthomosaics, prioritizing areas exhibiting lower patch density (to avoid surveying large patches in which in difficult to define the limits of a colony). The orientation of each transect line was perpendicular to the coastline and reef zonation lines. We considered in the analysis the *A. palmata* colonies that were at least 0.5 m away from a neighboring colony (in an axial view) and with heights between 0.3 to 1.5 m. Two photographs were captured for each colony, (1) axial view, oriented using a compass to align with the coastline direction (NW), and (2) sagittal view, using a tier and a scale bar to establish a horizontal reference line. We recorded the coordinates of each colony using a Garmin GPSmap 64 GPS device.

A total of 103 *A. palmata* colonies were photographed. To obtain morphological metrics for the colonies present in each reef zone image processing was performed using ImageJ free software (https://imagej.net/ij/). In sagittal view photos we measured the growth angle of as many branches as possible for each colony. In axial view photos we counted frequencies of horizontal orientations for all branches of the colonies. We assessed the growth angle of 306 branches and the horizontal orientation of 1366 branches. We employed One-way ANOVA to compare the mean growth angle among colonies in each reef zone, as well as coefficient of variation for the horizontal orientation frequencies. Data homoscedasticity was proved by Levene tests ($p > 0.05$); normality of the data as well model residuals was assessed though Q-Q diagrams. We created rose diagrams depicting the number of branches oriented to each cardinal point using the horizontal orientation frequencies.

B.4. RESULTS

The spatial cover of the *A. palmata* patches in Limones reef suffered a 25.09% change after the impact of both hurricanes, this is 1887 m² or *A. palmata* were either removed from the system (21.5 %) or dislodged (3.59 %) (Figure 2). Before the hurricanes the total area covered of the *A. palmata* patches was 10,979.16 m², while after the hurricanes (on October 16th) was reduced to 8,950.21 m² (Figure 2). Out of a total of 576 *A. palmata* patches, 75 remained undamaged during the hurricanes, while 371 experienced partial damage, and 130 vanished (Figure 3).

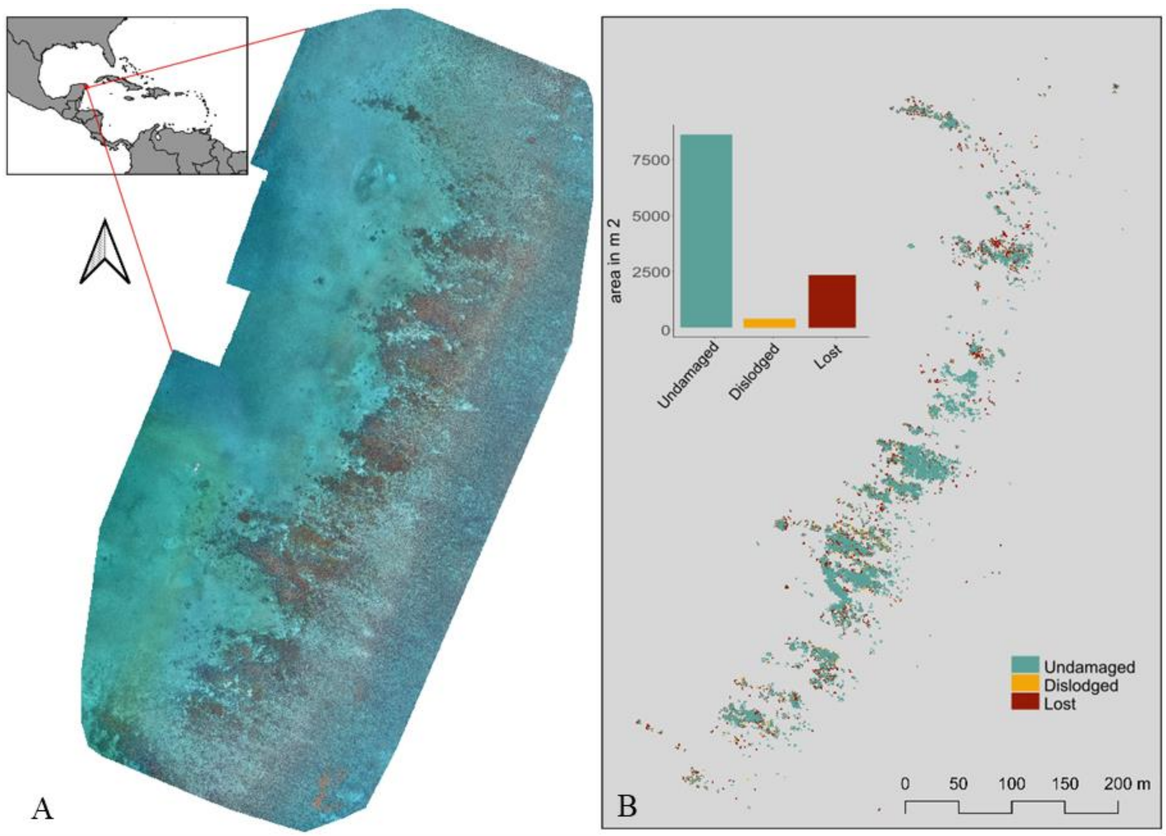

Figure 2. *Acropora palmata* patches on Limones reef in the Mexican Caribbean. A) Orthophoto of Limones reef constructed with 1048 aerial images on August 4th 2020, B) Vectorial files depicting the area (m^2) undamaged, lost and dislodged in the patches after the hurricane impacts. The inset shows total area undamaged, lost and dislodged for the entire reef. The spatial extent and orientation of A) and B) is the same.

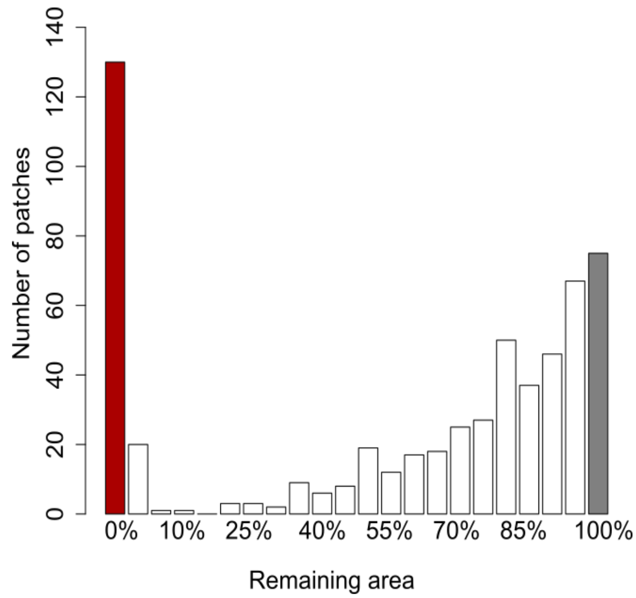

Figure. 3. Frequency histogram of the remaining area in the *Acropora palmata* patches. The red bar indicates the total losses (130 patches), the grey bar indicates the patches without any damage (75 patches), and the patches that suffered partial damage are shown in white (371 patches).

The binomial GLM (Table S.2) used to test the predictors of the probability to remain of *A. palmata* patches (independently of the damage) shows that the Shape index (SHAPE; β= 6.00, $p < 0.01$), the perimeter area ratio (PARA; β= 0.35, $p < 0.001$) and the backreef zone (β= 0.46, $p < 0.001$) were deemed as the significant predictors (Figure 4). Still, the effect of these variables was low compared to the non-significant effect of patch size, which suggests that larger patches had a greater probability of remaining (Fig. 4). The positive relationship with SHAPE indicates that more complex patches have a greater probability of persisting after a hurricane. The negative relationship with PARA implies that the decrease in the compactness of the patches reduces their chance of withstanding the disturbance. Patches in the backreef (contrasted with the crest, included in the model's intercept) have a lower probability of persisting after hurricanes. The high uncertainty associated with patch size is attributable to the fact that many of the smallest patches (< 5 m2) were lost, but also a considerable number of these small patches withstand the hurricane impact (Figure S2).

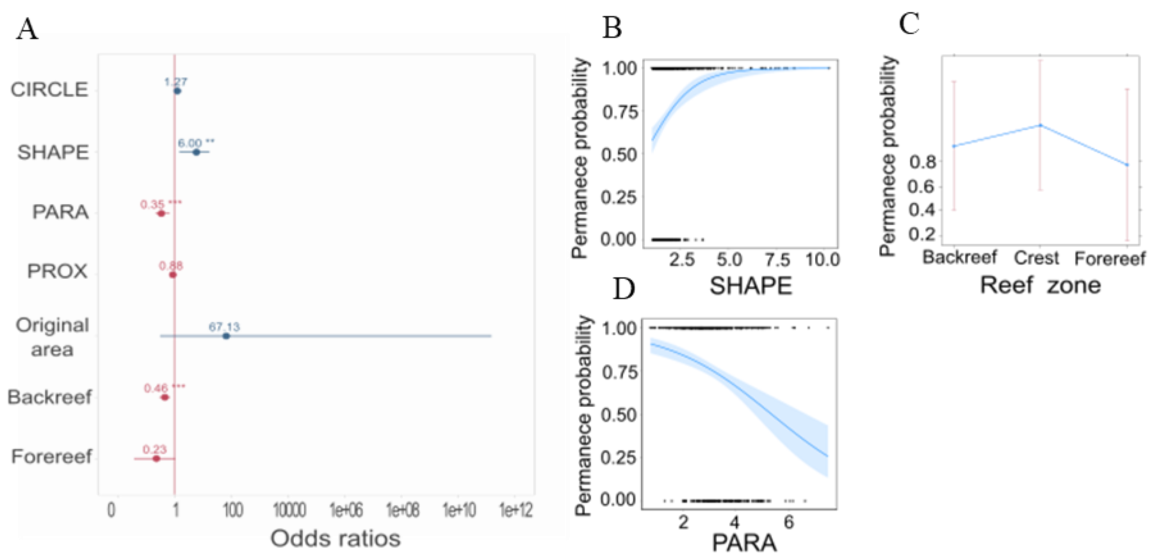

Figure 4. Variables effects on permanence probability. A) The predictor variables odds ratios of permanence probability of *Acropora palmata* patches derived from the binomial distribution GLM model. In the right model prediction of the permanence probability for B) Shape index (SHAPE), C) Reef zone, D) Perimeter-area ratio (PARA).

We then tested the predictors of the percentage area loss for the patches that remained after the hurricane impact (Figure 5). Only the backreef zone ($\beta = -0.222$, $p < 0.001$) had a significant contribution to explain the percentage of area remaining after the hurricane impacts. This is that patches located in the backreef underwent the greater losses in area. The remaining predictor variables, including CIRCLE, SHAPE, PARA, PROX, and patch size, did not show statistically significant relationships with remaining area in this model ($p > 0.05$). The uncertainty in the forereef is explained by the fact that there is only a small number of patches located in this zone (8 out of 576).

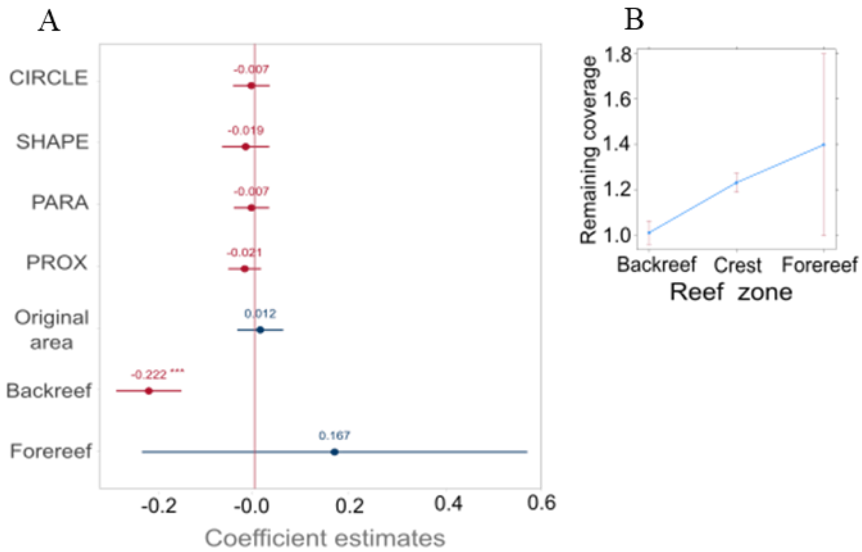

Figure 5. Variables effects on remaining area excluding the total losses. A) The effects of the predictor variables on the remaining area on *A. palmata* patches derived from a multiple linear regression model where the total losses were excluded from the response variable. B) Behavior of the models of Reef zone, the only significant variable.

The phenotypical plasticity of *A. palmata* colonies varies across reef zones (Figure 6). We characterized two main phenotypes within the three primary reef zones, the spear-like morphology, and the tree-like morphology. The former has the branch growth angle closer to the substrate and a tendency of branches to be oriented perpendicularly to the wave breaking line. The second one has branches growing straight up and no branch orientation tendency. We found that colonies in in the backreef zone tend to have branches with lower inclination angles, *i.e.*, colonies in this area tend to exhibit a more vertical growth pattern (Figure 6). In contrast, colonies in the reef crest and the forereef have branches higher inclination angles, so colonies in this zone tend to grow perpendicular to the substrate (Figure 6). ANOVA tests showed significant differences between reef zones for branch growth angle ($F = 11.77$, $P < 0.001$). Post-hoc Tukey's HSD revealed that differences were between crest and backreef zones (Table S.3).

Regarding to the orientation of branches, we observed that colonies located in the reef crest exhibited a higher frequency of branches oriented perpendicular to the beach line (NW), in contrast to the other two zones where branch orientations were more evenly distributed and did not display any discernible trends (Figure 6), although in the fore reef is clear that number of branches is considerably less than in the other two zones. ANOVA tests showed significant differences between reef zones for horizontal orientation ($F = 3.244$ $P < 0.05$). Post-hoc Tukey's HSD revealed that the differences were between crest and backreef zones.

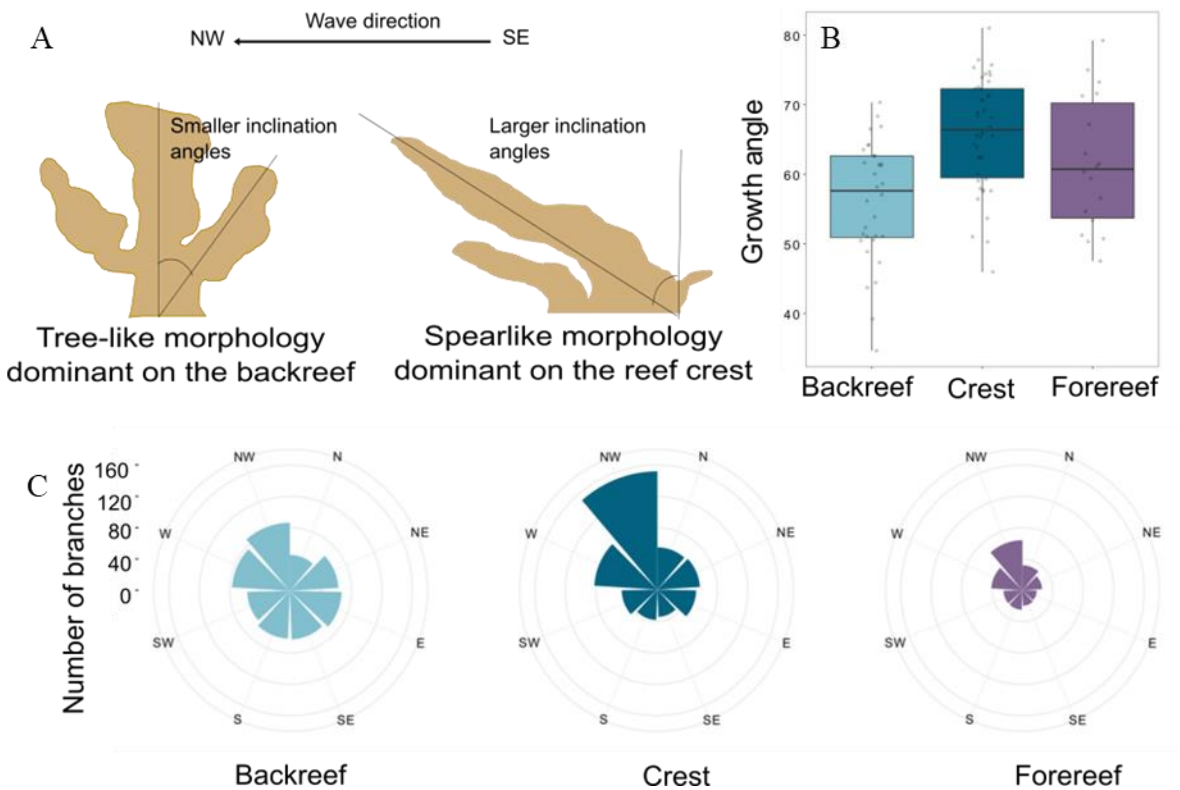

Figure 6. Phenotypical plasticity of *Acropora palmata* colonies along reef zones. A) Tree like and spear like morphology types descriptive diagram B) Data distribution of mean growth angle of *A. palmata* branches compared among colonies from the three reef zones. C) Frequencies of branch horizontal orientation of *A. palmata* colonies compared among reef zones.

B.5. DISCUSSION

Overall, we found that 25% of the original area covered by *A. palmata* patches was modified by the hurricanes Gamma (Saffir-Simpson category 1) and Delta (Saffir-Simpson category 2) in 2020. However, the probability of withstanding a hurricane impact was not equal for all patches. We observed that the probability of remaining of a patch depends on its shape, exposition to wave energy (reef zone) and, although not significative in our models, to some degree, its original size (Figure 4). In other words, small patches with a simpler shape in the back reef had the highest probability of disappearing. In contrast, patches in the reef crest had a higher likelihood of remaining after the impacts of the hurricanes. Furthermore, for patches that only lost a portion of their original structure, we observed the greatest losses in those located within the backreef (Figure 5). Colonies in the most exposed environments (reef crest) developed morphological attributes that allow them to thrive in these highly dynamic environments (e.g., branches growing closer to the substrate and oriented to the wave breaking line). This probably made those colonies and patches more resistant to the increased energy levels during the hurricanes, compared to the colonies inhabiting usually calmer waters in the back-reef.

Our findings show that the geometric features, and to some degree the size, of a patch influence the probability of permanence after a hurricane impact. More irregular patches (i.e., defined by high values in SHAPE) and more compact ones (low values in PARA) significantly increased the probability to persist after the two consecutive impacts. This likely because less compact and more complex patches better resist hurricanes as they present less structural resistance to the waves impact. These structural characteristics of reefs play a key role in structuring reef communities that has been studied in artificial reef construction specially in the early stages of benthic species (Schroeter et al., 2015; Jackson-Bué et al., 2024). This is probably related to the interaction between spatial traits, such as irregularity, and the system hydrodynamics among other factors (Jackson-Bué et al., 2024). The interactions between hydrodynamic processes and fragmented marine canopies are complex and influenced by many biotic and abiotic factors. These interactions are crucial for the structure, functioning, and services of ecosystems, as hydrodynamic processes cause mechanical stresses. Fragmented canopies have more spatially varied hydrodynamics compared to homogeneous canopies, leading to variability in stresses and other traits such as sheltering and nutrient distribution (Folkard, 2019). Regarding the size of the patch, even though we did not find a significant effect, our findings show that all patches that were completely lost belonged to small size categories (Figure S2). This indicates that smaller patches are more susceptible to be affected by the high-water energy associated to a hurricane strike. Furthermore, the big patches that withstand the hurricanes did suffer apparent area loss and fragmentation after hurricanes increasing the reef unit susceptibility to hurricane disturbance (Figure S3). This is because habitat fragmentation, along with patch size reduction, brings diverse consequences to marine ecosystems that ultimately could make them more vulnerable to external pressures (Gera et al., 2013).

Acropora patches in the back reef were the most affected, both in terms of increased probability of disappearing, but also the patches located in the zone and remained were the ones that underwent the greatest losses. Our explanation for this finding is the morphology of the colonies that inhabit different reef zones. We characterized a range of phenotypes that range from colonies with spear-like morphology, with few branches growing closer to the substrate and oriented against the wave breaking line, to colonies with a tree-like morphology with branches growing in multiple angles and directions (Figure 6). The former morphology is more prevalent in shallow-high energy environments associated with the reef crest, while the latter morphology is typical of calmer environments in the backreef, where the water movement and friction are significantly lower (Rijnsdorp et al., 2021). This phenotypical plasticity along the reef zones is a morphological response to the waves and current energy received during colony growth (Storr, 1964; Graus et al., 1977; Bottjer, 1980; Storlazzi et al., 2005; Lohr et al., 2020). While environmental conditions pre-adapted the colonies occurring in high-energy environments to dislodgement and damage caused by hurricane impacts, those in the backreefs are adapted to grow in calmer waters (Madin & Connolly, 2006). Under atypical climatic conditions during a hurricane strike, the water movement in the back reef greatly exceeds the levels of energy usual for corals inhabiting this zone (Drost et al., 2019; Lugo-Fernández et al., 1994), making them more vulnerable to the impact of hurricanes and therefore break or dislodge. Given fractal or repeated structure stetting across different spatial scales are common in nature (Cannon, 1984), including coral reefs (Zawada & Brock, 2009), we expect that aggregated spear-like colonies give the patches they conform the same structural characteristics that allow them to better resist the hurricane impacts as a repeated spatial trait from the colony level.

Despite differences in their susceptibility to physical impacts of increased water energy, patches in different reef zones also have substantial differences in their ecological contribution to the landscape that are worth mentioning. First, considering that *A. palmata* is a Caribbean coral with a major ecological and geological relevance for reef development and habitat provisioning to other species (Gonzalez-Barrios & Alvarez-Filip, 2018; Medina-Valmaseda, et al., 2020) we must point out that colonies occurring in different zones contribute differently to the ecological landscape of the reef. The structural morphology of

A. palmata colonies in the backreef is considerably more elaborated, with branches forming complex and intricate structures that likely provide a greater array of refuges to other species compared to the colonies (Figure 6; Lirman, 1999; Martínez et al., 2014). On the other hand, *Acropora* structures in the crest tend to grow primarily in one direction and flatten against the substrate, thus providing fewer niche spaces or refuges for different species. Secondly, the number of colonies and size of the patches are considerably larger in the backreef zones (Figure 2). These extensive patches were common in the Caribbean before its population decline in the 1980 decade, associated principally to the white band disease (Aronson & Precht, 2001). Larger patches of *A. palmata* are related to various ecological processes such as reef formation (Medina-Valmaseda, et al., 2020), specialist species populations preservation (González-Gómez et al., 2018) and the preservation of the populations of *A. palmata* itself (Busch et al., 2016).

The presence of larger patches in the backreef could be associated with the fact that, when receiving mechanical impacts, the colony fragments that break are not transported far away in contrast with the crest and the forereef due to the reef topography. Also, in a retroactive way, larger patches are probably also retaining more colony fragments than the isolated or small ones. In this matter, there is a lot of research regarding *A. palmata* colonies fragmentation as an asexual reproductive strategy (Lirman 2000; Roth et al., 2013; Forrester et al., 2014), so the patch area loss registered in our study does not necessarily means coral death. However, there are many factors that mediate the success of the fragment's attachment to the substrate such as fragment size, the location to where the fragments are transported (Lirman 2000), and other external pressures that threaten their survivorship like thermal stress and coral diseases (Williams et al., 2008; Roth et al., 2013). Also, there are other consequences of colony's fragmentation and displacement aside of the mechanical damage caused by hurricanes. A shift of the population, from full grown colonies with higher probabilities of survival to small fragments more susceptible to disappear has been observed in some cases (Lirman, 2000). Following this idea, sexual reproduction of *A. palmata* can be diminished after these events, since gamete production is only observed in fully grown colonies of the population, even after 3 years of a hurricane (Lirman, 2000). In the north Caribbean reefs specifically, the report of the effects hurricanes Gamma, Delta and Zeta, (the ones studied in this paper) says that the most common fragments found after the disturbance belonged to *A. palmata* colonies (Estrada-Saldivar et al., 2022). Also, that the only site where these fragments were fixed to the substate was precisely Limones reef, which can be related to the extensive size of *A. palmata* patches and the dense population of this species (Estrada-Saldivar et al., 2022).

In this study, we found a 25% damage associated with the impact of relatively minor hurricanes (category 1 and 2), which contrasts with other studies that have described relatively minor effects of hurricanes or tropical cyclones of similar or higher intensity (Anticamara & Go, 2017; Edmunds, 2019; Mudge & Bruno, 2023). At least three non-mutually exclusive circumstances might explain this apparent incongruence. First, we measure the change after two consecutive impacts; therefore, the accumulative effect of two relatively minor events could have been added up and produced significant damage to the system; this is particularly relevant if the first event (hurricane Gamma) left some structures already damaged that the second event (hurricane Delta) dislodged from the substrate or the colony structure. Similar situations of cumulative hurricanes causing additive damage have been documented elsewhere (Alvarez-Filip & Gil 2006; Alvarez-Filip et al. 2009; Gonzalez-Barrios et al., 2023). Secondly, the impact of hurricanes on the ecological integrity of an ecosystem largely depends on the initial ecological integrity of the system (Gonzalez-Barrios et al., 2023). Reefs with high coral cover, mainly if fragile species dominate them, are likely to undergo higher losses compared to those reefs with low coral cover and dominated by small encrusting species (Alvarez-Filip et al., 2009; Gonzalez-Barrios et al., 2023; Mudge & Bruno, 2023). This is even evident at regional scales when comparing reports of the damage caused by hurricanes category 5 in the Caribbean. In the 2000s, the relative damage caused by hurricanes was significantly lower compared to similar events affecting reefs in the 1980s (Rogers et al., 1991; Woodley et al., 1981; Edmunds, 2019), which can be explained by the fact that Caribbean coral communities have shifted to dominance of weedy coral species (Alvarez-Filip et al. 2011; Gonzalez-Barrios et al. 2021; Mudge & Bruno, 2023). Limones reef, however, was still considered one of the reef oases in the Caribbean, given its high coral cover and abundant populations of *A. palmata* (Fig.2.; Rodriguez-Martinez et al. 2014), making it therefore more susceptible to the impact of hurricanes compared to other contemporary reefs. A third consideration is that our method, that used high resolution orthomosaics to estimate two-dimensional changes in the cover of *A. palmata* in the entire reef unit, might not be directly comparable with the results obtained from traditional methods use to survey and asses changes after disturbances in coral communities; although, there was no significant difference found between traditional methods and a small area orthophoto assessment of coral community cover in Limones reef after the effect of the same two hurricanes in 2020 (Estrada-Saldivar et al., 2022), this could change in order the scale of the studied area increases. Estrada-Saldivar et al. (2022) estimated approximately 16% loss and dislodgement of colonies on the reef unit based on extrapolation of transect data, this is less that our estimation of 25% modification. Giving that our data comes from representations of all the patches bigger that $2m^2$ conforming Limones reef unit, and that changes were registered for each patch, our estimation of damage may be more accurate. Although, being a 2D representation it is possible that damages that aren't visible from the axial view aren't measured, for this 3D modeling would be needed. However, our methods principal contribution is the assessment of the relation between spatial traits of the reef and the resistance to hurricanes, predicting which reef patches or areas could be more prone to resist this kind of disturbance. Since the assessment of factors like extension, frequency, intensity, and cumulative effects of disturbance is crucial to understand now days on coral reef dynamics (Gonzalez-Barrios et al., 2023), this study is a valuable contribution to the variety of remote sensing methods that had been developed in recent years for the monitoring of coral reefs in this matter.

Overall, we have shown that using landscape indices to understand the drivers of change of a tropical coral reef spatial structure is an efficient method to evaluate, and even predict, the changes suffered by coral reefs after strong disturbance events. This information could be relevant in the management and conservation of coral reefs, also the sampling method could be used for reef constant monitoring activities. However, it is important to note that this method measures reef structural traits only from a two-dimensional perspective and a lot of information could be overlooked because of that. In contrast, 3D coral structure modeling, which is currently trending because of its precision in this matter (Hattori & Shibuno, 2015; Hedley et al., 2016), requires significantly more processing capacity than what was used in this study, especially given the extensive study area. The study of hurricane disturbance from a landscape perspective is also relevant to understand coral communities and populations, as reef-building structures because the resilience, diversity, and composition of populations are largely determined by spatial patterns and how disturbance is distributed within the reef (Rogers, 1993). Extensive evidence exists on how habitat heterogeneity modulates various ecological reef characteristics like the reef-fish assemblages (e.g., Grober-Dunsmore et al., 2007; Alvarez-Filip et al., 2011), algal cover (Graham & Nash, 2013), reef-fish movement (Hitt et al. 2011), ecological functions such as herbivory (Roff et al., 2019) and even ecological services provided by coral reefs (Graham & Nash, 2013). The relevance of spatial traits along the benthic ecosystem's seascape, and particularly coral reefs, is an open field for investigation and a framework to develop practical strategies for management and conservation of these ecosystems.

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C. CONCLUSIONES

C.1. *Impacto de los huracanes sobre los parches de A. palmata.*

Encontramos que el 25% del área original cubierta por parches de *A. palmata* fue modificada por los huracanes Gamma y Delta, de categorías 1 y 2 respectivamente en escala de Saffir-Simpson ocurridos en el año 2020 (Bravo-Lujano, 2020 a and b). Sin embargo, la probabilidad de que un parche sobreviva al impacto de los huracanes no fue la misma para todos. La probabilidad de permanencia de un parche depende de su forma, exposición a la energía de las olas (zona del arrecife) y, aunque no significativo en nuestros modelos, posiblemente de su tamaño original. Los parches pequeños, con formas más simples y ubicados en el arrecife posterior tienen mayor probabilidad de desaparecer. En contraste, los parches en la cresta del arrecife tienen una mayor probabilidad de permanecer después de los impactos de los huracanes. Además, para los parches que persistieron después de los eventos ciclónicos, las mayores pérdidas parciales también se encontraron en el arrecife posterior. Los parches en los entornos más expuestos como cresta del arrecife, presentan atributos morfológicos que les permiten prosperar en estos entornos altamente dinámicos, lo que probablemente los hizo más resistentes a los niveles de energía aumentados durante los huracanes. Por ejemplo, al estar conformados por colonias con forma de lanza, es probable que puedan tener atributos estructurales que les otorguen resistencia (mayor complejidad y compacidad). Respecto a las características estructurales de los parches, los más irregulares pero compactos, definidos por altos valores en SHAPE (shape index) y bajos en PARA (perimeter-area ratio), tienen una mayor probabilidad de resistir los impactos de los huracanes. Esto se debe probablemente a que los parches más compactos, pero de formas más complejas presentan menos resistencia al impacto de las olas, es decir que tienen formas más hidrodinámicas.

C. 2. *Impacto de los huracanes sobre las colonias de A. palmata.*

Los parches de *Acropora palmata* en el arrecife posterior fueron los más afectados, tanto en términos de mayor probabilidad de desaparecer como de sufrir las mayores pérdidas en los parches que permanecieron. La morfología de las colonias en diferentes zonas del arrecife es un factor clave para entender este hecho. Las colonias que crecen en ambientes de alta energía, como lo es la zona de la cresta arrecifal, presentan una morfología adaptada para resistir el impacto constante de las olas, mientras que las colonias en el arrecife posterior están adaptadas a crecer en aguas más tranquilas. Como resultado se obtiene un gradiente de morfologías, o de plasticidad fenotípica, que es una respuesta de las colonias de *A. palmata* a la energía de las olas y las corrientes recibidas durante el crecimiento de la colonia. Debido a la plasticidad fenotípica, los parches en diferentes zonas del arrecife están compuestos por colonias con diferencias sustanciales en su contribución ecológica al paisaje del arrecife. Las colonias de *A. palmata* en el arrecife posterior presentan estructuras más elaboradas y complejas que sirven como refugio para muchas especies (morfologías tipo árbol), mientras que las estructuras en la cresta del arrecife son más simples y proporcionan menos espacios de nicho (morfologías tipo lanza). Además, el número de colonias y el tamaño de los parches son considerablemente mayores en las zonas del arrecife posterior.

C.3 *Evaluación del método utilizado en el contexto del evento de disturbio estudiado.*

La modificación de área encontrada en este trabajo (25%), ya sea por perdida de área o desplazamiento, es alta para ser causada por el impacto de huracanes relativamente menores (categoría 1 y 2), sin embargo, hay que considerar que se estudia el efecto acumulativo de dos huracanes consecutivos. A demás, la integridad ecológica inicial del sistema juega un papel importante en este dato, ya que el arrecife Limones es una de las unidades arrecifales en mejor estado de conservación y con mayor cobertura de coral (Rodriguez-Martinez et al. 2014), por lo que la perdida de coral vivo será más alta que para otros sitios con una comunidad coralina más degradada (Gonzalez-Barrios et al., 2023; Mudge & Bruno, 2023). Una última consideración es que los métodos de medición utilizados en este estudio, representando cada parche de *A. palmata* y su pérdida de área, no son comparables con los resultados obtenidos mediante métodos de muestreo tradicionales, a pesar de ser eficientes para medir las consecuencias de este tipo de perturbaciones.

Las características del paisaje de los arrecifes juegan un papel clave en la conformación de las comunidades bióticas que los habitan. Estudiar la perturbación ocasionada por los huracanes desde una perspectiva de ecología del paisaje es relevante para comprender las comunidades y poblaciones arrecifales. Los patrones espaciales y la distribución de las perturbaciones dentro del arrecife que determinan en gran medida la resiliencia, diversidad y composición de estas poblaciones. El método aquí presentado, que usa índices del paisaje para entender los factores determinantes del cambio en la estructura espacial de los arrecifes coralinos, es una herramienta eficiente para evaluar y predecir los cambios sufridos por los arrecifes de coral después de eventos de perturbación fuertes, lo cual es relevante para la gestión y conservación de estos ecosistemas.

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E. MATERIAL COMPLEMENTARIO

Table S1. Moran's I index and Montecarlo simulations of Moran's I with 600 replications for the GLM and LMs residuals. No significant spatial autocorrelation was found for any of the model's residuals.

Model	Moran´s i statistic	SD	p value	MC simulation statistic	p value
Binomial GLM	-7.730758e-04	0.57753	0.2818	-0.00077308	0.2
LM without total loss	-3.051082e-03	-0.37994	0.648	-0.0030511	0.6067
LM with all data	-8.680735e-04	0.52047	0.3014	-0.00086807	0.1933

Table S2. GLM and LM results showing the effects of the selected variables on the permanence probability and the remaining area of the patches. Significance codes: * 0 '*' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.**

Binomial GLM				
	Estimate	Std. Error	Z Value	Pr (<|z|)
(Intercept)	1.9161	1.2009	1.596	0.110578
CIRCLE	0.2413	0.1297	1.861	0.062771 .
SHAPE	1.7911	0.6642	2.697	0.007002 **
PARA	-1.0505	0.3166	-3.318	0.000906 ***
PROX	-0.1272	0.1372	-0.927	0.353771
Original Size	4.2066	8.6988	0.484	0.628682
Reef Crest	0.7681	0.2209	3.476	0.000508 ***
Forereef	-0.6867	0.8359	-0.822	0.411322
LM				
	Estimate	Std. Error	Z Value	Pr (<|z|)
(Intercept)	1.009046	0.026938	37.458	< 2e-16 ***
CIRCLE	-0.006816	0.019479	-0.350	0.7266
SHAPE	-0.018785	0.025114	-0.748	0.4549

PARA	-0.006606	0.018799	-0.351	0.7255
PROX	-0.020808	0.017456	-1.192	0.2339
Original Size	0.011743	0.024483	0.480	0.6317
Reef Crest	0.221546	0.034726	6.380	4.51e-10 ***
Forereef	0.388964	0.206122	1.887	0.0598 .

Table S3. Post-hoc Tukey's HSD for the phenotypical plasticity (Branch growth angle and branch horizontal orientation) ANOVAs showing that differences between crest and backreef zones. 95% family-wise confidence level.

Branch growth angle among reef zones				
	Diff	Lwr	Upr	P adj
Crest-Backreef	9.758850	4.9637455	14.55396	0.0000154
Frontreef-Backreef	5.415345	-0.6054749	11.43617	0.0868819
Frontreef-Crest	-4.343505	-10.1005104	1.41350	0.1760232
Branch horizontal orientatiom among reef zones				
	Diff	Lwr	Upr	P adj
Crest-Backreef	0.3037471	0.04039869	0.5670956	0.0196131
Frontreef-Backreef	0.1547600	-0.17590503	0.4854251	0.5070611
Frontreef-Crest	-0.1489871	-0.46516338	0.1671891	0.5024221

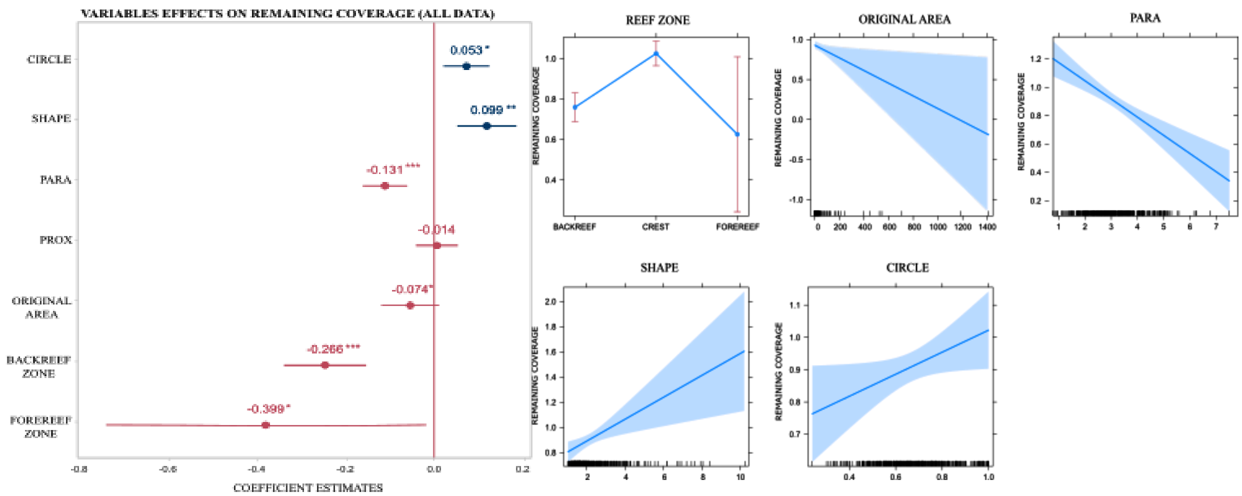

Figure S1. Linear regression analyses including all values of remaining area. Most predictor variables showed significance, as a result of the total loss influence. CIRCLE $\beta = 0.053$, $p < .05$), SHAPE ($\beta = 0.099$, $p < 0.01$), PARA ($\beta = -0.131$, $p < 0.001$), patch size ($\beta = -0.074$, $p < 0.05$), backreef zone ($\beta = -0.266$, $p < 0.001$) and forereef zone ($\beta = -0.399$, $p < 0.05$) all influenced remaining area. Only PROX wasn´t statistically significant ($p > 0.05$) with remaining area in this analysis.

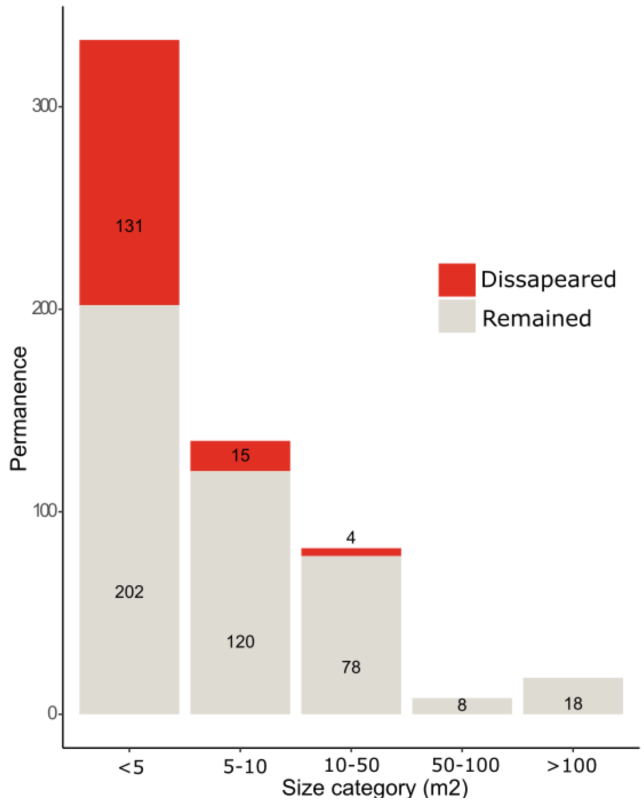

Figure S2. Size distribution of the totally lost patches showing that most of these patches were small (<5 m^2). However, a lot of patches of this size were not lost generating uncertainty in patch size as a predictor variable of patch permanence.

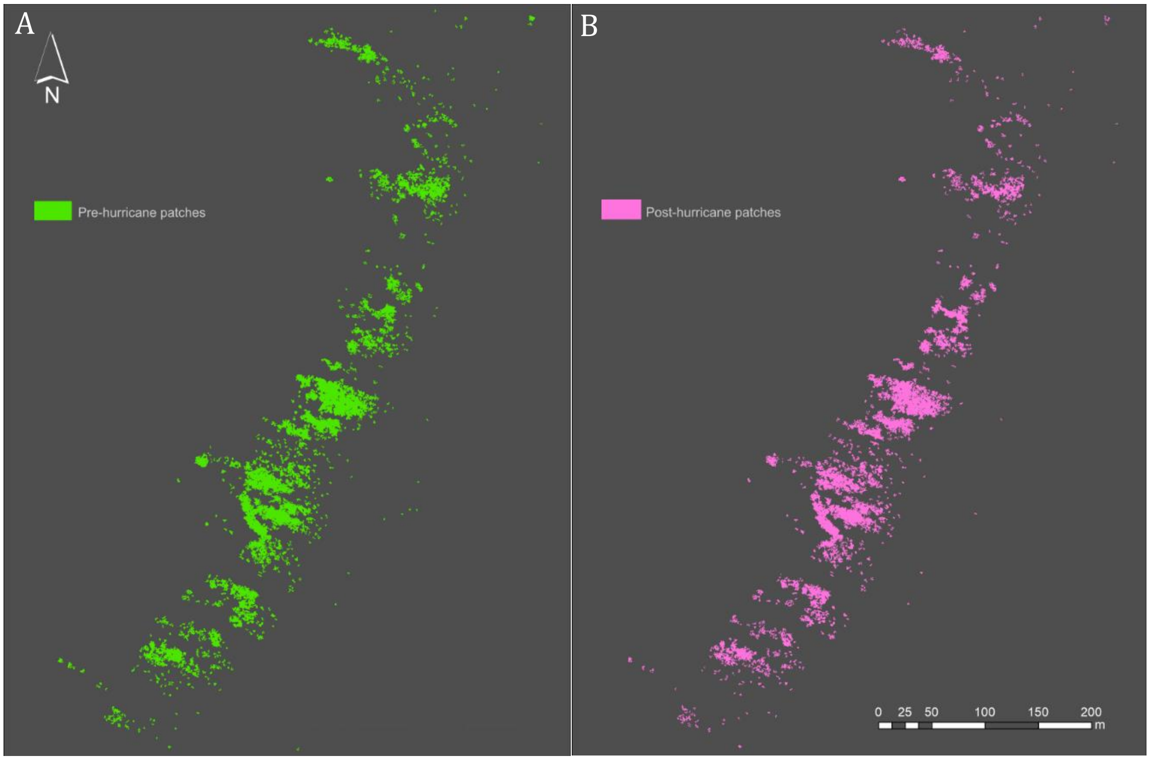

Figure S3. Vectorial files representing *Acropora palmata* patches of Limones reef (A) before and (B)after hurricanes Gamma and Delta. Looking in detail area loss and fragmentation can be observed in the patches after the pass of the hurricanes.