



**UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO**  
**POSGRADO EN CIENCIAS BIOLÓGICAS**  
**FACULTAD DE CIENCIAS**

**CAMBIOS DE DIVERSIDAD DE FAUNA ASOCIADA A ESPONJAS  
ARRECIFALES DEL GOLFO DE MÉXICO Y MAR CARIBE**

**TESIS**

QUE PARA OPTAR POR EL GRADO DE:

**DOCTOR EN CIENCIAS**

PRESENTA:

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**TUTOR PRINCIPAL DE TESIS: DOCTOR FERNANDO NUNO DIAS MARQUES SIMÕES**

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P r e s e n t e

Me permito informar a usted que en la reunión ordinaria del Comité de Posgrado en Ciencias Biológicas, celebrada el día **27 de noviembre de 2023** se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del estudiante **PÉREZ BOTELLO ANTAR MIJAIL** con número de cuenta **307142838** con la tesis titulada: "**Cambios de diversidad de fauna asociada a esponjas arrecifales del golfo de México y mar Caribe**", realizada bajo la dirección del **DR. FERNANDO NUNO DIAS MARQUES-SIMÕES**:

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Sin otro particular, me es grato enviarle un cordial saludo.

**A T E N T A M E N T E**  
"POR MI RAZA HABLARÁ EL ESPÍRITU"  
Ciudad Universitaria, Cd. Mx., a 04 de marzo de 2024

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**DR. ARTURO CARLOS II BECERRA BRACHO**



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# Índice

Resumen.....	1
<i>Abstract</i> .....	2
Introducción .....	3
Artículo 1 (Requisito): <i>Sponge-dwelling fauna: a review of known species from the Northwest Tropical Atlantic coral reefs</i> .....	8
Artículo 2: (Publicado) <i>Geographic range size and species morphology determines the organization of sponge host-guest interaction networks across tropical coral reefs</i> . ....	27
Artículo 3: (en revisión) <i>A multi-scale analysis of <math>\alpha</math>-diversity and <math>\beta</math>-diversity spatial variability on living islands</i> .....	51
<b>Discusión</b> .....	80
<b>Conclusiones</b> .....	82
<b>Referencias bibliográficas</b> .....	84
Apéndices .....	90
Apéndice I. Artículos publicados adicionalmente durante el programa doctoral.....	90
Apéndice II. Generación y mantenimiento del sitio web <i>Marine Species Interactions</i>	92

## Resumen

Las esponjas arrecifales son un componente biológico fundamental de la comunidad arrecifal, desempeñando diversas funciones. Entre estas funciones, destacan su papel como generadoras y facilitadoras de microhábitats, los cuales son utilizados por una amplia diversidad de especies, que abarcan desde microorganismos unicelulares hasta vertebrados. Algunas especies de esponjas ofrecen refugio y protección a los organismos asociados, mientras que otras contribuyen a la defensa química mediante la producción de metabolitos secundarios especializados, lo que beneficia a los organismos asociados al reducir su detectabilidad y aumentar su supervivencia. Si nos centramos solo en la fauna asociada a esponjas arrecifales es posible detectar una alta especificidad y variaciones en la diversidad de especies asociadas en función de la distribución y la morfología que presenta cada especie de esponja. En este contexto, la presente tesis tiene tres objetivos fundamentales: i) La integración coherente y estandarizada de la información disponible sobre la fauna asociada a esponjas en los arrecifes de coral del Atlántico Tropical Noroccidental. Este objetivo se cumplió a través de la recopilación de información proveniente de diversas fuentes bibliográficas y la creación de una base de datos estandarizada. ii) Analizar la estructura de la red de interacciones de esponjas arrecifales y su fauna asociada, evaluando la diversidad de interacciones por especie involucrada, la estructura de la red y el papel que cada especie de esponja desempeña en el mantenimiento de la estructura de esa red. Este objetivo se cumplió a través de un análisis de redes complejas el cual nos permitió cuantificar la diversidad de interacciones por especie y evaluar la importancia de cada esponja en la estructura de la red. iii) Analizar la diversidad  $\alpha$  y  $\beta$  de la comunidad asociada a la esponja tubular *Callyspongia aculeata* en tres escalas espaciales, a nivel de ecosistema, a nivel de hábitat y a nivel de microhábitat. Este objetivo se cumplió mediante salidas a campo, muestreos en ocho sistemas arrecifales distintos, identificación en laboratorio de organismos y pruebas de hipótesis estadísticas. Estos análisis revelaron patrones complementarios entre los diferentes componentes de diversidad analizados en función de la escala espacial. En conclusión, esta tesis contribuye significativamente al entendimiento de las complejas redes de interacciones que existen en los arrecifes de coral del Atlántico Tropical Noroccidental, ofreciendo una perspectiva integral de la importancia de las esponjas como especies clave en la estructura de las comunidades en sistemas arrecifales.

## *Abstract*

*Reef sponges play a fundamental biological role within the reef community, performing multiple functions. Among these functions, their capability to generate and facilitate microhabitats stands out, which are utilized by a wide range of species, from unicellular microorganisms to vertebrates. Certain sponge species offer shelter and protection to associated organisms, while others contribute to chemical defense through the production of specialized secondary metabolites, benefiting associated organisms by reducing their detectability and enhancing their survival. A high specificity and variations in species diversity based on the distribution and morphology of each sponge species is revealed if we only focus on the sponge's associated fauna. In this context, this thesis encompasses three fundamental objectives: i) The coherent and standardized integration of available information on sponges-associated fauna within the coral reefs of the Northwestern Tropical Atlantic. This objective was achieved through the compilation of information from various bibliographic items and the creation of a standardized database. ii) Analyzing the structure of the interaction network of reef sponges and their associated fauna, evaluating the diversity of interactions per species involved, the network's structure, and the role that each sponge species plays in maintaining the network's structure. This objective was fulfilled through the analysis of complex networks, allowing us to quantify the diversity of interactions per species and assess the importance of each sponge in the network's structure. iii) Analyzing the  $\alpha$  and  $\beta$  diversity of the community associated with the sponge Callyspongia aculeata at three spatial scales: ecosystem, habitat, and micro-habitat. This objective was achieved through fieldwork, sampling in eight different reef systems, laboratory organism identification, and statistical hypothesis testing. These analyses revealed divergent patterns among the different components of diversity analyzed according to the spatial scale under consideration. In conclusion, this thesis significantly contributes to our understanding of the complex interaction networks within the coral reefs of the Northwestern Tropical Atlantic, offering a comprehensive perspective on the importance of sponges as key species in the structure of communities in reef systems.*



## Introducción

La diversidad biológica, en un lugar y tiempo específicos, es el resultado de procesos históricos como especiación, vicarianza y dispersión, que moldean y regulan la distribución actual de la vida en el planeta Tierra (Holt, 1992). Estos procesos históricos generan una distribución no aleatoria de la vida, donde la heterogeneidad espacial y temporal del entorno físico, junto con la interacción entre organismos y ambiente, conducen a diversos procesos biológicos y ecológicos (Feldman, 1970; Legendre & Robson & Barmuta, 1998; Baselga & Gómez-Rodríguez, 2019; Legendre, 2012). Los factores que influyen en las medidas de diversidad biológica en un lugar y tiempo determinado son, el número de individuos de una comunidad, la distribución y abundancia de las especies de la comunidad y la distribución de cada individuo (Underwood et al., 2000; He & Legendre, 2002; McGlenn & Palmer, 2009; Chase & Knight, 2013; Chase et al., 2018). Cada uno de estos componentes puede interactuar de manera independiente o conjunta dentro de un ecosistema, lo que provocando cambios multidimensionales dependientes de la escala espacial o temporal que se analice (Chase et al., 2018).

Entender cómo se organizan millones de especies representa un desafío para cualquier estudio centrado en patrones de diversidad biológica (Dáttilo & Rico-Gray, 2018). Al mismo tiempo, la diversidad biológica tiene muchas facetas, por ejemplo, la diversidad de especies, genética, fenotípica, funcional, filogenética, metabólica y de interacciones (Andresen et al., 2018; Dáttilo & Rico-Gray, 2018; Martínez-Falcón et al., 2019; Pugh & Field, 2022). Para esta tesis utilizamos los conceptos de diversidad de interacciones (ver Artículo 1 y 2 de este escrito) y diversidad de especies (ver Artículo 3 de este escrito) para contestar las preguntas ¿Cuál es el arreglo de la red de interacciones huésped-hospedero de la fauna asociada a

esponjas arrecifales del Golfo de México y el Mar Caribe?, ¿Qué especies de esponja son claves en el mantenimiento de la estructura de la red de interacciones huésped-hospedero? y ¿Cuáles son los cambios de diversidad de especies de la fauna asociada a las esponjas arrecifales en tres escalas espaciales diferentes?

La diversidad de interacciones se puede definir como el número total de relaciones compartidas por todas las especies en un conjunto dado de organismos, también definida como riqueza de interacciones (Tylianakis et al., 2010; Pugh & Field, 2022). No obstante, la diversidad de interacciones suele medirse en términos relativos entre el número de “enlaces” entre especies y el número de especies en la red (Tylianakis et al., 2010). Y al mismo tiempo, las interacciones bióticas pueden ser de diferente tipo y naturaleza, antagonistas (competencia por recursos), mutualistas (polinización), tróficas (depredación) o no tróficas (huésped-hospedero), siendo el tipo y la naturaleza de la interacción dos mecanismos que promueven la especiación de la vida (Wulff, 1997; Watson & Pollack, 1999; Freilich et al., 2018; Pugh & Field, 2022).

A su vez, la diversidad de especies se tiene que definir de acuerdo con la escala espacial que se analice, dividida en tres componentes: la diversidad alfa ( $\alpha$ ), diversidad beta ( $\beta$ ) y diversidad gamma ( $\gamma$ ) (Whittaker, 1972; Whittaker et al., 2001; Andermann et al., 2022). La diversidad  $\alpha$  se refiere a la riqueza de especies dentro de una comunidad o unidad ecológica (Andermann et al., 2022). La diversidad  $\beta$ , por su parte, describe la diferenciación entre comunidades (Baselga & Gómez-Rodríguez, 2019; Andermann et al., 2022). Sin embargo, la interpretación exacta y la cuantificación de la diversidad  $\beta$  varían sustancialmente entre estudios (Tuomisto, 2010). Inicialmente, se definía como la relación entre la diversidad  $\gamma$  y  $\alpha$  ( $\beta = \gamma / \alpha$ , *sensu* Whittaker, 1972). Actualmente, una medida ampliamente utilizada para evaluar la diversidad  $\beta$  es la similitud entre comunidades, lo que

mide el recambio o variabilidad de especies entre unidades ecológicas (Anderson et al., 2013; Anderson & Santana-Garcon, 2015). Por último, la diversidad  $\gamma$ , describiendo la suma total de especies dentro de diferentes comunidades en una zona geográfica más extensa (Baselga & Gómez-Rodríguez, 2019; Andermann et al., 2022;).

Para esta tesis utilizaremos la diversidad  $\alpha$ , medida como la riqueza de especies en diferentes unidades ecológicas y la diversidad  $\beta$ , medida como la similitud entre pares de unidades ecológicas. A pesar de que la diversidad  $\gamma$  se define como un componente de la diversidad de especies, lo único que la diferencia de la diversidad  $\alpha$  es la escala espacial de análisis, por tal motivo se decidió no incluir la diversidad  $\gamma$  en esta investigación. La decisión se fundamenta en que la diversidad  $\alpha$  medida en diversas escalas espaciales provee la información necesaria para abordar las preguntas de investigación de esta tesis.

A nivel mundial, las esponjas destacan como componentes cruciales en los ecosistemas marinos, desempeñando diversas funciones esenciales (Rützler, 2004; González-Rivero et al., 2011). Por ejemplo, su capacidad para filtrar grandes volúmenes de agua y facilitar la producción primaria las posiciona como actores clave en la ecología de los sistemas arrecifales, generando un vínculo bento-pelágico entre los nutrientes disponibles en la columna de agua y la energía disponible en el lecho marino (Diaz & Rützler, 2001; Bell, 2008; Perea-Blázquez, 2011; Bell et al., 2013; Pawlik et al., 2013; Maldonado et al., 2017). De igual manera, las esponjas pueden ser especies clave como generadoras de hábitats, los cuales son activamente aprovechados por una amplia diversidad de especies, desde microorganismos hasta animales invertebrados y vertebrados (Diaz & Rützler, 2001; Ávila et al., 2007; Bell, 2008; Webster & Taylor, 2012; Maldonado et al., 2017; Bell et al., 2013; Pawlik et al., 2013). Por tales motivos, los cambios en abundancia específica y composición

comunitaria de las diferentes especies de esponjas ejercen impactos significativos en la comunidad arrecifal y en el funcionamiento global de este ecosistema (Bell, 2008).

Las esponjas además de ser facilitadoras de hábitats también brindan cierto grado de protección a los organismos que se asocian a ellas, ya sea por el uso directo de diferentes estructuras como refugio o camuflaje o por la protección indirecta derivada de la defensa química de la esponja (Dembowska, 1926; McLay, 1983; Bedini et al., 2003; Pawlik, 2011; Cruz Ferrer, 2014; Maldonado et al., 2017; Harada et al., 2020). Entre las esponjas reportadas, las de la Clase Desmospongiae son las que tienen un mayor número de asociaciones; además, esta es la Clase con mayor riqueza de especies en los arrecifes del mundo (Maldonado et al., 2016; Rossi et al., 2017). En relación con la defensa química, esponjas de los géneros *Agelas*, *Amphimedon*, *Aplysina* e *Ircinia* producen metabolitos secundarios especializados para su defensa contra la depredación, siendo compuestos tóxicos o poco palatables, que indirectamente protegen también a los organismos que viven asociados a ellas (Pawlik, 2011). Estas condiciones provocan que un tipo de interacción dominante en el *Phylum* Porifera sean las relaciones huésped-hospedero (Aerts, 1998; Wulff, 2006; Ávila et al., 2007). Este tipo de interacciones tienden a ser especie-específicas en distintos niveles taxonómicos, sin embargo, la naturaleza de la interacción (comensalismo, parasitismo y mutualismo) y la intensidad de la asociación (obligatoria o facultativa) varía considerablemente entre especies (Turon et al., 2000; Thiel & Baeza, 2001; Đuriš et al., 2011).

El análisis de las redes ecológicas facilita el estudio de las interacciones en una comunidad, en otras palabras, facilita el estudio de las conexiones entre especies (Dáttilo & Rico-Gray, 2018). Esta línea de investigación ofrece una perspectiva que integra la estructura de las redes con procesos ecológicos como, el mantenimiento de la diversidad de especies

en una región, la colonización de nuevas especies, el efecto de que podría tener la extinción local de especies, y la evolución y coevolución de las redes a medida que las especies avanzan en el tiempo (Martínez-Falcón et al., 2019; Dáttilo & Rico-Gray, 2018). Por otro lado, analizar los cambios de diversidad a diferentes escalas espaciales es esencial para comprender la respuesta de la fauna asociada a las esponjas arrecifales con diferentes factores ecológicos que ocurren a nivel ecosistémico, a nivel local y a nivel del microhábitat (Chase et al., 2018).

Por tales motivos los objetivos de esta tesis fueron: i) Integrar toda la información disponible sobre fauna asociada a esponjas en un solo sistema coherente y estandarizado, ii) analizar la estructura de la red huésped-hospedero de la fauna asociada a esponja arrecifales para identificar los patrones que determinan el arreglo presente en la red, y iii) analizar los cambios en la diversidad- $\alpha$  y - $\beta$  de la fauna asociada a *Callyspongia (Cladochalina) aculeata* (Linnaeus, 1759) en tres escalas espaciales diferentes las cuales son ecosistema, hábitat y microhábitat.

## Artículo 1 (Requisito): *Sponge-dwelling fauna: a review of known species from the Northwest Tropical Atlantic coral reefs*

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### Resumen

En los arrecifes de coral tropicales de aguas someras (menores a 50 m de profundidad), las esponjas marinas desempeñan un papel crucial al proporcionar microhábitats para una amplia diversidad de especies. A pesar de la existencia de numerosos estudios sobre las relaciones hospedero-huésped entre las esponjas y su fauna asociada, esta información ha permanecido dispersa y desconectada. Por lo tanto, el objetivo de este trabajo fue desarrollar y generar una base de datos que compile las interacciones relacionadas con las especies de esponjas marinas y la fauna asociada en los arrecifes de coral del Atlántico Tropical Noroccidental. Con este conjunto de datos compilamos 67 fuentes bibliográficas que reportan 101 especies de esponjas hospederas, agrupadas en 12 órdenes que interactúan con 284 especies huéspedes pertenecientes a seis *Phyla*. Esta base de datos tiene la característica de tener dos formatos interrelacionados: i) datos legibles por máquina y ii) datos legibles por humanos, lo que mejora su alcance y facilita su uso tanto en plataformas informáticas como para los usuarios. Además, se generó un entorno visual e interactivo de los registros de interacciones y un diagrama de cuerdas dinámico que representa las conexiones entre las especies huéspedes y las esponjas hospederas. Esta herramienta visual permite a los usuarios explorar y filtrar la información de manera intuitiva. De igual manera esta base de datos proporciona una fuente de información centralizada, de acceso libre, pública y de alta calidad sobre la fauna asociada a esponjas arrecifales incluyendo el tipo de interacción (mutualismo, parasitismo, comensalismo) y otros detalles cuantitativos. Además, se resalta la riqueza de especies que dependen de las esponjas arrecifales y se compara la diversidad entre el Mar Caribe y el Golfo de México. Esta base de datos representa una valiosa recopilación de información sobre las interacciones hospedero-huésped en los arrecifes de coral del Atlántico Tropical Noroccidental, facilitando futuros análisis y promoviendo la colaboración para enriquecer esta línea de investigación.



# Sponge-dwelling fauna: a review of known species from the Northwest Tropical Atlantic coral reefs

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## Abstract

### Background

Within tropical shallow-water coral reefs, marine sponges provide microhabitats for a wide range of fauna. Although there have been numerous studies and reports of symbiotic relationships amongst sponges and their associated fauna, those pieces of information are isolated and disconnected. For this reason, based on the available literature, we compiled a species-interaction dataset of coral reef marine sponge-associated fauna known to date.

### New information

We introduce a dataset that includes 67 literature items that report 101 species of sponge hosts clustered in 12 Orders having a host/guest interaction with 284 guest species from six Phyla present in the Northwestern Tropical Atlantic coral reefs. This dataset consists of two types of information: 1. Machine-readable data and 2. Human-readable data. These two types of coding improve the scope of the dataset and facilitate the link between machine platforms and human-friendly displays. We also created an interactive

visualisation of the species-interactions dataset and of a dynamic Chord Diagram of the host-guest species connections to generate a user-friendly link between the user and the dataset.

## Keywords

marine ecology, community ecology, interaction networks, symbiosis, mutualism, parasitism, commensalism

## Introduction

Symbiosis relationships have been recognised as an important speciation mechanism (Wulff 1997, Watson and Pollack 1999, Hagedorn et al. 2015, Brooker et al. 2019, Bauer 2004). A few years ago, Rossi et al. (2017) introduced the term "Marine Animal Forests" in a book with the same name. In this book, the authors compare the function of trees in forests with marine animal communities like corals, sponges and bivalves. These organisms share one particular characteristic: they can create three-dimensional habitat heterogeneity and structural complexity, providing shelter and a secure food source for a wide range of sessile and mobile animals (Tews et al. 2016, Rossi et al. 2017, Brooker et al. 2019). Sponges tend to be particularly abundant and diverse in coral reef ecosystems. Their architecture, morphology and capability to synthesise toxic substances can generate microhabitats where other species may live or have an adaptive advantage to explore (Bruce and Jones 1976, Duffy 1992, Henkel and Pawlik 2011, Pawlik 2011, Maldonado et al. 2017, Reyes-Bonilla and Jordán-Dahlgren 2017, Koukouras et al. 1995, Maldonado and Young 1996, Diaz and Rützler 2001, Rios and Duffy 2007).

Reef sponges are a well-studied group; however, the available information on marine sponges' intraspecific relationships is scattered, isolated and, in most cases, is only focused on a particular taxonomic group or a reduced geographical area. For this reason and based on published records from the Northwest Tropical Atlantic (NwTA) coral reefs, we compiled and created a standardised dataset that brings together information on sponge host/guest interactions in the region. Moreover, we also created two dynamic and interactive web visualisation tools to describe and analyse the information.

## General description

**Purpose:** In a climate change and biological diversity loss scenario, it becomes crucial to have a high-quality open-access baseline dataset on fundamental aspects, such as symbiotic interactions. This dataset provides an updated and standardised matrix of published records on host/guest interaction between tropical coral reef marine sponges and their associated fauna. Each interaction was codified into a machine- and human-readable format, according to the Global Biotic Interactions (GloBI) standard language (for more information, see Poelen et al. 2014; [globalbioticinteractions.org](http://globalbioticinteractions.org)). Furthermore, an



independent, dynamic, interactive and user-friendly data-visualisation display of this information is provided to maximise outputs in terms of data accessibility and usage.

**Additional information:** In this work, we screened 65 articles and two university theses on the NwTA coral reefs published between 1909 and 2019. The present review includes 101 sponge species divided into 12 Orders from the Demospongiae Class, interacting with 284 guest species from six Phyla. The Haplosclerida and Dactyloceratida orders presented the largest number of associated species. Regarding the host sponges morphologies, the tube, fan and vasiform shapes common to the genera *Agelas*, *Aplisyna*, *Ircinia* and *Callyspongia*, tended to have more guest species. *Ircinia strobilina* was the species with the highest number of associated species (dwelling species N = 89) followed by *Callyspongia aculeata* (dwelling species N = 63) and *Ircinia felix* (dwelling species N = 53). According to the sponges-dwelling fauna records, the phylum Arthropoda was dominant on species numbers (164 spp.), followed by Annelida (60 spp.), Mollusca (19 spp.), Chordata (20 spp.), Echinodermata (15 spp.) and Cnidaria (6 spp.).

When we compare the host/guest species richness between the Caribbean and the Gulf of Mexico, the Caribbean has the greatest sponge diversity with 84 sponge species, whereas, the Gulf of Mexico has 38 sponge species. Both regions share 22 sponge species. However, the Gulf of Mexico has 191 guest species against 145 guest Caribbean species. At the guest species richness part, both regions shared 52 guest species. If we count the interaction diversity (an integrated binomial of host/guest species), the current work register 451 host/guest interaction within the Gulf of Mexico, but only 399 inside the Caribbean coral reefs.

Meanwhile, mutualistic associations are a common interaction type with 86 entries, followed by the parasitic interaction with 44 entries and commensal interaction with 36 entries. Nonetheless, most of the literature entries do not classify the type of interaction, remaining at the symbiosis or dwelling-species level.

Sponges, like other bio-constructing species, are ecosystem engineers, shaping the environmental complexity and maintaining part of the habitat biodiversity (Jones et al. 1994, Rossi et al. 2017). The present species-interactions' dataset highlights the remarkable diversity of animals that depend on, or take advantage of, the sponges' presence. Besides, it is possible to have a host/guest distribution, host/guest species richness quantification and a few more quantitative metrics that will help to better understand and model the sponge-dwelling fauna.

## Sampling methods

**Sampling description:** In order to perform the literature search and compilation of the interaction dataset, based on bibliographic records, it was necessary to define our sampling unit. For this work, we define each article and thesis reviewed as a unit; each of these elements we name as "literature item" and each item could provide one or several interaction report entries.

First, we compiled all the articles and theses known to us that report a sponge host/guest interaction in the N.W.T.A coral reefs (known literature items). This initial baseline was complemented with a Web of Science, Pub Med, Crossref, Scopus and Google Scholar web search (web literature items) using the "Publish or Perish" software application (Harzing 2007; [harzing.com/resources/publish-or-perish](http://harzing.com/resources/publish-or-perish)). A specific string of keyword sequences and logic operators was used to simultaneously focus the search without losing inclusiveness and to improve the exploration yield [(“Sponge”) AND (“dwelling” OR “interaction” OR “association” OR “mutualism” OR “commensalism” OR “parasitism”) AND (“Annelida” OR “Arthropoda” OR “Chordata” OR “Cnidaria” OR “Echinodermata” OR “Mollusca” OR “Molluska”) AND (“coral reef”) AND (“Caribbean” OR “Gulf of Mexico” OR “Northwestern Atlantic”)].

To identify possible duplicate and pseudoreplicate literature items between the web search and the known literature items, we used the "Check for Duplicates" tool implemented in Mendeley software ([mendeley.com](http://mendeley.com)). This tool compares the publication type (Journal Article or Thesis), the literature title, authors, publisher and publication year for all the literature items within the bibliographic database. With this comparison, it was possible to discriminate both duplicate and pseudoreplicates literature items.

A literature item would be validated 1. if it were published in an indexed journal, according to the Science Citation Index Expanded (SCIE) or in a MSc or PhD University theses; 2. if the literature item were an indexed journal, necessarily had to match the geography of interest, contain details of the latitude and longitude information (or a detailed geographical description) and clearly stated the species involved. If the literature item were a University thesis, the previous criteria were used, but it was also indispensable that the species involved were deposited in a scientific collection. With this protocol, we ensured that all compiled literature items has the minimum essential information to be extracted. Whenever possible, the interaction type presence (commensalism, parasitism, mutualism), the species taxonomy details and the host body part where the guest lived, were also extracted. Finally, with the screened literature items, we compiled the sponge-dwelling fauna dataset. The compiling process consisted of generating independent entries, based on the sponge host/guest interaction reports inside a particular item.

**Quality control:** Data were standardised according to the GloBI standard language. This guideline consists of categorising each entry into different standardised vocabularies. We cross-checked the species scientific names with the World Register of Marine Species webserver (Costello et al. 2013; WoRMS; [marinespecies.org/aphia.php?p=match](http://marinespecies.org/aphia.php?p=match)), retrieving the actual classification and the universal identifier, Aphia ID, provided by the UN-Global Biodiversity Information Facility. The geographic information was integrated and codified according to the GeoNames ID platform ([geonames.org](http://geonames.org)). The interaction type and host body part name were standardised, according to the OBO Library ([obofoundry.org](http://obofoundry.org)). Lastly, for the reference management and citation style, we used Mendeley software. With this standardisation and quality control process, we ensured a high-quality integrated human-readable and machine-readable dataset.

**Step description:** Step 1: Define the sampling **universe**; this step was designed to mark the geographic and environmental limits.

Step 2: Literature **search**; in this step, we compiled the curated bibliographic database, without duplicates and pseudoreplicates between the known literature items and the web search literature items.

Step 3: Item **validation**; this step consists of a validation test that we used to select the literature items with the minimum necessary information.

Step 4: Entry **standardisation**; in this step, we homogenised all the sponge iteration entries into the GloBI standard language.

Step 5: Dataset compilation (Fig. 1)

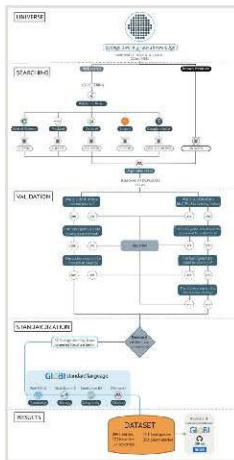


Figure 1. [doi](#)

Flow diagram of the steps followed to generate this dataset.

## Geographic coverage

**Description:** According to the large marine ecosystems' classification proposed by Spalding et al. (2007), the Northwestern Atlantic has five regions with major coral reef formations: the Gulf of Mexico, the Caribbean Sea formed by the greater and Lesser Antilles, Central America and the north shores of South America, North America, the Bahamian Archipelago and Bermuda at the north-eastern boundary of this major region.

## Taxonomic coverage

**Description:** This dataset is composed of the host/guest interaction between coral reef sponges (Pylum: Porifera) and six other major marine Phyla: Arthropoda, Annelida,

Mollusca, Chordata, Echinodermata and Cnidaria. All the information is at species resolution.

Taxa included:

Rank	Scientific Name	Common Name
phylum	Porifera	Sponges
phylum	Arthropoda	Shrimps, crabs, lobsters
phylum	Annelida	Worms, christmas tree worm
phylum	Mollusca	Clams, mussels, oysters and scallops
phylum	Chordata	Fish, goby
phylum	Echinodermata	Sea urchins, sea cucumbers, brittle-stars
phylum	Cnidaria	Sea anemones, hydroids

## Temporal coverage

**Data range:** 1909-1-01 - 2019-12-31.

## Usage licence

**Usage licence:** Creative Commons Public Domain Waiver (CC-Zero)

## Data resources

**Data package title:** Sponge dwelling-fauna from the North-western Tropical Atlantic Ocean: a bibliographic records database.

**Resource link:** <https://doi.org/10.5281/zenodo.3333023>

**Alternative identifiers:** [https://github.com/BDMYRepository/Sponge\\_Interactions](https://github.com/BDMYRepository/Sponge_Interactions)

**Number of data sets:** 1

**Data set name:** Sponge-dwelling fauna from the North-western Tropical Atlantic Ocean: a bibliographic records database.

**Download URL:** <https://zenodo.org/record/3333023>

**Data format:** .tsv

**Data format version:** 2.06



**Description:** The present database compile 65 articles (Baeza et al. 2016, Carrera-Parra and Vargas-Hernández 1997, Chace 1972, Chavarro et al. 2004, Böhlke and Robinson 1969, Cházaro-Olvera and Vázquez-López 2014, Christoffersen 1972, Coutière 1909, Coutière 1910, Crocker and Reiswig 1981, Crowe and Thomas 2002, D'Aloia et al. 2011, Dardeau 1981, Dardeau 1984, Dauer 1973, Duffy 1992, Duffy 1996a, Duffy 1996b, Duffy 1996c, Duffy 1998, Duffy and Macdonald 1999, Erdman and Blake 1987, García-Hernández and Hoeksema 2017, Hendler 1984, Henkel and Pawlik 2005, Henkel and Pawlik 2011, Henkel and Pawlik 2014, Herrick 1981, Hultgren and Duffy 2010, Huang et al. 2008, Hultgren et al. 2011, Hultgren et al. 2010, Lattig and Martin 2009, Lattig and Martín 2011, LeCroy 1995, Macdonald and Duffy 2006, Macdonald et al. 2009, Macdonald et al. 2006, Montenegro-González and Acosta 2010, Ortiz et al. 2011, Ortiz et al. 2013, Paerse 1932, Paerse 1950, Pawlik 2011, Pequegnat and Heard 1979, Randall and Lobel 2009, Rebolledo et al. 2014, Reimer et al. 2018, Richards et al. 2007, Rios and Duffy 1999, Robertson and Tassell 2019, Santana-Moreno et al. 2013, Scott et al. 1988, Swain 2012, Swain and Wulff 2007, Thomas and Klebaa 2007, Thomas and Klebba 2006, Tobb and Manning 1961, Tóth and Bauer 2008, Tyler and Böhlke 1972, Victor and Krasovec 2018, Villamizar and Laughlin 2011, Westinga and Hoetjes 1981, Williams 1984, Winfield et al. 2009, Winfield and Ortiz 2010, Wendt et al. 1985) and two university theses (Ugalde García 2014, Perez-Botello 2019) in a detailed sponge host-guest interaction dataset distributed in the Northwest Tropical Atlantic coral reefs, including a total of 2992 interactions between 101 sponge host species and 284 sponge-dwelling species, over 90 years of publications (Fig. 2). All entries are standardised to the GloBI language.

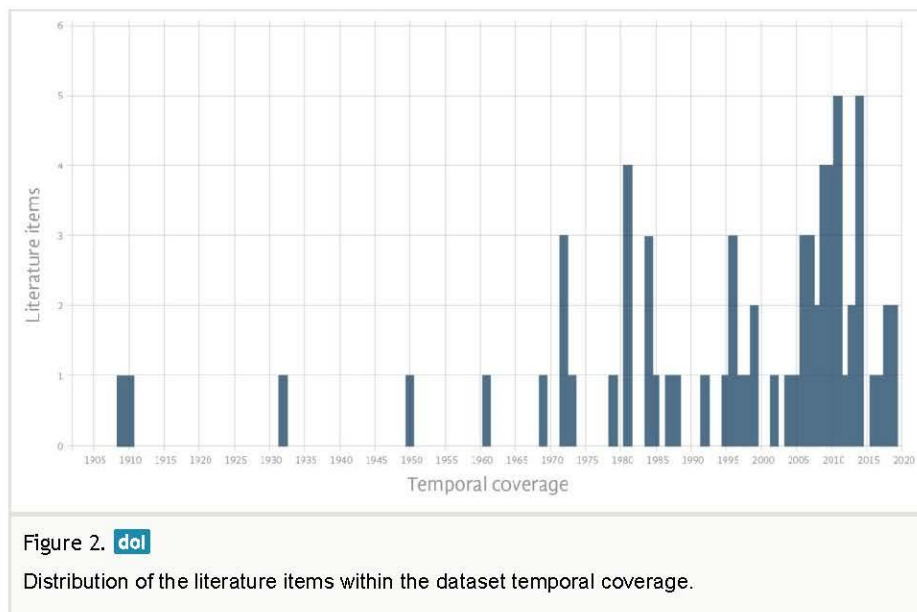


Figure 2. [doi](#)

Distribution of the literature items within the dataset temporal coverage.

Column label	Column description
sourceOccurrenceId	Globally unique id to reference the individual source organism.
sourceTaxonId	Taxon classification id of originating organism in some taxon name authority. WoRMS AphiaID
sourceTaxonName	Scientific name of taxon classification of source organism
sourceBodyPartId	Identifier of description of source body part is interacted with. As described by the OBO Relations Ontology
sourceBodyPartName	Human-readable description of source body part
sourceLifeStageId	Identifier of description of source life stage. As described by the OBO Relations Ontology
sourceLifeStageName	Human-readable description of source life stage
interactionTypeId	Id of interaction. As described by the OBO Relations Ontology
interactionTypeName	Human-readable description of interactions
targetOccurrenceId	Globally unique id to reference the individual target organism
targetTaxonId	Taxon classification id of target organism. WoRMS AphiaID
targetTaxonName	Scientific name of taxon classification of target organism of interaction
targetBodyPartId	Identifier of description of target body part is interacted with. As described by the OBO Relations Ontology
targetBodyPartName	Human-readable description of target body part.
targetLifeStageId	Identifier of description of target life stage. As described by the OBO Relations Ontology
targetLifeStageName	Human-readable description of target life stage.
localityId	Identifier of the Geo classification. As described by geonames.org
localityName	Human-readable description of locale
decimalLatitude	Latitude of geographic centre of interaction observation location
decimalLongitude	Longitude of geographic centre of interaction observation location
YYYY	Year of the recorded interaction
MM	Month of the recorded interaction
DD	Day of the recorded interaction
HH	Hour of the recorded interaction
mm	Minute of the recorded interaction
ss	Second of the recorded interaction
observationDateTime	ISO 8601 formatted date time string of the recorded interaction
referenceDoi	Digital Object Id used to the papers, datasets or other digital object that validate the interaction

referenceUrl	Some resolvable url that points to information related to species interaction record
referenceCitation	Human-readable reference related to species interaction record

## Additional information

### Interactive display and data visualisation

A virtual environment was generated to visual-analyse the dataset. We created a Tableau dashboard ([public.tableau.com](https://public.tableau.com)) and a AmCharts Chord Diagram ([amcharts.com/demos/toggleable-chord-diagram](https://amcharts.com/demos/toggleable-chord-diagram)). Both the interactive dashboard and the dynamic Chord Diagram are available at the project official web page: [marinespeciesinteractions.org/projects/visual-database/](https://marinespeciesinteractions.org/projects/visual-database/). The uses of the interactive dashboard are based on different lists that filter the displayed information according to the users' requests. The dashboard shows a map of the NWTA where the records of each interaction are plotted (Fig. 3a). In the middle are 10 filters with host Order, Family and Scientific species name, guest Phyla, Class, Order, Family and Scientific species name, the recorded locality (country) and the information source (Fig. 3b). On the right side, two bar graphics show either the sponge Order vs. guest species richness or the guest Phylum vs. guest Class species richness counts (Fig. 3c, d). The host/guest matrix is centred in the lower part of the dashboard, with the host sponges as rows and the sponge dwelling-fauna species as columns (Fig. 3e). In practice, the interactive dataset aims to be an intuitive step-by-step graphical interface. It is possible to select the source of information to observe and focus on a particular region or taxonomic group.

The Chord Diagram gives a general picture of everything in the universe of registered interactions (Fig. 4a). The thickness of the node represents the number of links that a species has and the colour represents the taxonomic group to which it belongs. The information can be filtered by guest Phylum (i.e. Annelida, Arthropoda, Chordata, Cnidaria, Echinodermata and Mollusca) (Fig. 4b), but not by the sponge Order (Fig. 4c). If the user wants to return to the original view, they can click on the guest Phylum name or the back button (Fig. 4d).

Although the complete dataset is fully accessible for downloading as a whole, with these two interactive visualisation tools, openly available through the internet and hopefully sufficiently intuitive, the user can interact with the dataset and pose questions filtered according to their particular interest.

### What's next?

With this dataset, we provide an updated and clustered report on the symbiotic relationships in coral reef sponges in the NWTA coral reefs. This information opens the door to many numerical and statistical analyses. Finally, we encourage you to collaborate with this project and, if you have any records that are not listed on this dataset, contact us. We will be glad to talk with you and add this information in the next version of the Dataset.

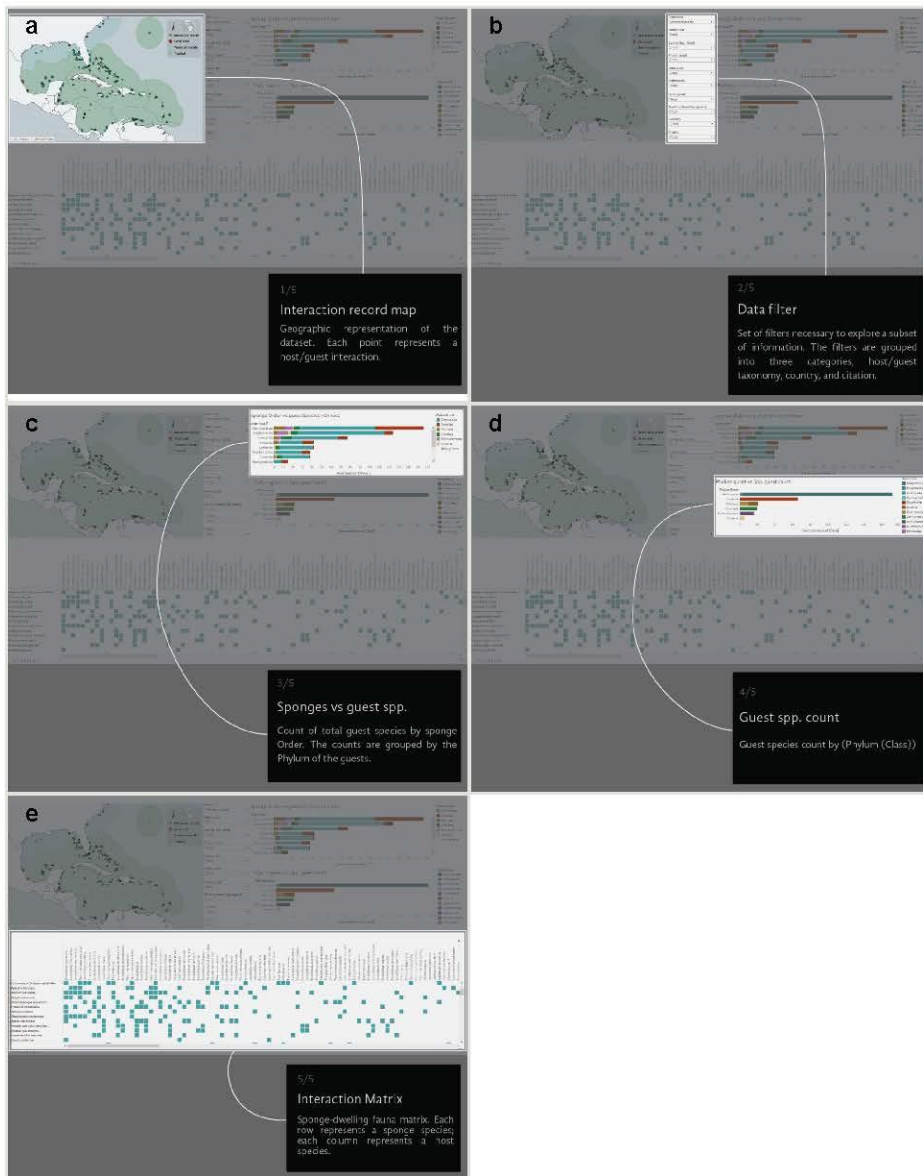


Figure 3.  
Example of the dashboard features.

### Concluding remarks

Compiling the available sponge host/guest interaction data in one place enhances the scope and shareability of the diffused information. Furthermore, the standardisation of the dataset into a global language creates a link between this dataset and several international repositories, such as The Encyclopaedia of Life and communication with other data



languages, such as Darwin Core. Moreover, with this work, a baseline is generated to compare and structure future works that focused on sponge host/guest relationships.

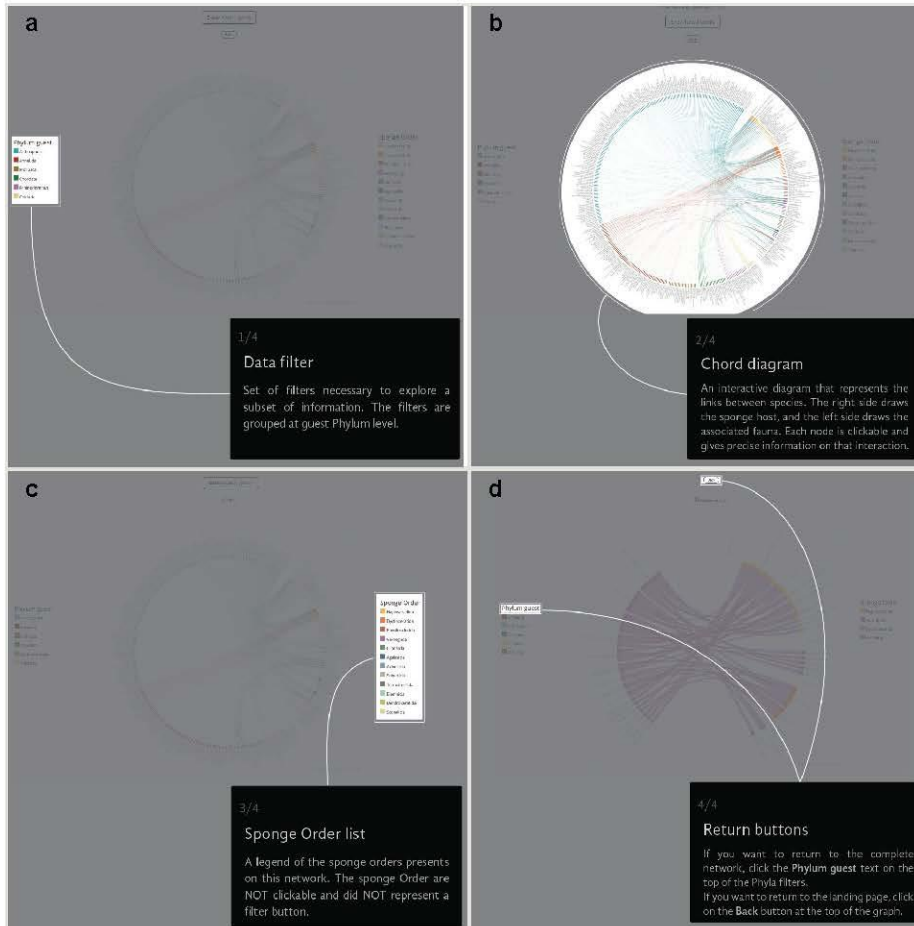


Figure 4.

Chord diagram features. A overview of how to use the network plot.

In conclusion, the state of knowledge about sponge-associated fauna is on the right path. However, the main obstacle during the data collection process was the lack of reported information. For example, the involved species' taxonomic identity and the interaction type are crucial pieces of information that are missing in several literature items. We suggest that future works make an effort to clearly identify both taxonomic entities, not only the guest or host species. Furthermore, it was possible to analyse the interaction matrix of sponge-dwelling species with a complex network approach identifying connected and key species with this dataset. To better understand possible changes in the sponge host/guest interactions, a niche-modelling approach could also be useful, displaying different future species-interaction scenarios.

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Artículo 2: (Publicado) *Geographic range size and species morphology determines the organization of sponge host-guest interaction networks across tropical coral reefs.*

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## Resumen

Las esponjas son organismos ampliamente distribuidos en los arrecifes de coral del Atlántico Tropical Noroccidental, brindando servicios como refugio, protección contra depredadores y fuente de alimento para una amplia diversidad de especies tanto de vertebrados como de invertebrados. La alta diversidad de fauna asociada a las esponjas puede generar complejas redes de interacciones a lo largo de gradientes espaciotemporales. Una forma de comenzar a descubrir la organización de las complejas redes de interacción entre las esponjas y sus huéspedes es comprender cómo el área geográfica acumulada, la morfología de las esponjas y la taxonomía de las esponjas contribuyen a la conectividad de las especies involucradas dentro de dichas redes. Este estudio es un metaanálisis basado en la literatura previa sobre interacciones entre esponjas y sus huéspedes recopilados en 65 publicaciones científicas. Esta recopilación resultó en un total de 745 interacciones entre esponjas y fauna asociada en ambientes de arrecifes de coral del Mar Caribe y el Golfo de México. El objetivo de este trabajo fue analizar la contribución de las especies de esponjas a la organización de las redes en los arrecifes de coral del Atlántico Tropical del Noroccidental mediante la combinación de siete descriptores a nivel de especie y la relación de esta contribución con tres rasgos funcionales principales: el área geográfica acumulada de las esponjas, la morfología funcional de las esponjas y el sesgo taxonómico de las esponjas. En general, observamos que las esponjas con una distribución amplia y un área geográfica acumulada mayor tenían una mayor contribución estructural a la red. Del mismo modo, encontramos que las morfologías funcionales en forma de copa y masivas tienden a ser formas con una mayor contribución a la organización de la red de interacciones en comparación con las morfologías erectas e incrustantes. Por último, no detectamos un sesgo taxonómico en la organización de la red de interacciones en relación con los órdenes de las esponjas. Estos resultados resaltan la importancia de una combinación específica de rasgos de las esponjas para promover la diversidad de asociaciones entre las esponjas arrecifales y sus especies huéspedes.

# Geographic range size and species morphology determines the organization of sponge host-guest interaction networks across tropical coral reefs

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## ABSTRACT

Sponges are widely spread organisms in the tropical reefs of the American Northwest-Atlantic Ocean, they structure ecosystems and provide services such as shelter, protection from predators, and food sources to a wide diversity of both vertebrates and invertebrates species. The high diversity of sponge-associated fauna can generate complex networks of species interactions over small and large spatial-temporal gradients. One way to start uncovering the organization of the sponge host-guest complex networks is to understand how the accumulated geographic area, the sponge morphology and, sponge taxonomy contributes to the connectivity of sponge species within such networks. This study is a meta-analysis based on previous sponge host-guest literature obtained in 65 scientific publications, yielding a total of 745 host-guest interactions between sponges and their associated fauna across the Caribbean Sea and the Gulf of Mexico. We analyzed the sponge species contribution to network organization in the Northwest Tropical Atlantic coral reefs by using the combination of seven complementary species-level descriptors and related this importance with three main traits, sponge-accumulated geographic area, functional sponge morphology, and sponges' taxonomy bias. In general, we observed that sponges with a widespread distribution and a higher accumulated geographic area had a greater network structural contribution. Similarly, we also found that Cup-like and Massive functional morphologies trend to be shapes with a greater contribution to the interaction network organization compared to the Erect and Crust-like morphos. Lastly, we did not detect a taxonomy bias between interaction network organization and sponges' orders. These results highlight the importance of a specific combination of sponge traits to promote the diversity of association between reef sponges and their guest species.

**Subjects** Biodiversity, Biogeography, Ecology, Marine Biology, Zoology

**Keywords** Caribbean reefs, Community ecology, Marine ecology, Gulf of Mexico reefs, Functional traits, Ecology

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## INTRODUCTION

The ecology of a species or community can be studied based on the functional characteristics of organisms (Gagic *et al.*, 2015; Schmitz *et al.*, 2015; Pimiento *et al.*, 2020). A functional trait or characteristic is an organism's distinguishable and quantifiable attribute, typically evaluated at the individual level and comparable across different species (Poff *et al.*, 2006; Weiher, 2011). Classifying biodiversity according to some trait or functional group emphasizes the phenotypic differences between taxa and breaks the species ancestor-descendent phylogenetic link (McGill *et al.*, 2006; Weiher, 2011; Gagic *et al.*, 2015; Bagousse-Pinguet *et al.*, 2019). Some functional traits such as feeding strategies, reproduction, dispersal, species distribution, response to environmental changes, species morphology or the ability of certain species to create microhabitats and vertical complexity, generally determine what, how, where and why we observe different species in an ecosystem (McGill *et al.*, 2006; Weiher, 2011; Costello *et al.*, 2015; Gagic *et al.*, 2015; Beauchard *et al.*, 2017; Pimiento *et al.*, 2020).

Sponges, some of the oldest animals on Earth with fossil evidence dating back over 580 million years ago (Chen, 2012), are crucial components of modern marine environments, acting as keystone species in benthic habitats (Rützler, 2004; Wulff, 2006, 2016; Bell, 2008; González-Rivero, Yakob & Mumby, 2011; Maldonado *et al.*, 2016; Brusca, Moore & Shuster, 2018). In particular, sponges can structure coral reef ecosystem performing multiple functions simultaneously, for example, sponge species are capable of filtering large volumes of water, enhancing primary production, participating in critical processes such as carbon, nitrogen, silicon, and oxygen cycles, and providing habitats for a wide variety of life forms which included organism with simple body plans (microorganisms) to complex ones (invertebrates and vertebrates) (Diaz & Rützler, 2001; Bell, 2008; Bell *et al.*, 2013; Pawlik *et al.*, 2013; Maldonado *et al.*, 2016; Rossi *et al.*, 2017). These previous cited studies have recognized the functional importance of sponges in coral reef ecosystems but this understanding has not always been translated into larger scale efforts (Bell, 2008; Gaiüzère *et al.*, 2022) and even less into no-trophic interaction networks ecology (*i.e.*, host-guest interactions).

Host-guest interactions, refer to the co-occurrence of two different species in both space and time (Watson & Pollack, 1999; Baeza, 2015; Overstreet & Lotz, 2016). The key attribute of these associations is the use of one organism as habitat by another organism of a different species (Baeza, 2015; Overstreet & Lotz, 2016). In this context, when we know the costs and benefits inherent to these relationships, it is possible to classify the host-guest interactions into parasitism, mutualism, or commensalism (Thiel, 1999; Watson & Pollack, 1999; Thiel & Baeza, 2001; Baeza, 2015). While it is well-documented that different sponge species can be habitat facilitators for a wide range of organisms, the specific costs acquired by the sponge species involved in these interactions remain poorly understood (Duffy, 1992; Wulff, 1997; Bell, 2008; Maldonado *et al.*, 2016). In order to maintain consistency in the interactions classification, the term "host-guest interaction" is assumed by this study to describe the relationship between sponges and the fauna that inhabit them.



Coral reefs are a dynamic and complex marine ecosystem involving a wide array of interacting organisms (Knowlton, 2001; Bauer, 2004; Hagedorn et al., 2015). The mutualistic relationship between cyanobacteria (*Symbiodinium* sp.) and scleractinian corals is crucial for the existence of this ecosystem, yet there are many other interspecific relationships that contribute to its complexity (Bauer, 2004; Hagedorn et al., 2015). One example is the host-guest relationship between sponges and the organisms that inhabit them (Diaz & Rützel, 2001; Hooper & van Soest, 2002b; Maldonado et al., 2016; Pérez-Botello & Simões, 2021). Sponges of class Demospongiae possess the highest number of host-guest associations diversity in coral reefs across the globe, highlighting *Agelas*, *Aplysina*, *Xestospongia*, and *Callyspongia* as the main hostesses genera (Maldonado et al., 2016). However, the study of ecological interactions in reef environments and even more in sponge-associated fauna focuses on analyzing interactions between paired species or on a small subset of networks.

In the Northwest Tropical Atlantic (NWTa) coral reefs (the Caribbean Sea, the Gulf of México, and Bermuda), sponges are a crucial benthic component along with scleractinian corals and macroalgae (González-Rivero, Yakob & Mumby, 2011). Phylum Porifera has a heterogeneous distribution, being Caribbean Sea reefs the ones with the highest species richness, then the Gulf of Mexico reefs, and finally Bermuda reefs (Ocean Biodiversity Information System (OBIS), 2020). These sponges could provide a series of services to several guest organisms; for example, sponges as habitat facilitators, can be a food source to the associated organisms, or can provide a certain degree of protection to the organisms that associate with them, either through the direct use of different structures as shelter or camouflage, or through the indirect protection derived from secondary metabolites produced by the sponge (Dembowska, 1926; McLay, 1983; Bedini, Canali & Bedini, 2003; Pawlik, 2011; Cruz Ferrer, 2014; Maldonado et al., 2016; Harada, Hayashi & Kagaya, 2020). Due to the multifunctionality that sponges present in the NWTa reefs, the community structure of sponge species directly influences other reef organisms (Bell, 2008). The NWTa sponge-associated fauna is incredibly diverse, with over 284 known associated species inhabiting 101 sponge species (Pérez-Botello & Simões, 2021). The main pattern is that host-guest associations are species-specific at sponge phylum level, meaning that sponges have the potential to maintain part of the biodiversity of reef systems (Maldonado et al., 2016; Pérez-Botello & Simões, 2021). However, when evaluating the sponge-guest species richness, a few sponge species, such as *Ircinia strobilina* (Lamarck, 1816), *Callyspongia* (*Cladochalina*) *aculeata* (Linnaeus, 1759), and *I. felix* (Duchassaing & Michelotti, 1864), concentrate 187 associated guest fauna (Dardeau, 1981; Carrera-Parra & Vargas-Hernández, 1997; Pérez-Botello, 2019), more than half of the associated species recorded, while 33 sponge species only interact with 51 spp., hosting between one to three spp. (for an exhaustive list of sponge-associated species diversity review Pérez-Botello & Simões (2021) and visit the website <https://marinespeciesinteractions.org/?p=2302>). These host-guest species interactions array generates a complex network where sponges act both as hosts and connectors within the network, emerging the question of what functional characteristics regulate the contribution that each sponge species has to the structure of the host-guest interactions network within the NWTa coral reefs?

In the present study, we evaluated three traits that could regulate the structure of the interactions network. First, the sponge-accumulated geographic area, or the habitat availability to be colonized, could regulate the contribution that each sponge species has to the structure of the network. In addition to the widely recognized ecological species-area pattern described by the Island Biogeography Theory (MacArthur & Wilson, 1963; Cornell & Lawton, 1992; Lawton, 1999; Losos et al., 2009), Galiana et al. (2018) proposed a relationship between geographic area and the probability of establishing a species interaction. We tested the hypotheses that there is a positive correlation between the sponge-accumulated geographic area and the network structural importance of each sponge species (Moulatlet, Dáttilo & Villalobos, 2023). The second tested trait is how habitat heterogeneity, measured as the functional sponge morphology, promotes the establishment of guest species. For example, sponges with large volumes could host a certain types of guest organisms than sponges with smaller volumes and more tightly packed shapes (Koukouras et al., 1996; Hooper & van Soest, 2002a; Maldonado et al., 2016; Pérez-Botello, 2019). For this reason, we also tested the hypotheses that there is a plausible suitable functional morphological group that promotes the establishment of sponge-guest interactions. Lastly, we tested if the sponges' taxonomy bias could affect the importance of each taxon in the interaction network structure. In other guest-host interaction models, particularly mutualism between sea anemones and crustaceans of the Caribbean Sea, it has been demonstrated a pairwise taxonomic relationship between anemones and shrimps (Mascaró et al., 2012; McKeon & O'Donnell, 2015; Kou et al., 2015; Pérez-Botello, Mascaró & Simões, 2021), such as *Bartholomea annulata* (Le Sueur, 1817) and *Condylactis gigantea* (Weinland, 1860), two sea anemones of the Actiniaria order that concentrate the major diversity of anemone-shrimps as *Alpheus armatus* Rathbun, 1901, *Ancylomenes pedersoni* (Chace, 1958), *Thor amboinensis* (De Man, 1888) and *Periclimenes yucatanicus* (Ives, 1891) (Silbiger & Childress, 2008; McCammon, Sikkell & Nemeth, 2010; McCammon & Brooks, 2014). Therefore, there may be a pattern in which sponge orders with a higher associated species richness are essential to maintain the structure of the host-guest interaction network on reef sponges.

Ecological networks can be visualized as a series of interconnected nodes and edges; these nodes represent different species within the ecosystem, and the edges represent the relationships and interactions between them (Ramírez-Flores et al., 2015; Cantor et al., 2018; Dehling, 2018; Martínez-Falcón, Martínez-Adriano & Dáttilo, 2019). These fixed representations of ecological processes help to identify keystone species that maintain and connect the network and predict changes in ecological communities, providing a comprehensive understanding of the dynamics of biological interactions (Bastolla et al., 2009; Cantor et al., 2018). Applying a network analysis to infer functional roles has been previously employed in other ecological systems, such as seed dispersal (Vidal et al., 2014), insect-plant mutualistic networks (Bastolla et al., 2009), vertebrate scavenging (Sebastián-González et al., 2021), and plant-pollinator—protective ant—seed disperser multi-interaction networks (Dáttilo et al., 2016).

In this study we perform a large-scale community-level network analysis on sponge-associated fauna, offering a valuable insight into the ecological importance of coral



reef sponges host-guest interactions. We aim to evaluate the structural importance of each sponge species and identify the keystone functions that maintain the organization of sponges host-guest interaction networks across NWT coral reefs.

## MATERIALS AND METHODS

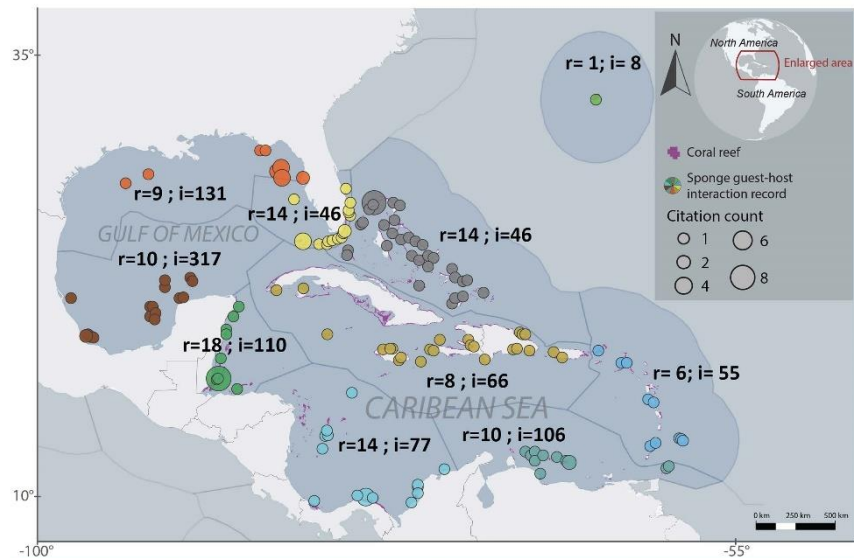
### Database

We employed a bibliographic Database containing 101 host sponges species that inhabit the NWT coral reefs, which were classified into 12 orders of class Demospongiae (Pérez-Botello & Simões, 2021; <https://zenodo.org/record/3333023>). In order to ensure the highest possible taxonomic resolution, the original database was filtered to include only sponge taxonomic entities at species level. The dataset analyzed in this meta-analysis comprised 65 scientific publications, yielding a total of 745 host-guest interactions between sponges and their associated fauna within the NWT coral reefs (Dataset S1).

We employed the Marine Ecoregions of the World (MEOW) to systematically organize the host-guest interactions dataset in a cohesive manner (Spalding *et al.*, 2007).

The analyzed ecoregions were Bahamian, Bermuda, Eastern Caribbean, Floridian, Greater Antilles, Northern Gulf of Mexico, Southern Caribbean, Southern Gulf of Mexico, Southwestern Caribbean and Western Caribbean. The number of interactions, locations and publications records per ecoregion varied, with Bahamian recording 46 interactions across 28 locations and 14 publications, Bermuda recording eight interactions across one location and one publications, Eastern Caribbean recording 55 interactions across 17 locations and six publications, Floridian recording 46 interactions across 22 locations and 14 publications, Greater Antilles recording 66 interactions across 23 locations and eight publications, Southern Caribbean recording 106 interactions across 14 locations and 10 publications, Northern Gulf of Mexico recording 131 interactions across seven locations and nine publications, Southwestern Caribbean recording 77 interactions across 19 locations and 146 publications, Southern Gulf of Mexico recording 317 interactions across 19 locations and 10 publications, and Western Caribbean recording 110 interactions across 15 locations and 18 publications. A total of 76 sponge species were recorded hosting 268 sponge-associated fauna (Fig. 1).

To assess publication bias and measure the effect that could have in terms of replication we relate the number of publications by ecoregion (observed publication sample sizes) with the publications total number in the dataset (expected publication sample size) (Egger *et al.*, 1997; Thompson, Smith & Sharp, 1997; Thompson & Sharp, 1999). With this citation proportion, we estimate the publication heterogeneity and evaluate the discrepancy between the observed and expected publication effort across ecoregions. The meta-bias analysis demonstrated that each ecoregion exhibited homogeneity in publications proportion ( $t^2$  estimator = Maximum-likelihood,  $p$ -value = 0.99), and no statistically significant publication bias was found between regions (bias method = Thompson,  $p$ -value = 0.28) (Fig. S1) indicating that the replication of the study across the different regions is reliable. We evaluated the publication bias using the functions 'metaprop' and 'metabias' from the package 'meta' in R (Schwarzer, Carpenter & Rücker, 2015; Balduzzi, Rücker & Schwarzer, 2019).



**Figure 1** Regionalized map of sponge host-guest interactions in the Northwestern Tropical Atlantic coral reefs. The ecoregions are based on the Marine Ecoregions of the World classification (Spalding *et al.*, 2007). Each region is labeled with the number of articles that provide information (r) and the number of recorded interactions (i). The sizes of each circle represent the number of citations that has each record. The colors of the circles represent the particular regionalization, gray for the Bahamian, light green for Bermuda, Blue for the Eastern Caribbean, light yellow for Floridian, dark yellow for the Grater Antilles, orange for the Northern Gulf of Mexico, sapphire for the Southeastern Caribbean, brown for the Southeastern Gulf of Mexico, light blue for the Southwestern Caribbean and dark green for the Western Caribbean. To interactively explore this map, visit the website <https://marinespeciesinteractions.org/?p=2302>. Full-size DOI: 10.7717/peerj.16381/fig-1

Interactive figures are available on Marine Species Interactions web site (<https://marinespeciesinteractions.org/?p=2271>) and the working datasets, are available on Zenodo (<https://doi.org/10.5281/zenodo.7549399>).

### Characterizing the structure of sponge-associated fauna network

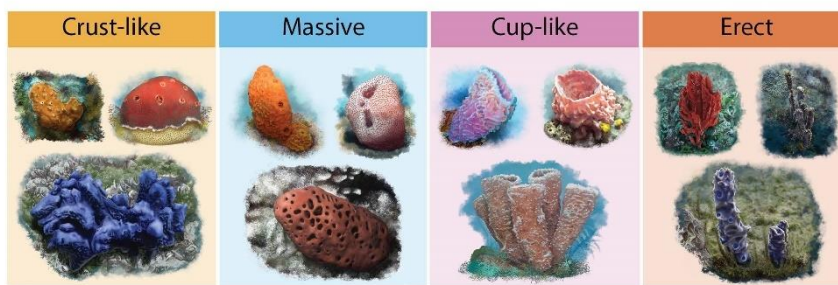
To analyze the sponge host-guest interactions, we employed a complex network approach (Dáttilo & Rico-Gray, 2018). The relationships (links) between different species are represented as interconnected nodes. Because the information on sponge-guest relationships used in this study came from different publication records employing several sampling methodologies and criteria for accounting interaction frequency, we used a qualitative network (Bellotti, 2014) in which a value of one represented the presence of an interaction between a sponge and one guest species, and 0 indicated the absence of a recorded interaction. This approach allowed us to analyze the contribution to network organization and species' importance without the influence of changing sampling methods and, therefore, ensuring that all species report the same type of biological information (Bellotti, 2014; Dáttilo *et al.*, 2016).


We begin by characterizing the contribution to network organization by using two structural properties frequently reported in species interaction networks: nestedness and modularity. In nested networks, species engaged in few interactions (*i.e.*, potentially specialists) are connected to a subset of species engaged in many interactions (*i.e.*, potentially generalists), while modularity describes a pattern where there are subgroups of species of one lower level (*e.g.*, sponges) that interact strongly with a subgroup of species of another higher level (*e.g.*, guests). Nestedness was estimated using the Nestedness Metric based on Overlap and Decreasing Fill (NODF; [Almeida-Neto, Frensel & Ulrich, 2012](#)), a nestedness descriptor that varies from zero (not nested) to 100 (perfectly nested). We estimated the Modularity ( $Q$ ) using the *QuanBiMo* algorithm, which repeatedly divides a network into modules (we set to 107 swaps) and re-calculates modularity until reaching an optimal  $Q$  value, which ranges from zero (no more links within modules than expected by chance) to one (maximum possible modularity). Then, we generated 1,000 random matrices to test the significance of nestedness and modularity according to a null model, in which the number of interactions and the number of links (and hence connectance) keep constant. We calculated nestedness and modularity using the function 'network level' from the package 'bipartite' in R ([Dormann, Gruber & Fründ, 2008](#)).

### Network structural contribution

We considered seven complementary species-level descriptors to measure the species' contribution to network organization: species degree, betweenness, closeness, Katz centrality, among-module connectivity ( $ci$ ), standardized within-module degree ( $zi$ ), and contribution to nestedness ( $cni$ ). We chose these descriptors because they provide complementary biological information on the contribution to network structure and, therefore, are expected to be more robust than on a single measure ([Vidal et al., 2014](#); [Corro et al., 2022](#)). Degree centrality is the number of interactions established by a species ([Borrett, 2012](#)). Betweenness centrality calculates the fraction of the smallest number of links between any two species in a network that pass-through a given species. Closeness centrality is a measure of the average of the geodesic distances (shortest path lengths) from a focal species to all other species in the network. Biologically, a species with high closeness centrality is considered to be centrally located and has quick access to resources effectively throughout the network. Katz centrality calculates the number of immediate neighbors and the direct and indirect paths of a species to other species in the network ([Katz, 1953](#)). Among-module connectivity ( $ci$ ) describes how evenly distributed are the interactions of a given species across modules ([Olesen et al., 2007](#)). Standardized within-module degree ( $zi$ ) calculates of the extent to which each species is connected to the other species in its module within the network ([Olesen et al., 2007](#)). Contribution to nestedness ( $cni$ ) is the degree to which the interaction of species increases or decreases the network's overall nestedness ([Saavedra et al., 2011](#)). Because all these descriptors were highly correlated ([Fig. S2](#)) we used a principal component ordination (PCO) to reduce the seven-dimensional space to a single generalized index summarizing species' contribution to network organization as often used in specialized literature. The first principal component (PCO1) accounted for 99.8% of the variability, indicating complementarity among the seven descriptors, where





**Figure 2** Illustrations of sponge's functional morphologies. Dark yellow for Crust-like, light blue for Massive, pink for Cup-like and orange for Erec. For more information on the morphological standardization used, please refer to Schönberg (2021). Full-size  DOI: 10.7717/peerj.16381/fig-2

species with higher PCO1 scores exhibit many interactions, are connected to other species by multiple direct and indirect pathways, and represent a higher contribution to network organization. Since the values obtained from PCO1 are both positive and negative and the magnitude of change exceeds the tens between the minimum and maximum value, we changed the starting point of the values to zero, and we did a square root transformation of PCO1 ( $PCO1^{1/2}$ ).

### Sponge functional traits

Information on two functional traits that may influence a sponges' ability to host a greater or lesser number of species was compiled: (1) The accumulated geographic area of host sponges and (2) host sponges' functional morphology. The accumulated geographic area of sponges was determined using records from the Global Biodiversity Information Facility (GBIF, 2021), the interaction records of Pérez-Botello & Simões (2021) (Dataset S2), and the Caribbean and Gulf of Mexico coral reefs shapefile from the Allen Coral Atlas (Allen Coral Atlas, 2022). A circular buffer area of 10 m<sup>2</sup> was calculated for each sponge record, and the area was cropped with the reefs' shapefile. The results in square kilometers (km<sup>2</sup>) were used as colonizable sponges' areas. Sponges functional morphology (Cust-like, Massive, Cup-like, and Erect; Fig. 2) were classified with the Schönberg (2021) morphological standardization (Dataset S3), and with the original descriptions of each sponge species when is available or with a species taxonomy update.

### Statistical analysis

To analyze the sponge contribution to the network concerning their geographic accumulated area, we used a generalized linear model (GLM: family = *Poisson*). This analysis provides a quantitative evaluation of the hypotheses that the sponges' organization contribution to the interaction network is positively related by the accumulated geographic area of sponges. The sponges that provide a large geographical colonizable area potentially had greater structural importance than those sponge species with a restricted distribution (Dataset S4).

At the same time, we conducted an analysis of variance (ANOVA) to compare the different morphologies and test the hypotheses that sponges functional morphology improve the sponge contribution to the interaction network organization, *i.e.*, some sponges morphologies are more suitable for hosting more guests than other morphologies (Dataset S4). We also evaluated the potential for sponges' taxonomy bias in the network organization's importance. To do so, we grouped the different sponge species by order and conducted another ANOVA to compare the taxonomic groups (Dataset S4).

## RESULTS

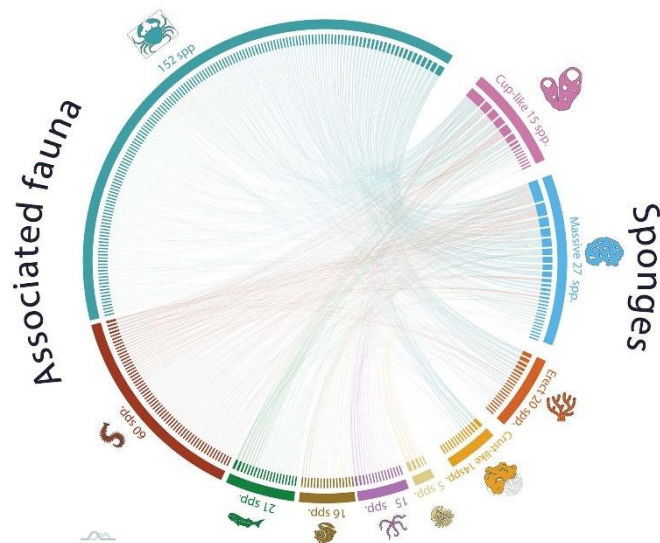
### Network-level properties

The analysis of nonrandom patterns in the sponge-host interaction network of NWT coral reefs demonstrated a statistically significant occurrence of nestedness and modularity in the organization of ecological network (NODF = 15.03 and M = 0.51, respectively. Both *p-values* < 0.001). A nested network exhibits a hierarchical organization of species interactions, specialist species engaged in few interactions are connected to a subset of generalist species with more interactions. Additionally, modularity describes a pattern where there are subgroups of guest species that interact more frequently with a group of host species. The presence of both nestedness and modularity network suggests a complex and dynamic structure within the sponge associated community, with host sponge species like *Ircinia strobilina* (PCO1<sup>1/2</sup> = 23.785; linked guest spp. 78) *I. felix* (PCO1<sup>1/2</sup> = 19.030; 46 guest spp.), *Callyspongia aculeata* (PCO1<sup>1/2</sup> = 18.121; 63 guest spp.), and *C. fallax* Duchassaing & Michelotti, 1864 (PCO1<sup>1/2</sup> = 16.389; 29 guest spp.) acting like species connectors and maintaining the network's structure. At the same time this pattern exhibits a high diversity of low connected species, for example, *Spongia (Spongia) obliqua* Duchassaing & Michelotti, 1864 (PCO1<sup>1/2</sup> = 0.037; 1 guest sp.), *Verongula rigida* (Esper, 1794) (PCO1<sup>1/2</sup> = 0.088; 1 guest sp.), and *Cribrochalina vasculum* (Lamarck, 1814) (PCO1<sup>1/2</sup> = 1.004; 2 guest spp.). Despite their limited interactions, these low connected sponge species contribute to the overall sponge host diversity within the network (Fig. 3).


The observed pattern highlights the remarkable dominance of interactions by a specific subset of sponge species within the ecological network. It is remarkable that a small number of sponge species play a crucial role in maintaining the organizational structure of the network through a high number of interactions, while a larger proportion of sponge species exhibit minimal associations with other species. In the same way, this pattern of a limited number of highly connected species making a significant contribution to the organization of the interaction network is constant regardless of the functional sponge morphology.

### Trait-level properties

The sponge accumulated geographic area exhibited a positive relationship with the contribution of each sponge to the network organization (Intercept = 1.178, *z* value = 13.206, *p-value* < 0.001). Our findings reveal that as the sponge cumulative area increases, so does the contribution of sponges to network organization (Fig. 4). Widely distributed sponges such as *Ircinia strobilina*, *I. felix* or *Callyspongia aculeata* are essential



**Figure 3** Sponge host-guest interaction network for the Northwestern Tropical Atlantic coral reefs.

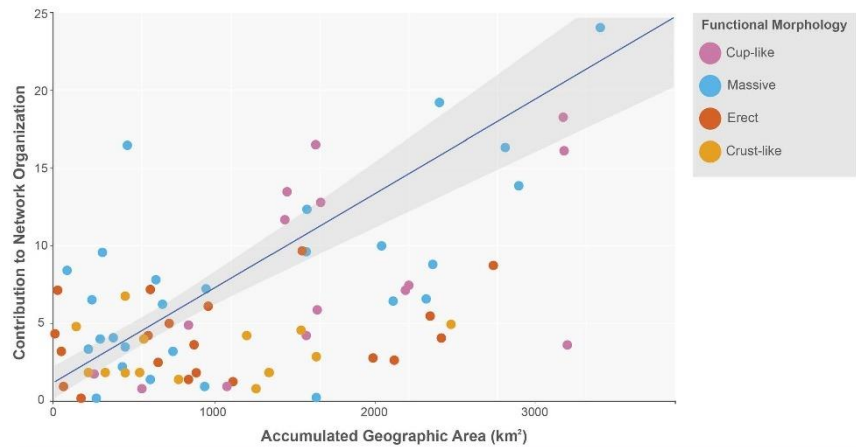
The left side of the network represents the sponge-associated fauna, dark blue denotes Arthropods, red Annelids, green Vertebrates, golden Mollusks, pink Echinoderms and light-yellow Cnidarians. The left side of the network represents the host-sponges. The sponges are classified according to its functional morphology (Schönberg, 2021), pink for Cup-like, light blue for Massive, orange for Erect, and dark yellow for Crust-like. To interactively explore the network, visit the website <https://marinespeciesinteractions.org/?p=2333>. Full-size  DOI: 10.7717/peerj.16381/fig-3

species with a significant structural contribution to the network and a higher accumulated area. In contrast, sponges with focal distributions or sponges with only reported in unique sites such as *Cliona vermifera* Hancock, 1867, *Aplysina bathyphila* Maldonado & Young, 1998 *Niphates erecta* Duchassaing & Michelotti, 1864 and *Ircinia ramosa* (Keller, 1889) had a lower contribution to the network organization. In the same way sponges functional morphology also influenced the magnitude to which it contributed to the structure of the guest-host interaction network (ANOVA:  $F_{2,731} = 5.389$ ;  $p\text{-value} < 0.002$ ; Fig. 5). Sponges with Cup-like (mean  $\pm$  s.e.:  $8.348 \pm 5.886$ ) and Massive morphologies ( $7.844 \pm 5.962$ ) had a significant superior contribution to network organization than Erect ( $4.153 \pm 2.625$ ), and Crust-like ( $8.348 \pm 1.746$ ) morphologies. Finally, there were no significant differences in the contribution of sponge orders to the network organization (ANOVA:  $F_{1,941} = 0.587$ ;  $p\text{-value} < 0.832$ ; Fig. 6).

## DISCUSSION

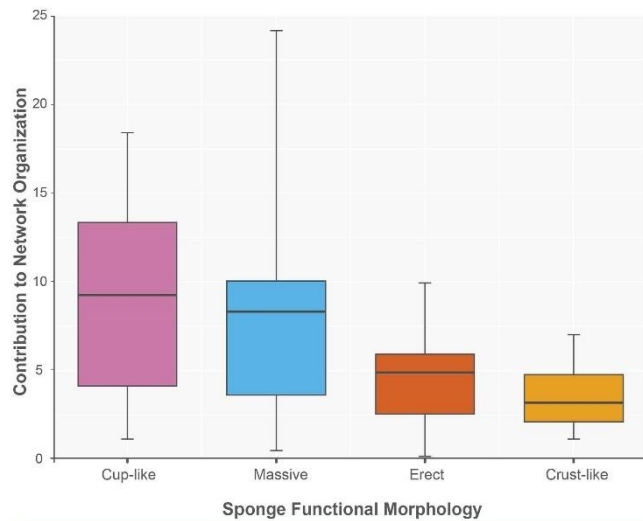
Our results provide evidence that supports the relationships between network organization, accumulated geographic area, and functional morphology in the interactions between sponge hosts and their associated guest species. The relationship between accumulated geographic area and network organization was already supported by the existing interactions theory (Galiana et al., 2018; Dallas & Jordano, 2021), however this





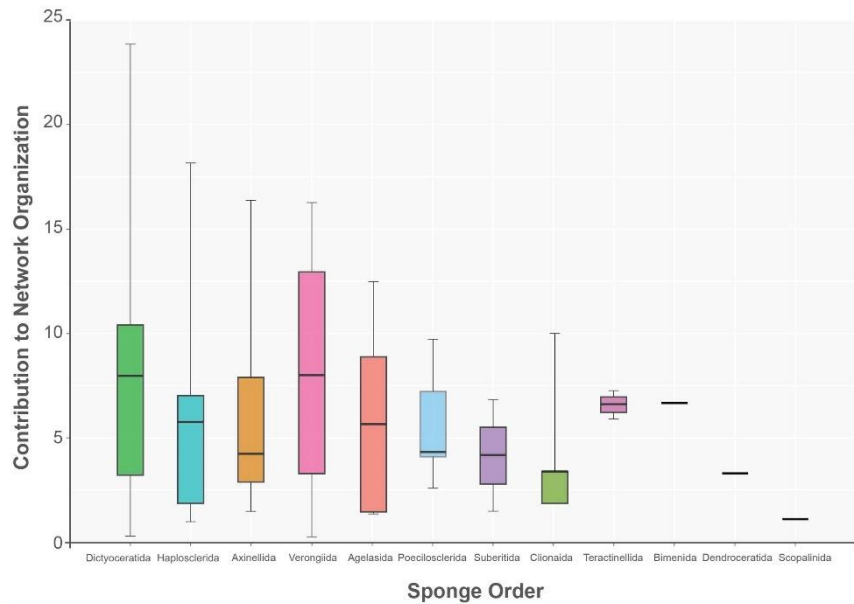
**Figure 4** Relationship between sponge contribution to network organization and sponges accumulated geographic area. General lineal model between sponge contribution to network organization and sponges accumulated geographic area (Intercept = 1.178,  $z$  value = 13.206,  $p$ -value < 0.001). The sponges are classified according to its functional morphology (Schönberg, 2021), pink for Cup-like, light blue for Massive, orange for Erect, and dark yellow for Crust-like.

Full-size DOI: 10.7717/peerj.16381/fig-4



**Figure 5** Sponge contribution to network organization according to sponge functional morphology. Crust-like and Massive morphologies are the statistically different groups (ANOVA:  $F_{2,731} = 5.389$ ;  $p$ -value < 0.002). The sponges are classified according to its functional morphology, pink for Cup-like, light blue for Massive, orange for Erect, and dark yellow for Crust-like.

Full-size DOI: 10.7717/peerj.16381/fig-5



**Figure 6** Sponge contribution to network organization according to sponge order. No statistical differences between sponge orders (ANOVA:  $F_{1,941} = 0.587$ ;  $p$ -value < 0.832) are founded. The boxplot interquartile black line provides the mean value. Upper and lower whiskers extend to visual represent all data distribution. Full-size [DOI: 10.7717/peerj.16381/fig-6](https://doi.org/10.7717/peerj.16381/fig-6)

result improves further theoretical development in coral reef interactions ecology.

In contrast, although there are numerous studies of the actual fauna that use sponges as microhabitats (Bell, 2008; Maldonado et al., 2016; Pérez-Botello & Simões, 2021), there has been not clarify the sponge morphological features that make them a suitable environment.

The positive relationship between sponges' contribution to network organization and its accumulated geographic area has a significant ecological implication. Our results indicate that as the accumulated geographic area increases so does the possibility to interact with a wide diverse guest species. For example, *Ircinia strobilina*, *I. felix* or *Callyspongia aculeata* are sponges with a wide distribution, also are generalist sponges in terms of hosted guest species. Isolated, each one of these three sponges can host up to 46 guest species of the five registered Phyla, like Arthropoda: *Synalpheus townsendi* Coutière, 1909, *S. fritzmulleri* Coutière, 1909 and *Colomastix heardi* LeCroy, 1995; Annelida: *Haplosyllis spongicola* (Grube, 1855) and *Loimia medusa* (Savigny, 1822); Chordata: *Elacatinus xanthiprora* (Böhlke & Robins, 1968); Mollusca: *Isognomon bicolor* (C. B. Adams, 1845); Echinodermata: *Ophiothrix (Ophiothrix) oerstedii* Lütken, 1856; Cnidaria: *Umimayanthus parasiticus* (Duchassaing de Fonbressin & Michelotti, 1860); and together these sponge concentrates 187 guest species of the 745 recorded host guest-interactions (25% of the recorded interactions). According to this relationship sponges with less geographic accumulated area like, *Aplysina bathyphila*, *Niphates erecta* and *I. ramosa* had a lower

contribution to the network organization, interacting with fewer guest species and showing a tendency to associate with guests like, *S. townsendi* and *H. spongicola* that are capable of colonizing a diverse array of sponge species. This relationship creates the situation where a sponge host already present in the network can increase the probability of interacting with a potential guest species if this sponge increases their geographical distribution, leading to a cascade effect between sponges' availability and potential guest diversity in tropical Atlantic coral reefs. However, it is important to note that there is a group of sponges with a low accumulated area and few occurrence records, but their geographical distribution covers both the Caribbean and the Gulf of Mexico reefs. For example, *Agelas dispar* Duchassaing & Michelotti, 1864, *Aplysina lacunosa* (Lamarck, 1814), *Ircinia campana* (Lamarck, 1814) and *Dragmacidon lunaecharta* (Ridley & Dendy, 1886). This feature could indicate that these sponge species are difficult to detect or identify to species level in the field or that they have low abundances in the different reef systems they inhabit. A variable that could be explored in the future is the paired-wise distance between records of sponges of the same species and analyzing if the sum of these distances is related to the structural importance of each sponge species.

In the same way, sponges provide a complex living space for a large number of species from many taxa (Renard et al., 2013; Pérez-Botello & Simões, 2021). Most sponge associated fauna live inside the sponge whether using the canals, oscula, or pores of the sponges (Westinga & Hoetjes, 1981; Koukouras et al., 1996; Hultgren & Duffy, 2010). This fact generates that the interactions between sponges host and their guest species can be influenced by a particular sponges morphological features. Our results indicate that certain sponge functional morphotypes have an effect on the organization of the host-guest interaction networks. Specifically, we found that Cup-like and Massive functional morphologies, frequently are more important in the network organization than Erect and Crust-like functional morphotypes. Cup-like sponges have concave upper surface and can efficiently separate their in- and exhalant openings (Renard et al., 2013; Schönberg, 2021). This functional morphology commonly has a roughly cylindrical (tubes and barrels) or inverted-cone symmetry (cups) with a larger internal volume and wide tube oscula (entrance) and, if multiple Cup-like structures aggregates in a group of a single individual sponge, the sponge heterogeneity enhances (Schönberg, 2021). In addition, massive sponges are very roughly as wide as high; in many cases, this functional morphology has a unified body mass comprised of fused subunits, resulting in the formation of interconnected small cavities and microcompartments (Schönberg, 2021) Also, massive sponges are characterized by its remarkable robustness, making them capable of providing a stable habitat compared to other functional morphologies (Bell & Barnes, 2000; Schönberg, 2021). In contrast with these two volumetric and tridimensional complex functional morphologies Crust-like shapes combine encrusting and creeping sponges, resulting in a low-profile body shape that extends parallel to the substrate; this morpho have a larger surface area compared to their height, and lack three-dimensional or vertical structures (Schönberg, 2021). On the other hand, erect sponges have a small attachment area and are positioned away from the substrate, they exhibit a predominantly vertical orientation, minimizing their horizontal surface areas (Schönberg, 2021). Their vertical



orientation and small attachment area make them susceptible to fragmentation, detachment, and removal by strong flow, waves, or storm surges (Wulff, 1995; Schönberg, 2021). This process could generate an unstable and dynamic habitat, despite the high sponge survival rate after fragmentation (Wulff, 1985, 1995, 1997, 2006).

Additionally, the abundance and species richness of sponge associated fauna could be regulated by three main morphological features. Firstly, sponges total volume. The number of sponges-inhabiting taxa is logarithmically related to sponge volume; larger sponges provide more substrate and resources for the colonization of different species, resulting in higher sponge-associated diversity (Westinga & Hoetjes, 1981). Secondly, the internal volume and diameter of the sponge's canals. The shape and size of the sponge inner canals can physically limit the size of organisms that can inhabit the sponge's interior; sponges with narrow canals provide suitable refuge for smaller organisms, while larger organisms are constrained by the reduced size and volume of the canals (Koukouras et al., 1996; Hultgren & Duffy, 2010). Lastly, the morphological heterogeneity of the sponge, including number of tubes, sponge surface, sponge total volume and sponge area, creates a complex and heterogeneous habitat that facilitate the colonization of different guest species (Pérez-Botello, 2019). As a result, it is the combination of these morphological features that makes Cup-Like and Massive sponges more significant in network organization and have a more diverse community of associated guests compared to Crust and Erect sponges.

In parallel, at sponge species level, it is very likely that the physical restrictions of each sponge species are promoting or limiting the diversity of the host-guest interactions. For example, volumetric and complex sponges like *Callyspongia aculeata*, *C. fallax* and *Ap. fistularis*, can establish a host-guest interaction with both small guest like *Leucothoe spinicarpa* (Abildgaard, 1789), *Colomastix irciniae* LeCroy, 1995 or *Ophiactis quinqueradia* Ljungman, 1872, that usually lives associated to the sponge surface and pores (Carrera-Parra & Vargas-Hernández, 1997; Crowe & Thomas, 2002; Winfield & Ortiz, 2010) and larger guest like *Synalpheus hemphilli* Coutière, 1909, *S. townsendi* or *Pagurus brevidactylus* (Stimpson, 1859) typically founded in the sponges canals (Christoffersen, 1979; Dardeau, 1981, 1984; Carrera-Parra & Vargas-Hernández, 1997; Ugalde García, 2014). In contrast restricted and spaceless morphologies, like the encrusting sponges *Petrosia (Petrosia) weinbergi* van Soest, 1980 or *Cliona celata* Grant, 1826 could mechanically limited the size range of potential guest species inhabiting the internal sponge cavities.

Furthermore, sponge morphology and guest behavior could regulate the diversity of observed interactions. Sponges with more complex, convoluted tube systems, such as *C. aculeata* and *Aiolochoira crassa* (Hyatt, 1875), tend to host more guest species than massive sponges with interconnected channels. For example, sponge species such as *Hyattella intestinalis* (Lamarck, 1814) are colonized only by *Synalpheus* species. These Crustaceans are extremely territorial, and some have a eusocial behavior like *S. regalis* defending the host sponge against other organisms (Duffy, 1996; Duffy & Macdonald, 1999; Duffy, Morrison & Macdonald, 2002). Probably the territorial behavior of certain guest species pushing another potential guest out of the sponge. The effect of this behavior

could be reduced in sponge species with a system of tubes that allow different degrees of segmentation of the internal sponge volume.

Finally, the taxonomic bias analysis revealed a no significant impact in the organization of the sponge host-guest interaction network. This result suggests that, at least at the sponges' order level, the relationship between sponges' order and host-guest network organization is primarily regulated by the sponge-accumulated geographic area and the functional sponge morphology and, to a minor degree, by evolutionary processes. This pattern implies that the sponges host-guest interactions depend not only on sponge taxonomic classification but also on the functional roles and specific adaptations each sponge-host and associated-guest species develops. While this analysis revealed no statistically significant relationship at sponges' order level, it remains plausible that certain guest species may exhibit specific associations with particular sponges. For instance, the annelid *H. aphysinicola* Lattig & Martin, 2011 was observed to exclusively interact with sponges belonging to the *Aplysina* genera, being a specialized host-guest interaction.

## CONCLUSIONS

One of the main findings of our study is the positive relationship between accumulated geographic area and network organization. These results provide valuable information to the theory of ecological interaction networks in a marine environment. This research further enhances our understanding of how geographical distribution influences the diversity and complexity of host-guest interactions. We further demonstrate that as the accumulated geographic area of sponge hosts increases, so does the potential for interactions with a wide range of guest species. This effect highlights the significance of sponge availability in promoting guest diversity in Tropical Atlantic coral reefs.

Also, our study demonstrates the crucial role of sponge functional morphologies in the organization of host-guest interaction networks. Cup-like and Massive morphologies exhibit greater importance in network organization compared to Crust-like and Erect morphotypes. Cup-like sponges, with their volumetric canals, and the potential to generate three-dimensional complexity, provide diverse living spaces. Massive sponges, characterized by their robust structures and interconnected small cavities, offer a stable habitat for guest species colonization. In contrast, Crust-like with their low-profile body shapes and erect sponges with vertical orientations, implies space limitations and potential instability due to fragmentation and detachment.

Importantly, our research demonstrates that taxonomic classification has not significantly influenced the organization of host-guest interaction networks. Instead, the ecological patterns observed in these networks are primarily shaped by accumulated geographic area, and functional morphology. This highlights the need to consider the functional traits and characteristics of sponge hosts and their associated guest species in ecological studies.

Finally with this research, we generate a comprehensive understanding of the regional structure generated in the network of host-guest interactions of reef sponges. Being able to detect emerging patterns and keystone species within that network. Sponges such as *Ircinia strobilina*, *I. felix*, *Callyspongia aculeata*, and *C. fallax* were crucial in maintaining the



network organization. The potential extinction of one or several of these species, or even a slight decrease in their presence within NWT coral reefs, could trigger cascading losses in abundance and diversity of their associated fauna.

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### Competing Interests

The authors declare that they have no competing interests.

### Author Contributions

- Antar Mijail Pérez-Botello conceived and designed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- Wesley Dáttilo conceived and designed the experiments, analyzed the data, authored or reviewed drafts of the article, and approved the final draft.

- Nuno Simões conceived and designed the experiments, authored or reviewed drafts of the article, and approved the final draft.

### Data Availability

The following information was supplied regarding data availability:

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### Artículo 3: (en revisión) *A multi-scale analysis of $\alpha$ -diversity and $\beta$ -diversity spatial variability on living islands*

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## Resumen

Las esponjas pueden ser especies clave en la estructura comunitaria de los arrecifes de coral tropicales. De agosto de 2016 a septiembre de 2019 se muestrearon ocho sistemas arrecifales a lo largo de los límites oceánicos de la Plataforma Continental de Yucatán en el Golfo de México. El objetivo de esta investigación fue analizar la diversidad  $\alpha$  y  $\beta$  de la comunidad asociada a la esponja tubular *Callyspongia aculeata* (como modelo experimental) a lo largo de tres escalas espaciales: ecosistema, hábitat y microhábitat. Nuestros resultados revelaron patrones complementarios entre la diversidad  $\alpha$  y  $\beta$  en diferentes escalas espaciales. A nivel del ecosistema, la diversidad- $\alpha$  de la comunidad asociada a *C. aculeata* no mostró correlaciones significativas con atributos del arrecife, como el perfil del arrecife, el sistema de arrecifes, la cobertura de coral y la posición longitudinal del arrecife. Además, no se encontraron diferencias sustanciales entre la diversidad- $\alpha$  ecosistémica y los puntos de muestreo, la distancia entre esponjas y la profundidad de las esponjas (escala hábitat). Sin embargo, a nivel de microhábitat, existe una relación positiva entre la diversidad  $\alpha$  de los huéspedes de las esponjas y la complejidad de las esponjas, lo que sugiere que el aumento de la complejidad estructural de las esponjas incrementa la posibilidad de albergar una mayor riqueza de especies. De manera complementaria al analizar la diversidad  $\beta$ , el recambio de especies entre los ocho sistemas arrecifales de la Plataforma Continental de Yucatán fue el factor principal que explica la mayor diversidad  $\beta$  a nivel ecosistémico. Los factores locales regularon los cambios a nivel del hábitat, sin embargo, ni la profundidad de las esponjas y ni la distancia entre esponjas fueron significativas. A nivel de microhábitat, la complejidad de las esponjas fue el principal impulsor del reemplazo de especies entre las esponjas muestreadas en sitios de arrecifes específicos. Nuestros resultados demuestran que la comunidad de especies huéspedes es un factor regulado por la escala espacial de análisis. Por ende, los patrones observados en fauna asociada a *C. aculeata* está condicionada por la dispersión de las especies huéspedes y la heterogeneidad ambiental en términos espaciales.



# Sponge dwelling fauna: A multi-scale analysis of $\alpha$ and $\beta$ diversity spatial variability on living islands

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## Abstract

This research aimed to analyze  $\alpha$  and  $\beta$  species diversity of fauna dwelling in the sponge *Callyspongia aculeata* at three nesting spatial scales: ecosystem, habitat, and micro-habitat. Macroinvertebrates dwelling in sponges were collected by intermittent sampling from August 2016 to September 2019 across eight reef systems along the oceanic boundaries of the Yucatán Continental Shelf in the Gulf of Mexico. Findings revealed a complementary pattern between  $\alpha$ - and  $\beta$ -diversity across scales. At ecosystem level,  $\alpha$ -diversity of the sponge-dwelling fauna showed no significant correlations with reef profile, reef system, coral coverage, or geographical longitude. At habitat level, no significant differences in  $\alpha$ -diversity were found between sample point, inter-sponge distances, or sponge depths. However, at the individual level,  $\alpha$ -diversity of the guest fauna was positively related to heterogeneity of sponge morphology; hence, variability in sponge morphology enhances species richness. Regarding  $\beta$ -diversity at the ecosystem scale, variability among reef systems within the Yucatán Continental Shelf was the primary factor that explained the observed changes in the guest fauna, primarily due to a non-directional species variation between reef systems. At the habitat scale,  $\beta$ -diversity was significantly influenced by site identity but not by sponge depth or inter-sponge distances; some of the changes appear to have been regulated by habitat factors yet unrecognised. At the micro-habitat scale, sponge morphological variability was the main driver of species variability and species turnover among sampled sponges at specific reef sites. In conclusion, the  $\alpha$ - and  $\beta$ -diversity patterns of these sponge-dwelling fauna depend on the spatial scale, influenced by ecosystem features, the dispersal capability of the sponge-dwelling species, and habitat/micro-habitat heterogeneity.

## Introduction

Species diversity has two main components,  $\alpha$ - and  $\beta$ -diversity, and these are strongly related to the spatial extent analyzed (Karkarey et al., 2022):  $\alpha$ -diversity characterizes the abundance and number of species or traits within communities, describing a static condition;  $\beta$ -diversity characterizes the variation in number of species or species composition between communities across spatial units, thereby describing a dynamic condition (Karkarey et al., 2022). The influence of ecological processes on species diversity must be better understood if management and conservation measures are to be effective (Karkarey et al., 2022; Levin, 1992; Socolar et al., 2016; Zintzen et al., 2017).

In marine environments,  $\alpha$ -diversity tends to increase with increasing area and heterogeneity of the habitat (Gray, 2001; Jordán-Dahlgren, 2002); however,  $\beta$ -diversity analysis suggests that this relationship is less clear when species replacement at various spatial scales is incorporated (Qian and Ricklefs 2007; Soininen et al. 2007; Anderson et al. 2013), particularly in modular organisms, such as corals and sponges, that harbor guest fauna.

Sponges contribute to coral reef ecosystems through multiple functions including water filtration, primary production, and participation in nutrient cycles (Bell, 2008). They can support diverse marine life forms including complex invertebrates, supplying their in-dwelling fauna with an ongoing stream of water with dissolved and particulate matter, including phytoplankton, organic and inorganic debris, and even sponge tissue (Corredor et al., 1988; García-Hernández et al., 2019; Pawlik, 1983). These conditions generate a microcosmos with well-defined boundaries (Uriz et al., 1992) that can be thought of as a 'living island' (Villamizar & Laughlin, 1991), several levels of interactions between the sponge host and the guest community take place simultaneously, frequently related with the aquiferous system of the sponge and its morphological variability (García-Hernández et al., 2019; Koukouras et al., 1996). Hence, reef sponges can be thought of as ecosystem engineers (Jones et al., 1994; Maldonado et al., 2016; Reyes-Bonilla & Jordán-Dahlgren, 2017).

The present study analyzes at three spatially nested scales the  $\alpha$ - and  $\beta$ -diversity of macroinvertebrates dwelling in the coral-reef sponge, *Callyspongia (Cladochalina) aculeata* (Linnaeus, 1759), from coral reefs. Across its geographical distribution from the Bahamas to

Trinidad and Tobago, this sponge could host at least 65 animal species (Pérez-Botello and Simões 2021). Its distinct tubular or elongate-tubular morphology, with a clearly demarcated boundary between its internal and external spaces, facilitates quantitative studies of its guest fauna.

The aims of our study were: (1) to analyze  $\alpha$ - and  $\beta$ -diversity of sponge-dwelling fauna across three spatial scales, and (2) to partition the variation of  $\beta$ -diversity across these spatial scales by determining the differences in taxonomic composition between communities of sponge-dwelling fauna. The hypothesis was that the  $\alpha$ -diversity and  $\beta$ -diversity measures of sponge-dwelling fauna are shaped by the contrasts between coral reefs, between local habitats within coral reefs, and between micro-habitats within each host sponge.

## **Materials and methods**

### STUDY AREA AND BIOLOGICAL MODEL

The Yucatán Continental Shelf is a heterogeneous and dynamic marine region at the eastern border of the Southern Gulf of Mexico ecoregion (Paz-Ríos et al., 2021; Spalding et al., 2007; Wilkinson et al., 2009). It is a broad platform characterized by carbonate substrates, with a shift to terrigenous sediments on its western part (Paz-Ríos et al., 2021; Tunnell et al., 2007). The main coral reef ecosystems are remotes and are on the outer shelf, at 130 to 200 km from the mainland (Tunnell et al., 2007); there, the Loop Current separates from the Gulf of Mexico and the Caribbean Sea, connecting water masses between the Atlantic and the Gulf's interior, and generates an upwelling at Cape Catoche, at the southeastern Gulf of Mexico (Sanvicente-Añorve et al. 2014, 2018a; Lara-Hernández et al. 2019). This dynamic creates seasonal cyclonic and anticyclonic eddies over the inner shelf (Sanvicente-Añorve et al. 2018a). The connectivity patterns in this region have seasonal variations and differ between the western part and the northeastern edge of the shelf (Sanvicente-Añorve et al. 2014). On the western shelf, connectivity flows northward from March to August and southward from September to February and maintains an almost unidirectional connectivity through the influence of the cyclonic eddies in the Campeche Bay (Sanvicente-Añorve et al. 2014). In contrast, the northeastern edge maintains a northeastern connection throughout October to December (Fernández et al. 2013; Sanvicente-Añorve et al. 2014).



Sponges (*Callyspongia aculeata*) and their guest fauna were collected intermittently between August 2016 and September 2019 from the main coral reef ecosystems on the outer shelf (Figure 1), namely Cayo Arcas, Cayo Arenas, Triangulos, Obispos, Banco Nuevo, Banco Pera, Alacranes reef, and Bajos del Norte (Supplementary 1).

## BIOLOGICAL SURVEY

We employed a sampling framework structured across three distinct spatial scales, which were nested hierarchically: a) ecosystem (*i.e. the reef systems sampled on the Yucatán Continental Shelf*), b) habitat (*i.e. the selected reef system sampling site*), and c) micro-habitat (*i.e. the sampled sponge*). The 146 sponges collected in the shallow reef subtidal zone (<25 m depth) came from the reef systems as follows: Cayo Arcas 28 sponges, Cayo Arenas 15, Triangulos 26, Obispos 17, Cayo Nuevo 8, Banco Pera 7, Arrecife Alacranes 26, Bajos del Norte 19. Each individual sponge was regarded as a discrete unit of observation (sample).

In the field, we compiled a preliminary overview of the morphospecies of the sponge-dwelling macroinvertebrates. These were subsequently identified in the laboratory to the lowest possible taxonomic level with the assistance of appropriate regional specialists and then checked against the World Register of Marine Species (WoRMS) Taxon Match Tool (WoRMS Editorial Board, 2023) (Supplementary 2).

The collected sponges have been deposited at the *Unidad Multidisciplinaria de Docencia e Investigación – Sisal* (UMDI-Sisal), and the associated fauna is held at the *Colección de Crustáceos de Yucatán* (YUC-CC) and the *Colección Regional de Equinodermos de la Península de Yucatán* (COREPY). These collections are held at the UMDI-Sisal facilities of the Mexican National University (UNAM).

Field collections were approved by the Mexican Department of Agriculture and Fisheries (SAGARPA), with permit numbers PPF/DGOPA-093/16 for sponges (Porifera: Demospongiae), PPF/DGOPA-066/16 for crustaceans (Arthropoda: Crustacea) and PPF/DGOPA-082/19 for echinoderms (Echinodermata).

## SAMPLE SIZE

An appropriate sampling effort was determined by using the 'SSP' library (Guerra-Castro et al., 2021) in R-project software. It compared the values of dissimilarity-based multivariate standard error (*MultSE*) obtained when data matrices were simulated to mimic the communities found in an in-field pilot survey. The pilot survey, in August 2016 at seven sites in Cayo Arcas reef, selected 26 sponges. The simulation revealed an optimal reduction of standard error between 7 and 11 sites per ecosystem, and an optimal sample effort per ecosystem of 7 to 10 sponges (Supplementary 3).

## SAMPLE DATA DISPERSION

As we had an unbalanced survey and to ensure the reliability of our dataset, the homogeneity of multivariate dispersions across these eight reef systems was evaluated by PERMDISP analysis (Anderson, 2006) using PRIMER v7 (Clarke & Gorley, 2015). There were no significant differences (*pseudo-F*= 1.22; *P* = 0.45), suggesting that our dataset is comparable for subsequent analyses.

## SPATIAL SOURCES OF VARIATION

Spatial data were compiled from databases, from measurements *in situ*, and from laboratory analyses.

*Ecosystem scale.* We quantified differences in  $\alpha$ -diversity and  $\beta$ -diversity of the fauna dwelling in *C. aculeata* in terms of reef system, coral coverage area, reef profile, and longitudinal position. For  $\alpha$ -diversity, we tested the relationship of species-with coral cover and the longitudinal gradient. We expect on one hand a positive correlation between the species richness in sponge-dwelling fauna and the coral coverage area (MacArthur and Wilson 1963; Losos et al. 2009), and on the other hand, a higher species richness in sponge-dwelling fauna at the eastern reef systems, as suggested for YCS coral reef species (Jordán-Dahlgren 2002; OBIS 2020). Regarding the  $\beta$ -diversity, we tested the null hypothesis that the sponge-dwelling fauna would be the same regardless of reef system identity, coral coverage area based on the coralline shape layer (Allen Coral Atlas 2022), reef profile classified into platform, atoll, or submerged keys (Jordán-Dahlgren & Rodríguez-Martínez, 2003), and geographical longitude.

*Habitat scale.* Effects on  $\alpha$ -diversity and  $\beta$ -diversity were quantified according to sample identity, inter-sponge distance, and depth of the host sponge. Inter-sponge distance was derived from the inverse of the sponge density at that site, as estimated from underwater video transects (UVTs): a 50 m line was laid out at each site and a diver positioned the camera perpendicular to the line to obtain a frame 0.6 m wide; this covered  $\sim 30\text{m}^2$  per transect (Aronson et al., 1994; Garza Pérez et al., 2010; Ninio et al., 2003). A total Of the 54 transects, Cayo Arcas had 12, Cayo Arenas 11, Triangulos 9, Obispos 8, Cayo Nuevo 2, Banco Pera 2, Alacranes 8, and Bajos del Norte 2. Each was parallel to the coastline to minimize changes in depth along the transect. Sponge depth was recorded on a dive computer at the time of sampling.

*Micro-habitat scale.* We quantified effects of sponge morphology on  $\alpha$ -diversity and  $\beta$ -diversity of the guest fauna. The characteristics used were covered area, surround volume, sponge volume, sponge surface area, and number of tubes. We tested whether the morphological variability of sponges (as an indicator of micro-habitat heterogeneity) regulates small-scale variability in the guest community. With the concept of a sponge as a living island, we predicted that a more homogeneous sponge would host a faunal community with lower  $\alpha$ -diversity and lower  $\beta$ -diversity.

To generate a three-dimensional model for each sponge, its height and width were measured and its tubes counted. Then the sponge was placed on a rotating motor that produced a  $360^\circ$  photographic imaging, and thence a digital record of each sponge. Each photographic dataset of 200 images was processed with 3DF Zephyr software (<https://www.3dflow.net>) to generate a 3D sponge model, which was scaled according to the height and width measurements. This allowed the use of Autodesk 3ds Max (<https://www.autodesk.mx/>) to calculate the area of substratum covered, the volume surrounding the sponge, sponge volume itself, and sponge surface area (Figure 2).

Measurements in different numeric scales ( $\text{cm}^2$  and  $\text{cm}^3$ ) were normalized. Then to reduce the multi-dimensional profile of a sponge to a synthetic heterogeneity index incorporating the individual variability of five characteristics, we performed a principal components ordination (PCO) to represent by means of the first principal component (PCO1) a heterogeneity index; this accounted for 89.7% of the morphological variability (Supplementary 4). Since the values obtained from PCO1 are both positive and negative, we changed the point of origin to zero.

## DIFFERENCES IN SPECIES RICHNESS AND SPECIES COMPOSITION

For  $\alpha$ -diversity of the sponge-dwelling fauna a Mixed Linear Model compared across the ecosystem, habitat, and micro-habitat scales, nesting the sample point in the reef system and nesting the reef system in the reef profile; we used as covariables the 'sample point longitude', 'reef coverage area', 'sponge depth', 'sponge density at the sample point' and 'sponge morphological variability'. All  $\alpha$ -diversity analyses used the 'lme4' library (Bates et al., 2015) in R-project software.

For  $\beta$ -diversity, we generated a pairwise dissimilarity resemblances matrix using a Bray-Curtis geometrical space among sampled sponges. This matrix led to a linear model based on permutational multivariate analysis of variance (PERMANOVA, Anderson 2017), nesting the 'sampled reef' (random factor) in the 'reef profile' (fixed factor), then the 'sample point' (random factor) in the 'sampled reef' and using as covariables the 'sample point longitude', 'reef coverage area', 'sponge depth', 'sponge density at the sample point' and 'sponge morphological variability'. We used a Type I (sequential) sum of squares and 9999 permutations. Also, we tested changes on  $\beta$ -diversity by factor levels of source of variations and quantified the proportion of variance by source of variation, measured with the square root of the coefficient of variation (Anderson, 2001, 2017; Anderson et al., 2011). All  $\beta$ -diversity analyses used PRIMER v7 software (Clarke & Gorley, 2015).

To analyze the differences in  $\beta$ -diversity across the three spatial scales, a metric Multi-Dimensional Scaling (mMDS) used the Bray-Curtis similarity index for each spatial scale: among sponges, among centroids of the different sample sites, and among centroids of the different reef systems.

## Results

### VARIATION IN $\alpha$ -DIVERSITY AND $\beta$ -DIVERSITY ACROSS SPATIAL SCALES

Spatial variation in  $\alpha$ -diversity (within-sample diversity) of sponge-dwelling macrofauna across ecosystem, habitat, and micro-habitat scales showed a notable homogeneity within each spatial scale (Table 1). At the ecosystem scale (figure 3), there was no significant association between  $\alpha$ -diversity and reef profile (LRT = 0.0187;  $p$  = 0.89134), reef identity (LRT = 3.3229;  $p$  = 0.06832), coral-reef coverage area (t-value = -1.095;  $p$  = 0.353), or reef longitudinal



location (t-value = 1.102;  $p = 0.337$ ). Likewise, at the habitat scale (figure 4), there was no significant association between  $\alpha$ -diversity and sample identity (LRT = 0.1713;  $p = 0.67892$ ), inter-sponge distance (t-value = 1.269;  $p = 0.212$ ), or sponge depth (t-value = -0.057;  $p = 0.955$ ). At the micro-habitat scale (figure 5), there was a positive relationship between  $\alpha$ -diversity of the guest fauna and the morphological variability of the sponge (t-value = 5.456;  $p < 0.01$ ); this supported the expectation that a higher morphological variability in sponges would result in a higher  $\alpha$ -diversity of associated species.

On the other hand,  $\beta$ -diversity of the guest communities showed a different trend (table 2). At the ecosystem scale (figure 3)  $\beta$ -diversity (between-reef diversity) was influenced by variation among the reef systems (pseudo-F = 1.873;  $p = 0.028$ ), rather than by reef profile (pseudo-F = 0.693;  $p = 0.831$ ), longitudinal gradient (pseudo-F = 1.364;  $p = 0.215$ ), or species-area relationship (pseudo-F = 0.614;  $p = 0.920$ ). At the habitat scale (figure 4) there were differences between sampled communities (pseudo-F = 1.410;  $p < 0.001$ ), but these showed no relationship to depth (pseudo-F = 1.163;  $p = 0.353$ ) or inter-sponge distances (pseudo-F = 0.810;  $p = 0.662$ ), suggesting that there are other unmeasured variables that could contribute to these differences. At the micro-habitat scale (figure 5), the  $\beta$ -diversity of sponge-dwelling fauna increased with increasing heterogeneity of the sponge host (pseudo-F = 3.000;  $p < 0.006$ ).

## GUEST SPECIES COMPOSITION AND SPATIAL SOURCES OF VARIATION

Found here in the tubular sponge *Callyspongia aculeata* were 76 macroinvertebrate species representing Arthropoda (64 species), Echinodermata (11), and Cnidaria (1). Within Arthropoda, the subphylum Crustacea was dominant, although confined to Malacostraca, except for a non-identified morpho-species that was assigned to Pycnogonida. Within Echinodermata, specimens represented one class (Ophiuroidea) and two orders (Amphilepidida and Ophiacantida). Within the Cnidaria, the one species found belonged to the Parazoanthidae (Anthozoa).

The factors that best explained the observed patterns of the  $\beta$ -diversity of sponge dwelling fauna differed between spatial scales (table 2). At the ecosystem scale,  $\sim 38.87\%$  of the variability was explained by 4 components, the most important being the reef system which explained 15.94% of total variation. At the habitat scale,  $\sim 19.80\%$  of total variation was

explained by 3 local components, with sample point explaining 14.64%. At the micro-habitat scale, 5.10% of the total was explained by variation in sponge morphology. Only 36.24% of the total variation reflected intrinsic differences among the components of the sponge-dwelling communities (residual variation).

## Discussion

While acknowledging dissimilarities in sponge-guest community assemblages between different spatial scales, our principal findings exhibited a complementary pattern between  $\alpha$ -diversity and  $\beta$ -diversity. Specifically, ecosystemic variation in  $\alpha$ -diversity and  $\beta$ -diversity was driven primarily by a difference in species composition between reef systems. At the habitat scale, the diversity indices differed between different parts of a reef but this was not attributable to differences in depth or in the in-between sponge distances. At the micro-habitat scale, both species richness ( $\alpha$ -diversity) and variance in species composition ( $\beta$ -diversity) increased with increasing structural heterogeneity of the host sponges.

### ECOSYSTEM-SCALE COMPONENTS OF SPECIES DIVERSITY

Patterns differed between  $\alpha$ - and  $\beta$ -diversity. Species richness of the macroinvertebrates dwelling in *Callyspongia aculeata* was not influenced by the area of the ecosystem. Nor did it reflect the longitudinal geographic gradient along this study area; hence, these macroinvertebrates did not follow the pattern of reductions in species richness predicted for coral reef species along the path from the Caribbean Sea to the Gulf of Mexico (Jordán-Dahlgren, 2002). Each reef system appeared to maintain a similar number of species irrespective of size of reef or geographical position.

However, the ecosystem-scale  $\beta$ -diversity index showed a clear reef-to-reef variability in composition of these sponge-dwelling communities. In other marine models, at ecosystem scales, a high  $\beta$ -diversity is expected when connectivity between environmental systems is low (Valanko, 2012). The process of emigration will persist, but the immigration of neighboring dominant species will be prioritized over less-dominant species (Matias et al., 2012; Mouquet & Loreau, 2003; Valanko, 2012). At the oceanographic level, over the entire Yucatán Continental Shelf the primary connection pathway occurs in the confluence zone between neritic and oceanic waters on the outer part of the shelf (Sanvicente-Añorve et al., 2014). Coral reefs of the northeastern shelf (Bajos del Norte and Alacranes) have a robust

interconnectivity influenced by atmospheric systems and their associated wind and current changes (Sanvicente-Añorve et al., 2014, 2018), and this could lead to higher self-recruitment in these reefs (Sanvicente-Añorve et al., 2014). These currents generate a sporadic connectivity between these shelf reef systems (Jordán-Dahlgren, 2002).

For benthic organisms, the planktonic larval stage is often the primary, and sometimes exclusive, method of dispersal, with critical implications for species colonization in new regions (Turon et al., 2000; Sanvicente-Añorve et al., 2018). Dispersion capability involves two crucial elements: larval energy supply and settlement strategies (Turon et al. 2000; Kendall et al. 2013); these determine the duration of the pelagic larval stage. Ultimately, planktonic larvae die if they fail to find a habitat suitable for settlement (Bonhomme and Planes 2000; Zapata and Herrón 2002; Lester and Ruttenberg 2005; Shanks 2009; Kendall et al. 2013; Sanvicente-Añorve et al. 2018a). We would expect those species with a longer pelagic larval stage to have an extensive distribution over the shelf, whereas those with a short larval phase or lacking planktonic larvae would be limited to self-recruitment within a single reef system. For instance, the primary community of macroinvertebrates dwelling in *C. aculeata* sponges across all reef systems in this study included *Synalpheus hemphilli*, *S. fritzmulleri*, *Lysmata pedersenii*, *Ophiothrix lineata*, *Ophiactis savignyi*, *Leucothoe kensleyi*, *L. ashleyae*, and *Colomastix tridentata*. Of these, *S. hemphilli* larvae can survive for up to 90 days (Knowlton, 1973), and *Lysmata pedersenii* larvae for 18–160 days and with the capacity to delay settlement through a final molt (Rhyne et al., 2009; Anger, 2001). The dual reproductive strategy of *O. savignyi* (Hendler et al., 1995) contributes to its extensive distribution across the shelf. In contrast, larvae of smaller ophiuroids such as *Ophiactis quinqueradia* may have a briefer pelagic phase and limited dispersal within specific sponge hosts (Mladenov and Emson 1988; Hendler et al. 1995). Amphipods have no larval stage, and this limits their dispersal capacity, although certain species such as *L. kensleyi*, *L. ashleyae*, and *C. tridentata* have a wider distribution, apparently by rafting on sponge fragments (DeBiase et al., 2016). Most amphipod species were limited to one, two, or three reef systems, with specific distributions noted (e.g., *Erichthonius brasiliensis* in Bajos del Norte, Obispos, and Cayo Arenas). Some organisms, such as *O. angulata*, *Periclimenes sandyi*, and *Umimayanthus parasiticus*, have a wider habitat range, not relying exclusively on sponges, and are found across various depths and substrates, including diverse sponge species (Hernández-Díaz et al., 2023; Pérez-Botello & Simões, 2021a; Santana et al., 2017; Ugalde

García, 2014), and this contributes to their widespread distribution among the coral reef systems on the Yucatán Continental Shelf. This study underscores the significance of the relationship between ecosystem processes such as marine currents and biological processes such as the pelagic larval phase of sponge-dwelling species. Only those species capable of synchronizing their reproduction and dispersal with the sporadic reef interconnectivity will have the opportunity to migrate to other reefs. In contrast, organisms unable to achieve synchronization, or having a brief pelagic larval phase, or lacking a larval phase, will be constrained in their distribution.

It is possible that reef-to-reef species homogeneity and species variation are regulated through i) the temporal connectivity of the coral reefs on this shelf and ii) the reproductive and dispersal strategies shown by the sponge-dwelling species themselves. This would result in dissimilarity among the sponge-dwelling communities on the shelf (higher ecosystem  $\beta$ -diversity) but maintaining stable the  $\alpha$ -diversity of the individual communities.

#### HABITAT-SCALE COMPONENTS OF SPECIES DIVERSITY

Although depth and density of sponges contributed 19.70% of the overall variation, neither of these factors was statistically significant. The sampling point itself was a significant influence on species turnover, but there appear to be other, as yet unquantified local variables contributing to an increase of  $\beta$ -diversity. For instance, repetitive attempts to colonize could lead to a cumulative effect of founder and initial colonizer events. Dispersibility tends to decrease after establishment on a new island (i.e., a new sponge), and the distance between sponges may be an impediment, so dispersion from the island may be outweighed by the recurrence of colonization events; these are likely to drive further differentiation among communities within a “sponge archipelago” (Roscher et al., 2014; R. J. Whittaker & Fernández-Palacios, 2007).

Depth can influence both species richness and taxonomic turnover to a degree that depends on the scale of analysis, whether tens, hundreds or thousands of meters (Anderson et al., 2013; Price et al., 1999). In our study, the sampled depth range extended from 1 to 25 m, revealing no distinct pattern in  $\alpha$ - or  $\beta$ -diversity; this suggests that the macroinvertebrates associated with *C. aculeata* show a comparable likelihood of colonizing sponges in both shallow and deeper environments.



The assessment here of sponge density may have oversimplified the true distance between the sponges within the reef, as each sampling site yields a unique sponge density value, from which we assume that sponges will be in closer proximity. It would be more precise to measure the in-field distance between the sampled sponges themselves, to test the effect of this separation between islands on the species diversity of their faunal communities. This could lead to a more realistic model of the diversity dynamics of the reef. Consequently, we propose that future research should measure distances between sampled sponges *in situ*, and if possible, also measure the first colonization effect and the implication that this could have in terms of the repeated founding events that could be happening at this spatial scale.

#### MICRO-HABITAT-SCALE COMPONENTS OF SPECIES DIVERSITY

The results suggested that species richness and species turnover in the guest community were higher in a sponge with a more heterogeneous morphology. In a reef ecosystem, an individual sponge could be considered as a micro-habitat patch available for colonization. At this spatial scale, the sponge-dwelling fauna of a reef can be conceptualized as an assembly of distinct focal communities, where each community corresponds to the fauna found on an individual sponge. Then, the assemblage of sponge-dwelling fauna over the reef can be characterized as a metacommunity, where several species interact across different sponges (Leibold et al., 2004). This perspective can be applied to the relationship between the patterns of diversity variation and the degree of heterogeneity of the sponge morphology. These patterns of diversity can be comprehended within the framework of the 'species-sorting' concept (Leibold et al., 2004), which identifies individual patches, such as distinct sponges in our context, as heterogeneous entities with diverse ecological factors. Consequently, the outcomes of species interactions depend upon specific factors of the environmental gradient that promote a species colonization-extinction dynamic (Leibold et al., 2004). Hence, the degree of heterogeneity in sponge morphology both within and between sponges could be regulating changes in the sponge-dwelling fauna by the change in the colonization-extinction rate of the guest species. This suggests that the greater the heterogeneity of the sponge, the higher the probability that it be colonized by a greater number of species and, in turn, that the more heterogeneous sponges promote the replacement of species within other sponges. Conversely, in smaller and simpler sponges there would be a higher probability that a guest individual would be expelled or unable to settle because of the limited colonizable space, and this would lead to a higher death rate and a lower rate of new colonizers.

## SPATIAL SCALES PARTITIONING ACROSS THE SPONGE-GUEST COMMUNITY

Analysis of community composition within a multi-scale space offers the ability to comprehensively detect and measure the differential contribution of each component of variation in the species turnover system (Anderson, 2017; Legendre et al., 2005). The notable  $\beta$ -diversity in the present study was primarily (38.26%) attributable to a regional-scale community turnover, signifying a pattern of species replacement across the reef systems of the Yucatán Continental Shelf, with a lower contribution of local-scale or individual-scale turnover in the community composition. This implies that, initially, it is essential to have a stock of species within each reef system (regional factors) capable of colonizing each sponge present in a given reef site (local factors). Finally, it is the heterogeneity of each host sponge (individual factors) that regulates whether a new species can successfully colonize it. This implies that successful colonization by these sponge-dwelling communities depends on a stock of their species within each reef system, capable of colonizing each sponge present in a given reef site, and with host sponges of sufficient morphological heterogeneity.

These results demonstrate that the environmental heterogeneity provided by an individual sponge influences the number of species it can host (individual  $\alpha$ -diversity) and also the number of those species in relation to the number of species in communities dwelling in other sponges (individual  $\beta$ -diversity). Hence, the morphology of sponges is one of the key factors regulating the small-scale processes occurring in the associated fauna of reef sponges. When combined with the behavior exhibited by each guest species, and the availability of guest larvae, the result is the community present in each host sponge.

In conclusion, the patterns of sponge-associated  $\beta$ -diversity are a function of scale, which, in turn, reflects the ecosystem features, the dispersal capability of the sponge dwellers and the heterogeneity of the habitat/micro-habitat. Hence, a comprehensive analysis of coral reef species diversity across a broad multi-scale spatial spectrum will facilitate a deeper understanding of how sponges and their associated biota will respond to dynamic impacts and shifting environmental conditions.

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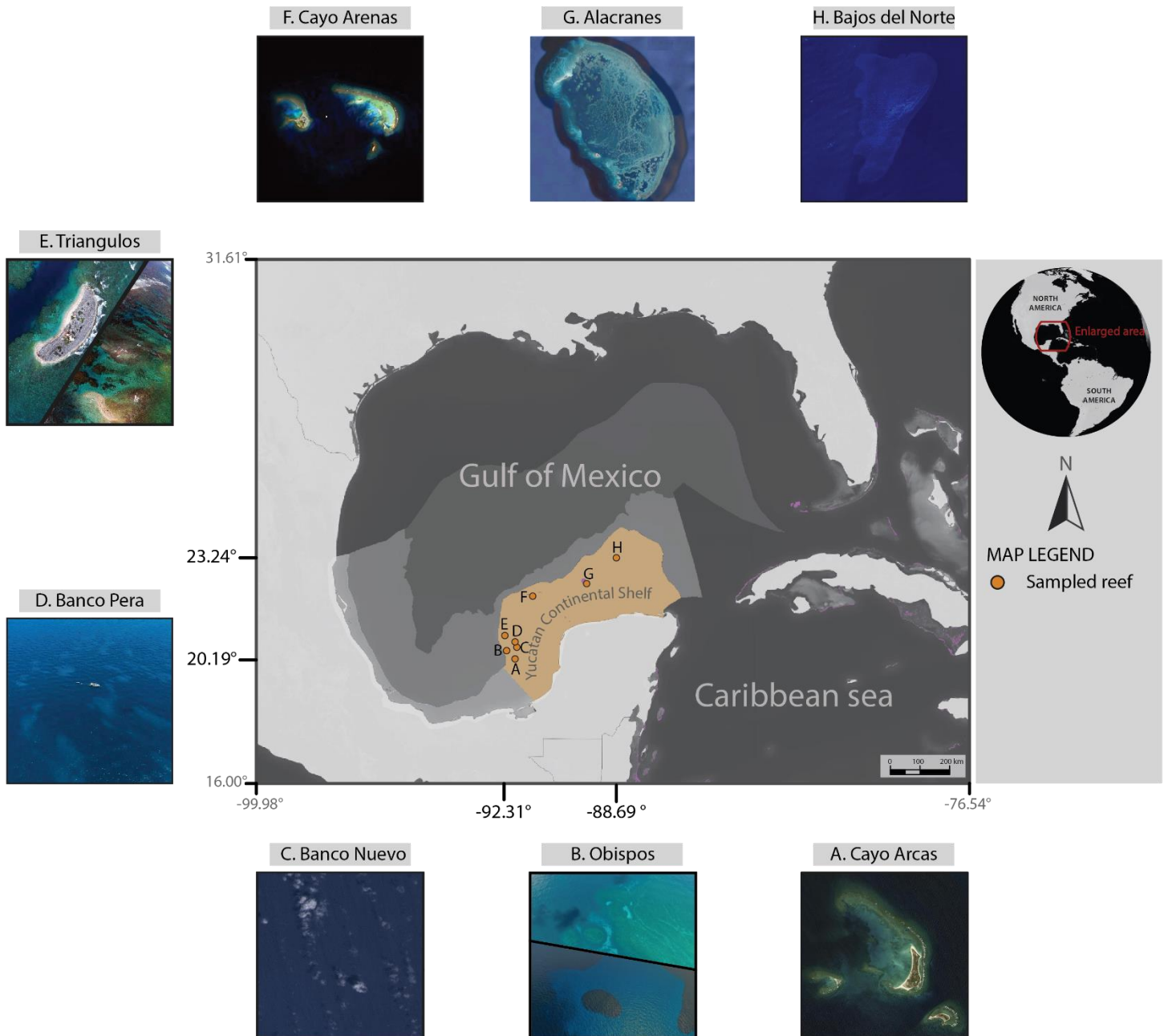
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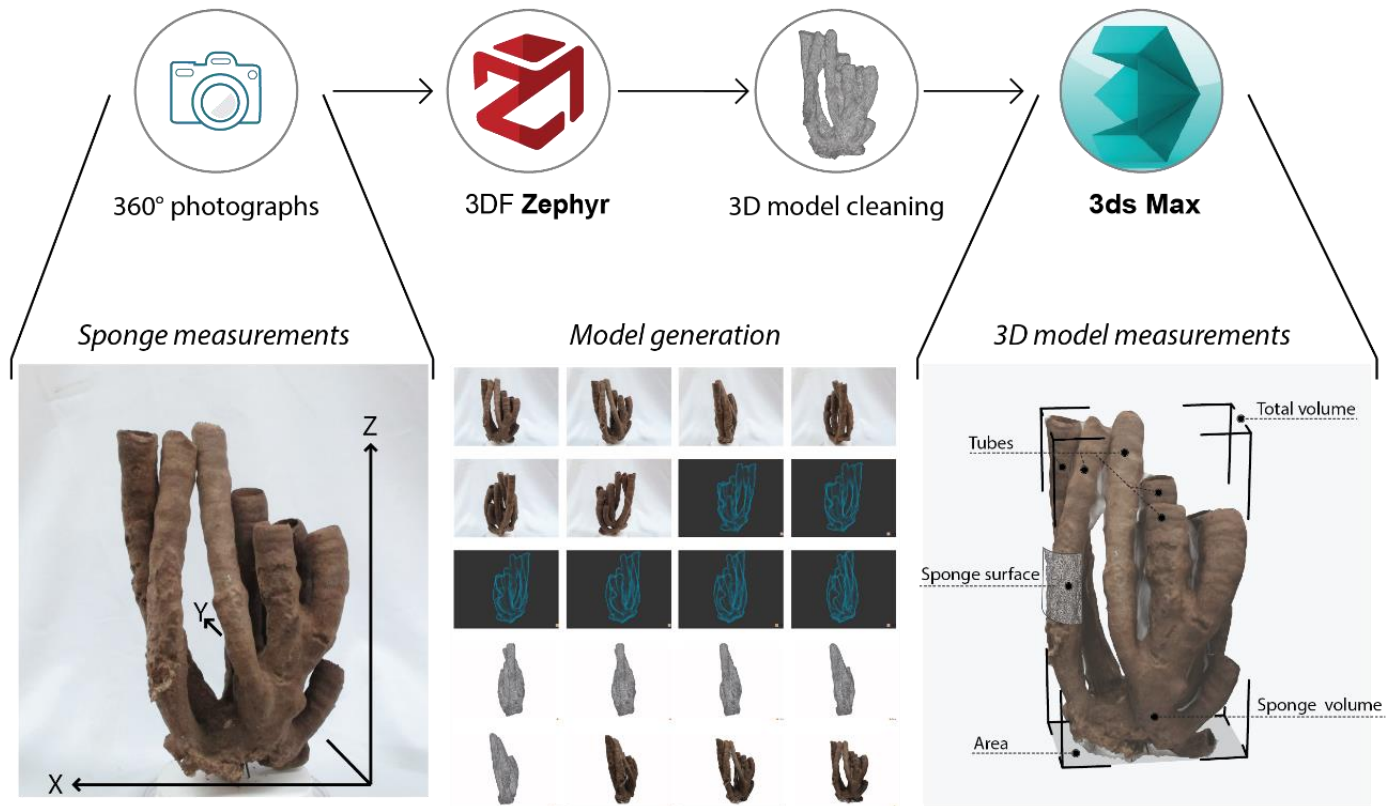
## Figures

**Figure 1. Sampling sites on the Yucatan Continental Shelf.** Reef systems: A, Cayo Arcas; B, Obispos; C, Banco Nuevo; D, Banco Pera; E, Triangulos; F, Cayo Arcas; G, Alacranes; H, Bajos del Norte

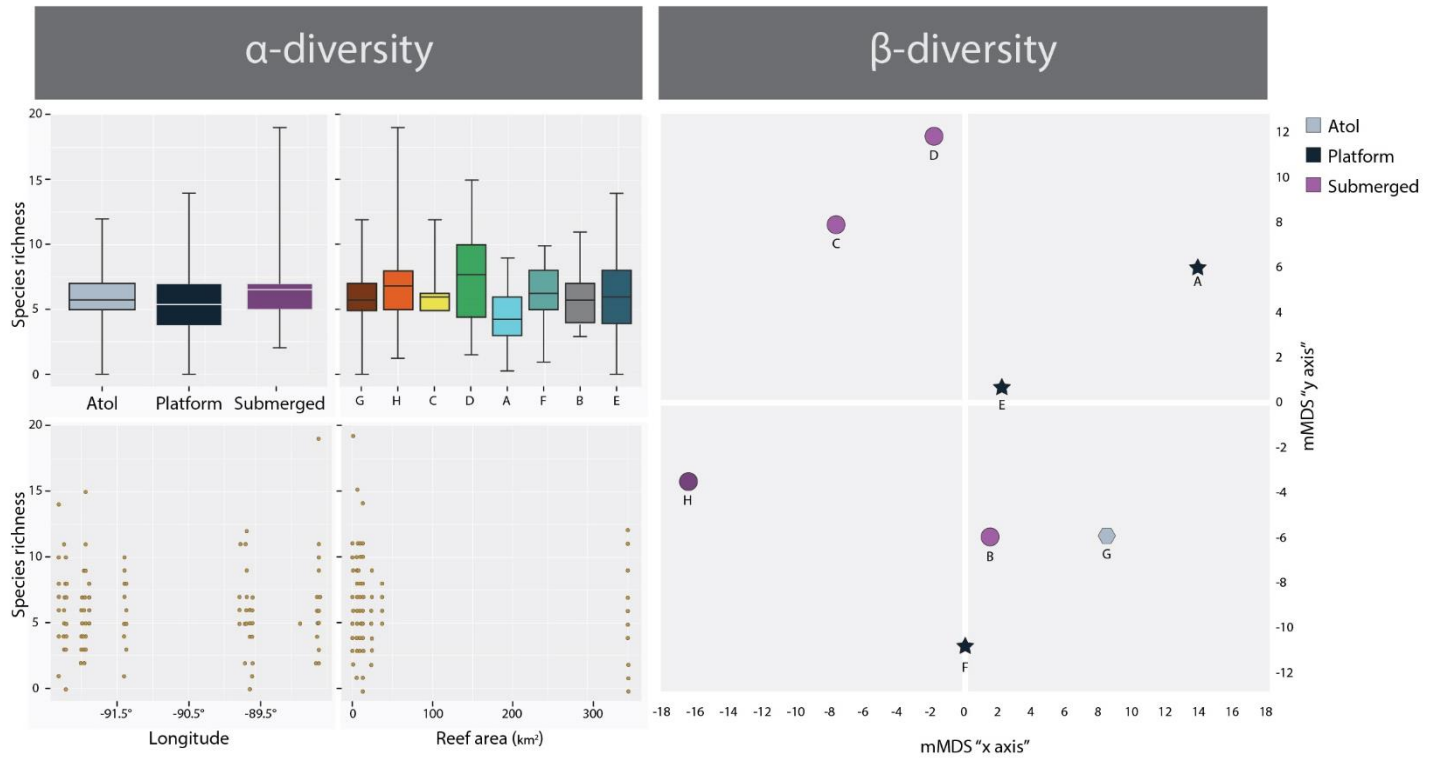




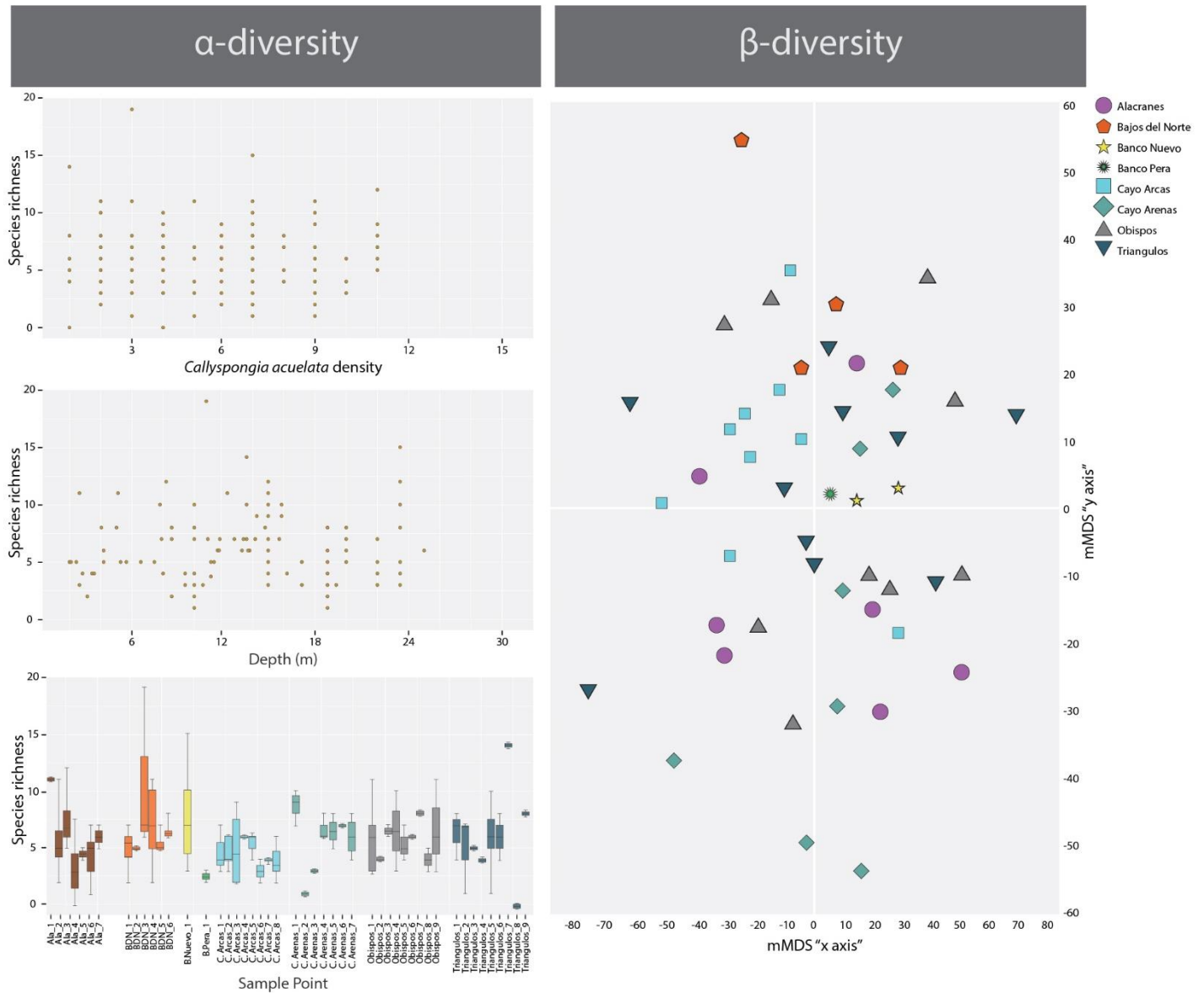
**Figure 2. Digitalization of a sponge morphology.** *Sponge measurements:* the length, width, and height of each sponge were measured, followed by capturing between 230 and 250 photographs from all perspectives of the sponge. *Model generation:* each photo was processed using 3DF Zephyr to generate a digital mesh of each sponge



**Figure 3.** Ecosystem-scale  $\alpha$  and  $\beta$  diversity. Left: relationship between  $\alpha$ -diversity and habitat components; for letters identifying reef systems, see Fig.1. Right: metric MDS showing similarity among reef systems based on the sponge-dwelling fauna. Reef profile: light blue, atoll; dark blue, platform; purple, submerged reef.



**Figure 4. Habitat-scale  $\alpha$  and  $\beta$  diversity.** Left: relationship between  $\alpha$ -diversity and habitat components. Right: metric MDS showing site similarity based on the sponge-dwelling community at each sample point. The colors on both sides of the figure correspond to the reef system identity: purple Alacranes Reef, orange Bajos del Norte, yellow Banco Nuevo, green Banco Pera, light blue Cayo Arcas, light green Cayo Arenas, gray Obispos, and dark blue Triangulos.



**Figure 5. Micro-habitat scale  $\alpha$  and  $\beta$  diversity.** Left relationship between  $\alpha$ -diversity and morphological variability of sponges. Right: mMDS showing similarity of guest communities among sponges. Reef systems: purple Alacranes Reef, orange Bajos del Norte, yellow Banco Nuevo, green Banco Pera, ligh blue Cayo Arcas, ligh green Cayo Arenas, gray Obispos, and dark blue Triangulos.



## Tables

**Table 1.** Mixed Linear Model revealing the significance of both random effects (top) and fixed effects (bottom) as sources of variation in the  $\alpha$ -diversity model.

Random effects								
Groups	Name	Variance	npar	Df	logLik	AIC	LRT	Pr(>Chisq)
Sample Point:(Reef System:Reef Profile)	(Intercept)	0.19	9.00	1.00	-355.58	729.17	0.17	0.68
Reef System:Reef Profile	(Intercept)	0.93	9.00	1.00	-357.16	732.32	3.32	0.07
Reef Profile	(Intercept)	0.11	9.00	1.00	-355.51	729.02	0.02	0.89
Residual		6.52						
Fixed effects								
		Estimate	Std. Error	Df			t value	Pr(> t )
(Intercept)		43.78	34.64	3.71			1.26	0.28
Longitude		0.42	0.38	3.71			1.10	0.34
Reef Area		0.00	0.00	3.02			-1.10	0.35
Depth		0.00	0.06	38.96			-0.06	0.96
Sponges density		0.11	0.09	38.95			1.27	0.21
Complexity		0.30	0.05	133.89			5.46	>0.01*

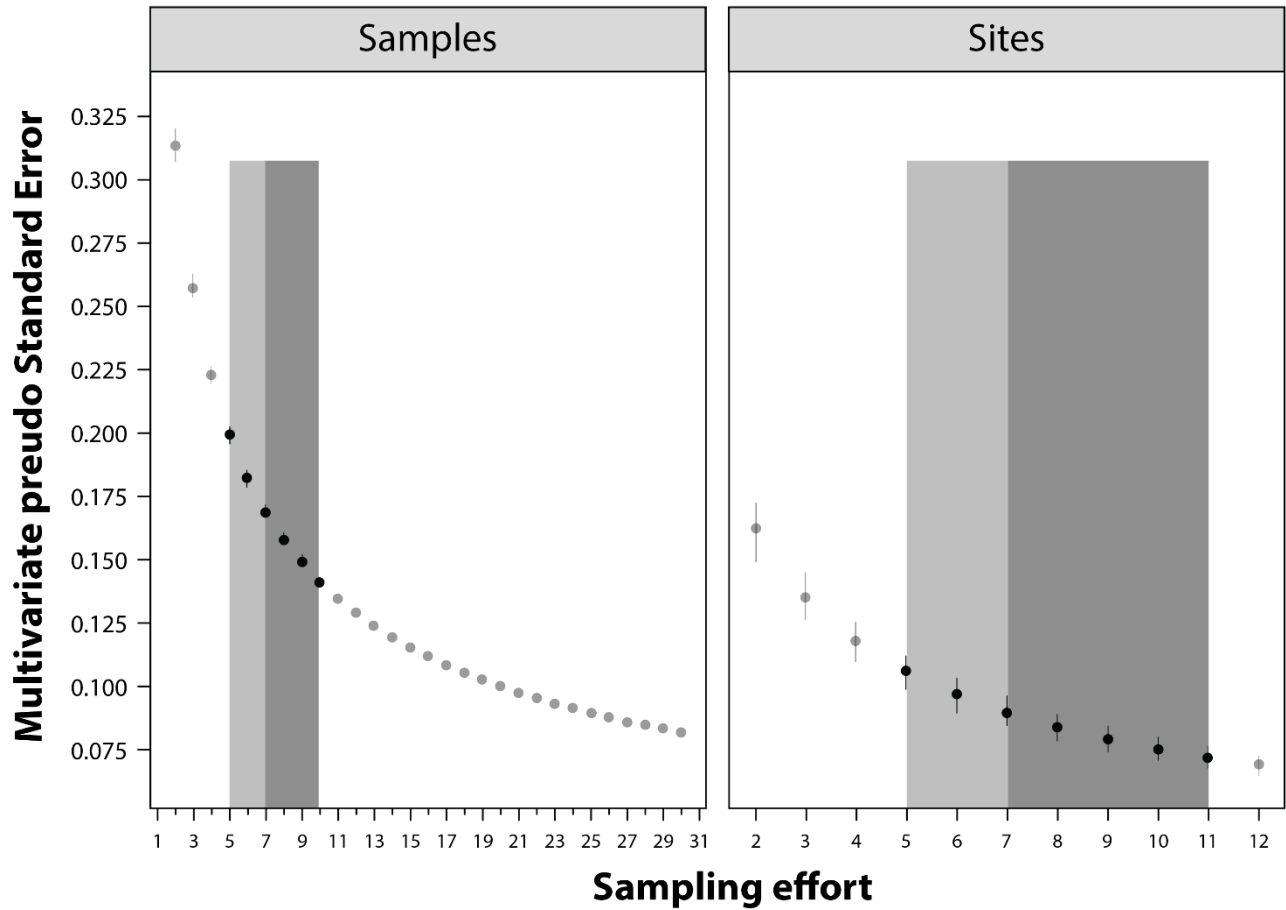


**Table 2.** Sources of variation in sponge-dwelling macroinvertebrate communities, based on the  $\beta$ -diversity model, and percentage contribution of each component to the overall model.

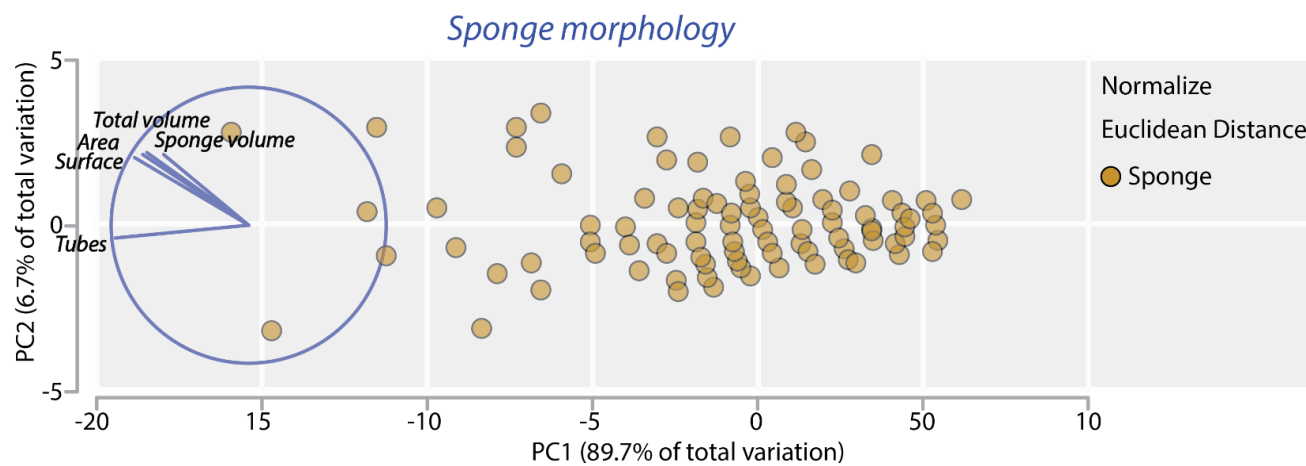
PERMANOVA							Estimates of Components of Variation
Source	Df	SS	MS	Pseudo-F	P(perm)	perms	% of variation
Complexity	1	5564.1	5564.1	3.00	0.01	9931	5.10
Sponges density	1	3514.3	3514.3	0.81	0.66	9929	2.65
Depth	1	5989.5	5989.5	1.16	0.35	9944	2.49
Reef Area	1	3070.0	3070.0	0.61	0.92	9935	6.49
Longitude	1	9730.5	9730.5	1.36	0.22	9921	5.55
Reef Profile	2	7083.1	3541.6	0.69	0.83	9924	10.89
Reef System(Reef Profile)	4	18124.0	4531.0	1.87	0.03	9920	15.94
Sample Point(Reef System(Reef Profile))	39	71181.0	1825.2	1.41	0.00	9746	14.65
Residuals	94	121600.0	1293.6				36.24
Total	144	2.46E+05					

## Supplementary Material

**Supplementary 3.** Sampling effort model based on the Multivariate Standard Error. This simulation shows the optimal range of sample sites and sampled sponges per reef system



**Supplementary 4.** Principal Component Ordination of sponge morphological variables.  
Yellow dot: sampled sponge.



## Discusión

Las esponjas, al igual que otras especies bioconstrutoras, son ingenieros ecosistémicos que generan complejidad ambiental y manteniendo gran parte de la biodiversidad asociada a los ecosistemas que habitan (Jones et al. 1994; Rossi et al. 2017). En esta tesis se ha demostrado que uno de los factores ecológicos que regulan la estructura de la red de interacciones huésped-hospedero es el área geográfica acumulada de las diferentes especies de esponjas. Este factor se puede interpretar como el hábitat disponible para ser colonizado por diferentes especies hospederas. En este sentido la diversidad de especies asociadas a cada esponja tiene un comportamiento similar al patrón ecológico de especies-área (MacArthur & Wilson, 1963; Macarthur & Wilson, 1967), siendo que a mayor área geográfica reportada para cada esponja mayor será la riqueza de especies huéspedes. A la par, la morfología funcional que desarrolla cada especie de esponja también es un factor fundamental en el arreglo de la red de interacciones. Las esponjas con formas funcionales más complejas serán especies seleccionadas por una mayor riqueza de especies hospederas en contraste con formas estructurales sencillas. Por último, estos resultados sugieren que en niveles taxonómicos inferiores no hay una relación taxonómica clara entre los organismos que colonizan esponjas y las esponjas mismas. Con estos análisis se demostró que, a nivel de Orden, las esponjas no presentan un patrón claro de asociaciones. No obstante, es importante resaltar que, si subimos un nivel taxonómico, la Clase Demospongiae fue dominante, siendo prácticamente la única Clase que presentó algún tipo de fauna asociada.

De igual manera, con el análisis multiescalar de diversidad  $\alpha$  y  $\beta$  fue posible evaluar cómo la fauna asociada a *Callyspongia aculeata* es regulada primero por los factores

ecosistémicos del sistema arrecifal, después por las características del hábitat, y por último por las características del microhábitat que proporciona cada esponja. Con estos resultados se demostró que los patrones de diversidad  $\alpha$  y diversidad  $\beta$  presentes en la Plataforma de Yucatán son complementarios. Específicamente, la diversidad de especies a nivel ecosistémico está siendo regulada por la variación comunitaria de la fauna asociada presente en los diferentes sistemas arrecifales. Similar a nivel del hábitat, la variación de la comunidad se da entre los distintos puntos de muestreo. Mientras que, a nivel del microhábitat, la variabilidad en la morfología de cada esponja regula la riqueza de especies presente, así como el recambio de especies asociadas a cada esponja. Estos resultados demuestran que, al menos para la fauna asociada a las esponjas en la Plataforma de Yucatán, existe una regulación descendente, lo que quiere decir que en primer lugar, es necesario tener un conjunto de especies dentro de cada sistema de arrecifes (factores ecosistémicos) que puedan colonizar cada esponja presente en un sitio de arrecife (factores del hábitat) y, en última instancia, es la heterogeneidad de cada esponja anfitriona (factores del microhábitat) la que regula si una nueva especie puede colonizarla.

Similar a los resultados obtenidos en esta tesis se ha observado que la riqueza de fauna asociada a esponjas podría estar siendo regulada por condiciones del hábitat como el nivel de exposición al oleaje, la profundidad o el tipo de sustrato (Briceño-Vera et al., 2021). De igual manera, en otros estudios se ha demostrado que la variabilidad morfológica de las esponjas determina la diversidad de especies que se pueden asociar a una esponja. Por ejemplo, para *Sphaciospongia vesparium*, la riqueza de especies huéspedes está correlacionada con el volumen total de la esponja, aumentando a medida que el volumen de la esponja aumenta (Westinga & Hoetjes, 1981; Hultgren & Duffy, 2010). En el caso de las esponjas *Amorphinopsis atlántica*, *Haliclona implexiformis* y *Neopetrosia exigua*, además



del volumen de la esponja, el diámetro promedio de los ósculos es un factor que influye en la riqueza de especies asociadas; un ósculo de menor tamaño implica una abertura más pequeña a la esponja, limitando así el tamaño máximo de los organismos que pueden colonizar cada esponja (Briceño-Vera et al., 2021; Beepat et al., 2015).

## **Conclusiones**

Esta tesis proporciona una perspectiva integral de la importancia de las esponjas como especies clave en la estructura comunitaria de los arrecifes de coral tropicales. La recopilación y análisis de datos, así como la aplicación de herramientas de análisis de redes, han proporcionado un entendimiento profundo y novedoso sobre las interacciones huésped-hospedero que ocurren en los arrecifes de coral tropicales. Esta aproximación es fundamental para el manejo y la conservación de los arrecifes de coral, ya que las esponjas son organismos centrales en la estructura de la red lo cual significa que gracias a ellas se mantiene gran parte de la diversidad de especies de los arrecifes de coral. Los resultados de esta investigación ofrecen una base sólida para futuros estudios y esfuerzos de conservación que buscan preservar la biodiversidad y la salud de los ecosistemas marinos. Además, el análisis de redes reveló la complejidad y la especificidad que se tiene en la fauna asociada a esponjas, destacando la función clave de algunas especies de esponjas, pero sobre todo la importancia funcional de la morfología de los organismos hospederos en el mantenimiento de la comunidad asociada a las esponjas arrecifales. Con este trabajo se demostró la relación entre la escala espacial de observación y los componentes de diversidad de especies al momento de analizar la biodiversidad asociadas a esponjas arrecifales, teniendo patrones distintos y complementarios tanto para diversidad  $\alpha$  como para diversidad  $\beta$  a nivel ecosistémico, a nivel de hábitat y a nivel de microhábitat. Por último, los datos generados en esta investigación representan una valiosa fuente de información actualizada sobre interacciones ecológicas huésped-hospedero en los arrecifes de coral del Atlántico Tropical

Noroccidental, generando una nueva línea base de conocimiento, lo que facilita futuros análisis.

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## Effects of floral display and abiotic environment on the foraging activity of bees on *Kallstroemia pubescens* (Zygophyllaceae)

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Foraging activity of bees depends on a combination of their biology, floral traits attractive for bees and environmental factors. We carried out this study to determine whether the variation of floral aperture, floral display and environmental factors throughout the day influence the foraging activity and composition of bee visitors in *Kallstroemia pubescens* (G. Don) Dandy. This research was conducted at the Chamela Biological Station, UNAM, Jalisco, Mexico. During anthesis, we collected bees and recorded the foraging behavior hourly. We measured hourly the environmental factors (temperature, relative humidity, and light intensity), floral aperture, floral display and floral reward. Using generalized linear mixed-effects models we tested which of the factors have more influence on floral aperture and foraging activity. To determine the dissimilarity of the species composition between the hours sampled, we used a one-way analysis of

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# The Importance of Home Cleaning: Sediment Transport by Alpheid Shrimps Provides a Competitive Advantage to Their Host Anemones

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*Bartholomea annulata* is a facultative host of the *A. armatus* species complex. In the Mexican Caribbean it is commonly found in cracks and crevices located where the vertical walls meet the sandy bottom or on large coral patches away from the sand. To protect themselves from predators, anemones often contract their hydraulic body into a cavernous den and extend the stinging tentacles toward the entrance. The high sediment dynamics of the region, however, result in a permanent risk of animal shelters to be obstructed by sand. By both analysing field data and conducting laboratory experiments with artificial shelters, the present study explored the den cleaning behaviour widely extended amongst alpheid shrimp, and its role in the alpheid-anemone symbiotic interaction. Videorecordings showed that den cleaning was composed of three main behaviours: digging, tossing and tamping. It commenced as soon as  $7.2 \pm 10.5$  min after anemones were recognised by alpheids, and behaviours were displayed systematically amongst all 12 replicates. Despite being completely burrowed in sand, *Alpheus* spp. were capable of finding the anemone and liberating the entrance of the artificial shelters in less than 2.5 h. In addition, manipulative experiments showed that anemones confronted with shelters that were obstructed with sediment had a 25% probability of fully retracting when *Alpheus* spp. were absent, compared to a 75% probability when shrimps had cleaned the shelter's entry and internal passage. The analysis of field data indicated that the presence of alpheid shrimps as symbionts of *B. annulata* was 30% higher amongst anemones in close contact with sandy bottoms than when inhabiting crevices on the top or lateral walls of hard substrates, away from the sediment. Overall, our study concludes that den cleaning constitutes a quick and effective mechanism to assure the anemone's full retraction into their den, and by keeping the sediment away, alpheids provide the necessary conditions that serve both



Apéndice II. Generación y mantenimiento del sitio web *Marine Species Interactions*  
[www.marinespeciesinteractions.org](http://www.marinespeciesinteractions.org)

