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Identifying key biodiversity areas as marine conservation priorities in the greater Caribbean

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Abstract
Increasing rates of Anthropocene biodiversity extinctions suggest a possible sixth mass extinction event. Conservation planners are seeking effective ways to protect species, hotspots of biodiversity, and dynamic ecosystems to reduce and eventually eliminate the degradation and loss of diversity at the scale of genes, species, and ecosystems. While well-established, adequately enforced protected areas (PAs) increase the likelihood of preserving species and habitats, traditional placement methods are frequently inadequate in protecting biodiversity most at risk. Consequently, the Key Biodiversity Area (KBA) Partnership developed a set of science-based criteria and thresholds that iteratively identify sites where biodiversity is most in need of protection. KBA methodology has been rarely applied in the marine realm, where data are often extremely limited. We tested the feasibility of KBA population metrics in the Greater Caribbean marine region using occurrence and population data and threat statuses for 1669 marine vertebrates. These data identified areas where site-specific conservation measures can effectively protect biodiversity. Using KBA criteria pertaining to threatened and irreplaceable biodiversity, we identified 90 geographically unique potential KBAs, 34 outside and 56 within existing PAs. These provide starting points for local conservation managers to verify that KBA thresholds are met and to delineate site boundaries. Significant data gaps, such as population sizes, life history characteristics, and extent of habitats, prevent the full application of the KBA criteria to data-poor marine species. Increasing the rate and scope of marine sampling programs and digital availability of occurrence datasets will improve identification and delineation of KBAs in the marine environment.

Keywords Targeted conservation · Marine protected area networks · Threatened species · Geographically restricted species · Conserving marine biodiversity

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Introduction

Anthropogenic biodiversity loss may be causing a sixth mass extinction event (Ceballos et al. 2015), as species extinction rates in both terrestrial and marine environments approach nearly 1,000 times background rates (Pimm et al. 2014). This escalating loss erodes the functional integrity of ecological processes and threatens the vitality of ecosystem services (Costanza et al. 1997). The preservation of biodiversity requires effective conservation planning (Brooks et al. 2004), but available resources are often limited (Pullin et al. 2013). Well-established and enforced protected areas (PAs) afford species and ecosystems the best prospect for preservation (Le Saout et al. 2013), but traditional approaches to PA placement often exclude species and habitats most in need of conservation (Rodrigues et al. 2004; Klein et al. 2015).

Biodiversity conservation goals, such as the Aichi Targets 11 and 12 (CBD 2012), often prioritize the implementation of PA networks that emphasize species most at risk for extinction, biodiversity hotspots, and areas integral to ecosystem services. However, many of the Aichi targets were not realized by the 2020 deadline, and focus on PA networks is expected to continue through the post-2020 biodiversity framework. It has become increasingly important to find ways to fulfill biodiversity conservation goals and targets related to PA networks. Thus, in order to identify sites most likely to conserve species and habitats most at risk, the International Union for Conservation of Nature (IUCN) Species Survival Commission, the World Commission on Protected Areas Joint Task Force on Biodiversity and Protected Areas, and other partners devised standardized criteria to identify Key Biodiversity Areas (KBAs), defined as sites that contribute significantly to the global persistence of biodiversity (Langhammer et al. 2007). KBAs complement existing PA networks by highlighting discrete geographic localities where biodiversity is most at risk (Langhammer et al. 2007). The identification of KBAs within existing PAs provides evidence that adequate spatial coverage to conserve some species and habitats exists. Alternately, KBAs identified outside of existing PA networks encourage collaboration of conservation planners and managers on where to best place future PAs.

The KBA criteria are based on the concepts of uniqueness (irreplaceability) and threat status (vulnerability) of biodiversity (Margules and Pressey 2000). Irreplaceable species and ecosystems are those with restricted ranges during one or more life-stages and sites where unique combinations of species occur; vulnerable species and ecosystems are those with a high risk of extinction (Langhammer et al. 2007), as quantified by IUCN Red List (RL) categories and criteria (Mace et al. 2008). The development of the KBA criteria drew heavily from previous initiatives that targeted mostly terrestrial and fresh water biodiversity, including Important Bird and Biodiversity Areas (IBAs: Grimmett and Jones 1989), Important Mammal Areas (Linzey 2002), and Alliance for Zero Extinction sites (AZEs: Ricketts et al. 2005). The inclusivity of KBA criteria standardizes the selective process of identifying where site-specific conservation measures are most needed across multiple taxonomic and environmental spectra (Eken et al. 2004a; Langhammer et al. 2007; Edgar et al. 2008).

The earliest versions of KBA criteria focused mainly on threatened terrestrial animals and plants (e.g. Madagascar: Eken et al. 2004a; Turkey: Eken et al. 2004b; Japan: Natori et al. 2012; Upper Guinea Forest Hotspot: Kouame et al. 2012), as sufficient data were available to apply the criteria to these taxa. Efforts to identify KBAs in the marine realm were generally limited in geographic and/or taxonomic scope (e.g. Galapagos Marine Reserve: Edgar et al. 2008; the Philippines: Ambal et al. 2012; and marine turtles in

Melanesia: Bass et al. 2011). The population and occurrence data required by the criteria existed mostly for charismatic or flagship species, many of which are threatened. Furthermore, RL assessments for many marine taxa did not begin in earnest until about 2005. However, recent consultation between KBA partners produced a revised and updated set of KBA criteria and thresholds (hereafter, the KBA Standard: IUCN 2016a) that incorporates several population estimation metrics, allowing for better inclusion of data-poor species and habitats into KBA analyses. However, these updated criteria have yet to be applied in the marine realm. This is increasingly important given global commitments by individual nations to marine conservation through the Aichi targets, and the ongoing efforts of the UN to provide legally binding mechanisms to protect the marine environment and to conserve and ensure the sustainable use of marine biodiversity in international waters under the Convention on the Law of the Seas (United Nations 2017).

The Greater Caribbean region, defined by Robertson & Cramer (2014) as the western central Atlantic Ocean, Caribbean Sea, and Gulf of Mexico (Fig. 1) is geographically complex and biologically diverse. Several critical marine habitats, including more than 10% of all global coral reefs, over 12% of global mangrove forests, and nearly 20% of global seagrass beds (Jackson 1997; Smith et al. 2002; Spalding et al. 2010; Burke et al. 2011) are found in the region. Encompassing an extensive and complex network of nearly 1500 international PAs (those designated by international organizations) and national PAs (those designated by national organizations) and including over 189 PA designation types (Fig. 1), the Greater Caribbean is an ideal case study in the application of the updated KBA criteria in the marine environment. In our scoping analysis, we focus on the first step of the KBA establishment process: the identification of potential KBA sites based on species' existing occurrence data and threat status. The resulting outputs can then be used by regional stakeholders to complete the second step: delineation, by identifying and establishing shared

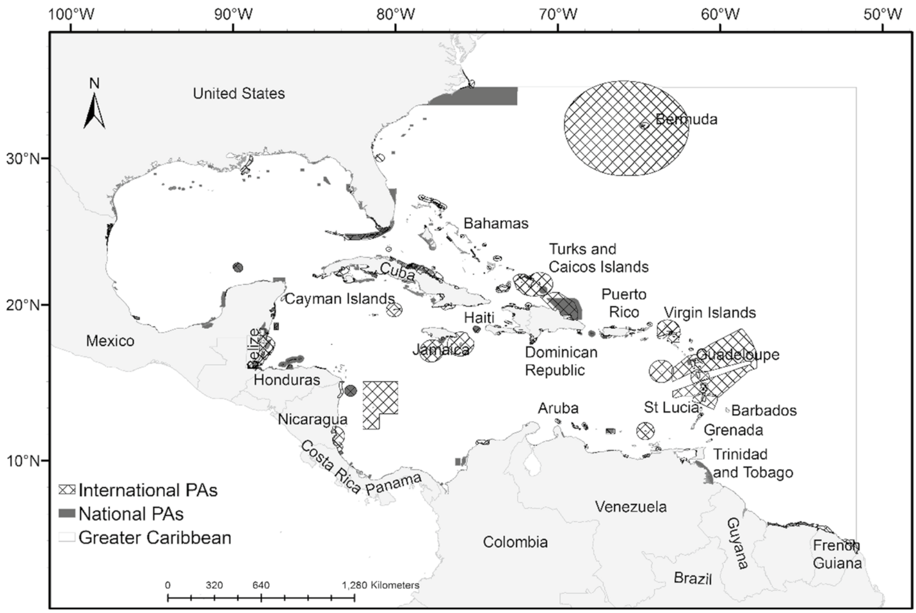

Fig. 1 The Greater Caribbean study area and existing national and international protected areas in the region

KBA management units. Through this process, we also highlight significant biological data gaps that hamper widespread application of the KBA criteria in the marine realm.

Methods

To identify potential KBAs in the Greater Caribbean, we first determined the availability of data required for KBA selection. Species-specific datasets included: point locality data, generalized distribution maps, threat statuses, and global population estimates. We also included physical and contextual spatial data, including marine ecoregion boundaries, political boundaries, distribution of marine habitats, and a measure of cumulative human impacts on marine species and habitats (see Appendix S1 for a summary of the data sources used in the analysis).

KBA criteria

The KBA Standard describes criteria by which sites may qualify as KBAs (IUCN 2016a). These 11 criteria are nested within five major categories: A—threatened biodiversity, B—geographically restricted biodiversity, C—ecological integrity, D—biological processes, and E—irreplaceability through quantitative analysis. The first two criteria (A1 and A2) address vulnerability of biodiversity, and the remaining nine criteria cover components of irreplaceability (Appendix S2; IUCN 2016a). All criteria require that a significant proportion of species' populations or amount of intact ecological communities be present at potential sites. Some criteria further require specific numbers of reproductive units of a species or a significant proportion (5–20%) of an ecosystem's global distribution at sites. Under Criteria A1 and B1-B3, the proportion of a species' global population at a site may be observed based on the number of mature individuals or inferred through a proxy (e.g. area of occupancy (AOO), extent of suitable habitat, range, number of localities, and distinct genetic diversity). However, for the biological processes and quantitative analysis Criteria (D1-D3 and E), only an observation of the number of mature individuals is permitted (IUCN 2016a). The 11 KBA criteria are summarized below and a table with the criteria, population and reproductive unit thresholds, and whether the criterion was applied in the study is provided in Appendix S2.

Species assessed under the IUCN RL criteria as Critically Endangered (CR), Endangered (EN), or Vulnerable (VU) may trigger sites under the threatened biodiversity Criterion, A1. Ecosystems assessed as threatened under the IUCN RL of Ecosystems may trigger sites under Criterion A2, where an ecosystem faces deterioration, transformation, or replacement by another ecosystem type (IUCN 2015).

The four criteria for geographically restricted biodiversity (B1-B4) pertain to species or species assemblages with restricted ranges or with wide-ranging distributions that occur in clusters of at least 10% of the global population size during all life-history stages. Geographically restricted species may occur individually or in groups, such as at centers of taxonomic endemism, biodiversity hotspots, or assemblages of regionally restricted biodiversity.

The ecological integrity Criterion (C) identifies sites where large-scale, wholly intact ecological communities maintain fully functional ecosystem types, contain historical abundances or biomass of associated species, support all inter- and intraspecific interactions and natural movements, and enable maximum functionality of all ecosystem processes in an ecoregion. As such, KBAs identified under Criterion C are relatively large, generally $\geq 10{,}000$ km^2. The biological processes Criteria (D1-D3) identify sites important to demographic aggregations, ecological refugia, and recruitment sources during one or more life-history stages. These sites are often connected to reproductive activities, such as bird rookeries, fish aggregations, or areas of refugia during inclement weather conditions. Criterion E is a complementarity-based, quantitative approach of measuring the relative contribution of sites to the persistence of biodiversity, on the species level. It requires data-heavy analyses, such as population viability analyses, that project the likelihood of a species surviving in the future based on current population levels and trends.

Determining species datasets

To determine potential trigger species, we filtered all species on the RL website (IUCN 2016b) by taxonomy (Mammalia, Aves, etc.), system (marine), marine region (western Central Atlantic FAO fishing zone), and Red List category (not extinct or extinct in the wild). However, as only a small proportion of marine birds have a marine region coded, we supplemented this initial output by including all marine birds (as defined by Croxall et al. 2012) that occur in the Greater Caribbean region. The exclusive choice of vertebrates allowed for consistency in the availability of point occurrence data that are readily available. Overall, 1669 species were assessed against the RL criteria as of November 2016.

Online data repositories provided point occurrences used to generate species' distribution point maps (GBIF 2016; OBIS 2016; Robertson & Van Tassell 2016). All occurrences that fell outside of species' distribution polygons, as published on the RL, were assumed to indicate waifs, misidentifications, or instances of vagrancy and were eliminated. We assigned confidence levels to indicate the relative reliability of occurrences, following KBA protocol (IUCN 2016a). High confidence occurrences, such as those reported relatively recently and from reliable institutions, collectors, or observers, were assigned a value of "1". We considered these occurrences as most reliable for populations and reproductive units when identifying potential KBAs. We considered occurrences of intermediate confidence, such as antiquated records (20 + years old) by reliable institutions, collections, or observers, as well as those reported by citizen scientists at any time in the past, as qualitatively plausible but unverified, and we assigned these occurrences a confidence value of "2". These reported occurrences are likely correct but may reflect the antiquated reports on the presence of species at sites that may no longer occur there. Occurrences of low confidence, such as those with no metadata or taxonomic uncertainty, received a confidence value of "0" and were not included.

Determining threatened and geographically restricted species

We defined trigger species as both threatened and geographically restricted species that could potentially trigger sites as KBAs (Langhammer et al. 2007). We identified threatened species as marine vertebrates, which comprised all marine mammals, birds, reptiles, sharks and rays, and bony shorefishes, with an elevated extinction risk (CR, EN, and VU) on the RL website. To identify geographically restricted species, we calculated the Extent of Occurrence (EOO) for all marine vertebrates in the Greater Caribbean that have been assessed for extinction risk by drawing a minimum convex polygon around the vetted occurrences for each species, including uninhabitable areas, such as land (for marine species) and potential physical barriers, as specified in IUCN protocol for calculating EOO

(IUCN 2012). Species with a calculated EOO < 100,000 km^2 were designated geographically restricted, following marine KBA analyses and protocols from earlier iterations of KBA criteria (Edgar et al. 2004, 2008; IFC 2012; IUCN 2014). More recently, the use of extent of suitable habitat (ESH) rather than EOO has been recommended to identify geographically restricted species (KBA Standards and Appeals Committee 2019); however, very few marine species have existing ESH maps, and the underlying data, both in terms of species-specific habitat requirements and high-resolution habitat distribution maps, are lacking. Co-occurring geographically restricted species were identified using a richness analysis of geographically restricted species' generalized distribution maps, which we ranked according to the number of overlaps at sites. A species qualified as bioregionally restricted if all known occurrences fell within the boundaries of a single, marine bioregion, defined as a biogeographic unit distinguished by similar climate, flora, and fauna that is typically an order of magnitude larger than smaller ecoregions nested within it. Ecoregions contain distinct assemblages of species and communities approximating the composition of plants and animals prior to major land-use changes (Spalding et al. 2007, 2011).

Using estimated Area of Occupancy (AOO) as a proxy for population size

An essential component of KBA identification for most criteria is population size. However, as these data are lacking for many marine species, we tested the feasibility of using AOO as a proxy for population size, as described in the KBA Standard (IUCN 2016a). While EOO includes the total area that encompasses all known occurrences of a species, AOO includes only the area within the EOO where specific habitat and food resources are found. In this way, AOO identifies portions of the species' distribution where individuals are most likely to occur (IUCN 2012). We determined species' AOO by converting the high- and intermediate-confidence occurrences into 4 km^2 raster cells (IUCN 2012). We considered the sum of the raster cells at potential KBA sites, relative to the total number of raster cells for a species, as a proxy for the proportion of a species' global population size at sites to compare against thresholds (IUCN 2016a). For example, if a species' global distribution encompassed 100, 4 km^2 raster cells, and 5 of those cells occurred at a given site, then we considered the site to hold 5% of the AOO and, by proxy, 5% of the global population. While this approach to estimating global population sizes for data-limited marine species represents the best available science in identifying potential KBAs for marine species, it introduces a range of limitations that potentially misrepresent the population sizes of species, particularly those of wide-ranging species. For example, patterns of presence often differ from patterns of abundance (Waldock et al. 2019), such that an area identified as having a high proportion of the total AOO may not have a high proportion of the total population. Furthermore, occurrences can reflect the concentrations of observers more than actual population densities, leading to inflated estimations of proportions of populations at some sites. Despite these limitations, AOO represents an acceptable methodology for estimating populations for most marine species.

Determining reproductive units

We used the metadata (number of individuals in collections, gender, life history stage, etc.) associated with high confidence occurrences (those less than 20 years old and reported by reliable institutions, collectors, or observers) to estimate the number of reproductive units at sites. For batch spawners, such as most teleosts, as well as marine birds and reptiles, we summed all occurrences of adult specimens at sites, making sure at least 1 adult female and 1 adult male was present at the site, and assumed the total number of adult individuals at a site to be the number of reproductive units. Marine mammals and some cartilaginous fishes required at least 1 adult male and 1 adult female at sites to constitute a single reproductive unit.

KBA criteria applied in this study

Due to the paucity of population data for most marine species, potential KBAs were identified using only criteria that allowed for proxies in estimating the proportion of species' populations at sites (i.e., Criteria A1, B1, B2 and B3), rather than those that require the number of mature individuals. Because ecoregions are smaller than bioregions, and the median range of most marine species is well over 100,000 km^2 (Edgar et al. 2004), we did not identify potential KBAs for ecoregionally restricted assemblages (Sub-criterion B3a), but we did identify potential KBAs for bioregionally restricted assemblages (B3b). While wholly intact marine ecological communities have not yet been identified in the Greater Caribbean (Criterion C), we performed a preliminary scoping analysis to identify areas where human influences have been limited. These areas may maintain assemblages similar to those present historically, and subsequent analyses may confirm that the functionality of ecosystem processes remains unimpeded.

We could not apply criteria A2 and B4, as the IUCN RL of Ecosystems' status assessments are not yet widely available. Additionally, no baseline data exist to quantify the most important occupied habitat for many marine species (Sub-criterion B3c), eliminating that criterion from the study. For Criteria D1-D3, only number of mature individuals may be used to observe population sizes, eliminating these criteria from the analyses. Finally, complementarity-based approaches to quantitatively estimate the relative irreplaceability of sites to the persistence of biodiversity (Criterion E) may be determined in one of two ways: either by the number of mature individuals at sites relative to the number of mature individuals in the global population or by the proportion of the spatial distribution of species at sites relative to the spatial distribution of species, globally. Both approaches require quantitative population viability analyses (PVA), which help identify sites that would ensure the global persistence of species with a probability of $\geq 90\%$ in 100 years, which is beyond the scientific scope and funding opportunities of this study. For a more detailed description of the quality and reliability standards for data collection and assimilation procedures, see Harvey (2018).

Identifying potential KBAs

We followed two basic steps to identify potential KBAs for Criteria A1, B1, B2, and B3b. First, sites had to meet the population proportion thresholds of trigger species, according to the KBA Standard, to be considered further; next, we based the selection of potential KBAs on reproductive unit thresholds (see Appendix S2 for the specific thresholds required for the criteria and subcriteria). Sites that satisfied reproductive unit thresholds with high confidence occurrence data, only, were designated proposed KBAs, while sites that used intermediate confidence occurrence data to meet reproductive unit thresholds were designated candidate KBAs. If sites met the proportion of population threshold but did not satisfy reproductive unit thresholds, they were designated research priorities. Candidate KBAs and research priorities have high conservation potential but require extensive further evaluation; therefore, we included only proposed KBAs in further analyses.

As suggested by KBA protocol (Langhammer et al. 2007), we first identified potential KBAs at existing PAs by iteratively evaluating each threatened and geographically restricted species present against relevant KBA criteria and thresholds. Potential KBAs outside of existing PA boundaries were identified utilizing a model in ArcGIS version 10.5.1. In this model, polygons were drawn around occurrence records of threatened and geographically restricted species outside of existing PA boundaries and within 50 km^2 of each other; this threshold was chosen to identify areas that would be large enough that the number of occurrences and reproductive units would most likely be able to satisfy KBA criteria and thresholds, but not so large that the site would be logistically impractical to manage. Polygons with overlapping boundaries were merged, such that each resulting polygon represented a geographically independent site. We identified sites that satisfied KBA criteria and thresholds as potential KBAs.

For the scoping analysis for Criterion C, we identified large, contiguous areas ($\geq$10,000 km^2) within the Greater Caribbean with mean cumulative impact scores < 1.8, according to the methodology presented in Halpern et al. (2015), indicating areas that likely have experienced the least amount of cumulative human impacts. These areas may harbor wholly intact ecological communities and pre-industrial era species composition and populations/densities, as required to qualify as a marine wilderness under Criterion C. Further surveys and studies would be necessary to confirm whether any of the sites identified during this scoping analysis would qualify for a marine wilderness designation.

Results

We identified a total of 90 geographically unique potential KBAs under the A and B criteria, 56 completely within and 34 completely outside of existing PAs (Fig. 2). Although existing PAs accounted for about two-thirds of identified potential KBAs, only about 4% of existing PAs met the criteria and thresholds for KBAs. The limited number of existing PAs triggering KBAs may be related to the small size of many Caribbean PAs. Existing PAs that triggered potential KBAs were larger than those that did not, across both nationally and internationally designated areas. The median size of existing national protected areas was 1.2 km^2, but the median size of national PAs that met the KBA criteria was 466.6 km^2 (Fig. 3). Similarly, the median size of international PAs was 42.0 km^2, but 75% of potential KBAs identified at international PAs was > 500 km^2. National and international PAs that did not trigger any potential KBA were relatively small; 83% were < 100 km^2, and nearly 93% were < 1,000 km^2.

Additionally, we identified four areas in the Greater Caribbean that have likely experienced the least amount of human-induced degradation and thus, are potential candidates to qualify as KBAs under Criterion C. Two were identified within the Exclusive Economic Zone (EEZ) of the Bahamas, and one, each, within the EEZs of the USA and Mexico (Fig. 4). These areas generally occurred away from high-density human populations, outside of main shipping corridors, and, for the most part, outside of the existing PA network. The exception is the site identified off the southeast coast of the USA; however, this site excludes the nearshore environment closest to the population centers.

Of the 1,669 marine vertebrates assessed for extinction risk in the Greater Caribbean, we considered a total of 308 potential trigger species: 108 threatened species

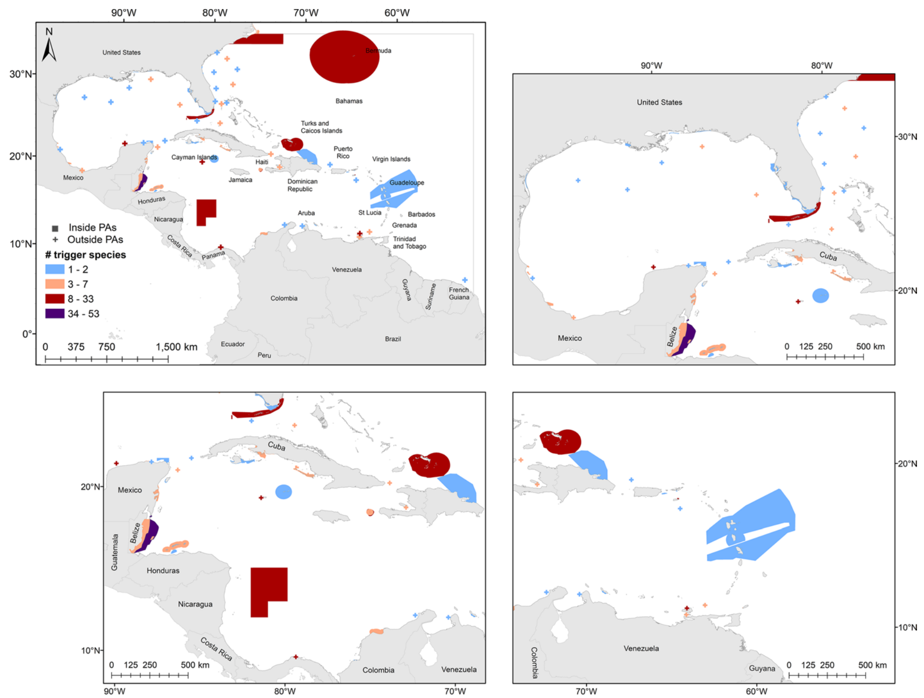

Fig. 2 Potential Key Biodiversity Areas (KBAs) identified within existing protected areas (polygons) and outside of existing protected areas (crosses) in the Greater Caribbean

(~6.5%) and 228 geographically restricted species (~13.7%). Twenty-eight species were both threatened and geographically restricted. Threatened taxa triggered or co-triggered ~82% of all potential KBAs identified at existing PAs, but nearly half of potential KBAs identified outside of existing PAs were triggered or co-triggered by geographically restricted species. While 57% of all potential KBAs were triggered only by threatened species, over three-quarters of all potential KBAs contained at least 1 threatened species, either independently or in addition to geographically restricted species (Fig. 5). Conversely, ~24% of KBAs were triggered by geographically restricted species only (Criteria B1-B3). Potential KBAs triggered as AZEs were rare: 2 in the Bermuda Whale Sanctuary, 1 in South Water Caye (Belize), and 1 in the Florida Keys; these sites were triggered by three bony fishes and one marine bird.

The number of potential KBAs triggered by each species was highly variable. Across all sites, 92 species triggered only one potential KBA (Fig. 6a, Appendix S3). On the other extreme, 2 species triggered more than 10 KBAs; the Nassau Grouper (*Epinephelus striatus*) triggered the most, with 14 potential KBAs. Most potential KBAs contained multiple trigger species (Fig. 6b). One existing PA (Belize Off-shore and Barrier Islands) was triggered by 52 threatened and geographically restricted species, more than all other identified potential KBAs. A site off Panama, previously unrecognized for its conservation potential, was triggered by 33 species (Fig. 2). In contrast, 32 sites were triggered by only one species.

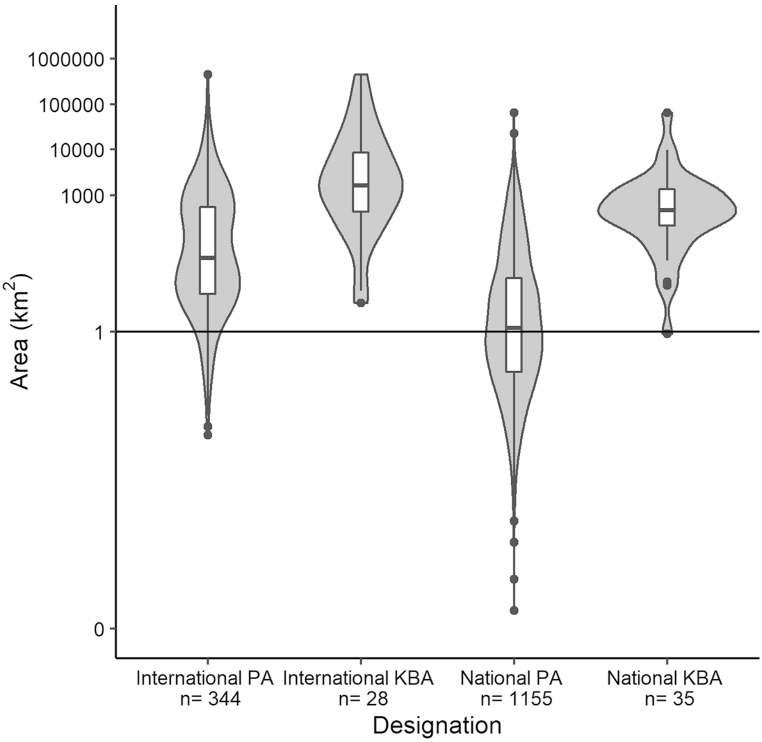

Fig. 3 Violin plots of the area (log-scale) of nationally and internationally designated protected areas (PAs) and PAs that were triggered as potential Key Biodiversity Areas. Each violin plot includes a standard box plot, which indicates the summary statistics (median, interquartile range and outliers), supplemented by a rotated, smoothed probability density distribution that describes the underlying shape of the data. Wider sections of the violin plot represent a higher probability of a PA being a given size, while narrower sections represent a lower probability

Patterns of KBA identification also varied by ecological role. For example, most of the 113 species in the core cryptobenthic fish families (as defined by Brandl et al. 2018) that triggered at least 1 KBA were restricted range, or restricted range and threatened. Only 9 of these species (7 *Coryphopterus*, 1 *Elactinus*, and 1 *Hippocampus*) triggered KBAs solely under the threatened species criteria. In contrast, about 70% of the 36 elasmobranchs and higher vertebrates (reptiles, birds, and mammals) that triggered at least one KBA were threatened. Cryptobenthic fishes tended to trigger the same KBAs, with 37 unique KBAs triggered by the 113 species. In contrast, elasmobranchs and higher vertebrates generally triggered different KBAs, with 45 unique KBAs triggered by the 36 species. Furthermore, relatively low overlap was found in the proposed KBAs triggered by small, cryptobenthic fishes and those triggered by elasmobranchs and higher vertebrates; only 9 KBAs were common to both sets of potential KBAs.

Most (224 of 308) potential trigger species triggered one or more potential KBAs (Appendix S3), but these were not evenly distributed among the taxa included. Bony fishes comprised about 83% of the species in the study, and they triggered or co-triggered the majority of KBAs (~60%). In fact, bony fishes triggered twice as many KBAs as all other classes, combined (Fig. 7). On the other hand, marine reptiles accounted for only ~0.3% of

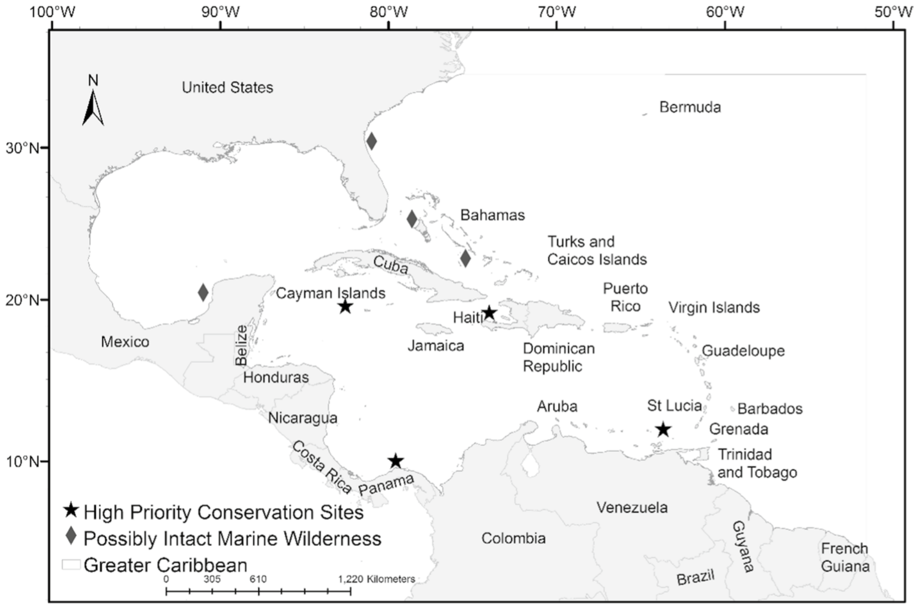

Fig. 4 Marine conservation priorities in the Greater Caribbean, where high numbers of threatened and/or geographically restricted species triggered potential Key Biodiversity Areas (KBAs) outside of the existing protected area network (stars), based on KBA identification protocol, and where cumulative human impact scores (Halpern et al. 2015) are lowest (diamonds)

species in the study, but they triggered or co-triggered about 14.5% of identified KBAs. For taxa that triggered at least one potential KBA, sharks and rays triggered the second most, and marine birds triggered the fewest. Eighty-one bony fishes, 1 marine bird, 8 sharks and rays, and 1 mammal triggered a single potential KBA, exclusively (Appendix S3).

More than 70% of both the threatened species and geographically restricted species triggered at least one potential KBA in the Greater Caribbean, suggesting fairly high coverage of at-risk biodiversity by KBAs. The potential trigger species that did not trigger a KBA were concentrated among the bony fishes, and to a lesser degree, the Chondrichthyes. For example, of the threatened species that did not trigger a potential KBA, about 40% were bony fishes and 43% were sharks and rays; 3 mammals, 1 sea turtle and 1 marine bird also failed to trigger a potential KBA (Appendix S3).

Discussion

In addition to identifying potential KBAs in the Greater Caribbean, this study highlighted gaps in the effectiveness of existing PAs in conserving biodiversity in the Greater Caribbean. Over 30% of identified potential KBAs were triggered outside existing PAs, identifying sites previously unrecognized for their conservation potential. Furthermore, we identified only about 4% of existing PAs as potential KBAs, with a strongly supported median area of 670 km^2 that is much larger than the median areas of existing PAs (Fig. 3). This suggests that relatively small PAs may not be capable of maintaining viable populations of threatened or geographically restricted marine

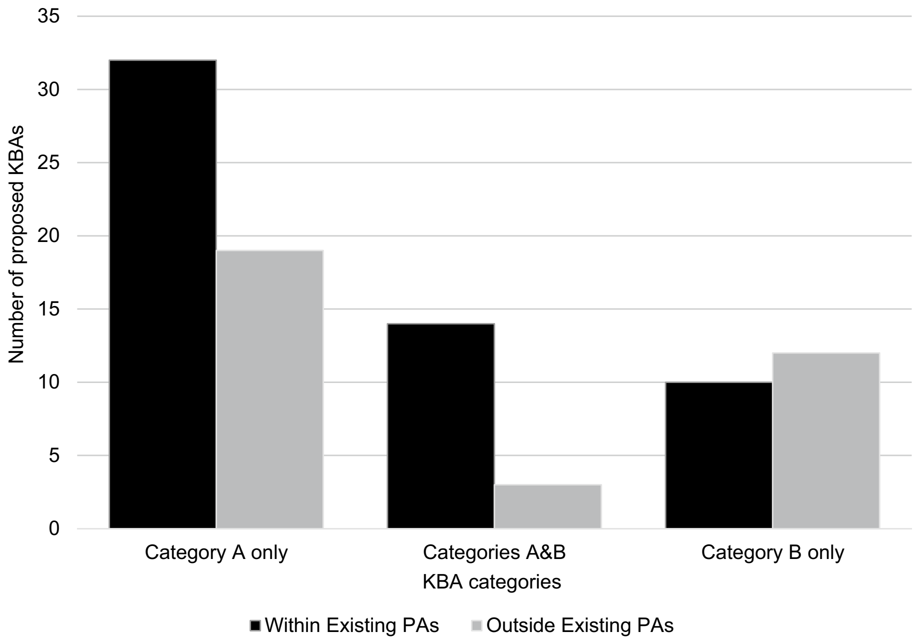

Fig. 5 The number of potential Key Biodiversity Areas (KBAs) identified as a function of KBA categories. Each bar represents the number of potential KBAs triggered and the criteria that triggered them. Category A represents only potential KBAs triggered under the threatened species criterion (A1). Category B represents only potential KBAs triggered under the geographically restricted biodiversity criteria (B1, B2, and B3). "Categories A & B" represents potential KBAs triggered under both the threatened species criterion and the geographically restricted biodiversity criteria

species. PAs are designated for a variety of biological and cultural reasons, and these results do not detract from the importance of PAs to conservation efforts. However, traditional approaches to PA placement, such as biological proxies or surrogates, land classes, marine habitats, or flagship species (Caro 2010), may not identify or protect the full range of biodiversity most in need of conservation (Allison et al. 1998). Without question, trade-offs and concessions made to accommodate some stakeholders in PA designation exacerbate the lack of protection for some species and habitats most in need of protection. Similar concessions are likely when conservation planners determine which potential KBAs should be protected. After the potential KBAs identified here are validated (to confirm that KBA thresholds have been met), delineated, and proposed, the confirmed KBAs could then be included in conservation prioritization processes conducted at national and regional scales. As not all KBAs will or should be protected, KBAs identified outside of the existing PA network, with the most threatened and geographically restricted species, may be given strong consideration for protected status (Fig. 4).

The results of this study further underscore the importance of including more, and diverse, taxa in KBA analyses. Many KBA analyses, especially in the marine realm, have focused on a small suite of taxa (e.g. Bass et al. 2011, which focused on marine turtles). However, the limited overlap in potential KBAs triggered by small, cryptobenthic fishes and those triggered by elasmobranchs and higher vertebrates suggests that

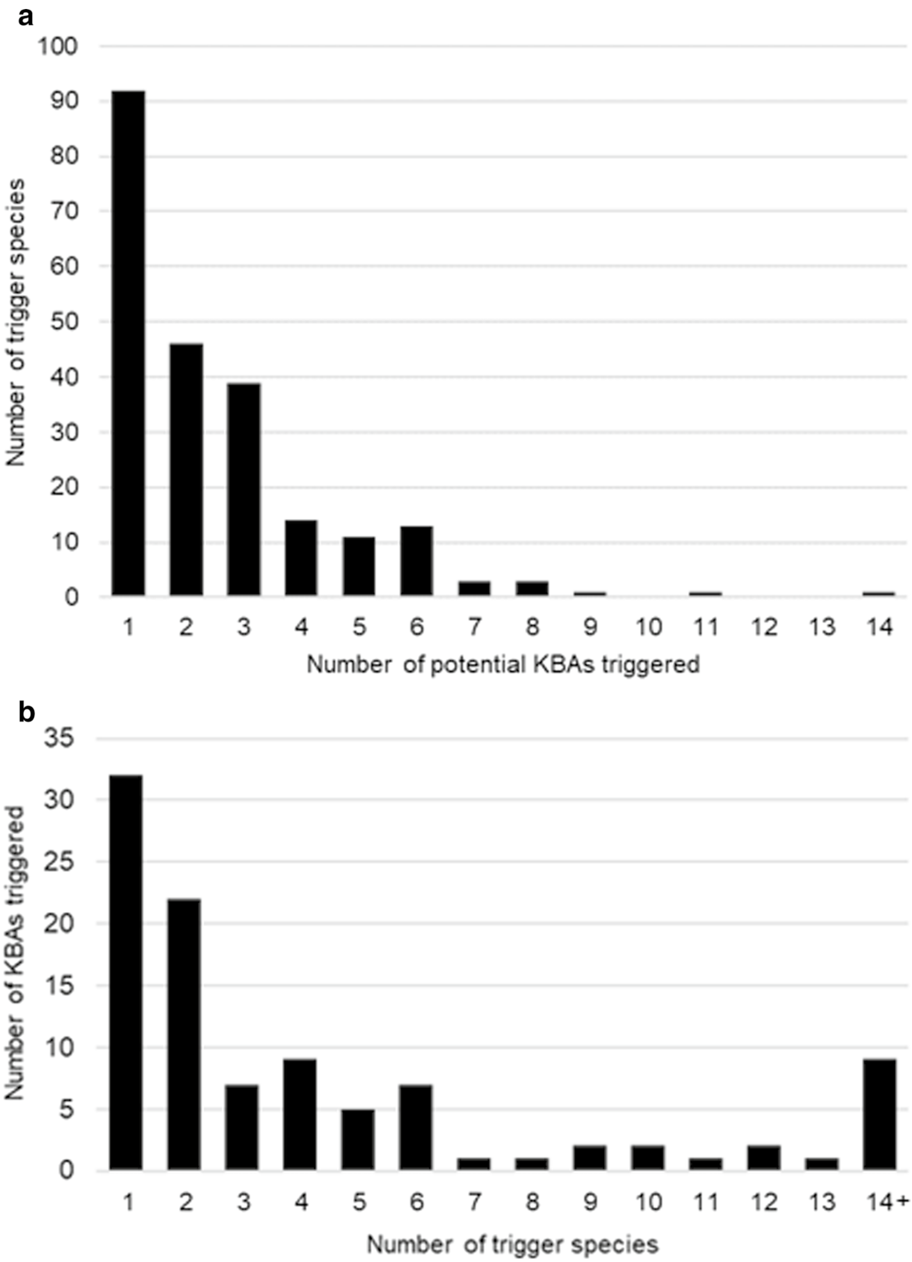

Fig. 6 **a** The number of species that triggered each unique potential Key Biodiversity Area (KBA) and **b** the number of unique potential KBAs identified as a function of the number of individual trigger species at each site

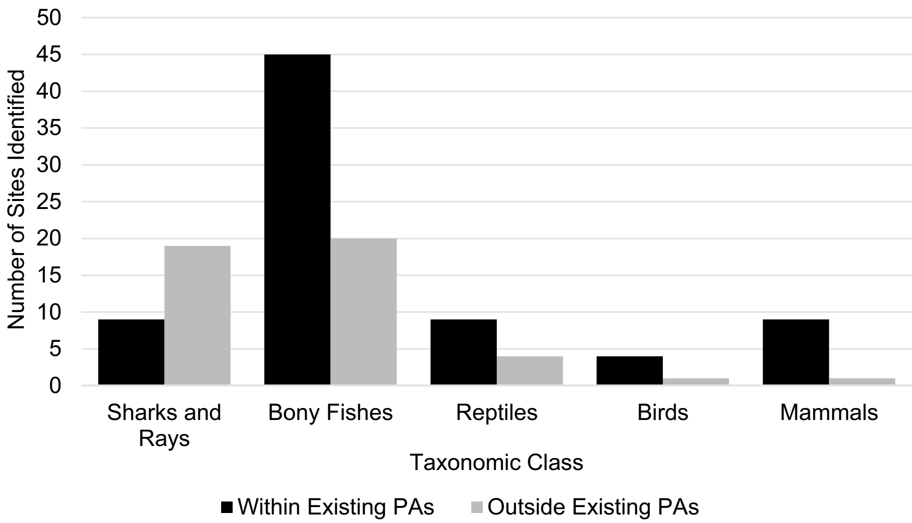

Fig. 7 The number of potential Key Biodiversity Areas (KBAs) triggered according to taxonomic group. Some potential KBAs are represented more than once under different KBA categories and criteria

KBAs based on charismatic megavertebrates alone may potentially miss biodiversity that could benefit from site-based conservation.

While this is the first application of the KBA Standard (IUCN 2016a) in a marine system, these results are qualitatively similar to those of KBA analyses using earlier versions of KBA criteria, mostly in terrestrial regions. For example, this study identified over twice as many geographically restricted species as threatened species in the Greater Caribbean; similar results were found in the Philippines (Ambal et al. 2012), the Upper Guinea Forest (Kouame et al. 2012), and the Indo-Burma hotspot (Tordoff et al. 2012). However, geographically restricted species are inherently characterized by a small distribution, often resulting in a reduced probability of sufficient occurrence data required to trigger a KBA under the B Criteria. Further, although threatened species are often less abundant and less frequently encountered in situ (Paleczny et al. 2015), the proportion of threatened species' occurrences in the literature, relative to their abundance, has increased since the 1960s (Boakes et al. 2010). As such, threatened species triggered or co-triggered about 82% of all potential KBAs identified in this study and between 66 and 83% of KBAs in other analyses (e.g. Ambal et al. 2012; Kouame et al. 2012; Tordoff et al. 2012). Geographically restricted species, though not well represented in existing PAs, triggered nearly half of potential KBAs outside of existing PAs, and indicate where future conservation efforts should be targeted.

Across the different groups of marine vertebrates included in this study, some taxonomic groups with relatively few species triggered disproportionately more potential KBAs than other taxa with more species. For example, bony fishes accounted for over 80% of the species in the study but only about half of all potential KBA trigger events. Conversely, marine reptiles made up only 0.3% of all species in the study but triggered or co-triggered 14.5% of all potential KBAs. This difference may be explained, in part, because the high threat status and charismatic nature of some species, such as sea turtles, increases public attention and support, thus bolstering funding for research on those species. As a result, more scientific research has been published on the migration, foraging, reproduction, population size and trends, and reported occurrences of sea turtles, data on which KBA identification depends, relative to most other marine species (McClenachan et al. 2012). As a result, a disproportionate number of potential KBAs were identified for marine turtles versus less charismatic, less studied taxa, such as hagfishes and non-commercially viable bony fishes.

Ultimately, successful KBA identification depends on the quality and quantity of available data. This study identified several data gaps that inhibited the full application of the KBA methodology across marine taxa. Occurrence data are lacking for many marine taxa, particularly invertebrates and plants (Appeltans et al. 2012). The lack of comprehensive occurrence data introduces bias in estimating populations sizes of species using AOO, particularly for wide-ranging, pelagic species, such as sharks, rays, and whales, as well as for small, cryptic, geographically restricted species where occurrence data may over-estimate the proportion of species' populations at a given site. These skewed data may cause over-estimation of KBA thresholds being satisfied at sites, leading to errors of commission in KBA identification analyses. These limitations also highlight the importance of site validation via increased local sampling efforts prior to KBA delineation. Furthermore, species-specific habitat requirements and high-resolution habitat distribution maps, required inputs for determining species' extent of suitable habitat, are not often available (Jetz et al. 2019). Erroneous or under-sampled occurrence data cause omission and commission errors (Fourcade et al. 2014) in the estimation of site-specific populations (Feeley & Silman 2011), which impact the accuracy of KBA site selection. These limitations could be addressed through large-scale initiatives to obtain additional occurrence data, including traditional field surveys, rapid biodiversity assessments, and public–private partnerships. However, these datasets would need to be readily accessible, integrated, and freely disseminated (Muller-Karger et al. 2018).

The spatial distribution of KBAs identified in this study was likely affected by the distribution of sampling effort in the Greater Caribbean. For example, in Haiti, Honduras, and Nicaragua, where reported marine biodiversity is relatively low (Miloslavich et al. 2010), sampling effort has been limited (Stockwell & Peterson 2002), and only 5 potential KBAs were identified in these countries' EEZs. Conversely, Belize, where the Caribbean Coral Reef Ecosystem program has studied coral reef ecosystems and associated species for 40 years, produced numerous potential KBAs, as well as the one with the most trigger species. As more accurate inventories of marine biodiversity are developed, more KBAs will be triggered in under-represented countries, producing a more connected and inclusive network.

Similarly, the variability in sampling intensity, both temporally and spatially, across countries and territories in the Greater Caribbean results in low estimates of marine biodiversity in under-sampled areas (Stockwell & Peterson 2002; Miloslavich et al. 2010). These biases in marine species datasets inhibit the identification of potential KBAs under not only the C criterion, but all KBA criteria. However, under Criterion C, sites which are wholly intact, contain full compliments of species' natural abundances, and are essentially undisturbed by anthropogenic influences qualify as KBAs. As scientists continue to identify and inventory which species occur in the Greater Caribbean (Bunge & Fitzpatrick 1993; Hoetjes & Carpenter 2010; Miloslavich et al. 2010; Feeley & Silman 2011), it remains impossible to accurately identify sites of historically intact ecological communities and community composition without a comprehensive understanding of which species occur there presently. Although data limitations inhibit definitive identification of KBAs under the C criterion, areas with limited human impacts are most likely where intact marine communities may exist. While four large (> 10,000 km^2) areas were identified here as having the lowest cumulative impact scores (Fig. 4), an alternate approach to determining marine wilderness conducted by Jones et al. (2018) suggested that limited area of marine wilderness exists in the Greater Caribbean region. More work is needed to determine whether these sites, or others, meet the thresholds to trigger a KBA under Criterion C.

The limited knowledge of the population structure and number of mature individuals for the vast majority of marine taxa impeded the application of the biological processes criteria (D1-D3), which identify sites that hold significant proportions of a species' population during specific life stages, such as marine bird rookeries and bony fish spawning aggregations. In these cases, where densities of individuals are skewed spatially and temporally, only the number of mature individuals provides meaningful estimates of species' populations. Accurate estimates of global population sizes (e.g. the number of mature individuals) are available only for birds and a few other select species of high commercial importance. As a result, the number of potential KBAs identified here is likely to be an underestimate for species that congregate for specific life stages. For example, BirdLife International identified 283 IBAs in the Caribbean, of which nearly 60% were triggered by IBA clustering criteria (Wege et al. 2008). Although these sites were primarily identified for terrestrial birds, marine birds triggered only 5 KBAs in this study, all under the threatened species Criterion (A1); as such, it is likely these sites do not represent the only areas important to marine bird conservation in the Greater Caribbean. Similarly, hundreds of fish spawning aggregation sites (Erisman et al. 2017), at least five marine mammal calving grounds (Debrot et al. 2017), and numerous sea turtle nesting sites (Piniak & Eckert 2011) occur in the Greater Caribbean. Although many of these are not freely disseminated for fear they would be targeted for exploitation (de Mitcheson & Erisman 2012), the inclusion of these aggregation areas would greatly enhance the coverage of important components of biodiversity in KBA networks.

The paucity of occurrence and population data for most marine species also inhibits the identification of potential KBAs through complementarity-based quantitative analysis of irreplaceability (Criterion E). Irreplaceability of a site is contingent on a site's probable contribution to the continued survival of species (IUCN 2016a). One of the main ways to estimate the probability of a population's survival is through a PVA. These analyses estimate the probability that a population will go extinct in a certain amount of time relative to minimum population sizes and demographic and environmental stochasticity (May 1973; Shaffer 1981). Analyses that estimate the effects of stochasticity over time rely on calculating the variance and covariance of life history characteristics of species' populations (Reed et al. 1998). As many of these variables are poorly understood for most marine species, it remains virtually impossible to identify potential marine KBAs under the E criterion.

This study represents the first step in the designation and official recognition of KBAs in the Greater Caribbean (Langhammer et al. 2007). Local stakeholder workshops that consider political, economic, and practical factors are needed to select and delineate sites most likely to preserve biodiversity. Delineating KBA boundaries needs to balance ecological considerations, such as the extent and type of habitat the trigger species need, with management practicalities. Sites with many trigger species or without existing protection merit special attention. For example, the current PA network is missing potentially important sites for biodiversity off western Haiti, Little Cayman island, and around the islands of Federal Dependencies of Venezuela, where no PAs exist but many potential KBAs were triggered, and off Panama, where existing PAs exclude a site with 31 species in need of conservation (Fig. 4). After sites are selected and delineated, the final list of proposed KBAs, IBAs, and AZEs should be reported to the appropriate organizations.

Despite limitations preventing the exhaustive application of all KBA criteria in the Greater Caribbean, the results of this study are consistent with other KBA analyses conducted in both terrestrial and marine environments using differing taxonomic classes and associated trigger species. This is due, in part, to the robust nature of the KBA criteria and thresholds, which allow for the identification of rare and unique sites and species across taxonomic and environmental spectra. However, as with other data-heavy analyses, the results reflect the comprehensiveness and accuracy of the underlying data. As the quality and availability of occurrence and population data of marine species increases, more sites, not yet known for their contribution to the persistence of biodiversity, will be identified.

The identification of these potential KBAs not only improves our understanding of how and where PAs may be effectively placed, but also serves to better monitor the progress made towards the conservation goals specified in the Aichi targets. Furthermore, these results can inform ecologists and conservation managers where best to collaborate with local Greater Caribbean stakeholders to optimally determine where to invest resources that most promote the global persistence of species and ecosystems.

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