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MODELOS DE NICHO ECOLÓGICO: DE LA TEORÍA HASTA SU APLICACIÓN PARA ESTIMAR LA FUNCIONALIDAD FÍSICA EN ARRECIFES DEL CARIBE

TESIS
QUE PARA OPTAR POR EL GRADO DE:
DOCTORA EN CIENCIAS
(Biología Marina)

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Dedicatoria

A mi madre y hermanas, con profundo amor y agradecimiento

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RESUMEN

Los arrecifes de coral son uno de los ecosistemas más diversos de la Tierra y brindan una gran variedad de servicios ecosistémicos. A pesar de ser ecosistemas tan valiosos, los arrecifes de todo el mundo se están degradando en respuesta a una serie de factores de estrés ligados principalmente a actividades humanas como la contaminación y el calentamiento del océano. En el caso particular de Caribe, la degradación que han sufrido en las últimas décadas se ha visto reflejada en perdidas de cobertura coralina viva de hasta un 80%, afectando la complejidad estructural del arrecife y su funcionalidad física. La complejidad estructural es un atributo clave del ecosistema del que dependen en gran medida su capacidad de albergar una alta diversidad biológica y la provisión de servicios ecosistémicos. Ante este panorama, lo manejadores de los recursos naturales se enfrentan al reto de desarrollar estrategias de conservación que ayuden a mitigar el impacto de los distintos estresores de manera efectiva. Sin embargo, para lograr estrategias de conservación efectivas es necesario conocer el estado inicial de los ecosistemas y cómo han cambiado en respuesta a los disturbios, así como también contar con información sobre el nivel de exposición a los distintos estresores. Para esto, los modelos de nicho ecológico son una herramienta importante para explorar patrones ecológicos y apoyar en el diseño de estrategias de conservación.

Bajo este contexto, en este trabajo primero se realizó una revisión de literatura sobre el uso de los modelos de nicho ecológico y distribución de especies en el ambiente marino. A continuación se combinaron técnicas de modelado de nicho ecológico con rasgos morfofuncionales de corales constructores de arrecife para estimar el potencial de funcionalidad física de los arrecifes del Caribe, para posteriormente evaluar el grado de divergencia de los arrecifes del oeste del Caribe al comparar las estimaciones de funcionalidad basadas en los modelos de nicho y los rasgos funcionales contra estimaciones de funcionalidad obtenidas en campo. Adicionalmente, se explora el nivel de exposición de los arrecifes con alto potencial de funcionalidad física al incremento de la temperatura en escenarios de cambio climático, con la finalidad de identificar aquellos menos expuestos que podrían funcionar como refugios climáticos.

Se observó que el uso de los modelos de nicho ecológico en el ambiente marino han crecido dramáticamente en los últimos años con diversos enfoques taxonómicos y de investigación, siendo uno de los más importantes el predecir el impacto potencial del cambio climático. Se encontró una alta variabilidad en el potencial de funcionalidad física de los arrecifes del Caribe, donde los valores más altos se observaron en el oeste del Caribe y los más bajos en zonas consideradas marginales para el desarrollo arrecifal. En el análisis de divergencia de los arrecifes del oeste del Caribe se estimó que 84% de los sitios analizados presentaron una reducción sustancial en su funcionalidad física. También se estimó que 46% de las celdas arrecifales identificadas como prioritarias y que podrían funcionar como refugios climáticos se encuentran actualmente desprotegidas. A nivel nacional, se identificó que entre los países del Caribe que tienen mayor oportunidad de proteger arrecifes con potencial de actuar como refugios climáticos se encuentran Bahamas, Puerto Rico, las Islas Turcas y Caicos, Panamá, Cuba, Belice, Haití, Honduras, Guatemala, y Jamaica.

Este trabajo tiene implicaciones importantes para la conservación de los arrecifes coralinos del Caribe desde la perspectiva del funcionamiento de los ecosistemas, ya que puede guiar los esfuerzos para definir áreas prioritarias para la conservación en el Caribe. Sin embargo, es importante resaltar la necesidad de tomar acciones para reducir el impacto de otros estresores que actúan a escala local, así como de acciones climáticas para reducir el impacto de las amenazas asociadas al cambio climático.

ABSTRACT

Coral reefs are one of the most diverse ecosystems on Earth and provide a wide variety of ecosystem services. Despite their value, reefs around the world are degrading in response to a series of stress factors linked mainly to human activities such as pollution and ocean warming. In the case of Caribbean reefs, the degradation they have suffered in the last decades has been reflected in losses of live coral cover of up to 80%, affecting the structural complexity of the reef and its physical functionality. Structural complexity is a key ecosystem attribute on which its ability to host high biological diversity and the provision of ecosystem services largely depend. Given this escenario, natural resource managers face the challenge of developing conservation strategies thet help mitigate the impact of different stressors effectively. However, in order to achieve effective consrvation strategies, it is necessary to know the initial state of ecosystems and how they have changed in response to disturbances, as well as to have information on the level of exposure to differet stressors. For this, ecological niche models are an important tool to explore ecological patterns and support the desing of conservation strategies.

Under this context, in this work, a literature review was first conducted on the use of ecological niche and species distribution models in the marine environment. Further, ecological niche modelling techniques were combined with morphofunctional traits of reef-building corals to estimate the reef functional potential of Caribbean reefs, and to assess the degree of divergence of western Caribbean reefs by comparing the estimates of functionality based on niche models and functional traits against estimates of reef functionality obtained with field data. Additionally, the level of exposure of reefs with high potential for physical functionality to the increase in temperature under future climate change scenarios was explored, in order to identify those less exposed to the increase in temperature that could function as climatic refugia.

It was observed that the use of ecological niche and species distribution models in the arine environment has grown dramatically in recent years with various taxonomic and

research objectives, one of the most important being to predict the potential impact of climate change. A high variability in the physical functional potential of Caribbean reefs was found, where the highest values were observed in the western Caribbean and the lowest in areas considered marginal for reef development. In the divergence analysis of the wester Caribbean reefs, it was estimated that 84% of the sites analyzed showed a substantial reduction in their physical functionality. It was also estimated that 46% of the reef cells identified as priority and that could act as climatic refugia are currently unprotected. At the national level, it was identified that among the Caribbean countries that have the greatest opportunity to protect reefs with potential to act as climatic refugia are the Bahamas, Puerto Rico, the Turks and Caicos Islands, Panama, Cuba, Belize, Haiti, Honduras, Guatemala and Jamaica.

This work has important implications for the conservation of Caribbean coral reefs from the peerspective of ecosystem functioning,as it can guide efforts to define priority areas for conservation in the Caribbean. However, it is important to emphasize the need to take action to reduce the impact of other stressors acting at the local scale, as well as climate actions to reduce the impact of threats associated with climate change.

CAPÍTULO 1: Introducción general y estructura de la tesis

INTRODUCCIÓN GENERAL

Los arrecifes de coral son ecosistemas marinos biogénicos formados por la acumulación de los restos de generaciones sucesivas de organismos calcáreos (Kaiser et al. 2011). La distribución geográfica de los arrecifes está restringida por la fisiología de los corales que los forman, por lo que están confinados a un rango relativamente estrecho de variables ambientales (Kleypas 1999). Dentro de los factores abióticos más importantes que determinan su distribución se encuentran la temperatura, la cual limita el desarrollo de los arrecifes entre los 30° norte y sur del ecuador, la salinidad, la penetración de la luz, las concentraciones de nutrientes y el estado de saturación de omega aragonita (Kleypas 1999, Kaiser et al. 2011).

Los arrecifes son uno de los ecosistemas más diversos y productivos del mundo. A pesar de que ocupan menos del 1% del fondo oceánico, albergan de un cuarto a un tercio de todas las especies marinas (Knowlton *et al.*, 2010; Plaisance *et al.*, 2011). Además, los arrecifes de coral proveen importantes servicios ecosistémicos que benefician a millones de personas alrededor del mundo, incluyendo pesquerías, turismo, compuestos biotecnológicos y protección a la costa del embate de tormentas (Woodhead *et al.*, 2019). Estos servicios han sido valuados en ~352,000 \$US/ha/año (Costanza *et al.*, 2014) y dependen principalmente de la capacidad de los corales constructores de arrecifes de secretar grandes cantidades de carbonato de calcio y crear estructuras tridimensionales complejas (Perry *et al.*, 2012; Graham & Nash, 2013).

A pesar de su importancia, en las últimas décadas los arrecifes de coral se han visto sustancialmente alterados por diversos estresores asociados a actividades humanas que actúan a escala local y global como la contaminación, la sobrepesca, el desarrollo costero y el cambio climático (Hughes *et al.*, 2017a). El efecto individual, acumulado o sinérgico de dichos estresores ha alterado fuertemente la ecología de estos ecosistemas, incluyendo disminución en la cobertura coralina, cambios en la estructura de las comunidades, disminución en la fecundidad y reclutamiento, y perdida de la complejidad estructural del hábitat y la reducción en su capacidad para acumular

carbonato de calcio, provocando la disrupción de la funcionalidad física de los arrecifes (Hoegh-Guldberg *et al.*, 2019; Perry & Alvarez-Filip, 2019; González-Barrios *et al.*, 2023).

La diversidad, abundancia y biomasa de taxa asociados a arrecifes está comúnmente relacionada positivamente con la complejidad estructural del hábitat; por lo tanto, la perdida de esta puede afectar negativamente la diversidad asociada (Rogers et al., 2014; Darling et al., 2017; Richardson et al., 2017b), afectando del mismo modo, la capacidad de los arrecifes de proveer servicios ecosistémicos (Hughes et al., 2018c; Smale et al., 2019; Eddy et al., 2021).

En los arrecifes someros tropicales, los corales constructores de arrecifes actúan como especies fundadoras y son los principales encargados de la construcción de la estructura física tridimensional (Perry *et al.*, 2012; Graham & Nash, 2013). Sin embargo, los corales presentan una gran variedad de estrategias de vida que se reflejan en una diversidad de morfologías y tazas de crecimiento que los hacen contribuir de manera diferencial en la construcción del arrecife (Richardson *et al.*, 2017a; Zawada *et al.*, 2019); por lo tanto, la identidad de las especies y sus rasgos asociados definirá en gran medida la dinámica y funcionamiento en los arrecifes coralinos (Alvarez-Filip *et al.*, 2011; González-Barrios *et al.*, 2021). Del mismo modo, el impacto que los distintos estresores tienen sobre los corales no es homogéneo en todas las especies, sino que está mediado en por su vulnerabilidad; de esta manera, los disturbios han generado cambios no aleatorios en la estructura de las comunidades (Spalding & Brown, 2015; Toth *et al.*, 2019). En el Caribe, la disminución en la complejidad estructural está asociada principalmente a la perdida de especies con morfologías complejas como *Acropora* spp. y *Orbicella* spp., y al incremento en la dominancia de especies menos complejas como *Porites astreoides* y *Agaricia agaricites* (Alvarez-Filip *et al.*, 2009, 2013; Perry *et al.*, 2015). Este cambio en la estructura de las comunidades ha afectado la funcionalidad física de los arrecifes, ya que las características de las especies ahora dominantes no les permiten desempeñar el rol funcional de las que dominaban previamente (González-Barrios *et al.*, 2021). Por ejemplo, estudios recientes han encontrado que en el Caribe mexicano, a

pesar de que se observó una recuperación en los arrecifes en términos de cobertura coralina viva, la funcionalidad física de los arrecifes no incrementó considerablemente debido a que las especies que más contribuyeron a la recuperación de la cobertura no son consideradas constructoras arrecifales importantes (Contreras-Silva *et al.*, 2020; González-Barrios *et al.*, 2021).

Desafortunadamente, se prevé que los disturbios continúen y que particularmente aquellos asociados al cambio climático como el calentamiento del océano, el cual se considera como una de las amenazas más serias a los arrecifes debido a que puede provocar eventos de blanqueamiento y mortalidad masivos, sean cada vez más frecuentes e intensos debido a las tendencias observadas de incremento en la temperatura (Hughes *et al.*, 2017b, 2018a; Sully *et al.*, 2019).

Ante este panorama de creciente degradación, es necesario generar estrategias de conservación que contribuyan a la supervivencia de las especies y la permanencia de las funciones y servicios del ecosistema. Idealmente, estas estrategias deberían ir más allá de la priorización espacial de la diversidad taxonómica, al incluir atributos y funciones clave que permitan proteger, además de la diversidad biológica, los servicios ecosistémicos, especialmente a largo plazo para hacer frente al cambio climático (Rogers *et al.*, 2014; Bellwood *et al.*, 2019; Chollett *et al.*, 2022).

Para apoyar la generación de estrategias de conservación eficientes y una adecuada planeación espacial, es importante conocer a gran escala las distintas presiones a las que los arrecifes están sometidos, así como su extensión y magnitud. La exposición de los arrecifes a las distintas amenazas no es espacialmente uniforme (González-Barrios et al., 2023). En el Caribe, la exposición a la temperatura ha mostrado una alta variabilidad espaciotemporal entre las ecorregiones (Chollett et al., 2012; Muñiz-Castillo et al., 2019). Sin embargo, a pesar de que la exposición de los arrecifes al estrés térmico y sus consecuencias han sido ampliamente estudiados (e.g. Hughes et al. 2018a), la exposición de otros atributos clave como la funcionalidad física de los arrecifes no ha sido evaluado. Una aproximación para integrar en los objetivos de conservación el

impacto de los estresores sobre otros atributos de los ecosistemas es el mapeo de sus funciones y la identificación de hotspots de diversidad funcional (Miatta et al. 2021). Una herramienta de gran utilidad para la biogeografía de la conservación son los modelos de nicho ecológico y distribución de especies (Guisan et al. 2013), que recientemente han sido utilizados para modelar diferentes aspectos sobre la estructura y composición de los ensamblajes ecológicos (e.g. D'Amen et al. 2017) y que además combinados con proyecciones climáticas, facilitan el manejo de los ecosistemas en un contexto de cambios dinámicos en el futuro. (Schoeman et al. 2023).

Tradicionalmente, la estrategia más adoptada en la conservación de los océanos es la creación de Áreas Marinas Protegidas (AMPs), las cuales pueden ser un fuerte instrumento de conservación si son adecuadamente diseñadas y cuentan con un manejo efectivo (Gill *et al.*, 2017; Roberts *et al.*, 2017; Álvarez-Romero *et al.*, 2018; Giakoumi *et al.*, 2018). Dentro de las estrategias para la creación de AMPs que consideran el impacto potencial del cambio climático y que han cobrado mayor interés se encuentra la identificación de refugios climáticos, los cuales pueden ser definidos como regiones menos expuestas al calentamiento con la capacidad de amortiguar a largo plazo los cambios en el ambiente que hacen a las áreas circundantes poco idóneas (Bruno *et al.*, 2018; Kavousi & Keppel, 2018). Algunos estudios han documentado la eficacia de los refugios climáticos para facilitar la supervivencia de los arrecifes en el pasado. Por ejemplo, se encontró evidencia de que el hidrocoral *Millepora intricata*, que se distribuye en el este del Pacífico, sobrevivió a eventos de blanqueamiento en refugios localizados en aguas más profundas, mientras que los organismos ubicados en aguas someras presentaron mortalidad (Smith *et al.*, 2014). En otro ejemplo, en una reconstrucción paleoambiental del periodo Cuaternario a lo largo de tres millones de años en el pasado, se observó que los refugios durante las fluctuaciones climáticas actuaron como centros de sobrevivencia para especies de peces y como moduladores de la diversidad actual (Pellissier *et al.*, 2014). Otros estudios han realizado análisis para identificar la existencia de refugios climáticos en el futuro para arrecifes, sin embargo, aunque incluyen un análisis más detallado sobre la incertidumbre asociada y diversos factores de estrés

además del incremento en la temperatura, no se consideran aspectos funcionales de los ecosistemas arrecifales para la determinación de los refugios (Beyer *et al.*, 2018; Chollett *et al.*, 2022; Dixon *et al.*, 2022).

En este contexto, resulta de vital importancia abordar el papel de las condiciones ambientales y de los rasgos funcionales de las especies coralinas en el funcionamiento de los arrecifes, para poder entender cómo han cambiado en respuesta a los disturbios, y cuál podría ser el impacto del cambio en las condiciones ambientales derivado del cambio climático en escenarios a futuro sobre estos ecosistemas. Esto permitiría generar conocimiento que apoye el diseño e implementación de estrategias de conservación que incorporen aspectos funcionales para la preservación del hábitat arrecifal.

JUSTIFICACIÓN E IMPORTANCIA

En los arrecifes someros tropicales, los corales constructores de arrecifes actúan como especies fundadoras y son los principales constructores de la estructura física tridimensional del arrecife al aportar grandes cantidades de carbonato de calcio (Perry *et al.*, 2012; Graham & Nash, 2013). Esta funcionalidad física favorece una alta diversidad de taxa asociados a través de la provisión de hábitats heterogéneos que regulan procesos ecológicos como el reclutamiento, depredación y competencia y es la base de los servicios ecosistémicos que brindan (Graham & Nash, 2013). Sin embargo, las especies coralinas han respondido de forma diferencial ante la variedad de disturbios, incluyendo el cambio climático, provocando cambios no aleatorios en las comunidades. Los corales presentan una gran variedad de estrategias de vida que se ve reflejada en una amplia gama de formas, tamaños y tazas de crecimiento, de esta manera la identidad de las especies y sus rasgos asociados definen en gran medida el funcionamiento y la dinámica de los ecosistemas (Richardson *et al.*, 2017a; González-Barrios *et al.*, 2021). Desafortunadamente, en el Atlántico oeste, las especies reconocidas como las constructoras más importantes, que aportan grandes cantidades de carbonato de calcio y complejidad estructural al sistema como *Acropora* spp. y *Orbicella* spp. han

sido las más afectadas dando lugar a ensamblajes comunitarios novedosos y una simplificación de la estructura física del arrecife, trayendo consigo severas consecuencias sobre la funcionalidad física del arrecife (Bruckner & Bruckner, 2006; Alvarez-Filip *et al.*, 2013; Rodríguez-Martínez *et al.*, 2014). En este contexto, la complejidad estructural y la funcionalidad física de los arrecifes son un componente integral de estos ecosistemas que debe ser incorporado en los objetivos de manejo y conservación (Graham & Nash, 2013). Comprender cómo los ensamblajes coralinos novedosos han divergido de su estado natural o previo a los disturbios, y el rol que los rasgos funcionales de las distintas especies y del marco ambiental en el que se desarrollan los arrecifes tiene sobre el funcionamiento de los ecosistemas y su capacidad para construir estructuras tridimensionales complejas a gran escala espacial, se vuelve fundamental para predecir el efecto de cambios ambientales y reconfiguración de las comunidades sobre el funcionamiento de los ecosistemas y los servicios que proveen. Además, permitiría guiar estrategias de conservación y manejo más efectivas al permitir la identificación de áreas críticas para la conservación que involucren atributos físicos de los hábitats que favorezcan la permanencia de las especies, comunidades, ecosistemas, servicios ecosistémicos y valores socioculturales, especialmente en escenarios de cambio climático.

OBJETIVOS Y PREGUNTAS DE INVESTIGACIÓN

El objetivo general es conocer y modelar cómo los requerimientos ambientales de las especies y sus rasgos funcionales modulan el funcionamiento de los ecosistemas e informan sobre su vulnerabilidad ante el cambio climático. El estudio se enfoca en el papel de los corales escleractinios ya que son los principales constructores de arrecifes, representan un grupo altamente diverso y presentan una gran vulnerabilidad al cambio climático.

En el **capítulo 1** se presenta el escenario sobre el que desarrolla esta tesis y su estructura. Incluye una introducción general sobre la problemática que se aborda y los antecedentes relevantes.

Reconociendo la importancia de las revisiones de literatura para la investigación, al aportar una descripción actualizada y estructurada, ofreciendo un conocimiento más profundo y preciso sobre temas de interés, especialmente en aquellos con creciente desarrollo; y considerando la relevancia de los modelos de nicho ecológico como aproximación metodológica clave para el desarrollo del presente trabajo, el **capítulo 2** explora el uso y las aplicaciones de los modelos de nicho ecológico y distribución de especies en el ambiente marino, respondiendo a la pregunta ¿Cuál es el estado actual del conocimiento sobre el uso y aplicaciones de los modelos de nicho ecológico y modelos de distribución de especies en el ambiente marino?

El **capítulo 3** se basa en la combinación de estimaciones de idoneidad ambiental obtenidas a través de modelos de nicho ecológico con rasgos morfofuncionales de las especies coralinas para explorar el potencial de funcionalidad física de los arrecifes del Gran Caribe, respondiendo a las preguntas ¿Cuál es el potencial de funcionalidad física de los arrecifes del Gran Caribe en ausencia de perturbaciones humanas?, y ¿Cómo han divergido los arrecifes de su potencial de funcionalidad física?

En el **capítulo 4,** utilizando en las estimaciones del potencial de funcionalidad física de los arrecifes del Gran Caribe, se evaluó el rol del esquema actual de la red de Áreas Naturales Protegidas del Caribe en proteger arrecifes con potenciales elevados de funcionalidad física, y el impacto potencial del incremento en la temperatura bajo escenarios de cambio climático sobre estos para responder a las preguntas: ¿Cuál es el estado actual de protección de los arrecifes con alto potencial de funcionalidad física? y, ¿Existen áreas arrecifales con alto potencial de funcionalidad y baja exposición al incremento en la temperatura que pudieran ser consideradas como refugios climáticos?

El **capítulo 5** incluye la discusión y conclusiones generales del trabajo y una propuesta de líneas de investigación complementarias como perspectivas a futuro.

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CAPÍTULO 2: Modelos de nicho ecológico y distribución de especies en el ambiente marino: una revisión de literatura y análisis espacial de la evidencia
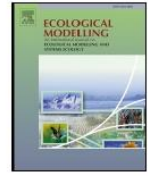
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Review

Ecological niche models and species distribution models in marine environments: A literature review and spatial analysis of evidence

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ABSTRACT

In recent years, the use of ecological niche models (ENMs) and species distribution models (SDMs) to explore the patterns and processes behind observed distribution of species has experienced an explosive growth. Although the use of these methods has been less common and more recent in marine ecosystems than in a terrestrial context, they have shown significant increases in use and applications. Herein, we provide a systematic review of 328 articles on marine ENMs and SDMs published between 1990 and 2016, aiming to identify their main applications and the diversity of methodological frameworks in which they are developed, including spatial scale, geographic realm, taxonomic groups assessed, algorithms implemented, and data sources. Of the 328 studies, 48 % were at local scales, with a hotspot of research effort in the North Atlantic Ocean. Most studies were based on correlative approaches and were used to answer ecological or biogeographic questions about mechanisms underlying geographic ranges (64 %). A few attempted to evaluate impacts of climate change (19 %) or to develop strategies for conservation (11 %). Several correlative techniques have been used, but most common was the machine-learning approach Maxent (46 %) and statistical approaches such as generalized additive models GAMs (22 %) and generalized linear models, GLMs (14 %). The groups most studied were fish (23 %), molluscs (16 %), and marine mammals (14 %), the first two with commercial importance and the last important for conservation. We noted a lack of clarity regarding the definitions of ENMs *versus* SDMs, and a rather consistent failure to differentiate between them. This review exposed a need to know, reduce, and report error and uncertainty associated with species' occurrence records and environmental data. In addition, particular to marine realms, a third dimension should be incorporated into the modelling process, referring to the vertical position of the species, which will improve the precision and utility of these models. So too is of paramount importance the consideration of temporal and spatial resolution of environmental layers to adequately represent the dynamic nature of marine ecosystems, especially in the case of highly mobile species.

1. Introduction

Ecological niche models (ENMs) and species distribution models (SDMs) are commonly used in theoretical and applied studies in ecology and biogeography (Peterson et al., 2015). Among the most common applications are determining suitable sites for species (Guisan and Zimmermann, 2000), predicting impacts of future climate change on species' distributions (Pearson and Dawson, 2003), evaluating the invasive potential of non-native species (Jiménez-Valverde et al., 2011), and conservation planning (Guisan et al., 2013).

Three main categories of models are recognized in this field: correlative models, the most common in the literature, which estimate the

ecological requirements of species by relating their known geographic distributions to a set of environmental variables (Araújo and Guisan, 2006; Franklin, 2009); mechanistic models that use detailed physiological information and first principles of biophysics (Kearney and Porter, 2009); and process-oriented models, which estimate distributions of species in terms of processes, including dispersal capability and biotic interactions (Peterson et al., 2015).

Throughout the history of modelling species' niches and distributions, such models have received a variety of names: "bioclimatic envelope models" (Araújo and Peterson, 2012), "habitat suitability models" (Hirzel et al., 2006), "species distribution models" (Elith and Leathwick, 2009), and "ecological niche models" (Peterson, 2006). This
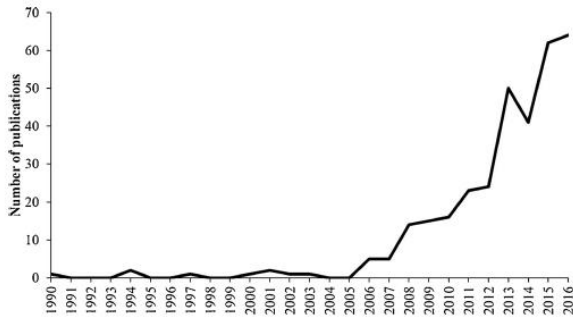
Fig. 1. Trends in the number of publications per year about ENMs and SDMs applied to marine species.

panoply of terms has led to confusion and sometimes misinterpretation of model results (Peterson and Soberón, 2012; Soberón et al., 2017). More recently, two terms for two kinds of models has gained attention; acceptance is growing for the terms ENM and SDM as two distinct approaches to answering different questions (Peterson and Soberón, 2012). ENMs estimate fundamental niches of species, and are applied when the aim is to know the potential distribution, as in the case of invasive species or projections in space and time. On the other hand, SDMs attempt to estimate objects in geographic space, referring to actual distributions of species (Peterson and Soberón, 2012; Soberón et al., 2017).

Implementation of ENMs and SDMs started with terrestrial species, with increasing numbers of publications each year (Robinson et al., 2011). Their application to marine species has been less frequent, however, niche models applied to marine systems have become more popular in recent years (Fig. 1; Robinson et al., 2017).

Modelling marine species may be a challenge owing to the particular physical and biological characteristics of marine habitats and species (Robinson et al., 2011). One of the main challenges is the three-dimensionality of marine habitats, especially when modelling pelagic species living in the middle layers of the water column (Dambach and Rödder, 2011; Bentlage et al., 2013). This challenge is mainly imposed by the fact that most available environmental data layers describe the uppermost layers or the ocean floor (Assis et al., 2017a), and because of the limited knowledge of many pelagic organisms' ecology and behavior (Bentlage et al., 2013). Another important challenge is the dynamic nature of marine ecosystems, and the multiple spatial and temporal scales in which species-environment relationships occurs (Redfern et al., 2006; Scales et al., 2017). This dynamism is essential in the case of highly mobile species for which transitory environmental conditions may determine distribution over short time frames (Fernandez et al., 2017, 2018). Another particularity is the lack of hard physical barriers to dispersal. For most marine organisms, dispersal depends upon ocean currents, so, the inclusion of ocean currents in the models, or taking species dispersal into account, should enhance the development of more reliable models (Dambach and Rödder, 2011).

Previous efforts to summarize the state on the field of ENM and SDM in the marine realm include the works of Dambach and Rödder (2011) and Robinson et al. (2011) who provided overviews of marine niche modelling applications and highlighted the particular challenges in modelling marine environments such as three-dimensionality, species interactions and ontogenetic shifts. Vierod et al. (2014) reviewed applications of niche models in deep sea ecosystems that are considered vulnerable, pointing out data limitations and implications of model predictions, and paying special attention to sampling bias, spatial autocorrelation, spatial scale and model evaluation and validation; issues of paramount importance that are still under discussion in the field of modelling. Marshall et al. (2014) analyzed the use of these models in planning marine conservation; they highlighted the fact that in most

cases models related to marine ecosystems are not linked to management decisions, and about the need to use these models into spatial prioritization programs. Moreover, they recommend the use of models in combination with layers of human footprint to add value to the models for conservation purposes. Marcelino and Verbruggen (2015) reviewed the use of these techniques to model invasive seaweeds, and pointed out some particularities when modelling invasive species, such as the assumption that those species are in equilibrium with its environment and about the fact that they retain their ecological niche. Most recently, Robinson et al. (2017) reviewed applications of marine models and developed a framework to guide future applications through the use of a flow diagram to guide the process towards model implementation, calibration and validation.

This review aims to answer key questions related to use of ENMs and SDMs in marine ecosystems, on the basis of 328 research articles published on the topic between 1990 and 2016. For most cases, both ENMs and SDMs are herein referred to as "models", except when we want to emphasize differences between them. This is the most comprehensive review yet compiled for marine environments, as it includes information from previous reviews, plus new additions that have not been summarized previously. Here, we summarize applications of the models and the taxa that have been targets of modelling studies. We identify gaps in modelling of marine species and point out emerging trends in the field; we consider aspects of modelling that are specific to marine environments.

2. Ecological niche concepts in ENMs AND SDMs

Species distribution modelling and ecological niche modelling rely on ecological niche theory. The ecological niche of a species was originally defined as the suite of ecological conditions within which a species is capable of surviving and reproducing without immigrational subsidy (Grinnell, 1917). Later, the term was recycled to refer to the functional role that a species plays in a community (Elton, 1927). Still later, distinction was drawn between the fundamental niche, the set of abiotic environmental conditions under which a species is able to persist indefinitely, and the realized niche, the part of the fundamental niche that is constrained by interactions with other species (Hutchinson, 1957). As such, species' ranges can be conceived of as a consequence of three factors, (Soberón and Peterson, 2005): (i) presence of environmental (abiotic) conditions under which the species can establish, survive and reproduce; (ii) the biotic environment determined by the presence of species interactions such as competition or predation in which species can persist, and (iii) the area that is accessible to the species *via* its movement or dispersal capabilities. These restrictions have been captured in the so-called BAM diagram (Fig. 2. A): **B**, biotic; **A**, abiotic; **M**, movement (Soberón and Peterson, 2005), which has become a central concern in designing models (Barve et al., 2011; Saupe et al., 2012). Species geographic ranges are the result of the dynamic interactions of those three factors. In niche modelling, inclusion of **B** presents a problem owing to the complexity of biotic interactions, and estimation of **M** is a complex challenge, since it involves knowledge of areas that have been accessible to the species over relevant time periods (Barve et al., 2011). Hence, most correlative models have been restricted to representations of **A**.

Peterson et al. (2011) presented the Eltonian Noise Hypothesis, which is the idea that biotic interactions seldom constitute a significant constraint on the distributional potential of species on large geographic extents and low resolutions. This is also a hypothesis about biological processes and represents a simplification of modelling methodologies, considering the difficulties to include biotic interactions in the process. Biotic interactions are hard to measure and represent in a raster grid format (Soberón and Nakamura, 2009). For some species, ecological interactions may not play a dominant role at the coarse resolution typically used for modelling, and niche models have demonstrated a good performance in describing their distribution on the basis of **A** (Costa
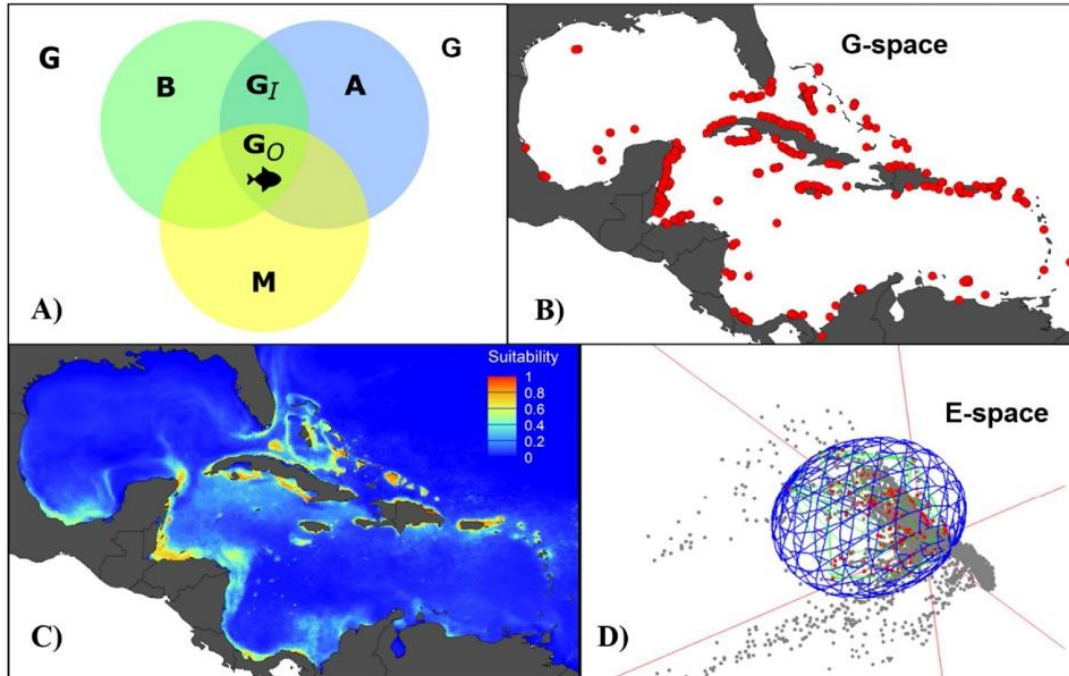
Fig. 2. A) BAM diagram representing the sets of factors influencing the geographic distribution of a species. *B*, represents the biotic conditions (*i.e.* coupled variables including biotic interactions appropriate for the species); *A*, region favorable for the species in terms of abiotic factors, typically used to represent limiting factors that would allow assessment of a species' fundamental niche (*e.g.* temperature and precipitation), and are typically of coarser spatial and temporal resolutions than biotic conditions; *M,* mobility or dispersal capacities of the species, encompassing the area that has been accessible for the species over relevant time periods (*e.g.* in a biogeographic context). **G***O*, occupied area, the actual area of distribution of the species where the three sets of components of the diagram intersect. **G***I*, invadable area, those places where biotic and abiotic conditions are adequate for species to survive but where the species has not yet reached because of some dispersal limitation. Modified from Soberón and Peterson (2005), and Soberón (2010). **B)** and **D)** are the representation of Hutchinson's duality: **B)** Occurrence localities for the scleractinian coral *Acropora palmata* obtained from OBIS and GBIF, representing the geographical space (G-space) occupied by the specie; **D)** three-dimensional model of the ecological niche of *A. palmata,* where gray dots represent all the environmental combinations (E-space) available in the Caribbean as a result of a principal component analysis, red dots represent the environments actually occupied by *A. palmata,* and the blue minimum-volume ellipsoid represents the fundamental ecological niche of *A. palmata.* **C)** Geographic projection of *A. palmata*'s niche model and corresponding suitability values. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

et al., 2010; Lira-Noriega et al., 2013). Conversely, for some species it has been demonstrated that accounting for biotic interactions improves model capability at predicting their distributions (de Araújo et al., 2014)

Another important concept in niche theory applied to niche and distribution models is the so-called Hutchinson's duality, which refers to the correspondence between niche (*i.e.* environmental or ecological) and geographic (*i.e.* distributional) spaces (Fig. 2, B and D). According to this hypothesis, a region of the niche space may correspond to more than one place in the geographic space, whereas each point in the geographic space corresponds to exactly one point in niche space (Colwell and Rangel, 2009). This hypothesis is of great utility for explaining the differences between ENMs and SDMs concepts, which mistakenly are often termed as equivalent (Peterson and Soberón, 2012). For practical considerations SDM refers to the modelling objects in G-space, whereas ENM refers to modelling objects in E-space (Soberón et al., 2017). ENM requires an explicit estimation of the species' fundamental niche, and are intended to model the processes that shape the area of distribution of the species, and frequently used to transfer those causal factors into projections in space or time (Peterson and Soberón, 2012). SDM can only focus on the species' distribution, and ideally must restrict model calibration to accessible areas (M), account for true absences and incorporate dispersal and colonization capabilities (Peterson and Soberón, 2012). It is clear that there is an intimate relationship between these two concepts, and delimiting one

or the other may be confusing, but in order to let the field grow, it is important to be consistent and rigorous with the use of the terminology.

3. Literature search and analysis

3.1. Literature search

Using the ISI Web of Science and SCOPUS databases, we performed an exhaustive literature search using the keywords: "species distribution models*", "habitat suitability models*", "ecological niche models*", and "bioclimatic* envelope models*", each accompanied successively by the words "sea", "marine" and "ocean". The initial search, restricted to articles published during 1990–2016, yielded more than 2000 articles. We discarded articles that did not make explicit reference to modelling species distributions or ecological niches in a Grinnellian sense (Soberón, 2007), and those focused on biotic interactions (*e.g.* studies of trophic niches). Articles regarding mangrove ecosystems were also discarded, though we included studies of marine species able to live in estuaries and rivers. Additionally, we searched the "references" sections of each article for relevant publications that might not have been detected in the initial search. In total, 328 articles were selected to be included in this review (Appendix A).

3.2. Summary of information

Each article was entered in a database with author(s), publication year, study region, and the following fields:

3.2.1. Extent of analysis

In order to know the analytical extent of the studies, these were classified as locals if they cover the territory of one country or less (*e.g.* Portuguese coast), as regionals for two or more countries (*e.g.* Mediterranean Sea) and global if they were accomplished worldwide.

3.2.2. Taxonomic group

The classification of target species by taxonomic group did not focus on a particular taxonomic category to illustrate the great variety of organisms studied. Thus, categories include phylum, subphylum, and class, and less formal groups such as "seaweed". For the purpose of this review, elasmobranch is taken as a group separated from the category fish which includes the Actinopterygii class.

3.2.3. Source of occurrence data and environmental variables

We registered sources of occurrences data and environmental variables in modelling studies. We also recorded the environmental variables used in each study (*e.g.* wind velocity, water temperature).

3.2.4. Type of model and modelling technique

We classified the studies as correlative, mechanistic, or process-oriented. Since most studies were correlative, we further classified all articles depending on the modelling technique that they used (*e.g.* Maxent, GLM, ENFA).

3.2.5. Model selection and validation

In order to know how model selection and validation is done, we registered the procedures (*e.g.* cross-validation) and metrics (*e.g.* AUC, TSS) used in each article.

3.2.6. Aim of the studies

Studies were classified according to 9 topic categories: present potential distribution, climate change impacts, invasive species, distributions under past climates, abundance models (populations and communities), habitat use, evaluation of methods, conservation planning and management, and "other". The latter category includes testing niche conservatism, evolution, or niche reconstruction, and review articles. Articles addressing more than one research question were assigned to several categories if necessary.

Finally, in order to enlighten the geographic distribution of ENM and SDM efforts, the study area described in each article was digitized with GIS software using as a reference a 1° spatial resolution global grid. We extended this spatial representation to the modelling purposes and the taxonomic groups studied in the articles.

4. ENMs and SDMs in the marine realm

To our knowledge, this review of 328 articles is the most extensive overview of applications of SDM and ENM in the marine realm. We found a great variety of applications, species being modelled, environments being studied, and a broad geographic distribution of studies. Below, we attempt to describe the main findings of the literature reviewed.

4.1. Regions studied and extent of analysis

Each ocean was covered by at least 39 modelling exercises. Research in marine systems most frequently concerned the North Atlantic Ocean; hotspots of studies were along the northeastern coast of the United States, the west coast of Europe, and the Mediterranean Sea (Fig. 3). The least studied areas were the northwestern Pacific Ocean and the Indian Ocean. Models have been used in all marine ecoregions (see also Robinson et al., 2017), with clear interest in the North Atlantic Ocean. Local studies predominated, followed by regional studies, only a few studies were at global scales (Fig. 4).

4.2. Taxonomic groups in marine modelling

Diverse marine taxonomic groups have been studied using ENMs or SDMs. Studies of fish and molluscs were most common (77 and 52 articles, respectively; Fig. 4). This concentration could be explained by the commercial importance that fisheries of those groups represent worldwide; according to the Food and Agriculture Organization of the United Nations (FAO), in 2015, fish and molluscs occupied first and second places, respectively, in global capture production in marine fishing areas (FAO, 2017). Most of the articles concerning these groups targeted commercial species such as anchovy and jack fish, and abalone and clams. A third group of importance in modelling were mammals ($N = 48$), which are among the most threatened species, facing severe population declines (Reeves et al., 2013), mainly owing to bycatch fisheries and pollution (Schipper et al., 2008), as well as ship strikes and noise disturbance (Aguilar de Soto et al., 2016; Pirotta et al., 2019), which now are recognized as major threats to marine mammals; hence, they are attractive for this kind of study. Another reason that makes these three groups suitable for modelling is the amount of data available. *Via* the OBIS portal (http://www.iobis.org/), > 20 million records are available for Pisces, > 3 million for Mollusca, and > 1 million for Mammalia. Other taxonomic groups well represented among the articles reviewed here were seaweed ($N = 34$), crustaceans ($N = 29$), seabirds ($N = 28$), and stony corals ($N = 25$). For seaweed, target species were mainly invasive, and crustacean included several economically important groups such as lobsters. Seabirds had a special interest for conservation, as well as stony corals since their ecological importance like habitat forming species.

Seagrasses are among the least studied groups ($N = 10$), even though they provide key ecological services, and there is a growing need for protection and conservation in the face of global threats (Orth et al., 2006). Two studies predicted the potential distribution and habitat suitability for the seagrasses *Zostera noltii* and *Z. marina* (Valle et al., 2011; Downie et al., 2013), yet we found just one article evaluating the impact of rising seawater temperatures and sea level rise on the distribution of *Z. noltii* (Valle et al., 2014). Other important habitat forming species that have received little attention are kelp forests and algae, but apparently they are receiving more attention since we found recent publications regarding kelp forests (Assis et al., 2018, 2017a), algae forest from the genus *Cystoseira* (Buonomo et al., 2018), and for the seagrass *Cymodocea nodosa* and *Posidonia oceanica* (Chefaoui et al., 2018; Chefaoui and Serrão, 2017). Other poorly represented groups were sponges, foraminifera, reptiles ($N = 9$ each), tunicates ($N = 7$), and bacteria ($N = 2$). Something worth mentioning is that we did not find articles regarding the study of viruses during years for which we conducted our review; however, a more recent article applies ENM to study the ecology and epidemiology of viral hemorrhagic septicemia virus of fish (Escobar et al., 2018). The study of marine diseases was less represented in the analyzed articles, nevertheless we think that distribution and niche models can help to better understand the complicated dynamic of epidemiological and diseases' processes in the marine realm.

In the category "reptiles" only turtles were found in the literature reviewed, which reflects the paucity of marine reptiles in comparison with fishes, but reptiles are probably receiving more attention since the recent publication of an article on niche modelling of sea kraits (Gherghel et al., 2018). "Other cnidarians" includes jellyfishes, anemones, black and red corals, the class Hydrozoa, and the extinct coral *Grewingkia*; all of these groups were much less represented in the literature. "Other invertebrates" includes the phyla Bryozoa, Placozoa, Entoprocta, Nematoda, Platyhelminthes, and Xenacoelomorpha; the

Fig. 3. Distribution of ENMs and SDMs studies worldwide taken from the 328 articles published between 1990 and 2016.

Fig. 4. Number of studies by taxonomic group of target species and extent of the study area. Numerous studies included more than one taxonomic group. Light blue, local studies; dark blue, regional studies; orange, global studies. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

class Priapulida; and the extinct class Trilobita. Many articles (*N* = 50) included multiple taxonomic groups.

4.3. Spatial patterns by taxonomic group

We found a strong interest in fish, molluscs, crustaceans, annelids, seaweed and sea grasses in western Europe and Mediterranean Sea (Fig. 5, Fig. B1 in Appendix B). Elasmobranch studies were more common in the Gulf of Mexico and near the United Kingdom; plankton studies were concentrated in the North Atlantic Ocean, mammals in the

eastern Pacific Ocean, and echinoderms in the southwestern Pacific Ocean. Studies of seabirds were spread more globally, but with a marked interest in the Southern Ocean.

4.4. Occurrence data for modelling

One of the most important inputs for model construction is occurrence data, which provide information about environmental conditions where the species is present and thereby allow estimation of niches *via* correlative methods. The occurrence data used in the reviewed

Fig. 5. Distribution of ENMs and SDMs studies per taxonomic group. For the other taxonomic groups see Fig. B1 in Appendix B.

Fig. 6. Tendency in the use of species occurrence data sources.

literature (Fig. 6) most commonly came from regional databases ($N = 121$) and field censuses ($N = 119$). Other sources included published literature ($N = 91$), global databases ($N = 61$) and scientific collections ($N = 20$). It was relatively common for studies to combine different sources, especially for poorly-known species. Global initiatives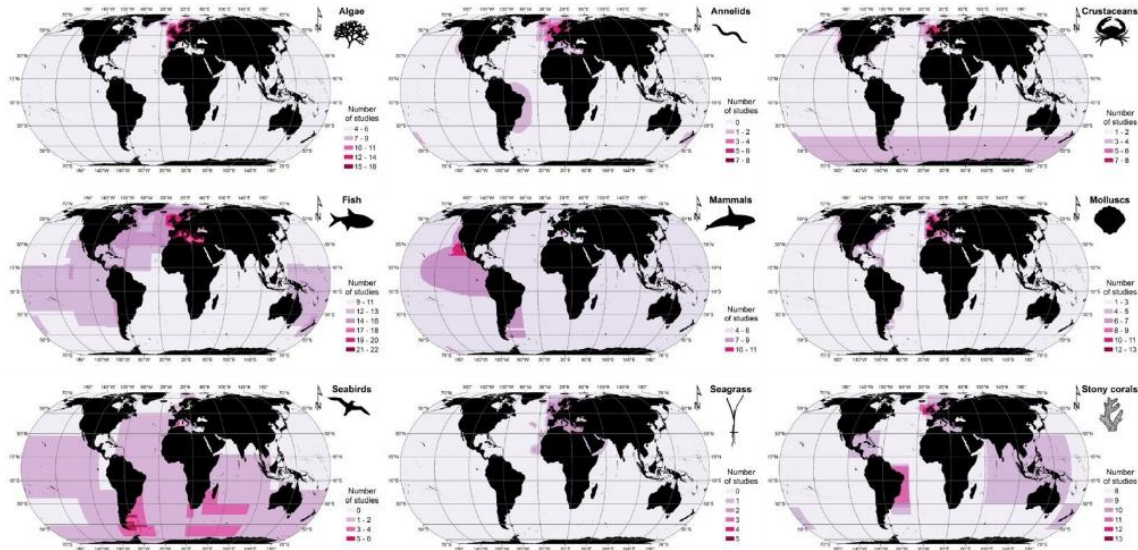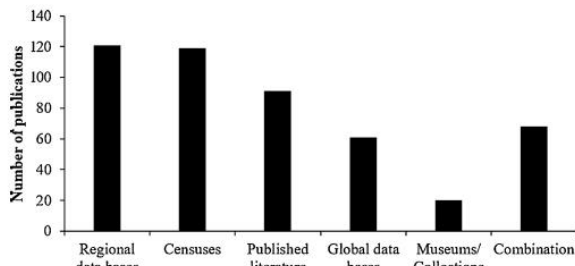 that provide open access to occurrence data include the Global Biodiversity Information Facility (GBIF, https://www.gbif.org/), Ocean Biogeographic Information System (OBIS, http://www.iobis.org/), FishBase (https://www.fishbase.de/), Fishnet2 (http://www.fishnet2.net/), and D4Science infrastructure (https://www.d4science.org/home). Other data sources are more specialized in particular taxa, such as the Microbis database from the International Census of Marine Microbes (ICoMM, https://vamps.mbl.edu/portals/icomm/icomm.php/microbis/) and the Global Diatom Database (Leblanc et al., 2012).

Example of regional efforts to compile accessible information on occurrences is the Continuous Plankton Recorder survey (CPR, https://www.cprsurvey.org/), in association with the Marine Biological Association of the UK, which holds historical data about biogeography and ecology of plankton from the North Atlantic and the North Sea (Helaouët and Beaugrand, 2009; Chust et al., 2014; Barton et al., 2016; Brun et al., 2016). Another example is the North Atlantic Right Whale Consortium (https://www.narwc.org/) that records historical sightings of right whales and other mammals, sea turtles, and large fish from the North Atlantic Ocean (Gowan and Ortega-Ortiz, 2014).

Alternative regional sources of occurrence data include commercial or recreational fisheries logbooks (Brodie et al., 2015; Gomez et al., 2015) and programs for assessment of fishing activity and stock

conditions (Maxwell et al., 2009; Tanaka and Chen, 2016). Among the latter, the International Bottom Trawl Survey in the Mediterranean (MEDITS, http://jadran.izor.hr/eng/international/medits.html) is a program that conducts continuous trawl surveys to assess the status of fishing resources, to support the policies and regulation of fisheries in the Mediterranean. Such data, besides providing information about occurrences, may also inform about their relative abundance, and thereby enable models aimed at studying effects of climate change on fish stocks. For instance, researchers have applied generalized linear and additive models to integrate swordfish *Xiphias gladius* and common sardine *Strangomera bentincki* fisheries data with simulations of future sea surface temperatures, to predict changes in their relative abundance and distribution off the coast of Chile (Silva et al., 2015).

Censuses were the second most common source occurrence data. Since most studies were at local scales, researchers can generate their own data. We found a variety of survey methods, including visual surveys (Pittman et al., 2007; Assis et al., 2015) and underwater video systems, especially for demersal species (Moore et al., 2009, 2016; Monk et al., 2010; McLean et al., 2016). Another common source was satellite tracking data, commonly used for sea turtles (Pikesley et al., 2015; Varo-Cruz et al., 2016; Whittock et al., 2016), seabirds (Skov et al., 2008; Catry et al., 2013; Ramos et al., 2015), and mammals (Edrén et al., 2010).

Information from natural history museums and scientific collections is another valuable source of primary data. Examples include the South Australian Museum (http://www.samuseum.sa.gov.au/collections; Bentlage et al., 2009), Museo Nacional de Historia Natural at Montevideo, Uruguay (http://www.mnhn.gub.uy/innovaportal/v/3090/12/mecweb/colecciones?leftmenuid=3090; Carranza et al., 2011), and the U.S. National Museum of Natural History (https://naturalhistory.si.edu/rc/; Georgian et al., 2014).

Occurrence databases frequently include important geographic biases, such as inaccurate geolocation and spatial autocorrelation among occurrence points, as well as species misidentifications. As with terrestrial ecosystems, it is common that certain marine areas are more visited than others because of their proximity or low-cost accessibility, which results in oversampling biases that turn into biases in the ecological niche space (Araújo and Guisan, 2006; also see Fig. 2). All modelling algorithms assume that occurrence data are unbiased (Araújo and Guisan, 2006), yet in reality they are sensitive to many

characteristics of the occurrence data (Araújo and Guisan, 2006; Loiselle et al., 2008; Fourcade et al., 2014). These biases can lead to model overfitting to environmental conditions associated with particular geographic spaces producing poorly reliable models (Araújo and Guisan, 2006; Boria et al., 2014), and also, impact model evaluation since in most cases there is no independent data to perform the test. A common practice is to randomly split occurrence data into training and testing subsets, despite both subsets keep sharing the same bias and may show an inflated metric for validation (Veloz, 2009). These remarks regarding biases and other problems associated to species occurrences are particularly important for pelagic and deep-water species that are hard to sample and, consequently, data-poor. Users and designers of occurrences databases must be aware of errors associated with this type of data acknowledging potential impacts on model performance, while also submitting occurrence data to exhaustive procedure of data cleaning (Peterson et al., 2011), and ideally by making specific mentions about data quality in metadata files at the time of making the data available.

4.5. Environmental data for modelling

Recent technological developments have enabled access to increasing amounts of environmental information, derived from remotely sensed data at high spatial resolutions, through data interpolation, or from modelled data (as with many climate data products). We found four main sources of environmental information: global data bases providing environmental parameters for whole oceans; information generated by the authors through either field measurements or computational methods; regional databases; and, in some cases, published information (Fig. 7). Global databases were by far the most common (*N* = 239). Among data portals most frequently used were the National Aeronautics and Space Administration (NASA) and National Oceanic and Atmospheric Administration (NOAA). Other data were accessed through the Ocean Color Web (https://oceancolor.gsfc.nasa.gov/), Physical Oceanography Distributed Active Archive Center (PODAAC, https://podaac.jpl.nasa.gov/), National Centers for Environmental Information (https://www.ngdc.noaa.gov/), World Ocean Atlas (WOA, https://www.nodc.noaa.gov/OC5/indprod.html), International Comprehensive Ocean-Atmosphere Data Set (ICOADS, http://icoads.noaa.gov/), AquaMaps (Kaschner et al., 2006; http://www.aquamaps.org/main/envt_data.php), MARSPEC (Sbrocco and Barber, 2013), GMED (http://gmed.auckland.ac.nz/), Bio-ORACLE (http://www.bio-oracle.org/), and The Copernicus Marine Environment Monitoring Service (CMEMS, https://www.copernicus.eu/en/services/marine), which is managed by the European Commission and offers products describing the physical and biogeochemical state of the global ocean and European regional seas. The most cited source for bathymetric data was the General Bathymetric Chart of the Oceans (GEBCO, https://www.gebco.net/), which offers a 15 arc-second resolution grid for the global ocean.

An example of a regional database is the Australian Bureau of Meteorology, consulted by Adams et al. (2015) to obtain data on wind speed and direction and solar exposure, with the goal of identifying environmental factors limiting seagrass survival in Moreton Bay,
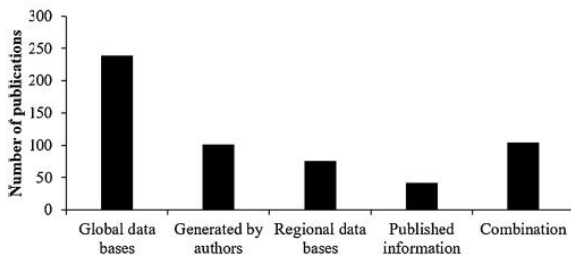

Fig. 7. Tendency in the use of environmental descriptors for ENM and SDM.

Australia. Sarà et al. (2013) used hourly seawater temperature data from the Italian Oceanographic Buoy Network at the Instituto Superiore per la Protezione e la Ricerca Ambientale to generate a mechanistic model of fitness and potential colonization areas for the invasive mussel *Brachidontes pharaonis* in the Italian portion of the Mediterranean. Finally, Carlucci et al. (2016) used bathymetric data from the European Marine Observation and Data Network (EMODnet, http://www.emodnet.eu/what-emodnet) to assess driving forces influencing the distribution of dolphin species in the Gulf of Taranto. Generation of environmental variables by the authors themselves was not common; however, one example is the use of multibeam echosounder systems to produce bathymetric data (Howell et al., 2011; Monk et al., 2011; González-Irusta et al., 2015; Piechaud et al., 2015).

Selection of key environmental variables in which to explore the niche of species is a crucial step in model design. Inclusion of too many environmental dimensions can cause model overfitting (Peterson et al., 2007); thus, as good practice, various biological or statistical criteria are used to select the best set of environmental predictors. Principal components analysis (PCA) is the most commonly used to reduce dimensionality of environmental spaces (Dennis and Hellberg, 2010; Freeman et al., 2013; Escobar et al., 2015). Another common procedure for variable selection involves the estimation of correlation among candidate variables, combined with the results of a jackknife analysis performed in Maxent; under this method, variable selection obeys low collinearity and high contribution values (Raghavan et al., 2019a,b).

In marine environments, the water column creates a three-dimensional structure that represents an extra challenge in modelling (Dambach and Rödder, 2011; Robinson et al., 2011). The study of pelagic organisms represents a particular challenge given the difficulties of access and sampling in open oceans (Bentlage et al., 2013). Most oceanographic data are representative of the topmost layers of the water column, and those representative of the seabed are often derived from bathymetric profiles (Assis et al., 2017a), which impedes modelling of pelagic and highly mobile species. Bentlage et al. (2013) modelled the potential distribution of the open-ocean jellyfish *Periphylla periphylla* on a global scale, they used oceanographic variables (WOA05) at multiple depths, and added the third dimension by transforming and combining all depth layers into a single, continuous, grid two-dimensional that replicated global oceans multiple times. As such, the model encompassed the whole environmental range occupied by the species in three dimensions. Duffy and Chown (2017) used similar approaches to estimate the probability of occurrence of four fish species in the northeastern Atlantic, highlighting the importance of explicit consideration of the vertical dimension.

The temporal resolution of environmental layers is important, especially in the case of highly mobile species, since their distributions may be associated with both short- and long-term variability in ocean environments (Fernandez et al., 2017; Mannocci et al., 2017). In the literature reviewed here, little attention was paid to this point, and the use of variables appeared more related to availability than to detailed analysis of impacts of temporal resolution on distributions of target species. An exception is the work of Scales et al. (2016), who used remotely-sensed environmental variables that temporally matched with tracking data for the Grey-headed Albatross *Thalassarche chrysostoma* to identify foraging areas. Fortunately, it seems that this field is gaining attention among the modelling community since contributions addressing this topic, although mainly focusing on mammals, have been recently published. It has been found that finer temporal scales may provide more accurate models, especially for species such as blue, fin and sei whales that are highly dependent on dynamic variables (Fernandez et al., 2018). Other studies regarding the spatio-temporal variability and habitat dynamism for modelling the distribution of blue whales in the Azores islands and the California coast in USA highlighted the utility of multiscale studies to capture the factors that affect the distribution of this highly migratory species (Abrahms et al., 2019; González-García et al., 2018); these contributions have been important
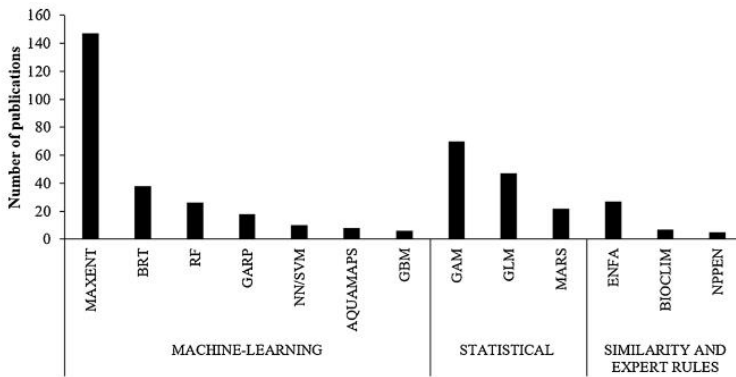
Fig. 8. Tendency in the use of ENM and SDM algorithms. We present only the most frequently used algoritms. MAXENT = Maximum Entropy; BRT = Boosted Regression Trees; RF = Random Forest; GARP = Genetic Algorithm for Rule Set Production; NN/SVM = Neural Networks/Support Vector Machine; GBM = Generalized Boosting Models; GAM = Generalised Additive Model; GLM = Generalized Linear Model; MARS = Multivariate Adaptive Regresion Splines; ENFA = Ecological Niche Factor Analysis; NPPEN = Non Parametric Probabilistic Ecological Niche.

to understand how species make use of, or shift among, dynamic habitats and to reinforce the importance of such models for conservation strategies.

Influences of data quality on model performance have been investigated for marine systems. Becker et al. (2016) compared the performance of two cetacean density models, one built with oceanographic information and the other with data measured *in situ*; they found no significant differences in the metrics evaluated, suggesting that modelled data, which are considerably easier and less costly to assemble, can support modelling efforts adequately. To assess effects of spatial resolution on model predictions, Basher et al. (2014) modelled distributions of shrimp species in the Ross Sea; they found that spatial resolution influences both the extent of the resulting suitable area, and the relative importance of environmental variables.

A great diversity of variables was used to describe species' niches, including physical and chemical properties of the water column, topographic characteristics of the seabed, factors describing the surrounding environments, and variables related to biotic interactions (Table C1, Appendix C). The most common descriptor used was water temperature, which was used in 240 of the articles reviewed. Temperature is among the most important determinants of species' distributions, and as a single environmental covariate can predict 53–99 % of present-day biogeographic units along coastlines (Belanger et al., 2012). Other physical variables included photosynthetically active radiation (PAR, $N = 26$) and diffuse attenuation coefficient ($N = 20$); chemical variables included salinity ($N = 147$) and chlorophyll-*a* concentration ($N = 97$); atmospheric variables included air temperature ($N = 15$) and precipitation ($N = 9$); environmental descriptors included sediment type ($N = 30$) and substrate/bottom type ($N = 27$); geographic variables included distance to shore ($N = 54$) and geographic coordinates ($N = 20$); hydrodynamic variables included current velocity ($N = 45$) and mixed layer depth ($N = 15$); topographic variables included bathymetry ($N = 210$) and slope ($N = 109$), ecological variables included habitat type ($N = 11$) and presence/absence/biomass of other species ($N = 7$); finally, temporal variables included season of the year ($N = 7$) and calendar year ($N = 4$).

4.6. Model types

4.6.1. Correlative models

Correlative modelling was far more frequent than mechanistic or process-oriented approaches. It usually begins with the known distribution of species, namely presence, presence-absence or abundance data, which are associated statistically with environmental variables describing dimensions such as climate (Kearney, 2006; Peterson et al., 2015). Its popularity is thanks partly to advances in statistical techniques, development of GIS tools, and availability of specialized modelling software, and also to growing availability of detailed data about biodiversity and the environment (Elith and Leathwick, 2009; Peterson

et al., 2015). In our review, 307 of the articles were exclusively correlative associations, so the general tendencies described above represent the main currents in correlative modelling in largest part. Thus, the main focus of this section is on description of methods used in correlative models.

Models differ in the way they select environmental predictors and measure variable contributions and predictive performance (Elith et al., 2006), but they have in common the goal of describing one part of environmental space as suitable, and the rest of that space as unsuitable. In the earliest marine models, Reilly (1990) applied analysis of variance to explore relationships between water mass properties (density and thermocline depth) and seasonal distributions of dolphin groups in the eastern tropical Pacific. Fiedler and Reilly (1994) and Reilly and Fiedler (1994) used canonical correspondence analysis (CCA) to study, respectively, habitat use and the relationship of dolphin abundance to habitat quality. More recently, a great variety of methods has been used for modelling species niches and distributions (Franklin, 2009). In our review, most popular methods were machine-learning methods ($N = 268$), followed by statistical methods ($N = 189$), and finally similarity-based and expert-rule approaches ($N = 54$); 74 studies used a combination of two or more techniques. Among machine-learning methods, Maxent (Phillips et al., 2006) was most frequent ($N = 147$; Fig. 8). Since the appearance of Maxent in 2006, it became one of the most popular modelling techniques, perhaps partly because it requires relatively little information, being designed to work with presence-only data (Phillips et al., 2006). Maxent has shown robust predictive accuracy (Elith et al., 2006; Graham et al., 2008) even with small sample sizes (Hernandez et al., 2006; Wisz et al., 2008), and provides great flexibility in model construction through a friendly interface (*e.g.* features and regularization multiplier) that allow the user to adjust the model to specific needs and available information (Merow et al., 2013; Muscarella et al., 2014). Other well-represented machine-learning methods have been boosted regression trees (BRT, $N = 38$) and random forests (RF, $N = 26$). In the case of statistical methods, most frequent were regression models (*i.e.* GAMs, $N = 70$ and GLMs, $N = 47$; Fig. 8). Among similarity-based and expert-rule models, most frequent was the ecological niche factor analysis (ENFA, $N = 27$; Fig. 8). In spite of their applicability and overall quality or popularity in the field of correlative modelling, it is has been recognized that there is no single "best" algorithm, and it is recommended, as a good practice, to test and justify a suit of algorithms in order to choose the best option for a particular research question (Qiao et al., 2015).

4.6.2. Mechanistic models

Mechanistic models use detailed physiological information and first-principles of mathematical reasoning to determine links between the environment and the fitness of the organism, which is later represented in geographic space (Kearney, 2006; Kearney and Porter, 2009; Peterson et al., 2015). In our review, only 13 articles used mechanistic

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approaches. Dynamic energy budget (DEB) models used chlorophyll-a to express food availability, and water temperature to express body temperature, to study relative fitness of native and invasive molluscs; this approach generated spatial predictions of their physiological performance and highlighted potential areas for colonization (Sarà et al., 2013; Montalto et al., 2015). Mechanistic niche models have been used to integrate solar radiation, salinity, and temperature in models designed to evaluate the invasive potential of the ascidian *Ciona intestinalis* and the seaweed *Codium fragile* (Madariaga et al., 2014). Other studies have assessed future changes in distributions of planktonic organisms in response to rising temperatures (Helaouët and Beaugrand, 2009; Thomas et al., 2012).

Other mechanistic niche models explicitly incorporate correlative approaches. For instance, Fordham et al. (2013a, 2013b) modelled the future ranges and abundance of two harvested abalone species (*Haliotis rubra* and *H. laevigata*), combining demographic processes and physiological responses with climatic factors. Other studies have used thermal thresholds of macroalgae to predict potential range shifts in response to global warming (Martínez et al., 2014), or have simulated effects of temperature and oxygen concentrations on growth and body weight in fish and invertebrates to predict patterns of change in species richness, invasion, and extinction worldwide (Jones and Cheung, 2014). For two ecologically and economically important mussels, *Mytilus edulis* and *M. galloprovincialis,* energetic responses to temperature were analysed to understand current and future potential distributions (Fly et al., 2015).

4.6.3. Process-oriented models

Dynamic models can take into account key processes that affect ranges of species through effects on demographic processes such as birth and death rates, and dispersal of individuals (Case et al., 2005; Holt and Keitt, 2005). Process-oriented models can measure effects of these processes across species' distributions (Peterson et al., 2015). In this review, only five of the articles included process-oriented modelling, almost all focused on molluscs and related to their dispersal capabilities.

Process-oriented models can be combined with correlative approaches. Among the articles reviewed, the earliest process-oriented model (Inglis et al., 2006) examined the utility of habitat suitability index models and particle dispersion models to project suitable habitat for the non-native bivalves *Theora lubrica* and *Musculista senhousia* in New Zealand. For *M. galloprovincialis,* which is invasive in southern Africa, Assis et al. (2015) combined niche modelling and Lagrangian particle simulations to assess its current distribution and evaluate effects of dispersal capacity and environment as controls on its potential to spread. In the Bay of Santander, Spain, Bidegain et al. (2013) combined niche modelling with a particle-tracking model to study larval transport, supply, settlement behavior and post-settlement mortality of the clams *Ruditapes decussatus* and *R. philippinarum*, to identify optimal habitat for settlement and assess connectivity between spawning and nursery grounds. Finally, Elsäßer et al. (2013) combined niche and particle dispersal models to identify suitable areas for adult translocation that could represent restoration sites for biogenic reefs formed by the horse mussel *Modiolus modiolus* in Northern Ireland. In our only example including fish, Cheung et al. (2009) analysed likely effects of climate change on distributions of 1066 commercially exploited marine fish and invertebrates using a dynamic model including environmental variables and simulations of abundances derived from a logistic population growth model.

4.7. Model selection and validation

Model selection and validation is a critical step in the model procedure, it is the measure of how useful and trustworthy our models are, most importantly when the intention is transferring the model to novel conditions (Wenger and Olden, 2012). Considering only correlative models, 224 articles used a cross-validation method, mostly by

randomly dividing occurrence data, whereas only 21 used independent test data. The most frequent evaluation measure was the threshold-independent area under the receiver operating characteristic (ROC) curve (AUC; $N = 177$), followed by the Akaike´s information criterion (AIC or AICc; $N = 42$), the true skill statistics (TSS; $N = 35$) and the Kappa statistic ($N = 26$); 111 articles combined more than one validation metrics.

Model selection is a debated topic in ENM and SDM currently (Warren and Seifert, 2011), and newer applications that run Maxent and other algorithms have adopted statistical model evaluations and metrics based on information criteria as the standard to choose among all possible combinations of model parameterizations (Muscarella et al., 2014; Cobos et al., 2019). Such approximations to model selection and evaluation represent a more robust protocol while implementing ENM, and have demonstrated to yield better results than only using default parameters.

4.8. ENMs and SDMs applications

4.8.1. Current species distribution patterns

Models are often used to investigate factors that limit species' distributions, and to fill gaps in information about species' ranges. In our review, 212 of the articles aimed to explore potential distributions of species or to elucidate which environmental factors are responsible for observed patterns. Most distributional studies concerned fish, mammals, molluscs, or seaweed (Table 1). For instance, ENM and SDM have been used to investigate the potential distribution of the harmful cyanobacteria *Lyngbya majuscula* in the Canary Islands (Martín-García et al., 2014), and to measure the effect of environmental variables on shaping the distribution of fish species (Beger and Possingham, 2008; Chatfield et al., 2010), for the kelp *Laminaria hyperborea* (Assis et al., 2016b), and for commercial cephalopods (Lauria et al., 2015). For several articles, a study of the distribution patterns was the first step toward answering more complex questions including topics such as climate change impacts and conservation planning.

4.8.2. Impacts of future climate change

The average global surface temperature of the Earth has increased by approximately 0.2 °C per decade over the past 30 years (Hansen et al., 2006). More than 90 % of the excess heat is absorbed by the ocean, driving to a rate of warming of about 0.11 °C per decade in the upper layer, and an increase in the global mean sea level of 0.19 m and a decrease of seawater pH by 0.1 units in recent decades (Rhein et al., 2013). Of the articles reviewed, 64 aimed to analyse some aspect of future climate change; the most frequent taxa in these studies were fish and molluscs (Table 1). Model scenarios have been used to improve understanding of how climate change may impact marine ecosystems and species; most have focused on predicting potential changes of species' distributions in response to climate change.

For example, Assis et al. (2016b) used niche modelling to predict consequences of future climate change on the distribution and genetic diversity of the kelp *L. hyperborea* in Europe. They suggested that changes in environmental conditions may lead to loss of suitability in areas where the species has persisted through time, and a possible northward range shift. A model of shallow coral reefs worldwide (Couce et al., 2013) assessed potential effects of increasing sea surface temperature and ocean acidification on these ecosystems; temperature would be the main driver in the decline of suitability, particularly in the Indo-Pacific region, and in producing a poleward range expansion of suitable areas.

4.8.3. Methodological advances

In the past two decades, use of models has grown rapidly (Lobo et al., 2010), with a concomitant increase in interest in improving their performance. Of the 328 articles reviewed here, however, only 41 addressed performance of the models. The most frequent way to evaluate

Table 1

Total number of articles and percentage by taxonomic group and application. For the purpose of this review elasmobranch are taken as a separate group from the category fish. Numbers are calculated considering only articles evaluating some aspect of a taxonomic group (324 in total), this excludes review articles. An article was counted more than once if two or more taxonomic groups or applications were modelled in a single study.

	Distribution	Climate change	Method evaluation	Conservation planning	Range shifts	Invasive species	Properties of populations and communities	Past climates	Other applications
N	212	63	41	36	31	32	31	18	14
Annelids	6	3	2	1		3		1	1
Bacteria	2	1							1
Crustaceans	10	6	5	2	1	6		3	1
Echinoderms	7	3	3	1		1	1	1	2
Elasmobranchs	9	4	1	2	2		1	1	1
Fish	37	16	13	9	6	6	11	3	2
Foraminifera	6	4	1	1		2		1	
Mammals	30	3	6	7	10		9	1	2
Molluscs	25	13	5	9		8	5	4	5
Other cnidarians	7	2	2	1					1
Other invertebrates	5	3	2						2
Plankton	4	6	1		1	1	2		1
Reptiles	6	4							
Seabirds	15	3	3	7	11			1	2
Seagrass	7	2	3	2					
Seaweed	21	9	4	1		11	2	4	1
Soft corals	12	5	5	3					1
Sponges	6	2	1	3					
Stony corals	15	7	3	1		3		1	1
Tunicates		1				6			

performance was to compare the results of multiple techniques in a single scenario. For instance, Jones et al. (2012) compared the performance of three different approaches, AquaMaps, Maxent, and Sea Around Us Project algorithms in modelling commercial fish distribution in the North Sea and North Atlantic. Bucas et al. (2013) compared outcomes of four modelling algorithms: GAMs, RF, MARS, and Maxent, in predicting the distribution and diversity of benthic species in the Baltic Sea.

Another contribution to methodological advance is ensemble modelling approaches; that is, results from different algorithms can be combined to produce a more robust model, including results from more than one set of model parameters (Thuiller et al., 2009). In the marine realm, ensemble models have been used to predict potential distributions of flatback turtles *Natator depressus* (Whittock et al., 2016), future suitability for the Barau's Petrel (*Pterodroma baraui*; Legrand et al., 2016), and impacts of climate change on fish diversity in the Mediterranean Sea (Albouy et al., 2015).

Other authors have evaluated transfer capability of models; for example, Lauria et al. (2015) evaluated model capacity to spatially predict density of the commercially important Norway lobster *Nephrops norvegicus* in fishing areas of the Northeast Atlantic; they found that most of the models were able to successfully predict lobster density among fishing areas, suggesting that simple regression models perform as well as complex models in space transferability. Verbruggen et al. (2013) studied the model transfer capability for the invasive seaweed *Caulerpa cylindracea*, they found that appropriate predictor selection plays an important role in transferability success. Projection exercises are a difficult task in the field of modelling because we don't have the capacity to validate that a successful model predicting the actual distribution of species is equally successful in predicting its distribution on novel conditions when projected to new areas or in climate change scenarios. It has been shown that when transferring models it is difficult to accurately estimate the existing fundamental niche of species, specially when it is not well represented in the calibration area (Qiao et al., 2019). It is also of high importance to evaluate the degree of environmental similarity between calibration and projection regions, as well as to make a proper selection of the modelling algorithm considering the completeness in the knowledge of the species fundamental niche (Qiao et al., 2019). Despite this, model projections represent a valuable tool to explore phenomena such as invasive species (Jiménez-Valverde et al.,

2011) or climate change impacts (Pearson and Dawson, 2003).

Implementation of new modelling methods represents efforts to improve ENM and SDM capabilities. For instance, Ready et al. (2010) presented the online approach AquaMaps (http://www.aquamaps.org), designed to estimate suitability for species on the basis of presence-only data and a set of environmental variables, while incorporating expert knowledge to account for potential bias in data sets. The performance of AquaMaps models have been found to compare well with other methods such as Maxent and GLM (Ready et al., 2010). Johnston and Purkis (2012) developed Invasionsoft, a web-based modelling tool designed to study marine invasions using a cellular automata algorithm to relate historical records of the invasion process of the species of interest with a set of environmental descriptors. In a test case using lionfish and seaweed, the algorithm was able to emulate the spread of those marine organisms, nevertheless we are not aware of other articles using this software.

4.8.4. Conservation planning

Conservation management can benefit from models that provide information about present-day distributions (Galparsoro et al., 2009), range shifts expected under climate change (Chust et al., 2014), potential spread of invasive species (De Rivera et al., 2011), and habitat use (Ballard et al., 2012; La Manna et al., 2016). Of the 328 articles reviewed, 36 included some aspect of conservation planning, most commonly for fish, molluscs, mammals, and seabirds. The most common goal was to designate marine protected areas (MPAs); for example, Ballard et al. (2012) combined ENMs of whales, seals, and seabirds along with information on their feeding habits, to identify sites in the Ross Sea most important for conservation. Similar studies have been conducted for marine mammals in Scotland (Embling et al., 2010), fish in New Zealand (Leathwick et al., 2008), and kelps in France (Bajjouk et al., 2015). Models have also been used to identify sites of vulnerability to pollution in seabirds (Lieske et al., 2014), vulnerability to fishing mortality for commercial species (Abecasis et al., 2014), and potential risk of bycatch for marine mammals (Briscoe et al., 2014).

4.8.5. Range shifts

Animal populations tend to move or shift their geographic ranges in response to specific conditions across marine habitats. These conditions may vary through the life history of a single organism, such as in

seeking predator-free sites, or optimal sites for feeding or spawning (Afonso et al., 2014; Fromentin and Lopuszanski, 2014). Species' distributions in space and time reflect spatial patterns in population dynamics, an important issue in conservation, and particularly for migratory species that have complex spatial dynamics, since they may change habitat preferences between migratory endpoints or during different life-history stages (McKinney et al., 2012). Of the 328 articles reviewed, 31 were related to these issues, particularly in seabirds and mammals. For instance, some authors have tried to predict foraging sites dynamics for seabirds, including the albatrosses *Diomedea exulans* (Louzao et al., 2013) and *Thalassarche chrysostoma* (Scales et al., 2016), and the gannet *Morus bassanus* (Skov et al., 2008). Models have also been used to identify optimal chick-rearing habitats for *Pygoscelis* penguin species (Cimino et al., 2013). For mammals, models have been applied to identify habitat partitioning in humpback whales between different reproductive states and behaviors (Lindsay et al., 2016); other cases include modelling species' distributions among seasons (Reilly, 1990; Pitchford et al., 2016). For fish, models have been used to identify optimal sites for feeding, spawning, and nursery areas (Florin et al., 2009; Druon et al., 2015, 2016; González-Irusta and Wright, 2016).

4.8.6. Invasive species

Invasive species represent one of the main causes of biodiversity loss (Bellard et al., 2016); they can displace native species, change the community structure and function, and cause significant economic losses by affecting ecosystem services (Molnar et al., 2008; Pejchar and Mooney, 2009). Consequently, understanding and predicting the potential for spread of invasive exotic species is crucial to effective management. Applications of models to invasive species have sought to evaluate their potential to spread (also see section on Methodological advances above).

Of the 328 articles reviewed, 32 were related to invasive species, particularly on seaweed (Table 1). For example, researchers have used models to investigate the potential for spread and the environmental factors that favor or limit the establishment of species such as the invasive kelp *Undaria pinnatifida* at local (Báez et al., 2010) and global (James et al., 2015) scales, the mussel *Mytilus galloprovincialis* in southern Africa (Assis et al., 2015), the scleractinian corals *Tubastraea coccinea* and *T. Tagusensis* in Atlantic waters Carlos-Júnior et al., 2015a,b), and the seastar *Asterias amurensis* in the Southern Ocean (Byrne et al., 2016). In another example, niche models were built to test niche conservatism of fish in the Mediterranean Sea (Parravicini et al., 2015); this topic, has rarely been explored in marine organisms.

4.8.7. Properties of populations and communities

Herein, "properties" refers to abundance, biomass, density, and richness. Of the 328 articles reviewed, 31 focused on these subjects, with fish and mammals as the most frequent taxa (Table 1). The most common topic was prediction of species abundance. Within the 1990–2016 literature search, the earliest work we found that used statistical procedures to relate abundance to environmental variables (Fiedler and Reilly, 1994) combined cetacean sighting data with *in situ* data of temperature and thermocline depth and thickness *via* canonical correspondence analysis to calculate a habitat quality index. For fish, niche models have been used to predict relative abundance of the mesopelagic fish *Electrona antarctica* in the Southern Ocean (Loots et al., 2007) and the swordfish *Xiphias gladius* in the Indian Ocean (Lan et al., 2014), and to predict potential changes in abundance for *X. gladius* and the sardine *S. bentincki* in the Pacific under climate change (Silva et al., 2015). Other groups of interest in predicting abundances have been rays (Dedman et al., 2015) and molluscs with commercial importance, such as abalone (Russell et al., 2012; Fordham et al., 2013a).

Density and biomass have been estimated for fish populations in the Pacific (Su et al., 2011) and Atlantic oceans (Lynch et al., 2015) considering climate change predictions, and for mammals in the Pacific

Ocean (Becker et al., 2012, 2016). Knudby et al. (2011) used ENMs to predict species richness, diversity, and biomass of fish in the Fiji Archipelago. Other studies have modelled biomass of kelp species in France (Gorman et al., 2013; Bajjouk et al., 2015), detected biomass hot-spots of bivalves in the Baltic Sea (Darr et al., 2014), and modelled bivalve densities in the Mediterranean Sea (Vázquez-Luis et al., 2014). Models have estimated species richness for fish in the Caribbean (Pittman et al., 2007), and potential changes in mammalian species richness worldwide under climate change scenarios (Kaschner et al., 2011).

4.8.8. Modelling past distributions

The Earth's climate has experienced continuous changes over the past 65 million years and beyond, shifting from extreme warmth to extreme cold (Zachos et al., 2001). Past and current evidence suggests that changing climates profoundly influence expansion or contraction in species' ranges (Pearson and Dawson, 2003); knowledge of species' responses to past climatic changes helps to anticipate responses to future climate changes (Araújo and Pearson, 2005; Kettle et al., 2011). Models have been used to explore the biogeographic history of several marine species; 18 of the articles reviewed were related to past climates, focusing on seaweed, molluscs, crustaceans, fish and mammals (Table 1). For example, Saupe et al. (2015) used ENM to evaluate the vulnerability to extinction of 92 bivalve and gastropod species that lived during the mid-Pliocene Warm Period, by relating niche breadth, geographic range size, and area availability. For seaweed, models have been used to explore influences of past climates on the distribution and genetic composition of *Saccorhiza polyschides* (Assis et al., 2016a), *Laminaria hyperborea* (Assis et al., 2016b), and *Fucus vasiculosus* (Assis et al., 2014) populations. For marine fish, Last Glacial Maximum distributional patterns have been modelled (Bigg et al., 2008; Kettle et al., 2011).

4.8.9. Other applications

Finally, 14 of the articles reviewed used models to study other aspects of marine taxa such as the relationship between phylogenetic structure and distributional patterns of gastropod species (Carranza et al., 2011), to test for niche shifts in invasive coral species (Carlos-Júnior et al., 2015a), to understand evolutionary niche dynamics of seaweed (Verbruggen et al., 2009), to test long term niche stability of benthic species (Brame and Stigall, 2014), to study niche divergence among closely related seabirds in combination with stable isotope analysis (Rayner et al., 2016), and to compare realized ecological niches of phytoplankton species categorizations of populations strategies and functional groups (Brun et al., 2015).

4.9. Spatial patterns by application

We observed an emphasis in western Europe on the study of distributions in current, future, and past climate scenarios. Studies of invasive species were mostly in the Mediterranean Sea, which has had numerous biological invasions, mainly thanks to the Suez Canal, and also from aquaculture and the aquarium trade (Katsanevakis et al., 2014, 2016; Galil et al., 2015); a secondary focus of invasive species was on the Brazilian coast. Conservation planning was of particular concern in the United Kingdom. Most studies concerning conservation or management were across small areas, appropriate in the context of conservation efforts for which legal responsibility relies in local agencies (Boersma and Parrish, 1999). Studies related to habitat use were more uniformly distributed across all oceans (Fig. 9).

5. Concluding remarks

Our examination of the published literature revealed an enormous interest in application of ENMs and SDMs to explaining and predicting distributional patterns and the processes shaping them for marine
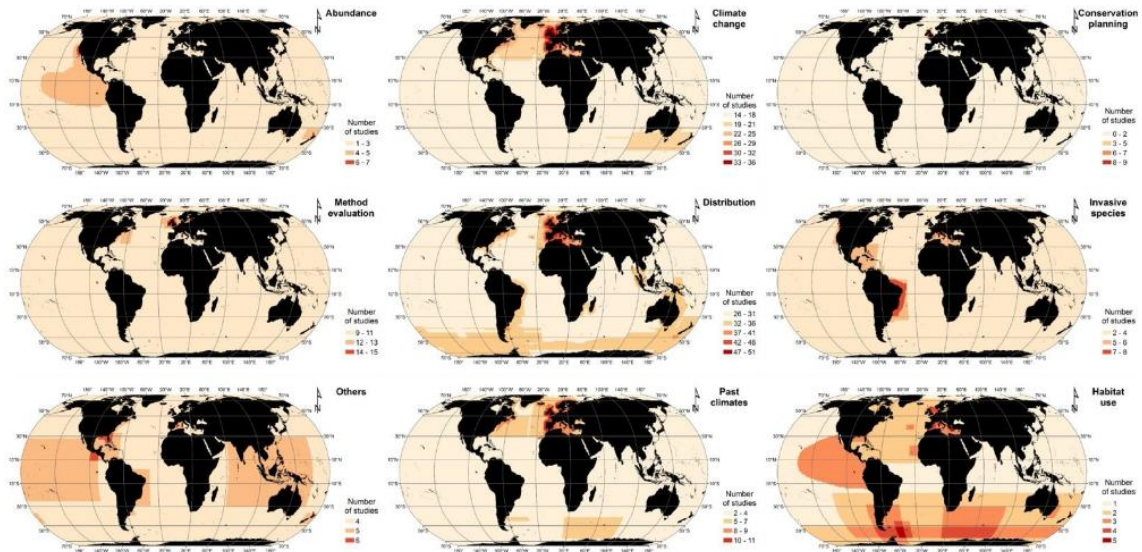
Fig. 9. Spatial distribution of ENMs and SDMs per model application.

species. The most common research questions are headed towards the understanding of the processes shaping species distributions and the impact of climate change on species habitat suitability and distribution. Taxonomic groups more studied are fish, molluscs and mammals, obeying the economic and ecological relevance of the first two, and conservation importance of the last. Taxonomic groups least represented are sponges, foraminifera, reptiles, tunicates and bacteria. We also found little representation of important habitat forming species such as shallow and deep scleractinian corals, kelp forests and seagrasses; even though recently have been published more studies about these groups, we think is of primer importance to keep addressing them in the research agenda in the face of growing threats to marine ecosystems.

A wide range of modelling techniques is available; the correlative approach is by far the most common, but mechanistic or process-oriented modelling approaches can be more appropriate in some cases, although are generally more difficult to implement given the amount and quality of data they require for proper calibration (*e.g.* physiological and demographic parameters, dispersal capacity). Mechanistic models, have the advantage that by incorporating physiological information have a stronger predictive power and thus, are more suitable in cases such as range shifts, climate change impacts or species invasions. Process-oriented models that include distribution potential and populations dynamics are adequate to predict species' distributions in spatially and temporally explicit frameworks, not only accounting for habitat suitability. As such we suggest strongly that choice of modelling technique follow the needs of the specific question and data availability.

Common problems and pitfalls rely on the lack of clarity in the concepts and on a proper use of ecological niche theory behind model design. Many articles do not differentiate clearly between ecological niche models and species distribution models. Proper use of these concepts is greatly encouraged, although, these issues are not exclusive to modelling in marine environments. Many articles failed to clarify the niche concepts used (*e.g.* fundamental, existing or realized niche) or the criteria used to define their modelling framework (*i.e.* the basis upon which the modelling technique was chosen). Many articles did not make clear that they had considered limitations of the data (occurrence

or environmental; *e.g.* spatial autocorrelation among occurrence points). We call for a rigorous process of model selection and validation in order to generate models as reliable as possible, specially when research questions go beyond theoretical interest, that is to say, with explicit interest in the application of models to conservation and management issues.

Unique aspects of marine modelling that impose and extra challenge are related to the dynamic nature of marine ecosystems. We highlight the need to understand and incorporate these complex dynamics especially in the case of highly mobile pelagic organisms by paying special attention to the temporal and spatial scales being handled in the models. The additions of a third dimension in representing the marine realm from a volumetric perspective has yet to be incorporated more broadly. These unique aspects of marine habitats urge to multi-disciplinary work that help us to understand how the processes inherent to the ocean, influence species' distributions. Improved understanding of how niche theory and modelling approaches apply to marine environments will lead to the development of more realistic niche models, especially in the case of conservation planning, climate change, and impacts of invasive species, where they represent useful tools in decision-making. Also, it is of utmost importance to develop models that can be truly incorporated in real life solutions to conservation and management needs, as well as to bet for the combinations of this models with other fields such as evolution, trait-based approaches, or even social and legislative matters, which can guide us to a better understanding of ecosystems processes and species' responses to extant and novel environmental conditions.

Oceans cover more than 70 % of Earth's surface and around the 95 % of it remains unexplored. Many marine resources are considered as "goods" for human beings, and we obtain from them an important number of services. There is a strong bond between oceans and humanity, and an urgent need to understand de complex dynamic and processes occurring in order to protect, conserve or recover our ocean ecosystems. ENMs and SDMs represent a valuable tool for this research, but only when more clarity infuses study design and conception, including correct use of concepts, niche theory, aims and methodology, will niche modelling be fully able to enhance in the marine realms.

Author contributions

SMMM and HRB conceived the idea. SMMM performed literature search and analysis of information. ALN contributed to the formal analysis, visualization and interpretation of results. SMMM wrote the original draft and ALN contributed to review and edit the manuscript.

Declaration of Competing Interest

Authors declare no conflict of interest.

Appendix A. Bibliographic list of the 328 articles included in the review

Abecasis, D., Afonso, P. and Erzini, K. (2014) Combining multispecies home range and distribution models aids assessment of MPA effectiveness. Marine Ecology Progress Series 513, 155–169.

Adams, M.P., Saunders, M.I., Maxwell, P.S., Tuazon, D., Roelfsema, C.M., Callaghan, D.P., Leon, J., Grinham, A.R. and O'Brien, K.R. (2015) Prioritizing localized management actions for seagrass conservation and restoration using a species distribution model. Aquatic Conservation: Marine and Freshwater Ecosystems 26, 639–659.

Afonso, P., McGinty, N. and Machete, M. (2014) Dynamics of whale shark occurrence at their fringe oceanic habitat. PLoS ONE 9(7), e102060. doi:10.1371/ journal.pone.0102060.

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Appendix B
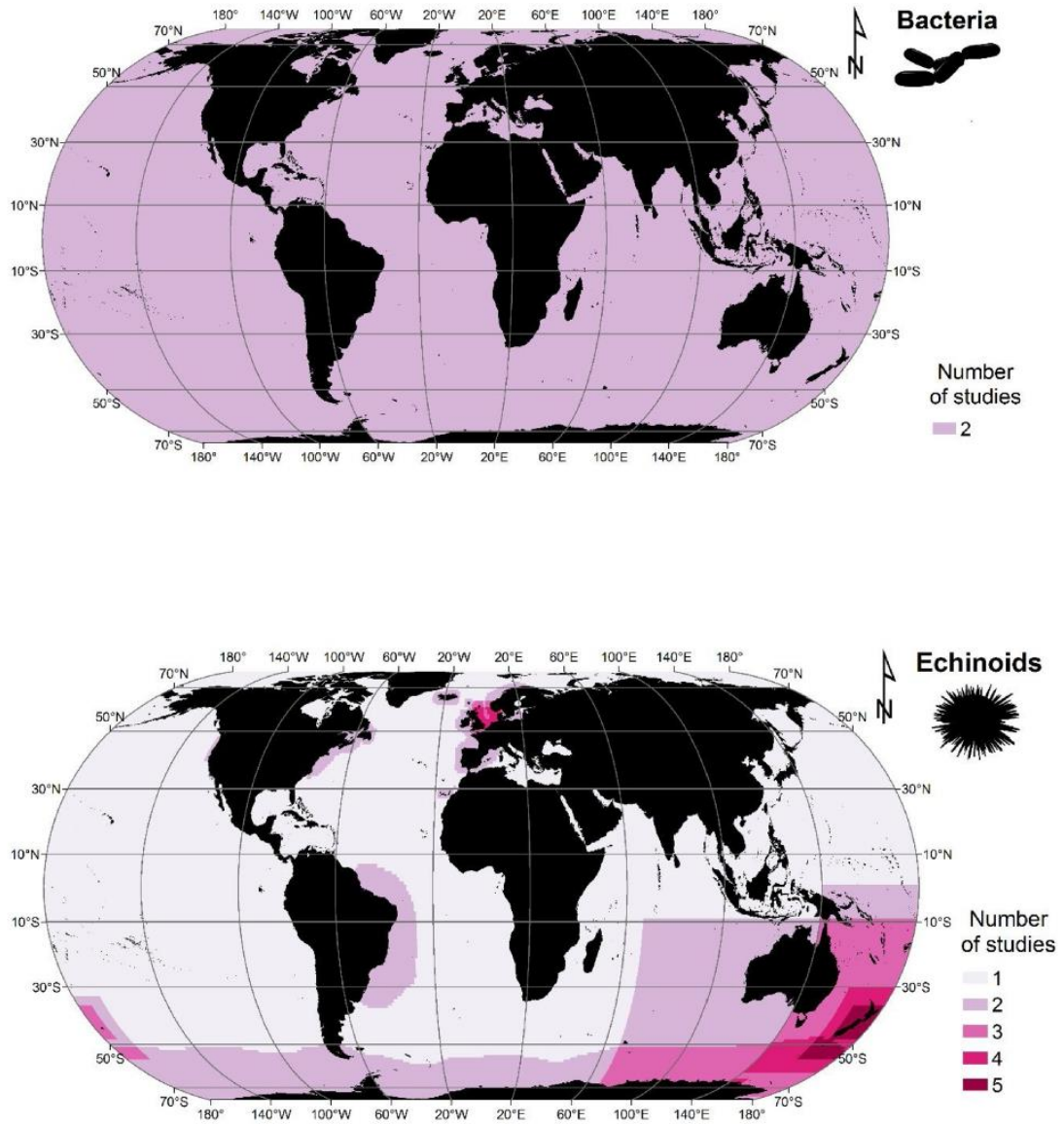
23

Fig. B1. Maps showing the spatial distribution of taxonomic groups not presented in the main text of the article.
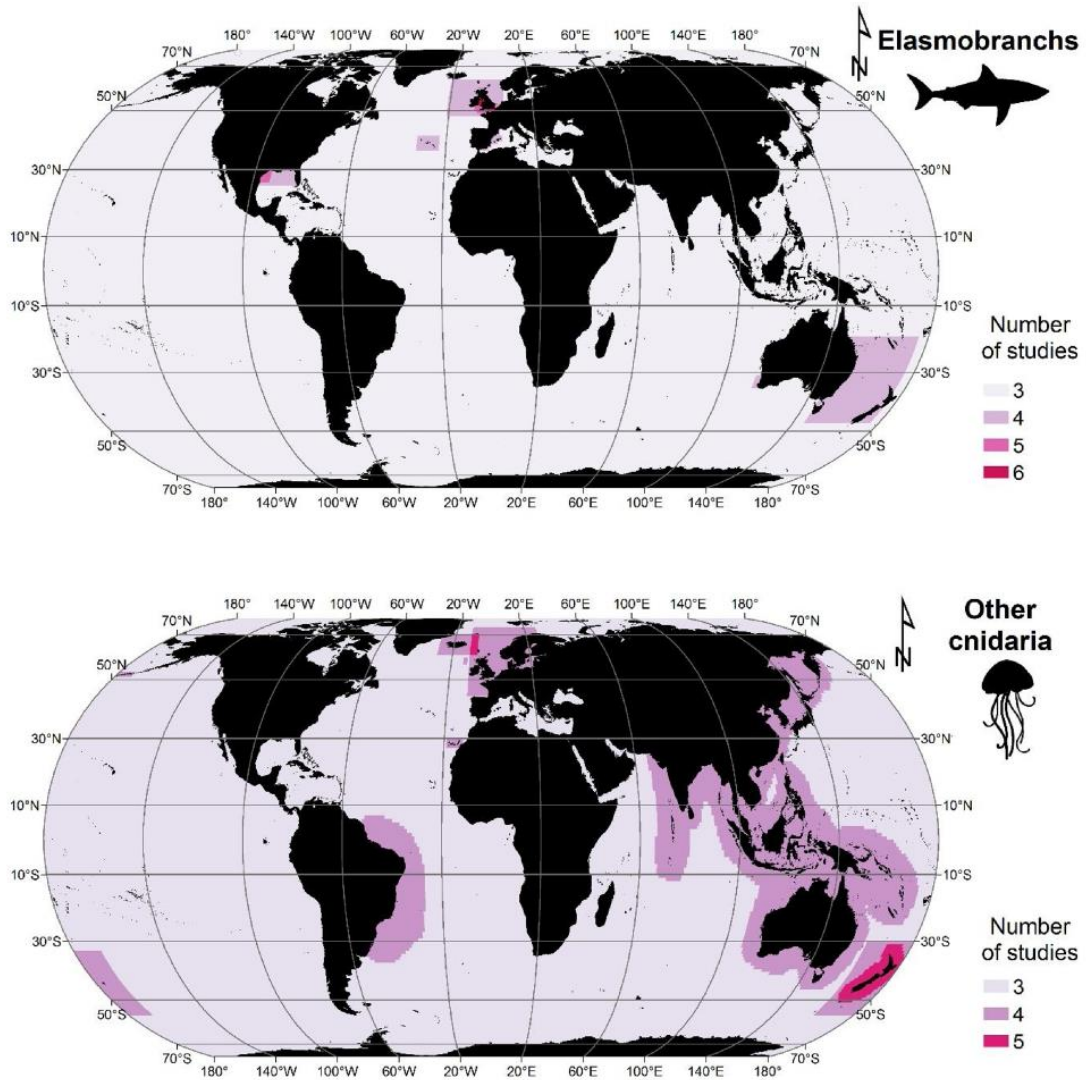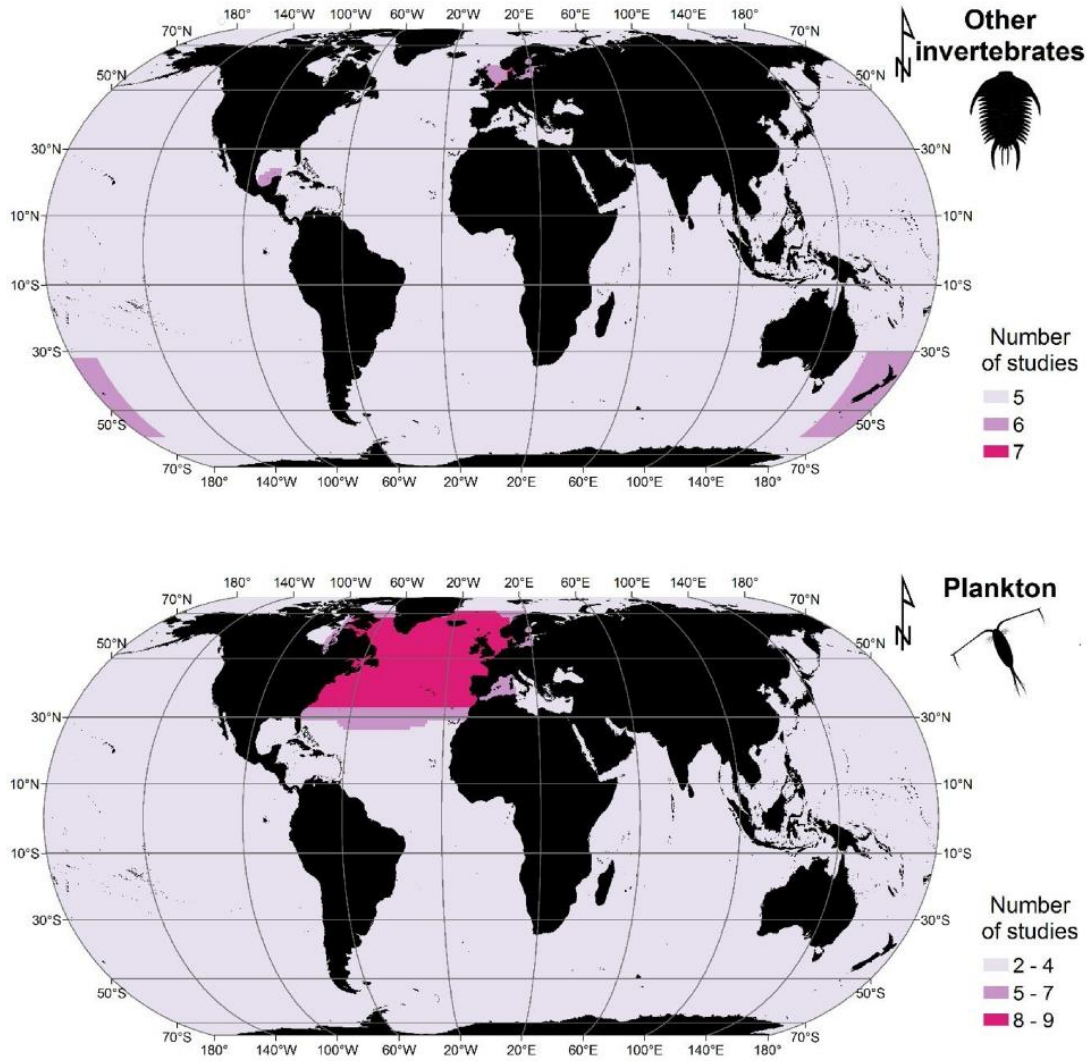
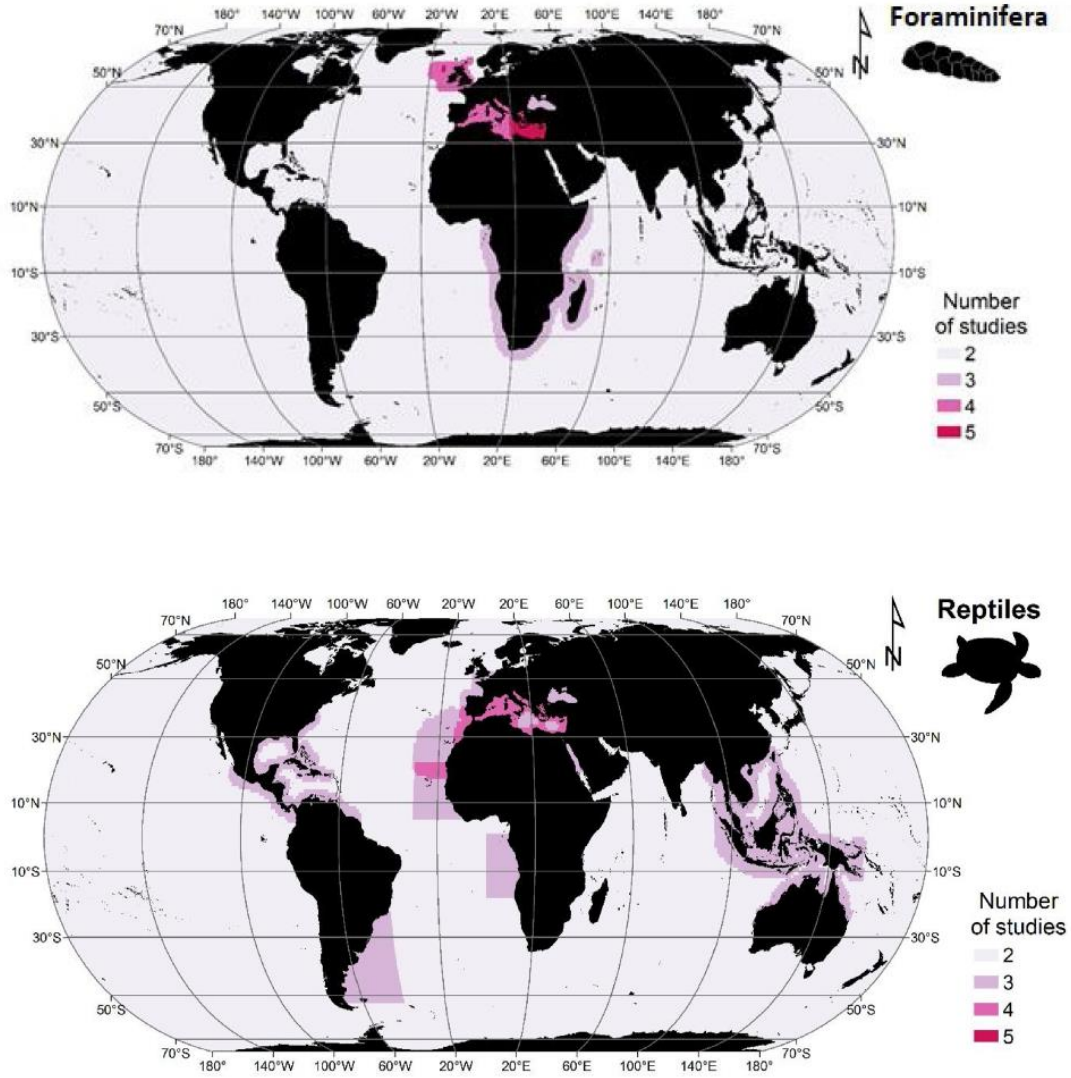Fig. B1. (continued)

Fig. B1. (*continued*)

Fig. B1. (continued)

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Fig. B1. (continued)

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Fig. B1. (*continued*)

Appendix C

Table C1

List of predictor variables used to model marine species in the literature reviewed. Variables were assigned to different categories; we show how many times appeared in the articles.

CATEGORY	VARIABLE	FREQUENCY OF USE
ATMOSPHERIC VARIABLES		
	Air temperature	15
	Precipitation	9
	Wind speed	9
	Cloud cover	7
	Thermal fronts	4
	Air humidity	3
	Cyclone activity	2
	Front probability	2
	Precipitation as snow	1
ENVIRONMENTAL DESCRIPTOR VARIABLES		
	Sediment type	30
	Substrate/bottom type	27
	Ice cover	24
	Wave exposure	13
	Benthic zone	3
	Land cover	1
	Presence/absence of tidewater glacier	1
	Treatment plant effluent exposure	1
	Land cover	1
	Percentage of area with seabank	1
	Presence of land	1
	Water run-off	1
	NAO (North Atlantic Oscillation)	1
	Shore-zone type	1
	Pacific Decadal Oscillation index	1
ECOLOGICAL VARIABLES		
	Habitat type	11
	Presence/absence/biomass of other species	7
	Phytoplankton concentration	3
	Zooplankton concentration	3
	Food availability	3
	Abundance	1
	Predation pressure	1

(*continued on next page*)

Table C1 (*continued*)

CATEGORY	VARIABLE	FREQUENCY OF USE
	Biogeographic province	1
	Vegetation productivity	1
PHYSICAL VARIABLES		
	Water temperature	240
	Photosynthetically active radiation	26
	Diffuse attenuation coefficient	20
	Turbidity	8
	Euphotic depth	6
	Vertical velocity	5
	Bed shear stress	4
	Light availability	4
	Eddy kinetic energy	4
	Irradiance	3
	Solar radiation	3
	Secchi depth	3
	Wave kinetic energy	2
	Insolation	2
	Visibility	2
	Ocean advection	1
	Magnetic anomalies	1
	Cumulative thermal stress	1
	Potential energy deficit	1
	Total kinetic energy	1
	Hue-saturation intensity	1
	Potential energy anomaly	1
	Geostrophic velocity	1
	Vorticity	1
	Potential energy deficit	1
GEOGRAPHIC VARIABLES		
	Distance to shore	54
	Geographic coordinates	20
	Distance to reefs	5
	Distance to bathymetric contours	5
	Distance to seamounts	4
	Distance from colony (birds)	3
	Distance to shelfbreak front	3
	Distance to ports	3
	Distance to soft substrate	3
	Distance to freshwater streams	3
	Distance to the nearest estuary	2
	Distance to roads	2
	Distance to the nearest city	2
	Distance to rocks	2
	Distance to rocky substrate	2
	Distance to ice	2
	Distance to persistent frontal activity	1
	Distance to moraine	1
	Distance to glaciers	1
	Distance from canyons	1
	Distance to southern boundary of Antarctic circumpolar current	1
	Distance from merchant shipping routes	1
	Distance to oceanographic fronts	1
	Distance from navy exercise areas	1
	Distance from industrial areas	1
	Distance from fishing areas	1
	Distance to nearest petroleum platform	1
	Distance to river mouths	1
	Distance from sediments	1
	Distance to colored substrate	1
	Distance to tidal inlet	1
	Distance to watersheds	1
HYDRODYNAMIC VARIABLES		
	Current velocity	45
	Mixed layer depth	15
	Sea level anomalies	10
	Sea surface height	8
	Wave height	7
	Thermocline depth	5
	Tide amplitude	4
	Tidal currents	3
	Vertical flow	2
	Sea ice thickness	2
	Tides	2
	Water mass	2

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Table C1 (*continued*)

CATEGORY	VARIABLE	FREQUENCY OF USE
	Beaufort sea state	1
	Wave direction	1
	Tidal state	1
	Ekman upwelling	1
	Thermocline strength	1
	Thermocline thickness	1
	Hydroperiod	1
	Current magnitude	1
	Prevalence of circumpolar deep water	1
	Pycnocline depth	1
	Coastal upwelling	1
	Geostrophic zonal currents	1
CHEMICAL VARIABLES		
	Salinity	147
	Chlorophyll-*a*	97
	Nitrate	41
	Phosphate	36
	Dissolved oxygen	36
	Primary productivity	34
	Silicate	26
	pH	24
	Calcite concentration	22
	Aragonite	13
	Saturated oxygen	12
	Alkalinity	11
	Apparent oxygen utilization	11
	Dissolved inorganic carbon	9
	Particulate organic carbon	9
	Suspended particulate matter	4
	Carbonate ion concentration	3
	Total nitrogen	2
	Ammonium	1
	Coloured dissolved organic matter	1
	Iron concentration	1
	Nitrogen oxide concentration	1
	Fluorescence activity	1
	Total phosphorus	1
	Dissolved organic matter	1
	Nutrient input	1
	Nitrogen concentration	1
TOPOGRAPHIC VARIABLES		
	Bathymetry	210
	Slope	109
	Rugosity	39
	Slope aspect	35
	Bathymetric position index	20
	Slope curvature	19
	Planimetric curvature	7
	Structure and complexity	5
	Profile curvature	5
	Topography	4
	Altitude	1
	Elevation	1
	Geomorphology	1
	Bathymetric gradient	1
	Hypsometric index	1
	Beach morphology	1
	Land use	1
TEMPORAL VARIABLES		
	Season of the year	7
	Year (calendar year)	4
	Length of day	3
	Time of the day	2
OTHER VARIABLES		
	Dust level	2
	Human population density	1
	Density of petroleum platforms	1
	Presence/absence of boat marinas	1
	Fishing effort	1
	Presence of fishing vessels	1
	Sampling depth	1
	Cargo traffic	1
	Boat speed	1
	Engine on/off	1
	Marine protected areas zoning	1

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CAPÍTULO 3: Divergencia funcional de las líneas base ecológicas en los arrecifes coralinos del caribe

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Research

Functional divergence from ecological baselines on Caribbean coral reefs

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Understanding how emergent ecological assemblages have diverged from natural states is fundamental in predicting future functioning and services of ecosystems. Coral reefs are of particular concern due to their high susceptibility to anthropogenic stressors. Yet, little is known about their pre-disturbance ranges of natural states, and most reports of decline are based on a limited number of sites and high levels of uncertainty. Here, we used a novel approach to estimate the physical functionality of reefs across marine ecoregions based on habitat suitability and morpho-functional traits for coral species. We calibrated ecological niche models for 49 reef-building corals of the Greater Caribbean based on occurrence records and environmental predictors, which we combined with species-specific functional coefficients derived from morpho-functional traits reflecting their contribution to the reef three-dimensional structure to estimate the reef functional potential (RFP). We then assessed the degree of divergence of western Caribbean reefs by comparing our physical functionality estimates against recent field data evaluations. We found spatial variability in RFP across the Caribbean, with the highest mean value in the western Caribbean and the lowest in areas with marginal environmental conditions. Hotspots of RFP exist along the coast of Belize and the southeast of Cuba. Overall, 84% of sites along the western Caribbean showed a substantial reduction in their physical functioning, with the highest reductions occurring within hotspots, implying that reefs displaying the greatest changes have high initial RFP. We conclude that combining niche models with species morpho-functional traits is a valuable and promising approach to estimate the large-scale functional potential of communities and the degree of change in the absence of ecological baselines. These findings have important implications and could be used to guide efforts to preserve coral reefs functionality and define priority conservation areas in the Caribbean.

Keywords: ecological niche models, functional traits, Maxent, species assemblages, stony corals, structural complexity

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Introduction

Ecosystem functioning and services largely depend upon the species combinations and traits that form biological communities (Mouillot et al. 2011). There is increasing evidence that environmental stress modifies the structure of these communities, but details on how functional traits of the resulting species combinations affect ecosystem functions are still uncertain (Funk et al. 2017). Trait-based approaches have a long history and are well established in ecological studies (Violle et al. 2007); nevertheless, their incorporation into ecological modelling is more recent (Zakharova et al. 2019). Overall, trait-based approaches incorporate any morphological or physiological trait measurable at the individual level, which indirectly affects organism performance (Violle et al. 2007). The use of functional traits thereby links an organism's performance to its functional role in populations, communities and ecosystems (Zakharova et al. 2019). The use of trait-based modelling approaches with emphasis on environmental gradients should therefore be more successful in providing general and predictable rules of a community's response to perturbations (McGill et al. 2006, Laughlin and Laughlin 2013, Mouillot et al. 2013, Scherrer et al. 2019). This is particularly relevant in the case of foundation species which, owing to their functional traits, create and define entire ecological communities or ecosystems, and whose loss can be severe for biodiversity and ecosystem services (Ellison et al. 2005).

In tropical shallow marine environments, reef-building corals are foundation species, and are the primary constructors of the physical three-dimensional structure by adding large amounts of calcium carbonate (Perry et al. 2012, Graham and Nash 2013). The physical functionality of reefs favors a high diversity of associated taxa through the provision of heterogeneous habitats that allow the regulation of ecological processes such as recruitment, competition and predation (Pratchett et al. 2008, Coker et al. 2009, Graham and Nash 2013).

Usually, the assessment of reef condition is based on estimations of total coral cover, without considering species-specific differences or functional traits (Gardner et al. 2003, De'Ath et al. 2012). However, corals exhibit a variety of life-history strategies that are reflected in a large range of growth rates and morphologies (Richardson et al. 2017, Zawada et al. 2019a). The identity of the species and their associated traits therefore largely define ecosystem functions and dynamics in coral reefs (Alvarez-Filip et al. 2011, Denis et al. 2017, Zawada et al. 2019b, González-Barrios et al. 2021). There are many corals traits that can be used to estimate functional diversity (McWilliam et al. 2018), but only a small subset contributes to the physical functionality of reefs and controls its capacity to create complex three-dimensional structures by means of calcium carbonate precipitation (González-Barrios and Álvarez-Filip 2018, Perry and Alvarez-Filip 2019). The three fundamental properties of coral species derived from their functional traits that contribute to reef physical functionality are: coral abundance or cover, calcification rate and structural complexity (González-Barrios and Álvarez-Filip 2018, González-Barrios et al. 2021). From an ecological perspective, the abundance or cover of individual species dictates their relative contribution in terms of functional traits to the ecosystem. The calcification rate denotes the capacity for reef accretion and regeneration, and how it influences the carbonate budget (Todd 2008, Perry et al. 2012). The structural complexity determines colony morphology and framework character that controls habitat complexity (Gratwicke and Speight 2005, Alvarez-Filip et al. 2011).

Coral populations are declining worldwide as a result of anthropogenic activities such as land-based pollution, overfishing, coastal development and climate change (Hughes et al. 2003, 2017). The resulting widespread coral mortality and the reduction of live coral cover is mediated by organism vulnerability and, as a consequence, human activities have caused non-random changes in community structure and in some cases novel assemblages (McKinney 1997, Bellwood et al. 2004, Alvarez-Filip et al. 2013, Spalding and Brown 2015, Toth et al. 2019). In the western Atlantic, *Acropora* spp. and *Orbicella* spp., both considered important reef-building corals (Jackson 1992, Roff et al. 2020), have been severely reduced and replaced by non-framework building or 'weedy' corals such as *Porites astreoides* and *Agaricia agaricites* (Bruckner and Bruckner 2006, Edmunds and Elahi 2007, Green et al. 2008, Rodríguez-Martínez et al. 2014, Perry et al. 2015, Estrada-Saldívar et al. 2019). However, the characteristics of these 'weedy' species prevent them from fulfilling the functional role of the former reef-building species (González-Barrios et al. 2021), therefore, compromising key ecosystem functions and services (Perry et al. 2018, Estrada-Saldívar et al. 2019, Perry and Alvarez-Filip 2019).

Understanding how such novel ecological assemblages have diverged from pre-disturbance or pristine ecological states is fundamental to predict the implications of these changes for ecosystem functioning and services (Schwerdtner Máñez et al. 2014, Thurstan et al. 2015). For that it is crucial to know the initial or baseline state of the community prior to human-induced changes or at a particular point in history (Kopf et al. 2015, Nogué et al. 2017). Such ecological baselines not only help quantify the extent of community change but also can help guide more effective conservation and management (Pitcher 2005, Schwerdtner Máñez et al. 2014).

Determining ecosystem baselines is challenging owing to the absence of reliable historical data (Bruno et al. 2014, Eddy et al. 2018). Very little is known about natural states of coral reefs, and most of historical data are usually defined at regional scale for a few reef locations and with a high level of uncertainty and potential biases (Knowlton and Jackson 2008, Eddy et al. 2018, Meesters et al. 2020). Moreover, attempts to estimate the pre-human baseline condition do not always consider species habitat preferences or large-scale environmental influences, which have a fundamental effect on the natural states of ecosystems (Bruno et al. 2014, Stein et al. 2014, McGarigal et al. 2016). In the absence of reliable historical data, a promising approach is therefore to reconstruct these baselines from ecological models of past ecosystems. Such approaches have been used to model historical changes in marine food webs or to construct models for

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past ecosystems to design sustainable fisheries (Pitcher 2005, Lotze et al. 2011).

Ecological niche models (ENM) have been widely used to study the ecological requirements of species by relating their known distribution to a set of relevant environmental variables (Peterson 2006), often focusing on species as individual entities. In recent years, however, new approaches have attempted to model different structural or compositional aspects of the assemblage (Pottier et al. 2013, D'Amen et al. 2017, Grenié et al. 2020). Such is the case of the so-called stacked species distribution models, which starts from modeling individual species to later stacking them to form assemblages (Dubuis et al. 2011, Guisan and Rahbek 2011).

Species richness is often the main property of the assemblages estimated using stacking models, and functional traits are often used to constrain species distributions or as assembly rules to reduce species richness overprediction (Guisan and Rahbek 2011, D'Amen et al. 2015). However, coupling the functional traits of habitat-forming species to the niche models estimating species fundamental niches, can also enable an estimate of the potential of physical functionality of communities across extensive areas, which we refer to as reef functional potential. This niche-trait based approach may therefore provide a promising way to link species environmental preferences, environmental variability and functional traits to improve inferences on the impact of environmental change on biodiversity and ecosystem functioning (Kearney et al. 2010, Funk et al. 2017).

To spatially estimate the reef functional potential (RFP) of Greater Caribbean coral reefs, we integrate ecological niche models of 49 reef-building coral species with morpho-functional traits. The modeled results are then compared to current estimates of the reef physical functionality derived from field data to quantify the degree of divergence of reefs along the western Caribbean. Our approach predicts the capacity to create complex three-dimensional structures rather than only portraying potential species distribution ranges. Because we use only environmental predictors, the estimates of reef functional potential do not consider other natural or anthropogenic disturbances acting over these ecosystems. Similarly, species richness and the functional characteristics of the communities are assumed to be controlled by the environment without consideration of processes such as biotic interactions and dispersal that shape ecological assemblages (D'Amen et al. 2017).

Methods

Species occurrence records

To create a geodatabase of occurrence records of Atlantic shallow-water reef-building corals we conducted a systematic search using the following sources: The Global Biodiversity Information Facilities (<www.gbif.org/>, GBIF Occurrence Download <https://doi.org/10.15468/dl.iwb5jx> (4 Sept 2017), GBIF Occurrence Download

<https://doi.org/10.15468/dl.n9x4nb> (12 Feb 2019)), the Ocean Biogeographic Information System (Ocean Biodiversity Infromation System (OBIS), Intergovernmental Oceanographic Commission of UNESCO, <https://obis.org/>), Biodiversity Information Serving Our Nation ((BISON), accessed 12 Feb 2019, <https://bison.usgs.gov/#home>), the Time Series Coral-cover from Florida and the Virgin Islands (Guest et al. 2018), the Caribbean Coastal Marine Productivity Program database (Linton 2001), the Atlantic and Gulf Rapid Reef Assessment database (Marks and Lang 2018), and data from the laboratory of Biodiversity and Reef Conservation, which was curated, systemized, and is now included in the Caribbean Reefs Information System database. Additionally, we performed a literature search to incorporate occurrence data for reef areas that appeared to be underrepresented when the pooled occurrences were plotted in the geographic space (i.e. none or very few records). Those areas were in Cabo Verde, Cuba, Guatemala, Honduras, Mexico, Nicaragua, Puerto Rico, Dominican Republic and Flower Garden Banks in USA (Supporting information). The compiled occurrences were reviewed to exclude duplicated coordinates per species, data coming from the fossil record and data with georeferencing errors (i.e. records on land).

Dataset treatment

Two important assumptions when developing niche models are that species are in equilibrium with the environment within their native range, and that the species niches are conserved over time (Richmond et al. 2010). The violation of these assumptions can cause underprediction of potential areas of suitability. In the case of Caribbean corals, there is evidence supporting that species composition and distribution ranges have been nearly homogeneous, even at geological time scales (Jackson 1992, Miloslavich et al. 2010, Veron et al. 2015). For instance, Toth et al. (2019) demonstrated that species composition in the Florida Keys Reef Trak has remained relatively stable since the Holocene. Yet, to avoid the violation of this assumptions in our models, we used short-time scale occurrence data for model calibration (from 1950 to 2019).

One more consideration regarding occurrence data is the effect of sampling bias on model performance. Most algorithms estimate the species environmental requirements by correlating occurrence records with environmental variables (Warren and Seifert 2011), which makes them especially sensitive to sampling bias and spatial autocorrelation (Segurado et al. 2006, Phillips et al. 2009). Geographical biases in occurrence data often result in environmental biases, which may lead to inaccurate models (Phillips et al. 2009, Yackulic et al. 2013). Despite the recognition of the importance of sample bias on ecological niche models, currently, there is no consensus about how to properly address this problem. To cope with this, we applied a spatial filter with a minimum nearest-neighbor distance between points in order to reduce spatial clumping of occurrences (Veloz 2009, Kramer-Schadt et al. 2013, Boria et al. 2014). To select

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the proper distance for the spatial thinning of occurrence data we tested models using ten coral species with different sample sizes and geographic range sizes as test examples. One group of models had no spatial thinning of the occurrence data; this yielded strong model overfitting coincident with a higher density of occurrences. A second group of models was run with a spatial filtering of 20 km applied to all data, and a third group was run with occurrences split in subsets according to different geographical clumping, where the data corresponding to the western Caribbean basin (higher clumping) was filtered with a distance of 40 km, and the rest of the data with a distance of 20 km. The resulting model outputs were converted to presence–absence maps using the minimum training presence threshold to cut off habitat suitability (Kramer-Schadt et al. 2013). We visually compared the two sets of presence–absence models with filtered occurrences against those generated with no thinning. As a result, we decided to use the 40–20 km filtering as these models showed a reduction in model overfitting, and better represented the known distribution of species. Once occurrence data were spatially filtered, the resulting subset was used as the training dataset, and the occurrences not included were used as testing dataset.

Spatial autocorrelation (SAC) is known to be an issue in distribution models. We investigated SAC in the data sets before and after the filtering process using the Moran's I statistics (R package 'ape' V 5.5, Paradis and Schliep 2019), and observed a substantial reduction in the SAC after the filtering process (Supporting information). We decided not to eliminate the remaining SAC further as we would risk underestimating the importance of the variables and losing explanatory power (Araújo and Williams 2000, Sillero and Barbosa 2021). Moreover, given that many abiotic factors commonly used in species distribution models are only independent at very long distances (Levin 1992), the control of SAC at large spatial scales is usually necessary when environmental factors are not considered the main drivers of ecological patterns (Diniz-Filho et al. 2003). Thus, we assumed that the remaining SAC in our data did not represent a problem as the models were calibrated at a macro-scale and were based on environmental controls.

Species selection

To select the species to be modeled, we applied a filter for those with more than 15 occurrence records after data treatment, resulting in a total of 49 coral species. The selected species represent approximately 48% of corals (scleractinia and hydrozoa) reported for the Caribbean (n = 102, Miloslavich et al. 2010) and include the main reef-builders in the region (Jackson 1992). These species exhibit different life-history strategies classified as competitive, 'weedy', stress-tolerant and generalists based on a trait-based approach accounting for colony morphology, growth, calcification, reproductive mode and symbiont richness (Darling et al. 2012). Furthermore, the species display different distributional ranges such as *Dendrogyra cilyndrus*, constrained to the

Caribbean basin, *Acropora cervicornis* and *A. palmata* which are found in the Caribbean and Gulf of Mexico, and species such as *Porites astreoides* and *Siderastrea siderea* which are also found in reefs from Brazil and among coral communities in west Africa.

Calibration areas

Choosing the extent of the calibration area (M) for ecological niche modelling is a key step to produce accurate models, preferably defined as the geographic region that has been accessible to the species over relevant time periods and reflects its ecology and evolutionary history (Barve et al. 2011). In the case of marine organisms, delineating the calibration area represents a challenge because of the lack of physical barriers and the fact that, for most organisms, dispersal depends upon ocean currents (Melo-Merino et al. 2020). Corals have complex life histories, including a larval phase that allow a greater dispersal through ocean currents, but whose success depends largely on the characteristics of the larvae (e.g. lifespan, presence of symbionts) and on environmental conditions, so they may not be able to occupy all areas to which they have access. Although the area of interest in this work is the Greater Caribbean, we considered it important to include the entire distribution of the species to make the niche estimation as realistic as possible. Therefore, we decided to use all the regions occupied by the species to calibrate the models. As a result, we defined two calibration areas dividing coral species into those that inhabit the Caribbean and Gulf of Mexico (M Greater Caribbean), and those that occupy a wider extent in the Atlantic and are found in Brazilian reefs and coral communities in Africa (M Atlantic; Supporting information).

Environmental predictors

We selected the environmental predictors recognized to influence the distribution of reef corals (Kleypas et al. 1999), and that have been used in other niche and distribution models for shallow water corals performed on a global scale (Couce et al. 2012, Freeman et al. 2013). These environmental variables are temperature, current velocity, diffuse attenuation coefficient, dissolved oxygen, nitrate, photosynthetically available radiation (PAR), phosphate, salinity and omega aragonite. We used the minimum, mean and maximum for each variable (but omega aragonite) from the Bio-ORACLE climate dataset (Tyberghein et al. 2012, Assis et al. 2018), except for PAR for which only the maximum and minimum were available and for pH for which only the mean was available. Additionally, we calculated the mean omega aragonite through the CO2calc software designed to estimate carbonate system parameters (Robbins et al. 2010) using salinity, temperature, total alkalinity (calculated following Lee et al. 2006), pH and depth (as proxy of pressure) as input values. All environmental predictors were downloaded and/or calculated at a 5 arcmin (~9 km) spatial resolution, and for the ocean surface layer.

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The final set of environmental predictors used to calibrate the models was selected using a combined procedure. We estimated the correlation among all metrics by Pearson's correlation coefficient and explored their contribution via a jackknife procedure implemented in preliminary Maxent models. For each species, the predictors with the highest contributions were usually derived from the same variable (e.g. dissolved oxygen max, min and mean, followed by diffuse attenuation max, min, and, mean) that showed strong correlations with each other. We therefore decided to perform an initial selection of predictors among groups of variables. We started by comparing the first two groups with the highest contributions and chose the metrics with the highest contributions if they were not correlated with each other. In the case where the metric with the highest contribution in one group was highly correlated ($r > 0.85$) with the highest in the second group, the one with the largest contribution was preferred over the other, and in the second group, the selected metric was the one uncorrelated with those previously selected. In the case of omega aragonite and pH that only had mean values and were correlated with each other, we selected the one with the highest contribution. We decided to use a single set of environmental variables for all the species since it is expected that closely related species occupy similar environmental niches (Wiens et al. 2010). For the final selection, we considered the variables that appeared with more frequency as the most important (estimated as percentage of relative contribution). The final selection included nine variables: minimum current velocity, minimum diffuse attenuation, minimum dissolved oxygen, maximum nitrate concentration, maximum PAR, mean pH, maximum phosphate concentration, minimum salinity and mean temperature (Supporting information).

Ecological niche models calibration and evaluation

We used the presence-background algorithm of Maxent ver. 3.4.1 (Phillips et al. 2006) as implemented in the 'kuenm' package (Cobos et al. 2019) in the R statistical environment (<www.r-project.org>). This package provides an automated way to tune the models by testing all possible combinations between regularization multipliers, feature classes and environmental predictors to choose the combination that best explains the data provided. We explored different parameterizations using 493 candidate models generated through the interaction of 17 regularization multiplayers (from 0.1 to 1 with intervals of 0.1, 1.5, 2, 2.5, and from 3 to 6 with intervals of 1), and all 29 possible combinations among five feature classes (l=linear, q=quadratic, p=product, t=threshold and h=hinge). The selection of the best candidate models was based on model significance, predictive ability and model complexity as implemented in 'kuenm'. First, the models were selected based on statistical significance using a partial ROC analysis (partial receiver operating characteristic; Peterson et al. 2008). Second, statistically significant models were tested to omission criteria using a threshold of 10% training omission rate (E=10%; Muscarella et al. 2014). Finally, model complexity was evaluated through the Akaike

information criteria corrected for small sample sizes and the models with the lowest AICc values were selected (Warren and Seifert 2011, Muscarella et al. 2014). With this framework for model selection (statistical significance, low OR and low AICc) the best models for the individual species showed different model parameterizations, but all models showed a good performance (Supporting information).

Final models for each of the 49 coral species were created using the specific settings from the best model and calibrated in their corresponding M (Greater Caribbean or Atlantic; Supporting information). We generated ten replicates of the model by bootstrap resampling for each species using the training-data subset. We selected the logistic output format, which estimates environmental suitability represented in a continuous scale from 0 (not suitable) to 1 (most suitable). To represent habitat suitability, we used the median values across replicates. When more than one model was selected as the best, we calculated the median among all models.

To evaluate final model performance, we used the AUC ratio and statistical significance of the partial ROC (area under the curve of the receiving-operating characteristic; Peterson et al. 2008). This metric takes values from 0 to 2 where values greater than 1 indicate that the predictions of the model are better than random. For all the models we allowed an omission rate of 10% (E=10%) and evaluated statistical significance of the partial ROC analysis. For all the species, models showed a good performance, with AUC ratios greater than 1, and all being statistically significant (Supporting information).

Coral reefs functional potential estimation

To estimate the reef functional potential (RFP) of Greater Caribbean reefs, we created a functionality metric by combining environmental suitability obtained using the Maxent models with coral morpho-functional traits.

We chose traits that are fundamental for determining the physical functionality of coral species in reef environments: calcification rate and skeletal complexity (given by colony rugosity and height). These morpho-functional traits are assumed to be strongly related with the functional role of corals in the ecosystem (González-Barrios and Álvarez-Filip 2018). Moreover, coral morphology has been considered to be an important part of a coral 'super trait' that captures large variations of biological and ecological processes (Madin et al. 2016). For the inclusion of coral morpho-functional traits, we used a previously published calculation of Caribbean coral species functional coefficients related to their capacity to build complex three-dimensional structures estimated by González-Barrios and Álvarez-Filip (2018). They used a combination of published literature and field data on extension rate, skeletal density and morphometric data to estimate corals calcification rates (kg $CaCO_3$ m^{-2} yr^{-1}) and colony complexity represented by its rugosity and height. Those three metrics were first standardized, and then averaged to represent the functional coefficient (FC) of the species, denoting their capacity to create complex three-dimensional structures in a reef. For those species not included in their publication

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(six species), we estimated their functional coefficient following González-Barrios and Álvarez-Filip (2018) methodology.

The Maxent output can be considered as a measure of environmental suitability, where higher values represent optimal conditions for the species (Phillips et al. 2006). So, as a first step before the stacking process we performed a raster operation to multiply the suitability raster layer of each species by its functional coefficient. Having done this, we estimated the RFP by stacking the product rasters based on the sum of the 49 raster layers derived from the multiplication (Fig. 1).

RFP layer post-processing

To restrict the area of analysis to the areas with reef development, the final output representing the RFP was cropped using a reef layer. To create this layer, we used the global map of shallow tropical coral reefs created by the World Resources Institute for the Reefs at Risk Revisited project (Burke et al. 2011). First, we created a fishnet shapefile with the same spatial resolution as the environmental variables (5 arcmin) encompassing the extent of the Greater Caribbean. Then, we selected all the cells in the fishnet that intersected with the reefs polygons. We added some additional reef locations that were absent in the initial polygon layer, located in the southwest Gulf of Mexico, the north of San Andres Archipelago, Honduras, Guatemala, Bahamas and Flower Garden Banks (Supporting information).

Once the RFP was limited to the areas with reef development, we analyzed the spatial patterns of the RFP using the ecoregion classification of the Marine Ecoregions of the
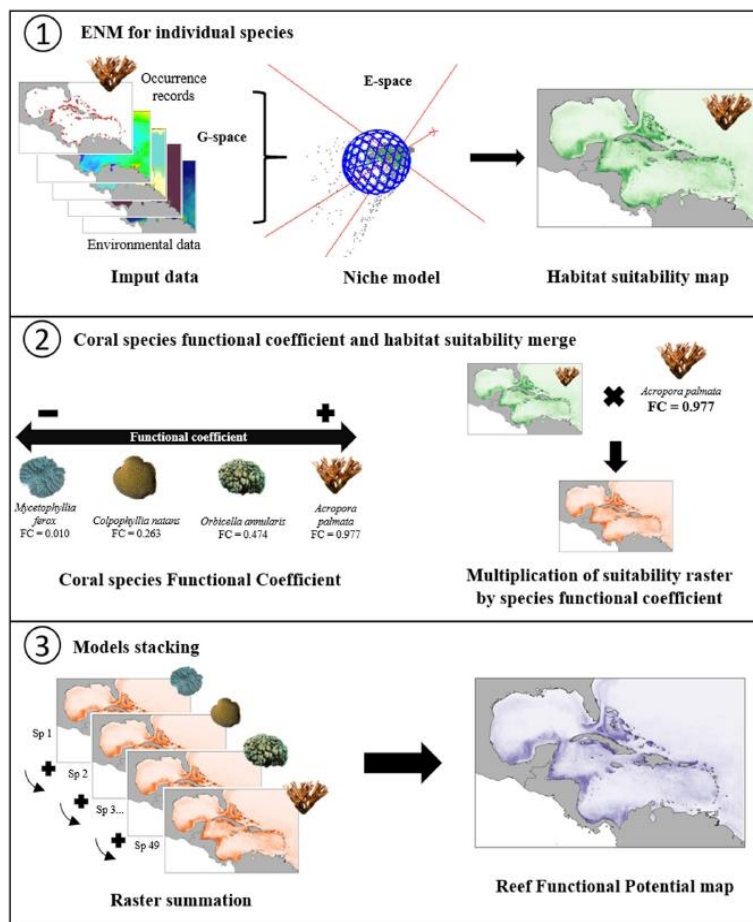

Figure 1. Schematic representation of the reef functional potential estimation procedure. Step 1: Generation of individual ecological niche models for the 49 species. Here, species occurrence records and environmental variables are interpreted by the algorithm in the ecological space, and then projected again in the geographic space as a suitability map. Step 2: Coral species functional coefficient and habitat suitability combination. Example of species with low, medium and high functional coefficient. Here, the habitat suitability raster is multiplied by the species functional coefficients. Step 3: Summation of the 49 raster layers obtained through the multiplication procedure to calculate the reef functional potential.

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World (Spalding et al. 2007). To determine the differences in the mean RFP among ecoregions we performed a one-way ANOVA test and a pairwise post hoc comparison Tukey test.

Hotspot analysis

To identify zones with the highest RFP we used the Getis-Ord G_i^* hotspot analysis (Getis and Ord 1992). This method compares proportionally the local sum of the variable (RFP value) in each cell and its neighbors with all the cells in the study area to measure the intensity of clustering of high or low values. When the local sum is higher or lower than expected by chance, the G_i^* has large positive or negative values. Thus, a z-score is estimated for each cell, where a large positive z-score denotes a hotspot and a large negative z-score a coldspot. As a z-score derived from a standard normal distribution, no further calculations are required. We conducted the Getis-Ord analysis with the function available in the ArcGIS 10.5 environment (Environmental Systems Research Institute (ESRI) 2015, ArcGIS desktop ver. 10.3).

Divergence of coral reefs functional potential

To estimate the degree of divergence in the RFP we used the western Caribbean (also known as the Mesoamerican reef) as study case. This region has been extensively surveyed to monitor coral reef condition along the ~1000 km reef system located within Mexico, Belize, Guatemala and Honduras, which is composed of fringing reefs, barrier reefs and atolls (Gress et al. 2019). For this analysis we used published information on the estimation of the reef functional index (RFI; González-Barrios and Álvarez-Filip 2018), complemented with information obtained through the Caribbean Reefs Information System database. Data collection follows the AGRRA protocol point intercept (Lang et al. 2010) and ReefBudget (Perry et al. 2012) methodologies.

A total of 242 sites were included in this analysis covering a period from 2010 to 2017. We selected this period as the coral cover remained relatively stable throughout the region given the absence of severe disturbance events (McField et al. 2018, Contreras-Silva et al. 2020). This period is so representative of the (poor) condition of many reef areas through the Caribbean (Jackson et al. 2014). Before this period, coral cover underwent considerable declines related to thermal anomalies, hurricane impacts, coral diseases and coastal development (García-Salgado et al. 2008, Eakin et al. 2010, Contreras-Silva et al. 2020), but since mid-2000s slightly (~ 5%) recovered, although with no evident effects on reef functionality (McField et al. 2018, Elías Ilosvay et al. 2018, González-Barrios et al. 2021). In 2018 a new deadly coral disease impacted the region, triggering further coral losses (Estrada-Saldívar et al. 2021). When information was available for more than one year for the same site only the most recent was used.

The RFI estimate is based on the species-specific functional coefficient that denotes its capacity to create complex three-dimensional structures and species-level coral cover data determining the relative contribution of each species to the overall RFI (González-Barrios and Álvarez-Filip 2018). Following Eq. 1, where Lcc_i is the percentage of live coral cover and Fc_i the functional coefficient of the species i.

$$RFI = \sum \left(\frac{Lcc_i}{100} \right) Fc_i \tag{1}$$

The RFI is obtained using the sum of the product of the FC by the cover of each species present in a site. To facilitate the numerical interpretation, the RFI is fourth-root transformed, such that the index varies from almost zero in reefs with low functionality to one in reefs with high functionality (González-Barrios and Álvarez-Filip 2018, Cabral-Tena et al. 2020).

The RFI obtained from field data was plotted against the modeled RFP to which we added an equivalence line. To construct this line, we used 0 as the minimum value for both axes and as maximum, the highest value that could potentially be achieved in each case. In the case of the FRI, the highest value would correspond to a hypothetical site with 100% of coral cover of the species with the highest functional coefficient, corresponding to a RFI of 0.977. In the case of modeled RFP the highest value would correspond to a cell in which the suitability value was 1 for all the 49 modelled species, in this case the RFP would be of 10.568. On the plot, a site with a coherent RFI and RFP values would be close to the line, sites with a higher RFI than RFP would be above the line, and sites with lower RFI than RFP would be below the line. As a measure of divergence from the RFP, we used the distance of each point to the equivalence line that we further transformed into percentage values.

Results

Reef functional potential

In general, distribution models for the 49 coral species showed a good representation of the known present-day species distributions. Using the stacked models, we found that Greater Caribbean marine ecoregions presented a high degree of spatial variability in RFP, with values ranging from 0.08 (low) to 9.35 (high) across the entire reef area. The ecoregion with the highest mean value of RFP was the western Caribbean, followed by the Floridean, Bahamian, Greater Antilles and the southwestern Caribbean (Fig. 2a). In contrast, ecoregions with the lowest RFP were Bermuda and the northern Gulf of Mexico (Fig. 2a). The western Caribbean was the ecoregion with the highest number of cells with high RFP values. Conversely, the southern Caribbean showed low values of RFP except for the Morrocoy National Park, Los Roques and Isla las Aves in Venezuela. The one-way ANOVA confirmed significant differences between ecoregions (p < 0.05). The pairwise-comparison test showed differences especially for the western Caribbean, which was significantly different to all other ecoregions (Fig. 3). The hotspot analysis identified the highest RFP along the coast of Belize and the
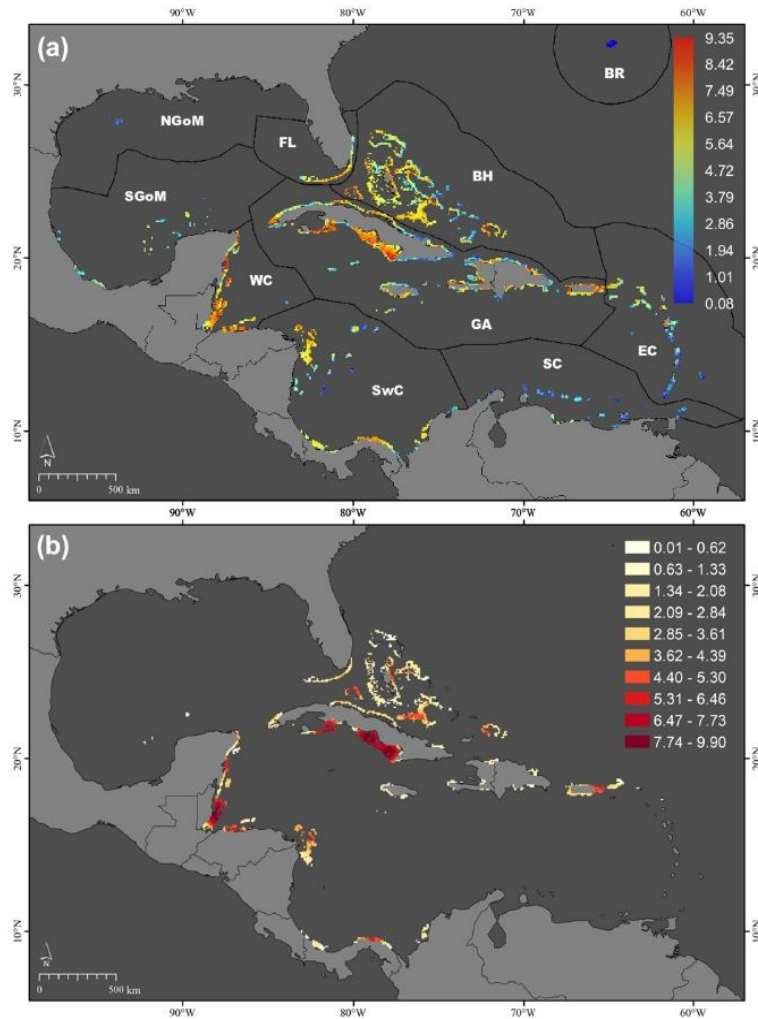
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Figure 2. Reef functional potential (RFP) and hotspot analysis of Greater Caribbean coral reefs. (a) Distribution of the RFP among ecoregions represented by the black lines: NGoM: northern Gulf of Mexico, FL: Floridian, BH: Bahamian, BR: Bermuda, SGoM: southern Gulf of Mexico, WC: western Caribbean, GA: Greater Antilles, EC: eastern Caribbean, SwC: southwestern Caribbean and SC: southern Caribbean. (b) Hotspots of reef functional potential in the Greater Caribbean using the Getis-Ord hotspot analysis. Legend shows the Getis-Ord G_i^* z-score values.

southeast coast of Cuba, followed by the central coast of the Yucatán Peninsula in Mexico, the west coast of Honduras, Cay Sal Bank in the Bahamas, the eastern Puerto Rico and the Kuna Yala province of Panama (Fig. 2b).

Divergence in reef functional potential

Of the reefs in the western Caribbean, 84% showed a reduction in their physical functionality with respect to the RFP estimation (blue dots; Fig. 4a), and nearly half of the sites presented a reduction superior to 30% (dark blue dots; Fig. 4a). Conversely, only a small proportion of sites, mainly located in Roatan island, Honduras and the north and south of the Mexican Yucatan peninsula showed higher RFI values than

those expected by the models, and the majority with a low difference (< 15%; red dots; Fig. 4a). We observed a spatially consistent pattern of decrease in physical functionality of reefs along the western Caribbean. Sites with the most drastic losses are mainly located in the north of the Yucatan peninsula and the Sian Ka'an Biosphere Reserve in Mexico, central and southern Belize and coastal Honduras (Fig. 4b). On average, the physical functionality of the western Caribbean reefs has decreased from the expected values by 30% (± 15% SD). Some of the reefs with the highest levels of decrease in physical functionality are located inside hotspot zones. A Spearman correlation analysis between percentage of divergence and hotspot G_i^*Zscore value showed a low but significant negative correlation (p < 0.001, rho = −0.47; Fig. 5).
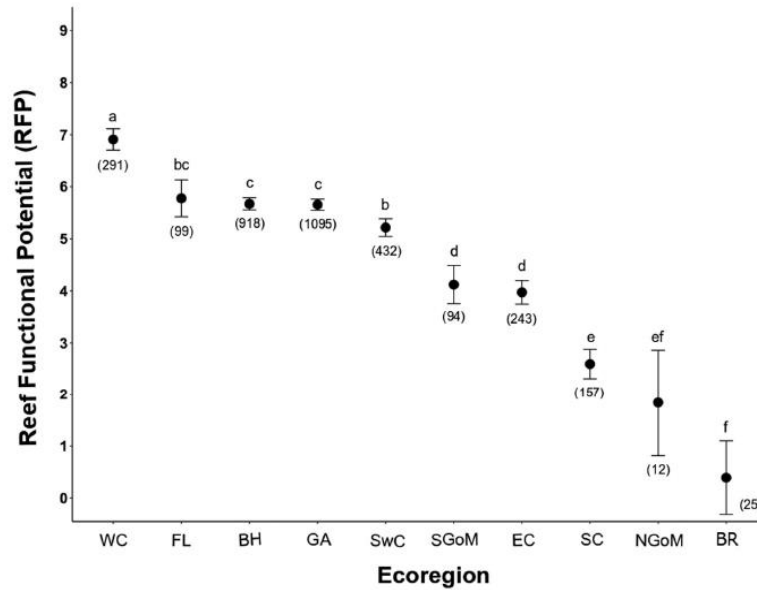
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Figure 3. Mean reef functional potential per marine ecoregion. Error bars represent the confidence intervals at 95%. Letters above the bars denote levels of significance, the means that do not share a letter have a difference that is statistically significant. Numbers in parentheses denote the *n* or number of cells in each ecoregion.
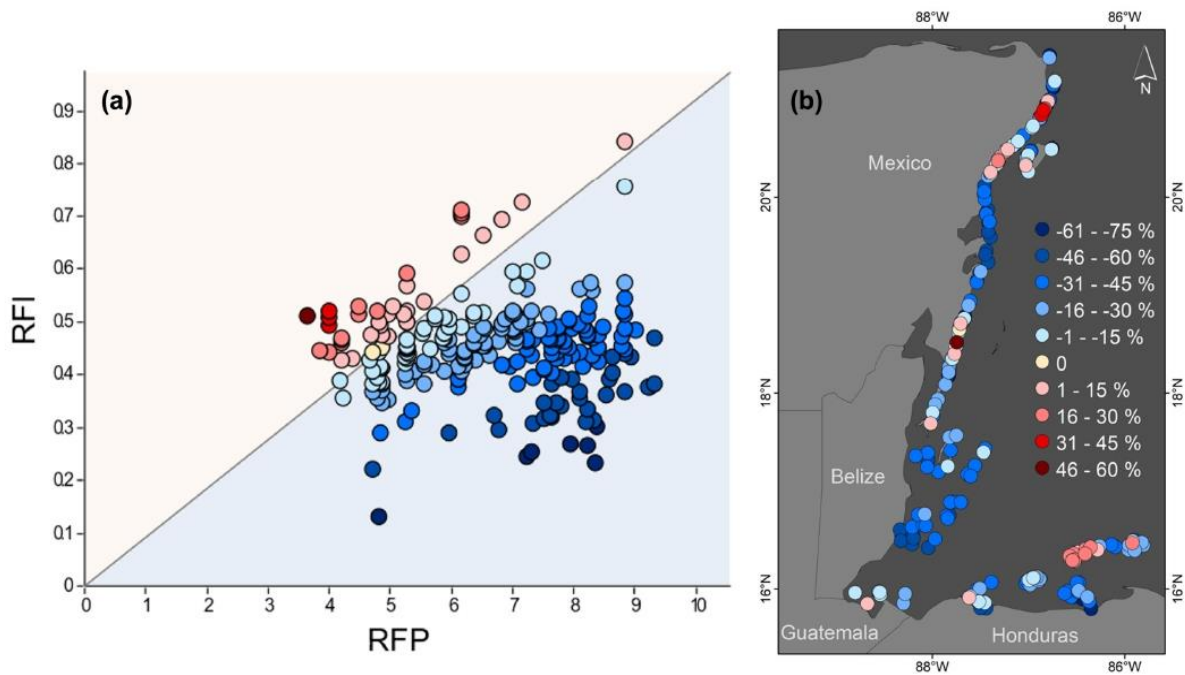

Figure 4. Divergence of reef functional potential. (a) Comparison between reef functional index (RFI) estimated with field data and reef functional potential (RFP) estimated through the models. Black line represents the correspondence between observed and predicted reef functioning. Red points above the regression line correspond to sites with observed values higher than modeled values. Blue points below the line correspond to sites with lower observed values than modeled values. The distance from the line represents a measure of the divergence from reef functional potential. (b) Representation of the divergence from reef functional potential in the geographic space, where legend represent values expressed as percentage.

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Discussion

In this study, we show that the combination of ecological niche models and species morpho-functional trait metrics is a promising approach to estimate the large-scale functional potential of ecological communities in the absence of anthropogenic disturbance. This approach directly incorporates a measure of the species performance and accounts for environmental variability, species environmental preferences and species-specific morpho-functional traits. Our findings reveal a highly variable reef functional potential (RFP) among reef areas within the Greater Caribbean ecoregions, but with lower values, as expected, in marginal environments. Furthermore, for the great majority of reefs in the western Caribbean, the potential for physical functionality has decreased by ~30% when compared with the RFI. These findings have important implications in evaluating the degree of degradation of coral reefs, as well as for the management, conservation and restoration of reef ecosystems.

The high degree of variation in RFP across ecoregions suggests a strong effect of local environmental conditions for reef development. Spatially adjacent coral reef areas can exhibit high environmental variability, which is reflected by different community structure, which in turns results in functional variation across assemblages (Alvarez-Filip et al. 2013, Gove et al. 2015, Zinke et al. 2018). The Caribbean basin exhibits a spatially heterogeneous physicochemical environment, mainly induced by local-scale variability in river outflow, terrestrial runoff, upwellings and bathymetric effects (Chollett et al. 2012). In our study, areas characterized by low values of RFP were located at the limit of reef development. At higher latitudes, environmental parameters such as temperature, light availability and aragonite saturation draw environmental limits for coral growth and reef development and, in some cases lead to a reduced coral diversity associated

with the marginality of environments (Kleypas et al. 1999, Perry and Larcombe 2003). Likewise, we observed low values of RFP in the southern Caribbean ecoregion. This portion of the Caribbean is subject to the influence of the southern Caribbean upwelling system that causes seasonal variability in light intensity, water temperature, salinity and nutrient concentrations, which invariably modifies abiotic conditions under which reefs develop (Rueda-Roa and Muller-Karger 2013, Eidens et al. 2014). For this reason, the southern Caribbean ecoregion exhibits different environmental conditions than the rest of the Caribbean basin, which caused the Maxent algorithm to identify it as less optimal for reef development. This is consistent with what has been described for reefs along the coast of Venezuela, where, in addition to the effect of the upwelling system, river outflow and unstable substrate (i.e. sandy bottoms) prevent a good reef development, leading to small coral communities with low diversity and no accretion, especially in the eastern portion (Weil 2003). However, our models accurately identified the areas where important reef development occur in the mainland of Venezuela located in the Morrocoy and San Esteban national Parks, and in the offshore islands in Los Roques Archipelago and Isla las Aves (Weil 2003, Debrot et al. 2019).

Areas characterized by high RFP were found particularly in the western Caribbean, which has been recognized as a biodiversity hotspot and considered as a conservation priority with great ecological and economic value (Olson and Dinerstein 2002, Roberts et al. 2002). The high values of RFP observed in this ecoregion might be explained by the attributes of the reef system and the seascape. In the western Caribbean is located one of the largest reef formations in the Caribbean constituted by a near-continuous reef system of about 1000 km long (Gress et al. 2019). This particularity confers a spatial continuity of the habitat favoring the connectivity between biological communities. As in terrestrial ecosystems,
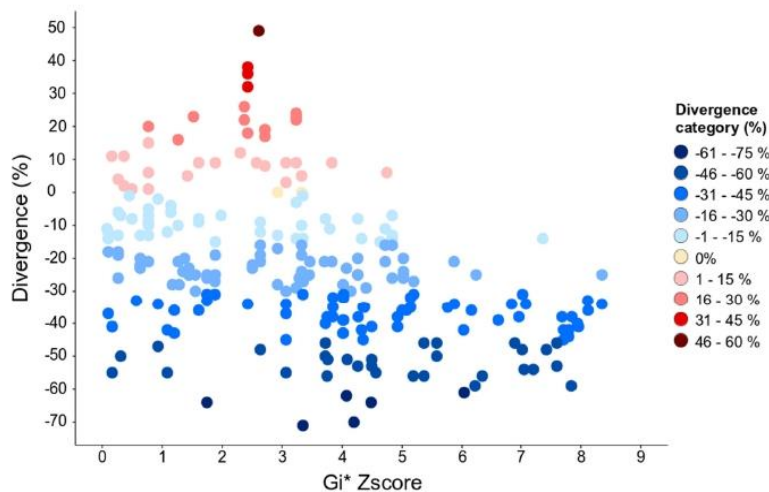

Figure 5. Relationship between the divergence from reef functional potential and hotspot value estimated using the G_i^*Zscore. The graph shows a low but significant negative correlation among variables (Spearman's rho = −0.47, p < 0.001).

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forests with a long temporal and near-continuous presence are often associated with high biodiversity (Mölder et al. 2019). Another attribute of the western Caribbean reef system that allows it to support a high diversity is the area available for species. The species–area relationship suggests that larger areas support higher richness (Lomolino 2001). This has been observed in coral reefs where species richness and density of coral colonies increase in larger reefs (Huntington and Lirman 2012).

The observed reduction in the physical functionality of reefs in the western Caribbean is consistent with their historical degradation. Live coral cover across the Caribbean basin has declined drastically in recent decades, with reductions of up to ~80% (Gardner et al. 2003, Côté et al. 2005, Contreras-Silva et al. 2020). These declines, however, have not been consistent across functional groups of reef building corals (Bruckner and Bruckner 2006, Edmunds and Elahi 2007, Rodríguez-Martínez et al. 2014). For instance, the mass mortality of *Acropora palmata* and *A. cervicornis* due to local human impacts and disease outbreaks killed ~80% of their populations (Gladfelter 1982, Cramer et al. 2020). This mass mortality of reef-building *Acropora* spp. has heavily altered the structure and functioning of Caribbean reefs, due to their fast growing, high carbonate accumulation rates and large branching morphology (Lange and Perry 2019).

Accompanying the demise of key reef-builders, many Caribbean reefs have undergone relative increases in the dominance of non-framework corals which despite providing benefits as carbonate producers and protection from erosion (Perry et al. 2015, Toth et al. 2018), contribute considerably less to the physical functionality of the reefs (González-Barrios and Álvarez-Filip 2018). Furthermore, even though some reefs have experienced a recovery in terms of live coral cover (Edmunds and Carpenter 2001, Contreras-Silva et al. 2020), most of these recoveries concerns non-framework 'weedy' corals, particularly *P. astreoides* and *A. agaricites* (Green et al. 2008, Perry et al. 2015). A recent study revealed that despite a low but significant increase in coral cover, the physical functionality of reefs was not considerably improved, owing to the life-history traits of the species that contributed most to the increase (González-Barrios et al. 2021). At present, coral reefs are still under increasing pressures from climate change, diseases, coastal development and the loss of ecosystem resilience (Roff and Mumby 2012, Hughes et al. 2018, Suchley and Alvarez-Filip 2018, Perry and Alvarez-Filip 2019, Estrada-Saldívar et al. 2020), which compromise their physical functionality and could even further exacerbate the reduction in functionality observed in this study.

Despite the considerable loss in physical functionality at most western Caribbean sites, our findings also show that some have a higher RFI than predicted by the models (i.e. RFP). One likely explanation for this counterintuitive increase is the disproportionate weight that single species with high functional contribution provide when they are present in the reefs at a relatively high cover. An obvious example is the genus *Acropora*, as these species consistently have the highest calcification rates and morphological complexity (González-Barrios and Álvarez-Filip 2018), and when present at relatively high cover (even more than 80% of relative cover) increase the RFI disproportionally. For instance, on the southwest coast of Roatan, Bay Islands, Honduras an extraordinary high cover for *A. cervicornis* has been reported (Keck et al. 2005, Riegl et al. 2009); similarly, in the northeast of the Mexican Caribbean, surveys report some of the most prolific populations of *A. palmata* in the western Caribbean region (Rodríguez-Martínez et al. 2014). Also, at Coral Gardens off the Belize coast, large populations of both species of *Acropora* also occur (Busch et al. 2016, Greer et al. 2020). A similar but lower effect is also identified when other functionally important species occur at high levels of coral cover (e.g. *Orbicella* spp, *Agaricia tenuifolia* and branching *Porites* spp.) (González-Barrios and Álvarez-Filip 2018, González-Barrios et al. 2021).

A more consistent finding is that the greatest losses in functional potential occur at those sites that initially had considerably high functional potential (Fig. 5). Given that anthropogenic impacts are global, the geographic distribution of these effects are not uniform, and the most affected ecosystems are in tropical regions because of their high biodiversity (Dirzo et al. 2014, Young et al. 2016, Barlow et al. 2018). For example, the Brazilian Atlantic forest is a bird-diversity hotspot and has been identified as a priority area for conservation; nevertheless the deforestation is so high that many species have likely been eliminated from their habitat (Jenkins et al. 2013). Similarly, diverse tropical coral reefs are extremely vulnerable to human-related stressors and are often highlighted as ecosystems of conservation priority (Roberts et al. 2002). Coral reef hotspots have been defined following the more traditional hotspot definition proposed by Myers (1988) that considers attributes such as species richness, endemism and threats for their delimitation as a biodiversity region of conservation concern (Roberts et al. 2002, Allen 2008). However, it has been pointed out that for corals and reef fishes centers of species richness and endemicity are not spatially concordant with hotspots (Hughes et al. 2002). Furthermore, studies considering other facets of biodiversity, such as functional diversity, argue that establishing conservation strategies should not only be conducted based on species richness patterns (Stuart-Smith et al. 2013, Grenié et al. 2018). In the Caribbean region, the identified RFP hotspots occur where environmental suitability and coral-species configuration enable high calcification capacity and the formation and accumulation of complex three-dimensional frameworks. This functionality approach allows the inclusion of reef structural complexity as an important attribute in the identification of targets for reef conservation or restoration, which would be valuable for maintaining and protecting their functional integrity.

In the absence of historical baselines, our approximation of the physical functional potential of reefs by integrating niche models and morpho-functional traits allows to estimate the large-scale functionality divergence of reefs. This methodology can be transferred to reefs in other geographic regions, as well

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as to other species, ecosystems and spatial scales. However, it is important to recognize that coral reefs are highly dynamic ecosystems that can exhibit alternative states of benthic cover composition through time (Norström et al. 2009). Therefore, divergence estimates are dependent on the data used to represent the 'current condition' of the coral communities, and results should be interpreted in this context. For example, in this study we used a slice in time (2010–2017) well-known to reflect a degraded state of most Caribbean reefs (Jackson et al. 2014), including our study region (Contreras-Silva et al. 2020).

In addition, we identified possible opportunities for improvement of our approach. First, we assumed that the 49 modelled species are present in all reef areas, and their contribution to the functional potential is proportional to environmental suitability. This ignores evidence of the role of biotic interactions on species distribution patterns and the assembly of ecological communities (Thuiller et al. 2013). Similarly, we did not nonsider the effects of dispersal capacity, historical and evolutionary processes, and abiotic constraints on the spatio-temporal dynamic of the species ranges and community assembly (D'Amen et al. 2017). Furthermore, factors such as wave energy exposure, hurricanes impact, strong boundary currents, tidal regimens, upwellings and other attributes of the reefs such as geomorphology are known to influence species distributions and diversity patterns on coral reefs (Couce et al. 2012, Veron et al. 2015, Medina-Valmaseda et al. in press). It has also been identified that historical processes such as plate tectonics acting over geological timescales played an important role in defining current tropical reefs biodiversity (Keith et al. 2013, Leprieur et al. 2016). For the Caribbean, major geological events are related to plate tectonics and the closure of the Isthmus of Panama, that separated the Atlantic and eastern Pacific oceans and slowly changed the oceanographic conditions on both sides (Cortés 2007, Reyes-Bonilla and Jordán-Dahlgren 2017). While mechanistic or process-based models that can account for some of the aforementioned factors exist, the nature of correlative models as applied here assumes that species environmental preferences govern their large-scale distribution (Pearson and Dawson 2003), thus, they must be interpreted under this context.

It has also been suggested that to make better spatial prediction of attributes of biological communities, the linkage between species ecological niche and functional traits must be estimated by considering the prevailing environmental conditions at each observation site to capture trait variability along environmental gradients (Guisan et al. 2019). Trait variability can be observed at different organizational levels: within a single individual, among individuals from the same population, and among populations, which implies that trait values are not equally represented across regions (Carmona et al. 2016). One of the causes for intraspecific trait variability is phenotypic plasticity in response to varying environmental conditions (Violle et al. 2012). For corals, it is well acknowledged that their morphology changes in response to prevailing environmental conditions, especially for light irradiance and water movement (Todd 2008). For instance, some foliose species such as the Indo-Pacific coral

Turbinaria mesenterina take a more flattened form under moderate or low light intensity conditions to increase photosynthetic energy acquisition (Hoogenboom et al. 2008). In the tropical Pacific, corals from the genus *Pocillopora* show spatial variation in branch-morphology in response to water flow conditions (Paz-García et al. 2015). Furthermore, the calcification process is affected by environmental conditions: growth parameters such as skeletal density, extension rate and calcification rate can vary for a single species along temperature gradients, and under thermal stress conditions in which calcification rates tend to decrease (Carricart-Ganivet 2004, Carricart-Ganivet et al. 2012). Given that, the performance of coral species can be different within the study area and their functional coefficient may also vary. In our models we did not consider intraspecific trait variability since detailed trait variability is still needed, especially in extensive areas such as the Greater Caribbean. However, we considered that the simplification made using mean trait values is valid to estimate the physical functionality at an ecosystem level, given that the effect of environmental conditions was captured by the niche models, and that interspecific-trait variability should be significantly larger than intraspecific-trait variability (McGill et al. 2006, Carmona et al. 2015). Our functional approach could be strengthened when more detailed morpho-functional trait data, together with a broader taxonomic and biogeographical coverage become available, as in efforts such as the Coral Trait Database (Madin et al. 2016).

In conclusion, our results can provide an important basis for reef protection, management and restoration actions not only based on diversity estimates but considering the ecosystem physical functionality to prevent the loss of key services coral reefs provide. Our approach offers an opportunity to assess how the physical functionality of reefs might change under future climate change scenarios. As environmental changes are expected to continue to occur in coming decades, it is essential to consider how these changes might affect key reef-building corals and the potential consequences on the physical functionality of reef ecosystems. Future studies should focus on the evaluation of habitat suitability changes under different climate scenarios for key reef-building corals, which could in turn help to establish restoration priorities based on habitat suitability from the perspective of species contribution to the physical functionality of coral reefs.

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Author contributions

Sara M. Melo-Merino: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Methodology (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Andrés Lira-Noriega**: Conceptualization (equal); Data curation (supporting); Formal analysis (equal); Methodology (equal); Writing – original draft (supporting); Writing – review and editing (equal). **F. Javier González-Barrios**: Conceptualization (supporting); Data curation (supporting); Formal analysis (equal); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (equal). **Héctor Reyes-Bonilla**: Conceptualization (equal); Data curation (supporting); Formal analysis (equal); Methodology (supporting); Writing – original draft (supporting); Writing – review and editing (equal). **Lorenzo Alvarez-Filip**: Conceptualization (lead); Data curation (supporting); Formal analysis (lead); Methodology (equal); Writing – original draft (lead); Writing – review and editing (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.0rxwdbs27> (Melo-Merino et al. 2021).

Supporting information

Any supporting information associated with this article is available from the online version.

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CAPÍTULO 4: Arrecifes con alto potencial de funcionalidad física en el Caribe necesitan protección bajo escenarios de cambio climático

ABSTRACT

Over the past decades, climate change has become one of the major threats to global biodiversity, with negative consequences for the integrity and functioning of ecosystems and the provision of services to people. To mitigate these impacts the identification of climate refugia that allow the persistence of the structure and function of the already transformed reef habitats is essential. Most refugia analysis focus on thermal exposure alone to define priority areas, whereas other ecological o physical aspects of the ecosystems are neglected. Here, we present the first assessment of climate refugia based on thermal exposure of one of the most important attributes of coral reefs, their physical functionality. We used a regional scale estimation of the reef functional potential for Greater Caribbean coral reefs, and predictions of future thermal anomalies based on two Shared Socioeconomic Pathways (SSP). We defined priority cells as those with high potential for physical functionality and the lowest exposure to climate change anomalies. Results show that 54% off priority reef cells meeting the refugia criteria are covered by a marine protected area polygon. We identified Caribbean countries with the highest potential for increasing protection of functionally important reefs in the Bahamas, Puerto Rico, the Turks and Caicos Islands, Panama, Cuba, Belize, Haiti, Honduras, Guatemala, and Jamaica. These results represent a valuable tool to be considered along with other climate or local stressors, ecological processes as well as socioeconomic aspects to define priority conservation areas in the face of climate change.

Key words: climate change, climate refugia, conservation prioritization, ecosystem functioning, spatial planning

INTRODUCTION

Climate change has become one of the major threats to global biodiversity, with negative consequences for the integrity and functioning of ecosystems and the provision of services to people (Smale *et al.*, 2019; Brown *et al.*, 2020). Coral reefs are one of the most sensitive ecosystems to climate change, as rising sea temperatures and thermal stress trigger widespread mass bleaching and coral mortality events (Hughes *et al.*, 2017b, 2018b). Coral species have differential responses to stressors depending on their susceptibility, thereby, thermal stress has resulted in non-random changes in species configuration and communities' functional traits composition (Okazaki *et al.*, 2017; Hughes *et al.*, 2018b; Bellwood *et al.*, 2019). Unfortunately, most afflicted species are those considered major reef-builders (Alvarez-Filip 2013; Hughes et al. 2018), causing the disruption of the reefs physical functionality compromising the ecological stability of the entire system (González-Barrios & Álvarez-Filip, 2018; Hughes *et al.*, 2018b, a; Perry & Alvarez-Filip, 2019).

To mitigate the impacts of climate change on coral reefs, identifying priority conservation areas that allow the persistence of the structure and function of the already transformed reef habitats is essential (Reside *et al.*, 2018). One potential management response is the creation of Marine Protected Areas (MPAs) in regions expected to warm less having the capacity to provide long-term mitigation of

environmental changes that make surrounding areas unsuitable, defined as climate refugia (Bruno *et al.*, 2018; Kavousi & Keppel, 2018). Nevertheless, in current schemes of protection that use biodiversity value as target, taxonomic diversity is the most considered metric while other dimensions of biodiversity such as functional or phylogenetic are neglected (Devictor et al., 2010). In the marine realm, a few studies have demonstrated the spatial mismatches between current MPAs and hotspots of phylogenetic, genetic or functional richness (e.g. Mouillot *et al.*, 2016; Ng *et al.*, 2022). In this context, effective conservation actions must consider climate change associated impacts to contribute to ecosystems and their functions to persist in the long term under changing conditions. Further, the incorporation of climate change into coral reefs conservation strategies is considered the single greatest challenge because of the associated uncertainty (Bellwood et al. 2019). Among the attempts to include climate change into coral reefs conservation, is the identification of locations of high priority for protection considering acute and chronic thermal stress and the potential response of corals to the stress regime trough acclimatization (Mumby *et al.*, 2011). Another example is the identification of priority sites for conservation through the analysis of environmental characteristics associated with reef persistence, such as past and future thermal exposure, the influence of hurricanes and larval connectivity, reinforced with knowledge of local threats and government priorities for spatial prioritization (Chollett *et al.*, 2022).

The heat exposure that the world's reefs have faced has exhibited a high spatiotemporal variability among geographical regions (Bruno *et al.*, 2018; Hughes *et al.*, 2018c,a). As

climate induced threats are not spatially uniform, the spatiotemporal predictability of threats that can be incorporated into MPAs design, might increase the possibility to achieve greater conservations benefits. Although the exposure of coral reefs to thermal stress and its consequences have been studied (Hughes *et al.*, 2018c; Muñiz-Castillo *et al.*, 2019), most of the studies focus on coral bleaching, the associated mortality and coral cover loss (e.g. Babcock *et al.*, 2021), while the consequences it has over other ecological attributes, like how is transforming the physical functionality of reefs (three-dimensionality) is recently being considered (e.g. Hughes *et al.*, 2018c).

The spatial estimation of the potential for physical functionality of Caribbean coral reefs developed by Melo-Merino et al. (2022), can aid to inform management strategies with the purpose of incorporating functional aspects of the ecosystems, and to the identification of potential climate refugia if combined with future climate change scenarios that can be considered as priority sites for conservation. The approach identified areas where reefs might have the capacity to create complex three-dimensional structures by means of calcium carbonate precipitation, and provided insights about how current coral assemblages might have diverged from their natural estates as a result of human induced changes.

Additionally, as the lack of financial resources is among the main shortfalls for effective management (Gill et al. 2017), this approach can help local managers and governmental authorities to guide investments for MPAs in sites where conservation is more likely to successfully fulfill ecological goals.

Here we evaluated the protection status of reefs with high potential for physical functionality in the Greater Caribbean and predict the extent to which these reefs might serve as refugia in the face of rising global temperatures. We first identify the reefs with the highest functional potential that are still outside the current network of MPAs for each of the countries and territories in the Caribbean. Then, we investigate the exposure of these reefs to future temperature anomalies under the Shared Socioeconomic Pathways climate change scenarios using the 2020-2049 time-span. We identify reefs with high RFP least exposed to temperature increase that might be considered as priority sites for conservation as climatic refugia.

METHODS

Reef Functional Potential

To examine possible physical functionality of Caribbean reefs, we used the estimates of reef functional potential (RFP) from Melo-Merino et al. (2022). They estimated the RFP by combining habitat suability from ecological niche models and the morpho-functional traits of reef-building corals (i.e., calcification rate and colony complexity). These traits determine the contribution of different coral species to the physical functionality of reefs and are represented by a coefficient (González-Barrios & Álvarez-Filip, 2018). The niche models were calibrated based on occurrence records and environmental predictors for 49 reef-building corals, and denoted environmental suitability for each species in the Greater Caribbean. The functional coefficient of each coral species was combined with its respective habitat suitability estimation through a

raster multiplication, and subsequently, the 49 raster-layer product of the multiplication were stacked based on the sum resulting in the RFP layer.

Protection status of RFP

The protection status of RFP of Greater Caribbean coral reefs was analysed using the Caribbean Marine Protected Area Management Network and Forum geospatial database (CaMPAM, accessed March 2021) from the Specially Protected Areas and Wildlife sub-protocol of the UNEP Caribbean Environment Programme. The CaMPAM database consists of a compilation of detailed information about MPAs which are predominantly marine, but also include some terrestrial components. In order to limit the study to MPAs that protect coral reefs, we performed a sequence of spatial operations. First, as a coarse filter, we performed a spatial union between the CaMPAM layer and the RFP layer; the MPAs that remained were then intersected with the Reefs layer. The MPAs that intersected the RFP layer but not the Reefs layer, were revised with more detail to decide upon exclusion or inclusion. The MPAs that intersected the reefs layer were revised to exclude those that protected coastal ecosystems (e.g. mangroves) but not coral reefs. When available, MPA layer metadata was used to make these decisions, and if none was available the polygon was retained. As a second source of MPAs data, we used the World Database on Protected Areas (WDPA, accessed March 2021). Following the same procedure, we identified MPAs polygons that were not included in CaMPAM layer and created a joint database. From the entirely marine MPAs, those only managed for fisheries, marine mammals and deep coral reefs were not included in the analysis. With the completion of this procedure our

analysis included a total of 562 MPA polygons (Fig. S1). To determine the protection status, RFP cells that intersected MPA polygons were considered protected or unprotected otherwise.

Considering that decision-making relies first on national governments, the analyses were performed at a country level. To assign each RFP cell to its respective country, we performed a spatial union between the RFP polygon and the exclusive economic zone layer from the Marine Regions Organization (V11; accessed march 2021; https://www.marineregions.org/about.php). Coral reefs in the United States were separated into two groups: Flower Garden Banks and the Florida reefs, since they belong to clearly different ecoregions (Spalding *et al.*, 2007). For the same reason, the coral reefs of Mexico were divided into Gulf of Mexico reefs and Caribbean reefs.

Exposure of RFP to climate change

The exposure of RFP to temperature increase was assessed for two future high emission scenarios that are part of the Coupled Model Intercomparison Project Phase 6 (CMIP6) forced under the Shared Socioeconomic Pathways (SSP). Projections of future climate change under the SSP family of scenarios have been developed with different levels of socioeconomic challenges to mitigation and adaptation to climate change (O'Neill *et al.*, 2016), and have been considered to better represent climate than the previous Representative Concentration Pathways (RCP; Kwiatkowski *et al.*, 2020). Future emissions scenarios chosen were the middle ground SSP3-7.0 and the upper ground SSP5-8.5 considering that recent studies suggest that CO_2 emissions are more

consistent with upper range scenarios (Schwalm *et al.*, 2020), as well as Caribbean reefs warming rates (Bruno *et al.*, 2018). The SSP3 represents a world with poor progress toward sustainability and high challenges to mitigation and adaptation (Fujimori *et al.*, 2017; O'Neill *et al.*, 2017). The SSP5 is characterized by high socio-economic challenges to adaptation and a strong dependence on fossil fuels, causing high levels of greenhouse gas emissions (Kriegler *et al.*, 2017; O'Neill *et al.*, 2017).

Future climate data for ten Earth System Models (Table S1) were downloaded from the Physical Sciences Laboratory of the National Oceanic and Atmospheric Administration (https://psl.noaa.gov/ipcc/cmip6/ccwp6.htm) as temperature anomalies, *i.e.*, the difference between the mean temperature in the future and the mean temperature of a historic baseline period. As baseline period we chose the 1985-2014 period and, for future projection the 2020-2049 period. Because of the inherent variability in climate models, we estimated a multi-model mean anomaly, and the inter-model variability was represented as the standard deviation (Fig. S2).

The spatial resolution of the temperature anomaly layers is 1 x 1° latitude/longitude (~111 km at the equator) thus, to even the spatial resolution with the RFP layer (~ 9×9 km latitude/longitude) and to reduce discontinuities in the grid boundaries, we downscaled the anomaly projections by applying an inverse distance weighting interpolation using the ArcGIS software version 10.3 (Environmental Systems Research Institute (ESRI) 2015, ArcGIS desktop ver. 10.3). Finally, to measure the vulnerability of RFP to temperature increase, we assigned to each RFP cell the corresponding temperature anomaly by intersecting both layers.

The exposure of RFP cells to future ocean warming was assessed by intersecting the temperature anomalies with the RFP layer, thus each RFP cell was assigned with its respective temperature anomaly. To spatially represent the exposure level, we created a bivariate choropleth map by dividing both variables (x= reef functional potential, y= temperature anomalies) by equal intervals obtaining three categories (low, medium, and high). Cells defined as "priority for future protection" were those that met the criteria of having the highest RFP and the lowest exposure to climate change anomalies.

RESULTS

Coral reefs in the Greater Caribbean exhibited a high spatial variability in their potential for reef functionality (RFP) with values ranging from 0.08 to 9.35. Reefs with high RFP values were observed in the Greater Antilles, the Western Caribbean, and the Bahamian ecoregions. Further, reefs with low RFP values are in the northern Gulf of Mexico and Bermuda ecoregions. Approximately half of the cells containing reefs in the Caribbean are protected (48%), but there is little difference in RFP between protected and unprotected reefs (Fig. 1). Also, protected reefs with medium to high RFP values are in the Western, Southwestern and Floridian ecoregions. But there are several unprotected reefs with high RFP values in the Greater Antilles and Bahamian ecoregions (Fig. 1).
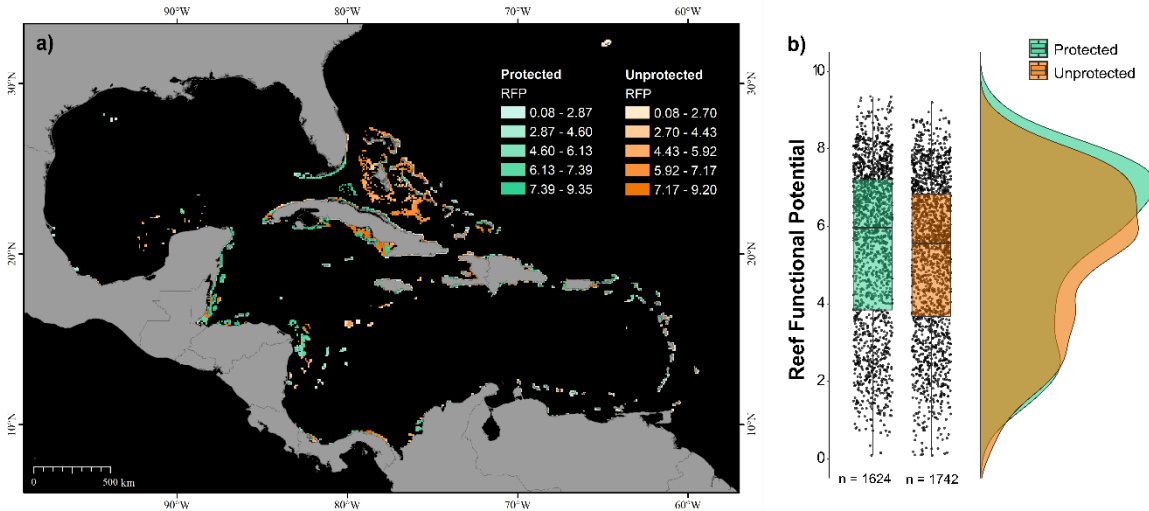
Figure 1. Protection status of Greater Caribbean reefs according to the Reef Functional Potential. a) Spatial distribution of protected and unprotected reef cells and their respective Reef Functional Potential value. b) Boxplot and density plots showing the distribution of Reef Functional Potential values in protected and unprotected reef cells.

We identified four groups according to reef protection status and their RFP: *1)* countries where all or almost all reefs are protected regardless of their RFP values; *2)* countries where reefs with the highest RFP values are protected; *3)* countries where reefs with high RFP are unprotected; and lastly *4)* countries where all or most reefs are unprotected (Fig. 4). We observed a substantial variation in RFP among countries belonging to the third group, yet a lack of MPA coverage on reefs with high RFP was particularly evident in Belize, Puerto Rico, Honduras, Cuba and Turks and Caicos (Fig. 2).
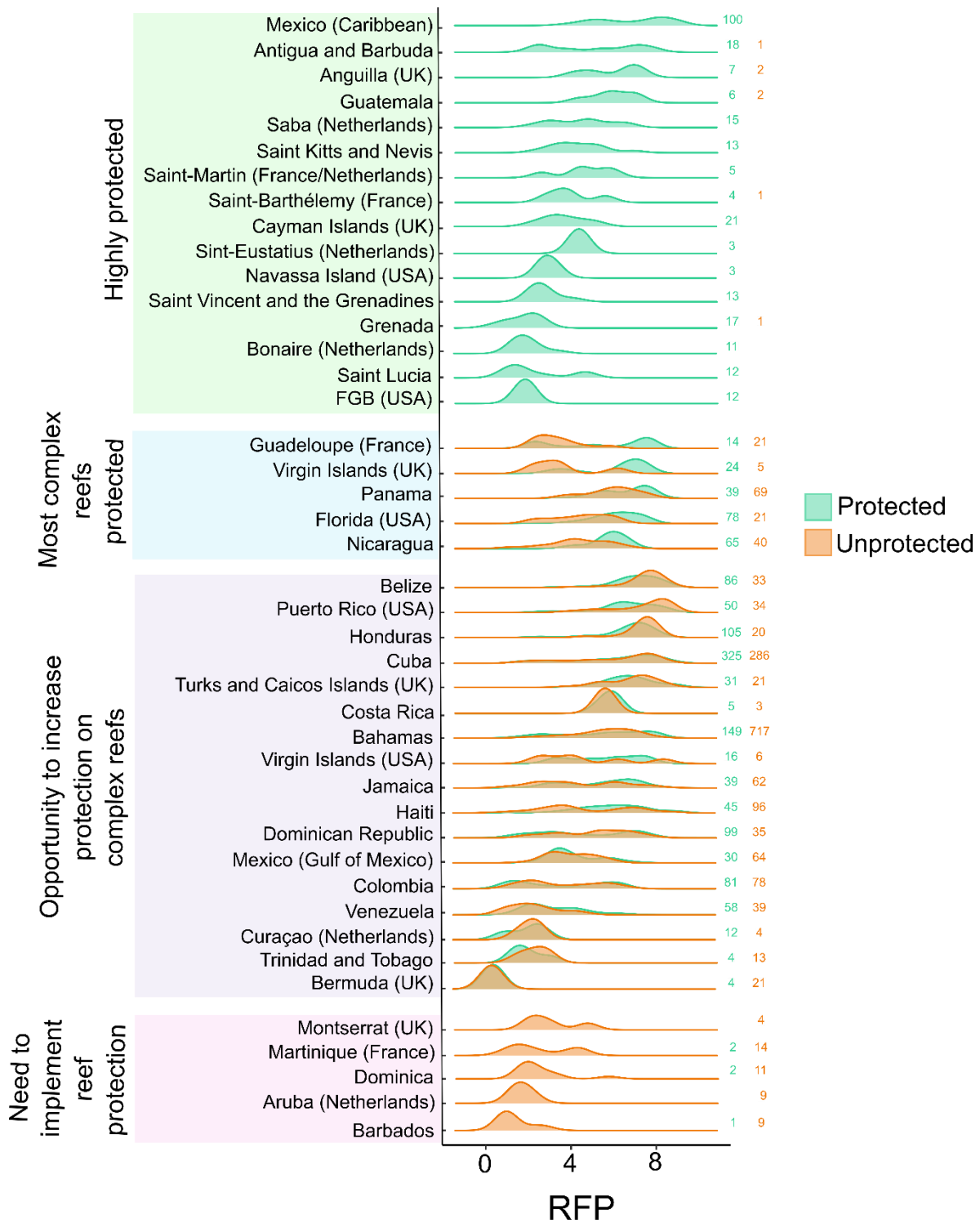
Figure 2. Protection status of reefs according to the Reef Functional Potential (RFP) in the countries and territories of the Greater Caribbean. Countries are grouped in four categories according to the reef protection status and RFP values. Numbers represent the cells in each category.

The reefs in the Greater Caribbean display spatial variability in heat exposure to 2049. The expected thermal anomalies increased from SSP3-7.0 to SSP5-8.5. In the SSP3-7.0 temperature anomalies ranged from 0.81 to 0.98 °C (mean = 0.88, SD = 0.03) and from 0.89 to 1.16 °C (mean = 1, SD = 0.03) in the SSP5-8.5. Both scenarios predict higher temperature change at higher latitudes in the Northern Gulf of Mexico and Bermuda ecoregions. The reefs with greatest exposure to temperature increase were those in Flower Garden Banks (USA) that reach up to 1.12 °C in the SSP5-8.5 scenario (Fig. 3). In contrast, countries exposed to future lowest temperature anomalies are found in the eastern Caribbean represented by Trinidad and Tobago and Grenada (Fig. 3). The Kruskal-Wallis test used to compare the median of temperature anomalies across all countries showed significant differences among them in both scenarios (Kruskal-Wallis chi-squared = 2449.8, df = 42, p-value < 0.05). Some countries exhibit greater variability among reef cells, this was most evident in Mexico (Gulf of Mexico), Colombia and Cuba. For some, this variability increased from SSP3-7.0 to SSP5-8.5 scenarios like in Mexico (Gulf of Mexico) and Bahamas, whereas for others such as Colombia, Guadeloupe, and Mexico (Caribbean) decreased meaning that the reef exposure to thermal anomalies becomes more homogeneous (Fig. 3).
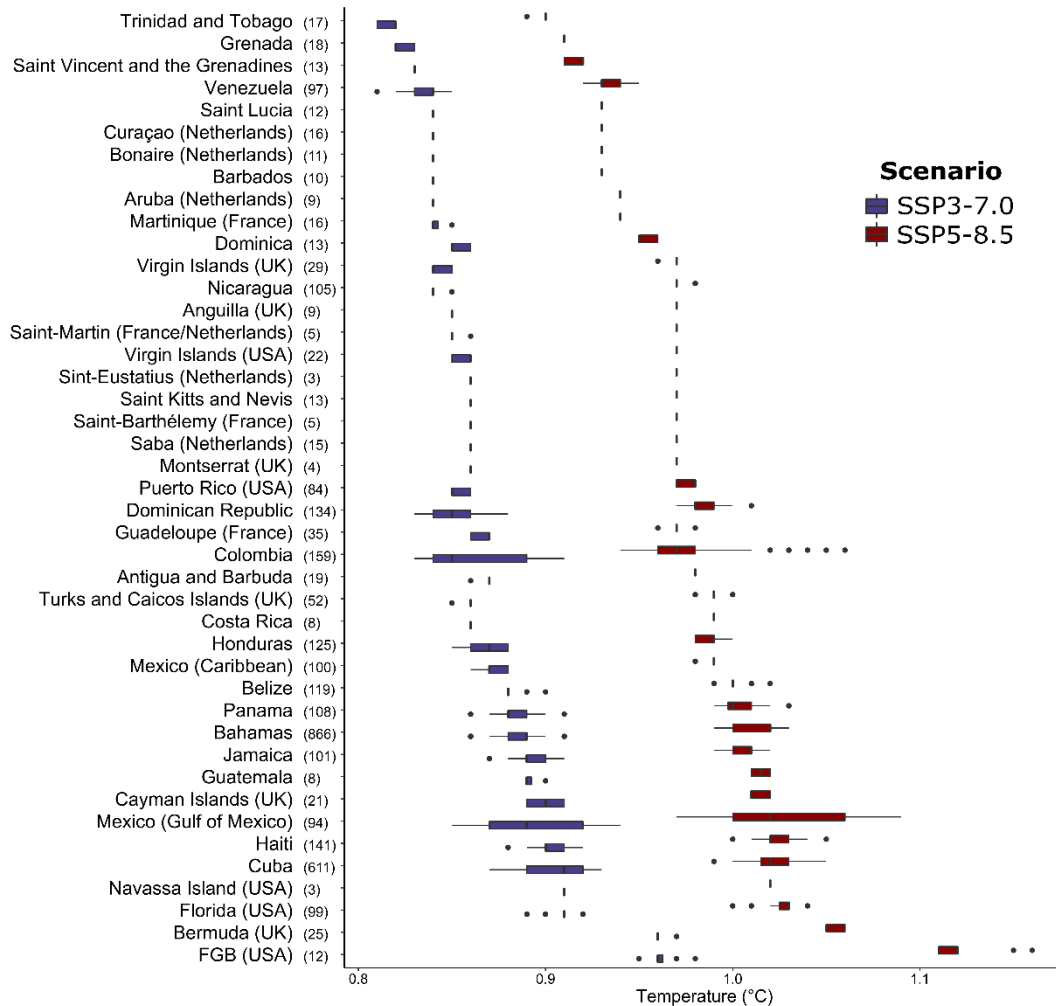
Figure 3. Temperature anomalies per country in the Greater Caribbean under future climate change scenarios SSP3-7.0 and SSP5-8.5 to 2049 time-frame. Numbers in parentheses indicate the number of reef cells.

The assessment of the RFP exposure to temperature anomalies revealed that in the SSP3-7.0 scenario the vast majority of reef cells with high RFP are exposed to the lowest category of temperature increase (< 0.92 °C; Fig. 4). The magnitude of the exposure increased between the SSP3-7.0 and the SSP5-8.5 where the majority of reef cells with high and medium RFP values (40% and 38% respectively) are found in medium temperature anomaly category, while practically no reefs are exposed to the

lowest exposure category in SSP5-8.5 (Fig. 4). The mean temperature anomalies for reef cells with high RFP increased from 0.88 °C in the SSP3-7.0 scenario to 1°C in the SSP5-8.5. To a country level, only a small proportion (0.45%) of reef cells with high RFP, all located in the south coast of Cuba were predicted to be exposed to the most severe warming category (>1 °C) under the most drastic scenario (Fig. 5). Countries with high percentages of reef cell exposed to elevated temperature anomalies are Flower Garden Banks (USA) and Bermuda for which 100% of their reef cells are exposed to the most severe warming category under the SSP5-8.5 scenario (Fig. 5).

Figure 4. Spatial representation of the exposure of Reef Functional Potential to future thermal anomalies under SSP3-7.0 and SSP5-8.5 climate change scenarios. Legend shows the Reef Functional Potential value in X axis and temperature anomaly according to the 1985-2014 historic baseline in Y axis. Percentage values in each quadrat indicate the proportion of reefs (cells).
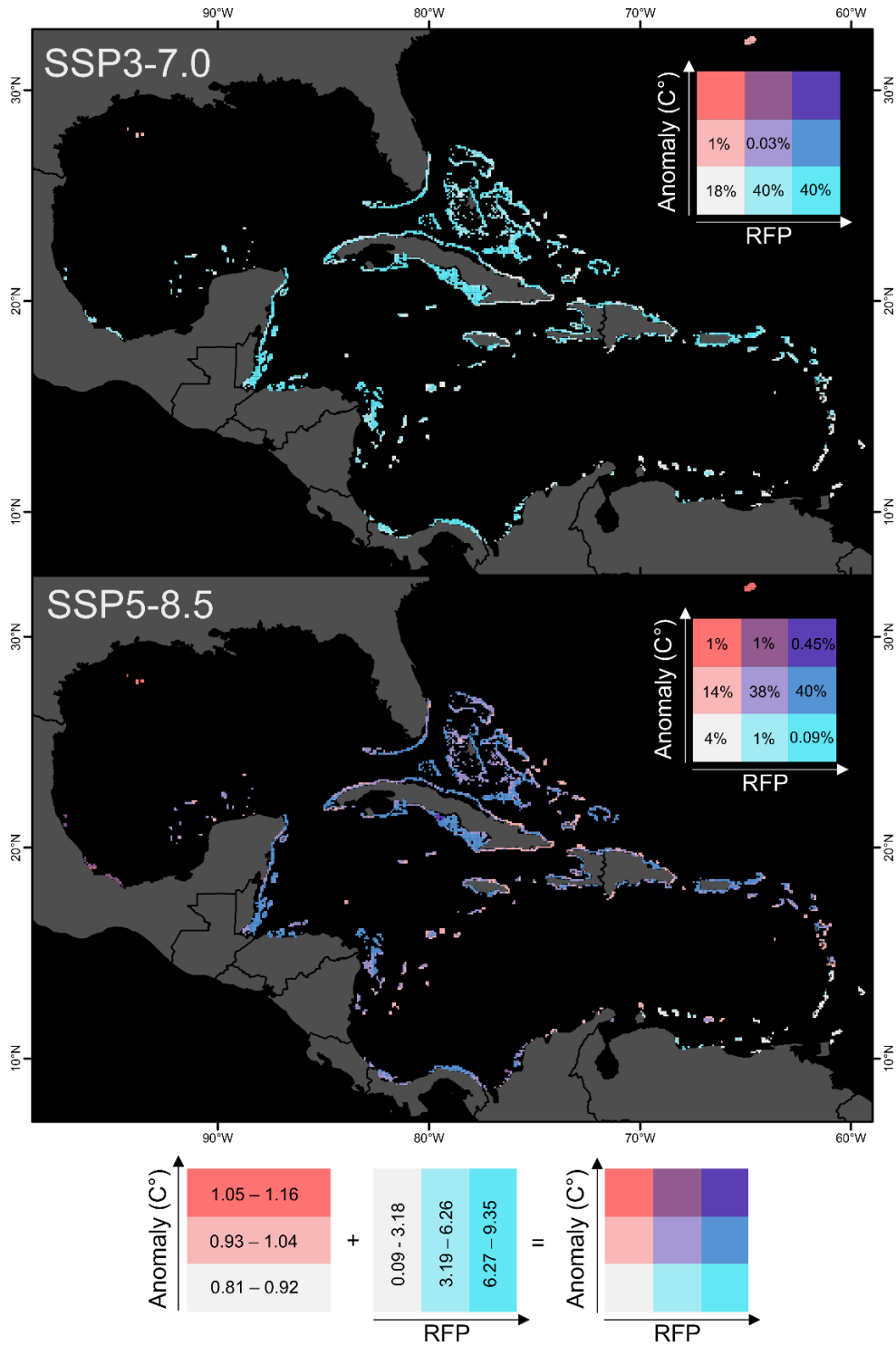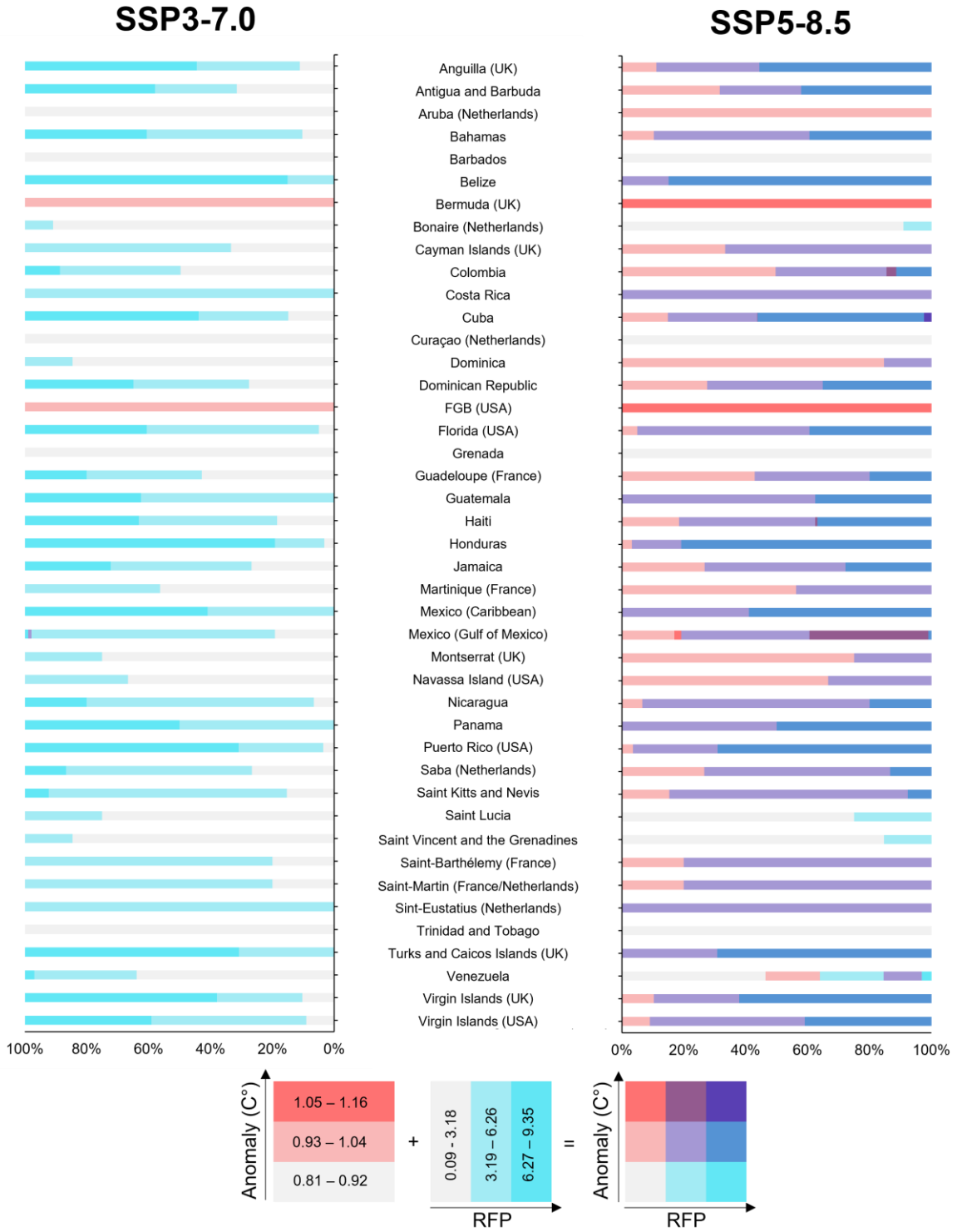
Figure 5. Country level exposure of Reef Functional Potential to future thermal anomalies under SSP3-7.0 and SSP5-8.5 climate change scenarios.

Our assessment allowed the identification of the countries with the greatest opportunity to increase reef protection under climate change scenarios. Overall, in both future scenarios 40% of reef cells in the Greater Caribbean meet the criteria of having the highest RFP and the lowest exposure to temperature anomalies. From the total of the identified priority cells, only the 54% are covered by a MPA under the current scheme of the Caribbean Marine Protected Areas networks. Proportionally, in both scenarios, countries with most priority reef cells are Belize and Honduras (>80%, Fig. 6), but those with the highest opportunity to increase protection for functionally important reefs, based in the percentage of unprotected priority cells are Bahamas, Puerto Rico, Turks and Caicos Islands, Panama, Cuba, Belize, Haiti, Honduras, Guatemala, and Jamaica (Fig.6).

■ Priority protected ■ Priority not protected

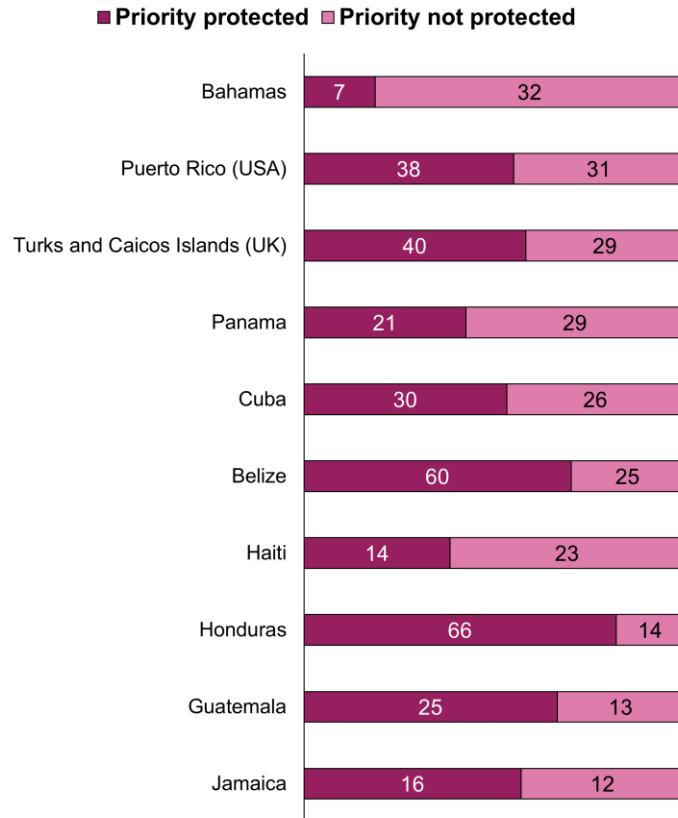| Country	Priority protected	Priority not protected
Bahamas	7	32
Puerto Rico (USA)	38	31
Turks and Caicos Islands (UK)	40	29
Panama	21	29
Cuba	30	26
Belize	60	25
Haiti	14	23
Honduras	66	14
Guatemala	25	13
Jamaica	16	12

Figure 6. Proportion of reef cells classified as priority for future protection in the top 10 countries with more unprotected priority reef cells. Numbers in the boxes represent percentages estimated for the SSP3-7.0 scenario. Countries are ordered in decreasing percentage of unprotected priority cells.

To represent the identification of priority cells we use Cuba as an example because it was the only one with reef cells exposed to the highest thermal anomalies category. We observed most priority cells distributed in the south cost of the island. The number of priority cells decreased from 56% in the SSP3-7.0 to 54% in the SSP5-8.5 due to the impact of elevated temperature anomalies in the Ana Maria Gulf. From the identified cells, only the 30% are currently inside an MPA. Priority cells lacking MPA coverage are

mainly located in the Guacanayabo Gulf in the south coast, and in the Guanahacabibes Gulf in the west coast (Fig. 7).
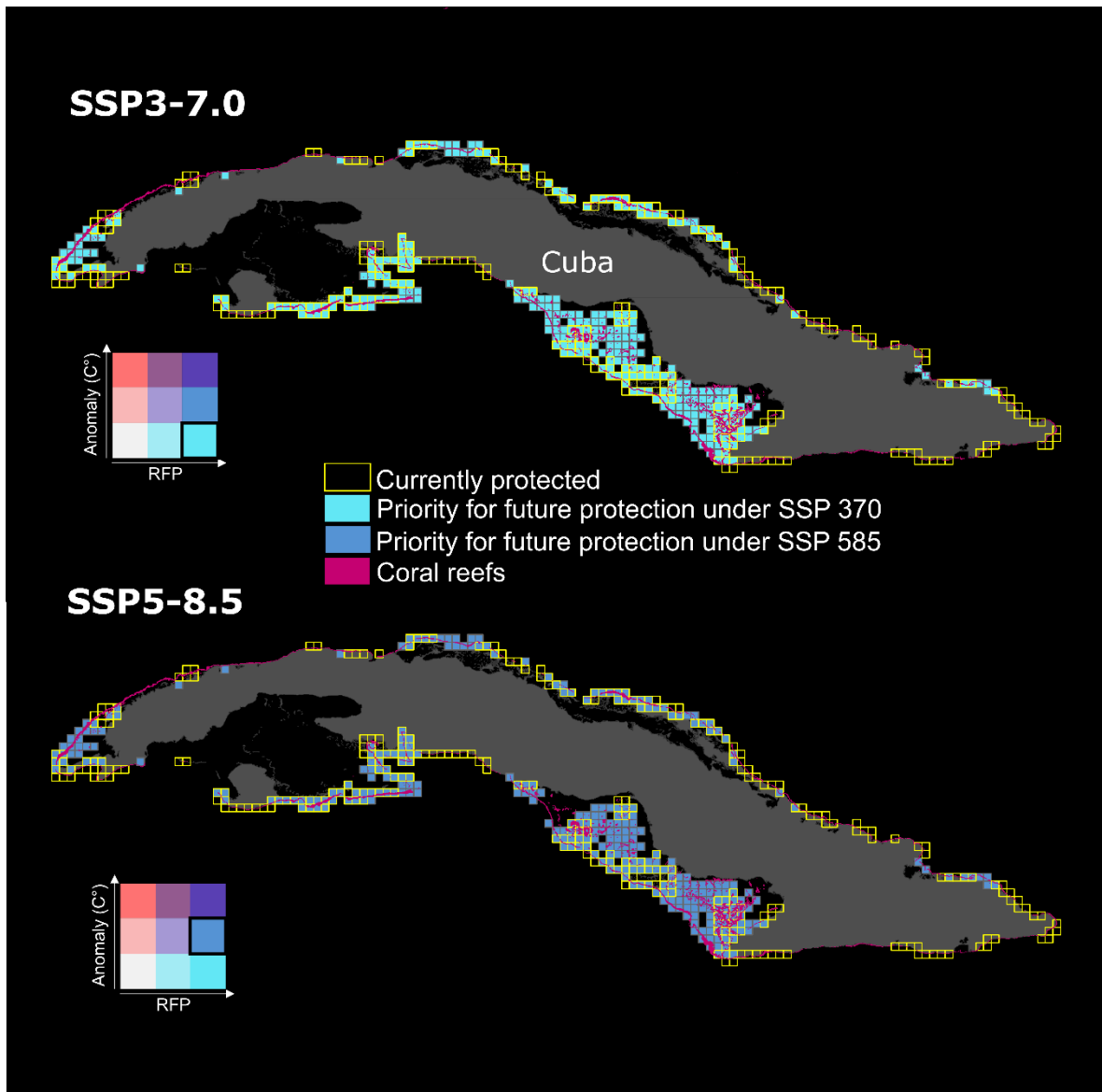

Figure 7. Reef cells identified as priority for future protection in Cuba under SSP3-7.0 and SSP5-8.5 climate change scenarios to 2049. The highlighted quadrat in the bivariate legend shows where priority cells belong to. Yellow framed cells represent cells currently covered by Marine Protected Areas.

DISCUSSION

Over the past decades, ocean warming as a result of climate change has profoundly impacted coral reefs' ecology and function (Hughes *et al.*, 2018b). This highlights the need for improved conservation measures to minimize associated losses and maximize protection, as well as the need to identify conservation goals that aid to maintain the ability of reefs to support high biological diversity and ecosystem services for people who depend on them, especially in the face of climate projections. In this study, we combined information on the capacity of reefs to build complex three-dimensional structures with projections of expected thermal anomalies to provide decision support about which places might be of priority in the present and under future climate change scenarios. These sites represent climatic refugia for coral reefs with a high potential for physical functionality less likely to be affected by rising temperatures. Our findings reveal that under the current scheme of the Greater Caribbean marine protected areas network, almost half of reefs that meet the characteristics to be considered climate refugia with high potential for physical functionality are unprotected.

With the intensifying pressure on coral reefs, marine protected areas (MPAs) have become extremely valuable conservation tools, but, in order to be effective in the long term they must consider the future impacts of climate change (Chollett *et al.*, 2022). In this sense, the identification, protection, and management of climate refugia have had a progressive growth as an adaptation action to support the persistence of species, communities, ecosystems, and sociocultural values (Morelli *et al.*, 2020). However,

recent studies have emphasized the need to consider other aspects beyond exposure in refugia analyses, and urge the representation of ecological complexity aspects such as species traits and the physical features of the ecosystems (Michalak *et al.*, 2020; Morelli *et al.*, 2020; Miatta *et al.*, 2021). Our results allowed the identification of reef areas with a high potential for physical functionality that are currently outside of marine protected areas, highlighting the importance of including functional aspects into spatial prioritization for Caribbean reefs. These spatial mismatches have been observed in other taxonomical groups of marine organisms when assessing functional traits. For instance, the assessment of reef fish biodiversity distribution comparing taxonomic and trait metrics reveled new hotspots of functional diversity in areas not considered for conservation (Stuart-Smith *et al.*, 2013). In this context, even though no single parameter can effectively describe the functioning of an entire ecosystem (Rees *et al.*, 2012), the incorporation of the reefs physical functionality estimations along with climate change exposure we made in our approach can be a promising tool to preserve one of the most important attributes of coral reefs: their complex three-dimensional structure.

At a national level, determining where conservation efforts should focus to provide adequate protection and a good destination of financial resources is highly important. In this sense, our results can aid in addressing gaps in conservation coverage. Our results suggest they are abundant opportunities to strengthen protection in existing MPAs covering physically important reefs, as well as for creating new MPAs to

represent those that lack protection, particularly for those countries with elevated numbers of unprotected priority sites (Fig. 6). To properly achieve this, local authorities and decision makers must also account for the impact of local stressor such as coastal development and marine pollution (Kavousi & Keppel, 2018), that allow the creation of integrative and more effective conservation measures. A study that evaluated the effect of ocean warming and acidification and local eutrophication over habitat suitability for coral reefs showed that accounting for these three impacts only the 6% of the worlds coral reefs may act as temporary refugia.

In the context of using integrative approaches, the priority areas we identified in Cuba are consistent with priority areas identified in other studies accounting for climate change impacts associated stressors and uncertainty (Chollett *et al.*, 2022). Additionally, the same reef area was identified as having potential to host reefs with high coral diversity when considering diversity models and environmental characteristics (Selmoni *et al.*, 2023). These consistencies underline the utility of our approach, demonstrating that it could strengthen decision-making; since the areas identified as important for conservation from the physical functionality perspective are also important from the biological diversity perspective, and are less exposed to related climate change impacts other than temperature increase such as the case of hurricane impacts and favored by larval connectivity (Chollett *et al.*, 2022; Selmoni *et al.*, 2023). Larval connectivity is particularly important for coral reefs persistence in the future, so is of primary importance prioritize reef sites that are valuable sources of larvae providing recovery

opportunities to degraded reefs. A study of reef connection networks suggested the that priority reefs are not only those in climate refugia, but those able to maintain high levels of connectivity for larval supply (Greiner *et al.*, 2022).

A consistent finding is the observed reduction in the percentage of priority cells with refugia potential in Cuba, which decreased from 56% to 54% in the high emission scenario. As has been observed in other studies of climate refugia for coral reefs, when temperatures reach higher values, the number and extent of coral refugia decrease, or even can completely disappear. Dixon et al. (2022) found that under warming scenarios of 1.5°C only the 0.2% of climate refugia remains, whereas under the 2.0°C warming scenario there are no climatic refugia for coral reefs.

With our approach, we identified priority sites based solely on heat exposure; nevertheless, a more comprehensive view of vulnerability to climate change should be considered when conducting climate refugia analysis. Differences in how species respond to climate change (species sensitivity) and their ability to adapt (adaptive capacity) will influence the location, duration and success of climatic refugia (Morelli *et al.*, 2020; Chollett *et al.*, 2022). It has been proved that corals have the ability to adapt to variable temperatures by switching symbionts, changing protein expression, or experiencing warmer temperature anomalies (Palumbi *et al.*, 2014; Boulotte *et al.*, 2016; Sully *et al.*, 2019; Scharfenstein *et al.*, 2022). The availability of this information on a

large spatial scale is practically nonexistent (but see McClanahan *et al.*, 2020); moreover, when available, it must be used to reinforce conservation measures.

The multi-model mean anomalies used here project the chronic thermal exposure, however, they do not reflect the potential impact of climate extremes (i.e. acute thermal exposure) than can have major ecological impacts on coral reefs. In recent years, extreme climatic events associated to ocean warming have caused devastating changes in coral reefs; for instance, the 2014-17 global-scale coral bleaching event resulted in very high coral mortality on many reefs and a rapid deterioration of the reef structure and changes in community composition (Hughes *et al.*, 2018c; Eakin *et al.*, 2019). Here, thermal anomalies expected under the worst scenario (SSP5-8.5) reach up to 1.16 °C, while during this bleaching episode some geographic regions showed maximum intensity of up to 4 °C (Holbrook *et al.*, 2019). Unfortunately, there is no certainty in how marine heat waves and other warming phenomena will change under climate change, but they are expected to become more frequent (Frölicher *et al.*, 2018; Laufkötter *et al.*, 2020).

In this study we revealed a significant opportunity to increase protection for reefs with high potential for physical functionality in the greater Caribbean countries, which might represent climate refugia. Moreover, strong climate action is needed; the lack of refugia in some areas may indicate the need for reducing greenhouse gas emissions so that reefs and their function can persist as we know them. Furthermore, our results may be

conservative, due to some Marine Protected Areas having poor reinforcement or lack of financial resources to operate properly, offering a false sense of protection. Future studies should further evaluate the importance of other climate change related impacts, such as storm exposure, ocean acidification and deoxygenation, as well as relevant ecological processes such as reef connectivity, and socioeconomic factors in defining or maintaining climate refugia.

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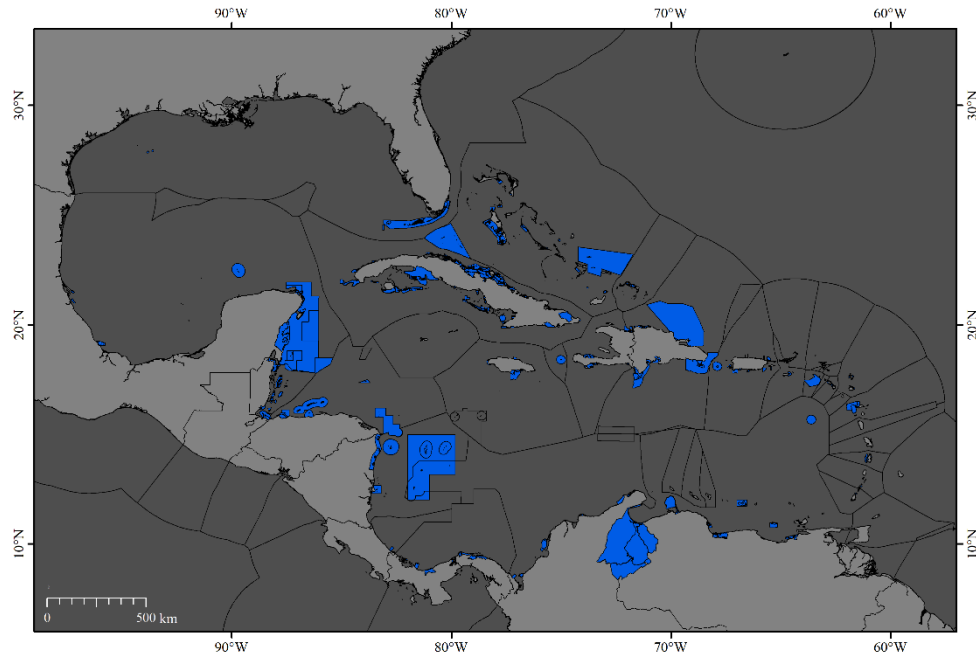
Supplementary materials

Figure S1. Map of the Marine Protected Areas included in the study. Black lines represent the Exclusive Economic Zone of the countries and territories.
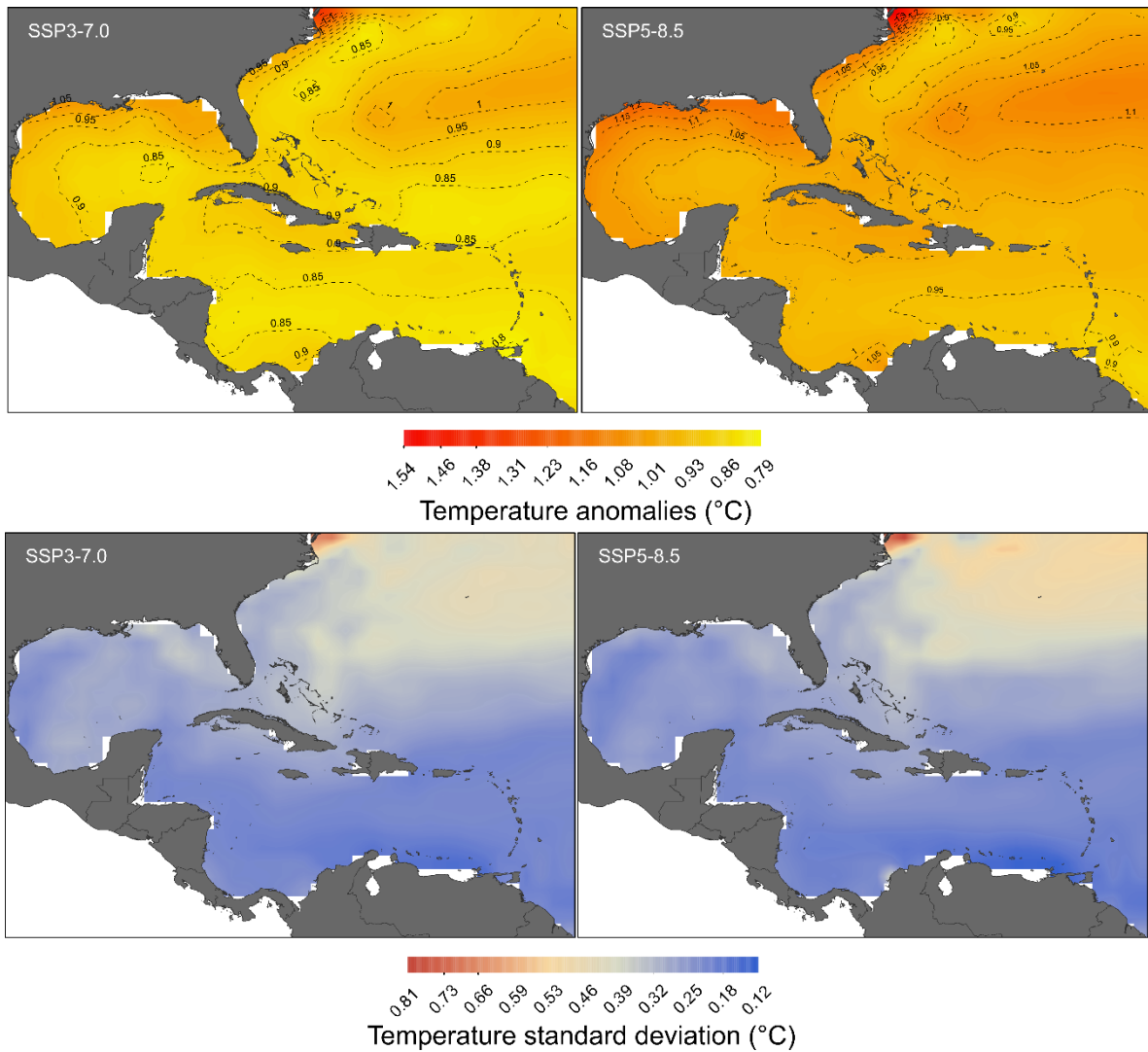
Figure S2. Future temperature anomalies under Shared Socioeconomic Pathways SSP3-7.0 and SSP5-8.5 for 2020 – 2049 timeframe. a) and c) Mean temperature anomalies. b) and d) standard deviation representing inter-model variability.

Table S1. CMIP6 Earth System Models used to build the multi model ensemble to represent temperature anomalies in climate change scenarios.

MODEL	SOURCE
ACCESS-ESM1-5	Australian Community Climate and Earth System Simulator Earth System
CanESM5	Canadian Centre for Climate Modelling and Analysis
CESM2-WACCM	National Center for Atmospheric Research, USA
EC-Earth3	EC-Earth Consortium, Europe
GISS-E2-1-G	NASA Goddard Institute for Space Studies, USA
INM-CM5-0	Institute of Numerical Mathematics, Russia
MCM-UA-1-0	University of Arizona, USA
MIROC6	Japan Agency for Marine-Earth Science and Technology, Atmosphere and Ocean Research Institute, Japan
MPI-ESM1-2-HR	Max Planck Institute for Meteorology, Germany
UKESM1-0-LL	Met Office Hadley Centre, UK

CAPÍTULO 5: Discusión general, conclusiones y perspectivas

DISCUSIÓN GENERAL

Las actividades humanas han inducido la pérdida de biodiversidad y el deterioro de los ecosistemas, por lo que tomar acciones de conservación y estrategias de manejo resulta vital para la conservación de los recursos naturales. La implementación de estrategias de conservación puede ayudar a conservar o restaurar la biodiversidad y los bienes y servicios asociados a los ecosistemas; sin embargo, a pesar de que se reconoce la importancia de considerar aspectos sobre la ecología funcional de las especies o los ecosistemas en el diseño de las estrategias de conservación, estos raramente son incluidos (Miatta *et al.*, 2021). En el caso de los arrecifes coralinos, uno de sus atributos más importantes es su funcionalidad física, -definida como su capacidad para la formación de estructuras tridimensionales complejas-, la cual les permite albergar una gran diversidad biológica a través de la provisión de hábitats heterogéneos que regulan los procesos ecológicos como la competencia y depredación (Graham & Nash, 2013). Sin embargo, los esquemas de conservación actuales que se rigen por criterios de biodiversidad, usan comúnmente medidas de diversidad taxonómica (Roberts *et al.*, 2002; Devictor *et al.*, 2010). Por lo anterior, es importante generar estrategias que faciliten el entendimiento de aspectos funcionales de los ecosistemas y su incorporación en estrategias de conservación.

En esta tesis, el objetivo fue estudiar cómo la variabilidad ambiental y la composición de rasgos funcionales de los ensamblajes ecológicos influencian el funcionamiento de los ecosistemas y pueden aportar información sobre su vulnerabilidad al cambio climático. Se exploró el uso de modelos ecológicos espacialmente explícitos como una herramienta útil para comprender los patrones y procesos detrás del funcionamiento de los ecosistemas y para informar sobre estrategias de conservación enfocadas a la preservación de funciones. Con este tipo de modelos, se generaron estimaciones del potencial de funcionalidad física de los arrecifes del Gran Caribe, y se midió el grado de divergencia funcional de los arrecifes comparando el potencial de funcionalidad

estimado versus el observado con datos colectados en campo; y por último, se midió la exposición de los arrecifes al incremento en la temperatura del agua en escenarios a futuro con la finalidad de identificar arrecifes con alto potencial de funcionalidad física menos expuestos al incremento térmico que pudieran funcionar como refugios climáticos.

Una forma eficiente de evaluar aspectos funcionales de los ecosistemas es a través de modelos ecológicos, como los modelos de nicho ecológico y distribución de especies. Estos modelos se han convertido en valiosas herramientas en estudios de biogeografía, ecología y cambio climático; y han sido ampliamente utilizados como apoyo en la generación de estrategias para el manejo y conservación de las especies y los ecosistemas (Melo-Merino *et al.*, 2020). Sin embargo, a pesar de que estos modelos generalmente solo incluyen información sobre las condiciones abióticas y registros de presencia de las especies individuales (Peterson, 2006), se han desarrollado metodologías que permiten utilizarlos para modelar diferentes aspectos estructurales o de composición de los ensamblajes ecológicos (Pottier *et al.*, 2013; Grenié *et al.*, 2020). En este sentido, la presente tesis representa una propuesta metodológica novedosa al combinar las estimaciones de idoneidad ambiental obtenidas en el modelado de nicho ecológico con rasgos morfofuncionales de las especies coralinas. De esta manera, la aproximación desarrollada incorpora medidas del desempeño de las especies considerando la variabilidad ambiental espacial, las preferencias ambientales de las especies, y sus respectivos rasgos morfofuncionales.

Los resultados obtenidos sugieren una alta variabilidad espacial del potencial de funcionalidad física de los arrecifes del Gran Caribe en las distintas ecorregiones. Esta variabilidad podría estar asociada al fuerte efecto que las condiciones ambientales locales tienen en el desarrollo de los arrecifes, ya que áreas espacialmente adyacentes pueden presentar grandes variaciones ambientales que se ven reflejadas en diferencias en la estructura y composición de las comunidades, lo que a su vez resulta en variaciones funcionales de los ensamblajes (Alvarez-Filip *et al.*, 2013; Gove *et al.*, 2015; Zinke *et al.*, 2018).

La comparación realizada entre el potencial de funcionalidad estimado con los modelos contra el índice de funcionalidad obtenido utilizando datos de campo sugiere que para la mayoría de los arrecifes del oeste del Caribe su funcionalidad física pudo haber disminuido en un 30%. Este hallazgo podría ser soportado si consideramos la historia de degradación a la que estos arrecifes han estado sometidos. Por ejemplo, se estima que en décadas recientes la cobertura coralina viva a lo largo del Caribe ha disminuido hasta un ~80% (Gardner *et al.*, 2003; Contreras-Silva *et al.*, 2020). Esta disminución en la cobertura coralina no ha sido consistente entre los distintos grupos funcionales de corales, sino que han sido los principales constructores de arrecife las especies más afectadas (Bellwood *et al.*, 2019). Por ejemplo, las mortandades masivas de *Acropora palmata* y *A. cervicornis* provocadas por brotes de enfermedades y actividades humanas redujo sus poblaciones en un ~80% (Gladfelter, 1982; Cramer *et al.*, 2020). Esta pérdida de corales del género *Acropora* ha impactado profundamente la estructura y funcionamiento de los arrecifes del Caribe, ya que se trata de especies de rápido crecimiento, con morfologías complejas y gran capacidad para acumular carbonato de calcio (Lange & Perry, 2019).

Al observar la distribución espacial de los valores estimados del potencial de funcionalidad física de los arrecifes, es notable que los valores más bajos se encuentran en la zona límite para el desarrollo de los arrecifes en latitudes altas, donde los parámetros ambientales como la temperatura, la disponibilidad de luz, y la saturación de omega aragonita limitan el crecimiento de los corales y el desarrollo de los arrecifes, y en ocasiones propician una baja diversidad de especies (Kleypas *et al.*, 1999; Perry & Larcombe, 2003). Por el contrario, los arrecifes con los valores de funcionalidad más altos se observaron principalmente en el oeste del Caribe, lo cual podría ser explicado debido a los atributos de los sistemas arrecifales ahí presentes, los cuales representan una de las formaciones más grandes de todo el Caribe compuesta por un sistema casi continuo, lo cual facilita la conectividad entre las comunidades biológicas (Mölder *et al.*, 2019).

Con la intensificación en la degradación de los arrecifes y el impacto potencial del cambio climático, es de vital importancia la identificación de estos arrecifes con alto potencial de funcionalidad física expuestos a bajas anomalías térmicas que puedan funcionar como refugios climáticos (alto potencial de funcionalidad y baja exposición a anomalías térmicas elevadas), y así contribuir a la mejoría de las medidas de conservación. Los modelos espacialmente explícitos sobre la exposición de los arrecifes a las anomalías térmicas permitieron la identificación, a nivel nacional, de las áreas que podrían funcionar como refugios climáticos, y que, por lo tanto, podrían ser objetivo para fortalecer la protección de arrecifes con alto potencial de funcionalidad física, o para la creación de nuevas AMPs que incluyan arrecifes con alto potencial que carecen de protección bajo el esquema actual de la red de AMPs del Caribe. La efectividad de los refugios climáticos ha sido evidenciada estudios realizados con hidrocorales, tal es el caso del coral *Millepora intricata*, para el cual se cuenta con evidencia de que sobrevivió a eventos de blanqueamiento en refugios localizados en aguas más profundas, mientras que organismos ubicados en aguas someras sufrieron blanqueamiento y mortalidad (Smith *et al.*, 2014).

Al determinar refugios climáticos es importante considerar que un análisis de exposición a las amenazas no refleja el panorama completo. Una evaluación más amplia sobre el impacto del cambio climático debería considerar una visión de vulnerabilidad, es decir, la exposición, la sensibilidad de las especies y su capacidad de adaptación (Morelli *et al.*, 2020; Chollett *et al.*, 2022). Se ha probado que los corales tienen la habilidad para adaptarse a las variaciones en la temperatura, cambiando de simbiontes, mediante expresiones de proteínas, o al experimentar anomalías térmicas repetidas (Palumbi *et al.*, 2014; Boulotte *et al.*, 2016; Scharfenstein *et al.*, 2022). Esta información no se encuentra disponible a grandes escalas espaciales, sin embargo, cuando lo esté, podría ser de gran utilidad para informar futuros estudios.

Otro argumento importante de considerar es el efecto potencial de los eventos climáticos extremos. En este trabajo, se utilizaron anomalías térmicas promedio, lo cual podría no reflejar el impacto de dichos eventos, los cuales tienen la capacidad de

provocar impactos graves en los arrecifes, como se han observado en los eventos de blanqueamiento masivos y la mortalidad coralina asociada (Hughes *et al.*, 2018a; Eakin *et al.*, 2019).

Los problemas globales de conservación de la naturaleza pueden ser atacados a través de acciones de conservación locales que estén coordinadas globalmente a través de la colaboración internacional. Para ello, la evaluación a nivel nacional sobre las áreas prioritarias aporta valiosa información sobre cuáles arrecifes podrían ser de particular interés. Sin embargo, es indispensable mejorar las condiciones locales para reducir el impacto y mejorar la resiliencia de los arrecifes (Kavousi & Keppel, 2018).

CONCLUSIONES

Los resultados de este trabajo tienen implicaciones importantes para el conocimiento y manejo de los arrecifes coralinos de aguas someras del Gran Caribe (Mar Caribe, Golfo de México y Bermudas de acuerdo con Robertson & Cramer, 2014). Los análisis realizados brindan elementos para contribuir a un manejo efectivo y eficiente sobre áreas geográficas grandes: la estimación del potencial de funcionalidad física de los arrecifes Caribe, el análisis de divergencia funcional en los arrecifes del oeste del Caribe, la evaluación de la exposición de los arrecifes al incremento de la temperatura en escenarios a futuro y la identificación de refugios climáticos potenciales en áreas que permanecerían relativamente protegidas del incremento en la temperatura.

Los modelos de nicho ecológico y distribución de especies mostraron tener un gran potencial de aplicaciones para el estudio de diversos patrones y procesos ecológicos de especies marinas bajo diferentes enfoques de investigación como los mecanismos detrás de los rangos de distribución de las especies, el impacto potencial del cambio climático o como herramientas de apoyo en la generación de estrategias de conservación. Dentro de los grupos taxonómicos más estudiados se encuentran los peces, mientras que los corales escleractinios están entre los menos representados. Se resalta la importancia de

considerar los aspectos únicos de los ambientes marinos, como la adición de una tercera dimensión dada por la columna de agua, las distintas escalas espaciales y temporales de las relaciones especie-ambiente, especialmente para especies altamente móviles; así como considerar la falta de barreras físicas para la dispersión; esto con la finalidad de obtener resultados más precisos y confiables en los ejercicios de modelación.

Los modelos de nicho ecológico también demostraron ser una herramienta útil en el estudio de atributos funcionales de los ecosistemas arrecifales. La combinación de las estimaciones de idoneidad ambiental obtenidas con los modelos de nicho ecológico con los rasgos morfofuncionales de las especies coralinas demostró ser una aproximación exitosa para ligar el efecto de la variabilidad ambiental, de las preferencias ambientales de las especies y sus rasgos morfofuncionales para estimar el potencial de funcionalidad física (capacidad para construir estructuras tridimensionales complejas) de los arrecifes del Gran Caribe. Los arrecifes mostraron una alta variabilidad espacial en su potencial de funcionalidad, probablemente asociada a la variabilidad en las condiciones ambientales. A nivel ecorregión, el oeste del Caribe presentó el mayor número de celdas arrecifales con altos valores de funcionalidad física; por el contrario, las ecorregiones con los valores de funcionalidad más bajos fueron Bermuda y el norte del golfo de México, consideradas regiones marginales para el desarrollo arrecifal. Se identificaron hotspots de potencial de funcionalidad física en las costas de Belice y la costa sur de Cuba. En el análisis comparativo de la estimación de funcionalidad física obtenida con los modelos con las estimaciones de funcionalidad física calculadas con datos de campo, sugiere una disminución importante en el potencial de funcionalidad de los arrecifes del oeste del Caribe, lo cual concuerda con el historial de degradación al que han estado sometidos y que se ha visto reflejado en la disminución de la cobertura de las especies constructoras más importantes, que ha conllevado a la perdida de tridimensionalidad y, por lo tanto, una disminución en la funcionalidad física de los arrecifes.

Se observó que algunos países tienen todos o casi todos sus arrecifes protegidos independientemente de su potencial de funcionalidad, mientras que otros tienen todos o casi todos sus arrecifes desprotegidos. Los arrecifes con alto potencial de funcionalidad física que se encuentran fuera de Áreas Naturales Protegidas se encontraron particularmente en Belice, Puerto Rico, Honduras, Cuba y las islas Turcas y Caicos. La exposición de los arrecifes al incremento en la temperatura bajo los escenarios de cambio climático SSP7-3.0 y SSP5-8.5 al año 2049 mostró variabilidad espacial; sin embargo, las anomalías térmicas proyectadas fueron más elevadas en latitudes altas, por lo cual los arrecifes que podrían experimentar anomalías de hasta 1.12 °C se localizan en Flower Garden Banks (USA) y Bermudas. La exposición de los arrecifes con alto potencial de funcionalidad física a anomalías térmicas elevadas se incrementa del escenario SSP7-3.0 al SSP5-8.5. La evaluación de celdas arrecifales con potencial para funcionar como refugios climáticos (alto potencial de funcionalidad y baja exposición a anomalías térmicas elevadas) ante el incremento en la temperatura identificó a Bahamas, Puerto Rico, las Islas Turcas y Caicos, Panamá, Cuba, Belice Haití, Honduras, Guadalupe (Francia) y Jamaica como los países con mayor número de celdas con potencial de actuar como refugios climáticos no protegidas.

Las perspectivas generadas en este trabajo ofrecen una oportunidad para salvaguardar la riqueza biológica, los servicios ecosistémicos y el valor sociocultural de los arrecifes coralinos para las futuras generaciones. El cambio climático podría afectar de manera importante la disponibilidad de refugios climáticos que protejan a los arrecifes del incremento en la temperatura en el océano, por lo que medidas para reducir las emisiones de CO_2 atmosférico y disminuir otros impactos a los arrecifes es urgente para intentar preservar estos valiosos ecosistemas.

PERSPECTIVAS A FUTURO

Con base en la información generada en el presente trabajo, se proponen líneas de investigación complementarias que puedan ser realizadas en futuros estudios:

1. Evaluar el efecto del incremento en la temperatura sobre la idoneidad ambiental de los corales en escenarios a futuro y las consecuencias sobre el potencial de funcionalidad física de los arrecifes del Caribe.

2. Incluir información más detallada sobre los umbrales de tolerancia térmica de las distintas especies de corales constructores de arrecife para mejorar las predicciones del impacto del cambio climático y de la vulnerabilidad de los arrecifes.

3. Evaluar la factibilidad de los refugios climáticos desde la perspectiva socioeconómica de los distintos países.

4. En todas las intervenciones de conservación es importante reducir el efecto de otras amenazas para mejorar la resiliencia de los ecosistemas. Mientras que este trabajo ayuda a identificar áreas donde los arrecifes podrían sobrevivir al incremento en la temperatura, futuros trabajos deberían considerar también el efecto de otras amenazas asociadas al cambio climático, como la acidificación, los cambios en el nivel del mar y la desoxigenación.

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