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Biodiversity hotspots are not congruent with conservation areas in the Gulf of California

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Abstract

As marine systems are threatened by increasing human impacts, mechanisms to maintain biodiversity and ecosystem functions and services are needed. Protecting areas of conservation importance may serve as a proxy for maintaining these functions, while also facilitating efficient use and management of limited resources. Biodiversity hotspots have been used as surrogates for spatial conservation importance; however, as many protected areas have been established opportunistically and under differing criteria, it is unclear how well they actually protect hotspots. We evaluated how well the current protected area network and priority areas selected through previous systematic conservation planning exercises preserve biodiversity hotspots in the Gulf of California, Mexico. We also determined spatial congruence between biodiversity hotspots based on different criteria, which may determine their ability to be used as surrogates for each other. We focus on the Gulf of California because it is a megadiverse system where limited information regarding species diversity and distribution has constrained development of strategies for conservation and management. We developed a species occurrence database and identified biodiversity hotspots using four different criteria: species richness, rarity, endemism, and threatened species. We interpolated species occurrence, while accounting for heterogeneous sampling efforts. We then assessed overlap of hotspots with existing protected areas and priority areas, and between hotspots derived by distinct criteria. We gathered 286,533 occurrence records belonging to 12,105 unique species, including 6388 species identified as rare, 642 as endemic, and 386 as threatened. We found that biodiversity hotspots showed little spatial overlap with areas currently under protection and previously identified priority areas. Our results highlight the importance of distinct spatial areas of biodiversity and suggest that different ecological mechanisms sustain different aspects of diversity and multiple criteria should be used when defining conservation areas.

Keywords Marine Spatial Planning · Species richness · Rarity · Endemism · Threatened species

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Introduction

Marine and coastal systems worldwide, and the ecosystem services they provide, are increasingly threatened by human activities including overfishing and lax fisheries management, climate change, habitat fragmentation and destruction, and pollution (Halpern et al. 2008; 2015). These impacts have led to a substantial decline in the global abundance and diversity of species (Jackson et al. 2001; Worm et al. 2006). In response, numerous conservation initiatives aimed at protecting biological diversity and the provision of ecosystem services in marine and coastal areas have been implemented (Halpern et al. 2010; Boulton and Ekebom 2016). However, selecting priority areas for conservation is not straightforward and limited resources requires thoughtfully defining priorities (Villalobos et al. 2013). Spatial closures and area protection need to minimize the costs associated with restricting economically or socially-important human activities, and also minimize implementation costs (Gruby et al. 2017) while assuring that conservation resources are directed effectively. Thus, it is important to identify clear conservation objectives for ecological, socioeconomic, and climate change components, to set implementation and management goals, and to identify areas that can meet the goals most effectively (Green et al. 2014; Munguia-Vega et al. 2018).

As a response to the urgent need to preserve habitats and the ecosystem services they provide, different approaches to marine and coastal area conservation have been developed. Systematic conservation planning incorporates readily available biological and environmental data and selects areas using expert knowledge, additive scoring systems (Klein et al. 2014), or prioritization algorithms (i.e. Ball et al. 2009; Moilanen et al. 2004), that meet conservation objectives while minimizing costs (Pressey and Bottrill 2009). An expedient approach for conservation has been to use surrogate biodiversity "hotspots," which in practice are defined as areas that "rank highly in one or more of the following biological criteria: species richness; species endemism; number of rare, threatened, or endangered species; complementarity; taxonomic distinctiveness; and degree of habitat loss" (Ceballos and Ehrlich 2006; Briscoe et al. 2016). This approach assumes that hotspots are areas of high biodiversity that capture key ecosystem functions and services (Naeem 2006), including productivity (Palumbi et al. 2008), stable food web dynamics (Dulvy et al. 2004), and evolutionary history (Sechrest et al. 2002), and that can be used to define conservation importance (Briscoe et al. 2016). In practice, however, selection of protected areas has often been opportunistic, and implementation determined by political circumstances, feasibility, and local goodwill (Beger et al. 2003).

Biodiversity-based approaches require detailed species records, but often these data are restricted to a few well-described taxa (Beger et al. 2003). The development of ocean biodiversity informatics—computer technology applied to manage marine biodiversity information, including data capture, storage, search, retrieval, and visualisation—has allowed the growth of global biogeographic databases (OBI) where occurrence data that indicate broad-scale biodiversity or species distribution is readily available (Costello and Berghe 2006; Costello et al. 2014). However, mapping species richness at large scales based on aggregated databases is challenging, due to spatially heterogeneous sampling efforts and because widespread species dominate distribution patterns (Raedig et al. 2010). Additionally, taxonomic and spatial errors are present in global data portals, and these can result in inflated measures of species richness and mismatched observations (Hopkins 2007; Robertson 2008).

Here, we evaluate the degree of overlap between existing protected areas, priority areas, and biodiversity hotspots as an indicator of how well these conservation areas may preserve biodiversity. We apply a data-driven approach that relies on computational tools that provide ready access to the increased availability of occurrence data, and on a recently developed statistical approach that corrects for unequal sampling effort. We used the Gulf of California, Mexico, as a case study because it is a region of high biodiversity where conservation strategies rely heavily on Natural Protected Areas (Figueroa and Sánchez-Cordero 2008), where priority areas have been selected through systematic conservation planning (Arriaga Cabrera et al. 1998; Sala et al. 2002; Enriquez-Andrade et al. 2005; Morgan 2005; Ulloa et al. 2006; CONABIO 2007), and where existing conservation planning efforts seek to extend the total area under protection and include areas important for fisheries recovery, species connectivity, and climate change adaptation (Álvarez-Romero et al. 2013, 2018; Turk-Boyer et al. 2014; The Nature Conservancy 2016; Munguia-Vega et al. 2018).

Our objectives were to:

(a) Identify biodiversity hotspots based on different criteria, including: species richness, or the total number of species reported; rarity, or species with a narrow geographical ranges ("ecologically rare," Izco 1998); endemism, or species that only occur within a specific biogeographic region (Fattorini 2017); and threatened species—any that are threatened with extinction and/or are of such high conservation value or national importance that they have been awarded national protection or international recognition (DOF 2002; IUCN 2017).
(b) Assess overlap between biodiversity hotspots and the current protected area network and priority areas selected through systematic conservation planning exercises. High spatial overlap between biodiversity hotspots and current protected area networks and priority areas may suggest that these areas meet multiple conservation goals; while low spatial overlap may indicate that future conservation initiatives should carefully prioritize conservation goals or use methodologies that achieve multiple goals (Shriner et al. 2006).
(c) Determine to what degree biodiversity hotspots based on different criteria are congruent, which may determine their ability to be used as surrogates for one another (Orme et al. 2005).

Methods

We determined the spatial congruence between biodiversity hotspots identified in this study and current protected areas and priority areas selected through previous systematic conservation planning exercises. Briefly, we first generated a comprehensive database of existing species occurrence records for the Gulf of California by harnessing the expanded biodiversity informatics infrastructure and recently developed analytical tools for data processing. Then, we modeled biodiversity hotspots using four criteria—species richness, rarity, endemism, and threatened species—using an approach that accounts for uneven sampling effort and is suited for rare species (Raedig et al. 2010). We examined spatial coincidence between our determined biodiversity hotspots and the existing network of protected areas, as well as previous marine conservation planning exercises, using the Kappa statistic, which measures cell-by-cell overlap. We used this same approach to examine spatial congruence for each hotspot. Finally, we assessed the relation between species composition of biodiversity hotspots defined with different criteria using regression analysis. Each of these steps is described in detail in the following subsections.

The data analysis was carried out in the R statistical framework (R Development Core Team 2011) on Linux virtual machines running Ubuntu Server 16.04 on Microsoft Azure cloud computing (Microsoft Inc., Redmond, WA). R packages used are listed in Table S1. The species occurrence database, species lists, and accompanying metadata are deposited at the Knowledge Network for Biocomplexity (KNB) repository (https://knb.ecoinformatics.org, https://doi.org/10.5063/F1348HKM). The R code used for the analysis is available from https://github.com/hmorzaria/biodiversity.

Study area

The Gulf of California is one of the world's most biologically rich marine regions and an area of conservation importance (Enriquez-Andrade et al. 2005; Lluch-Cota et al. 2007). The marine and coastal areas of the Gulf of California cover over 267,000 km^2 (Fig. 1) and harbor a variety of habitats, including mangrove lagoons, salt marshes, salt flats, hard and soft-sediment sea bottoms, rocky and coral reefs, seamounts, and rhodolith, sargassum, and eelgrass beds (Nagler et al. 2001; Sala et al. 2002; Brusca et al. 2004; Hinojosa-Arango et al. 2014; Jorgensen et al. 2016; Lopez-Calderon et al. 2016). In combination with the Gulf of California's unique oceanographic processes, e.g. mixing, coastal upwelling, currents, waves, and seasonal thermodynamics (Brusca et al. 2017), these habitats support high primary productivity (Lavín and Marinone 2003), a complex food web (Díaz-Uribe et al. 2012), large populations of marine taxa (Lluch-Cota et al. 2007), breeding grounds for multiple species (Soria et al. 2013), and fisheries production representing about half of Mexico's total catch (Brusca 2010). The Gulf is one of the world's top 10 ecosystems for endemic species (Roberts et al. 2002); its diversity of habitats, position as a neotropical transition zone, geology, and role as a barrier to gene flow to peninsular and insular areas, facilitated the divergence of its many endemics (Krings 2000; Zapata and Ross Robertson 2006).

The Gulf of California's biodiversity and associated ecosystem services are threatened by anthropogenic impacts, including overfishing, climate change, pollution, and coastal development (Lluch-Cota et al. 2007; Páez-Osuna et al. 2017). To date, 61 marine and coastal protected areas have been established in the Gulf of California (Fig. 1; Table S2); these sites protect over 29,700 km^2 of marine and coastal habitats or ~ 11% of Gulf's total area. Under Mexican legislation, these protected areas operate under different legal frameworks including biosphere reserves, national parks, wildlife reserves, Ramsar wetlands of international importance, and fishery refuges (Morzaria-Luna et al. 2014; Koch 2015). Additionally, many coastal and marine areas have been identified as priority for future implementation of conservation tools and practices through conservation planning exercises (Álvarez-Romero et al. 2013).

Species records

We obtained species occurrence points for all available taxa in marine and coastal areas in the Gulf of California within the polygon bounded by 32.139900, 20.164036 N and −115.142516, −104.95342 W (Fig. 1). This area included the spatial extent of wetland areas habitats previously compiled by Munguia-Vega et al. (2018). Species records were

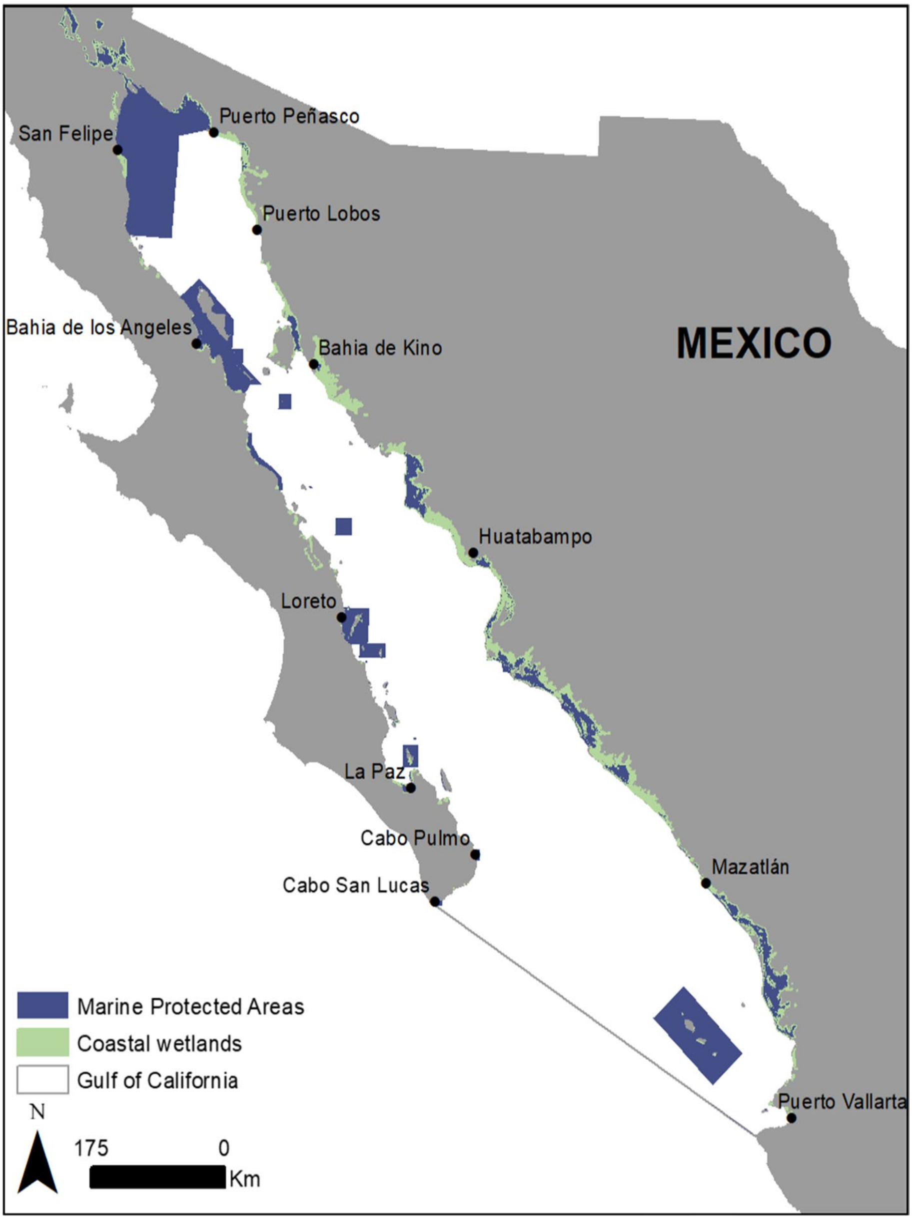

Fig. 1 Gulf of California and marine and coastal protected areas. See Table S2 for full list of areas. Figure indicates key coastal communities mentioned in the text (Colour figure online)

drawn from global, national, and regional biogeographic databases that aggregate data collected using different sampling designs, and from local studies. We queried ten global biogeographic databases (Table S3). When available, we used an application programming interface (API), a service that allows querying data portals in a standard format; otherwise we programmatically scraped the web portals or manually queried the corresponding records. We obtained species records from the National System for Biodiversity Information database managed by Mexico's National Council for Biodiversity (Comisión Nacional para el Conocimiento y Uso de la Biodiversidad - Sistema Nacional de Información sobre Biodiversidad), which aggregates Mexican biodiversity data. We included regional datasets of species occurrence for seagrasses, rhodoliths, and sharks (Ulloa et al. 2006; Hinojosa-Arango et al. 2014; Lopez-Calderon et al. 2016), commercial target species (Cudney-Bueno and Rowell 2008; Cudney-Bueno et al. 2009; Loaiza-Villanueva et al. 2009; Pérez-Valencia et al. 2011; Turk-Boyer et al. 2014), and intertidal and subtidal monitoring (CEDO Intercultural 2003; Reyes-Bonilla et al. 2005; Aburto-Oropeza et al. 2015; Munguía-Vega et al. 2015).

We revised the occurrence database to minimize, as possible, taxonomic and spatial errors that are prevalent in global data portals (Zuckerberg et al. 2011; Boyle et al. 2013). We used the R program *Taxize* to assess the taxonomic name validity of recorded species. Marine species taxonomy was resolved using the World Register of Marine Species (WoRMS; www.marinespecies.org), which provides expert-validated standarized source for taxonomy of marine organisms (Costello et al. 2013), except for macroinvertebrate species-level taxonomy, which was drawn from the Gulf of California Invertebrate Database (Brusca and Hendrickx 2018). Taxonomy for other coastal species was resolved through the Integrated Taxonomic Information System (ITIS), Tropicos, and the International Plant Names Index (IPNI). Once name validity was verified and corrected, we programmatically eliminated duplicate spatial records. Finally, we manually reviewed the species list for misspellings or other large-scale location errors.

Biodiversity hotspots

We used a conditional triangulation approach developed by Raedig et al. (2010) that is based on a specified interpolation distance to estimate biodiversity hotspots, using four criteria: species richness, rarity, endemism, and threatened species. This approach accounts for heterogeneous sampling effort, is useful for presence-only data representing only areas that have been visited and the species have been found, and can model species with few occurrences (Raedig et al. 2010). Biodiversity hotspots based on species richness used the complete species occurrence database. Rare species were defined as species with a narrow geographical range ("ecologically rare," Izco 1998), found in five or fewer grid points in spatial proximity, or 45 km^2. The endemic species subset contained 1400 species that were identified through a review of published sources (Table S4). Threatened species are those classified as such in the Mexican threatened species regulation NOM-059-ECOL-2010 (DOF 2002), or in the IUCN Red list (IUCN 2017), and assigned to either vulnerable, endangered, or critically endangered categories.

We derived richness models for biodiversity hotspots under each criterion. We briefly describe the algorithm for the models, and more details are found Raedig et al. (2010). First, we overlayed species occurrence point data on a 9 km^2 grid to create a point-to-grid map. We used this grid size to match the resolution of previous studies that analyzed species distribution (Álvarez-Romero et al. 2018) and fishing zones (Moreno-Báez et al. 2012) in the region. The point-to-grid data only contains observed species occurrences; the actual species ranges are expected to be larger. We tested for the point-to-point correlation between pairs of point-grid maps of species occurrence using the Spearman rank correlation, a nonparametric method for evaluating the degree of correlation between two independent variables (Gautheir 2001).

The algorithm then performs a distance-weighted interpolation based on a conditional triangulation approach using the centroids of the grids, given a set interpolation distance and a weighing term. We set the interpolation distance to five grid cells for centers of rarity, and to 10 grid cells for the other types of biodiversity hotspots. We used a weighting term of 0.5, which resulted in a combination of high weights for small distances and relatively low weights for large distances. Interpolated species ranges were summed across species to create an estimate of species richness. To reduce the impact of uneven spatial sampling effort, the algorithm incorporates an additional weighting factor based on the ratio of the number of species recorded in a grid cell and the maximum number of species reported for each species richness cluster; clusters are defined based on interpolated species richness, we used the 90% quantile as cut off. The richness estimate is expressed as normalized index between 0 and 1. The robustness of the interpolation is then assessed by repeating the interpolation in subsamples of species points to cross-validate the interpolated species ranges. The cross-validated richness estimate is divided by the weighted species richness to obtain the mean robustness per quadrat.

Overlap analysis

We delineated biodiversity hotspots based on the clusters of interpolated species richness. We estimated spatial coincidence between hotspots, defined under the four different criteria of richness, rarity, endemism, and threat, the existing network of marine and coastal protected areas, and priority areas designated by previous systematic conservation planning exercises in the Gulf of California using map similarity measures. We considered as marine and coastal protected areas the marine and wetland habitats within: (1) Federally-designated sites managed by the National Commission of Natural Protected Areas (CONANP 2016); (2) Ramsar Wetlands of International Importance (Ramsar Convention Secretariat 2008); and (3) areas managed as fishery refuges by the National Commission for Aquaculture and Fisheries (Aceves-Bueno 2013). These areas include a combination of spatial restrictions, including no-take areas, fishery gear restrictions, and seasonal use limits. The complete list of sites is in Table S2. Spatial polygons for existing marine and coastal protected areas were obtained from Mexico's National Commission for Natural Protected Areas (CONANP, http://sig.conanp.gob.mx/website/pagsig/ Ver. January 2017) and directly from managers (Fig. 2). We used priority areas selected through six planning exercises that prioritized coastal or marine areas in the Gulf of California between 1996 and 2006. Álvarez-Romero et al. (2013) previously reviewed these planning exercises. They range across spatial scales: (1) Sub-continental, Baja to Bering (B2B, Morgan 2005); (2) National, Marine Priority Regions (RMP, Arriaga Cabrera et al. 1998) and Marine Priority Sites, (SPM, CONABIO 2007); (3) Regional, Coalition for the Sustainability of the Gulf of California (CSGC, Enriquez-Andrade et al. 2005) and Ecoregional assessment (ERA, Ulloa et al. 2006); and (4) Sub-regional, Marine Reserves Network (MRN, Sala et al. 2002). Table 1 contains brief descriptions of the planning exercises and Fig. 2 shows the distribution of priority areas along the Gulf.

All spatial layers were converted to categorical data before comparison (where 1 is presence and 0 absence), and to the same spatial resolution. We used the Kappa statistic (Cohen 1960), which is the most commonly used measure of cell-by-cell overlap between spatial layers (Wilson et al. 2005; Álvarez-Romero et al. 2013). Kappa measures overlap using a misclassification matrix, that counts how many cells were "wrongly" assigned to each category in both maps, after removing overlap due to chance (Rose et al. 2009). This statistic can range

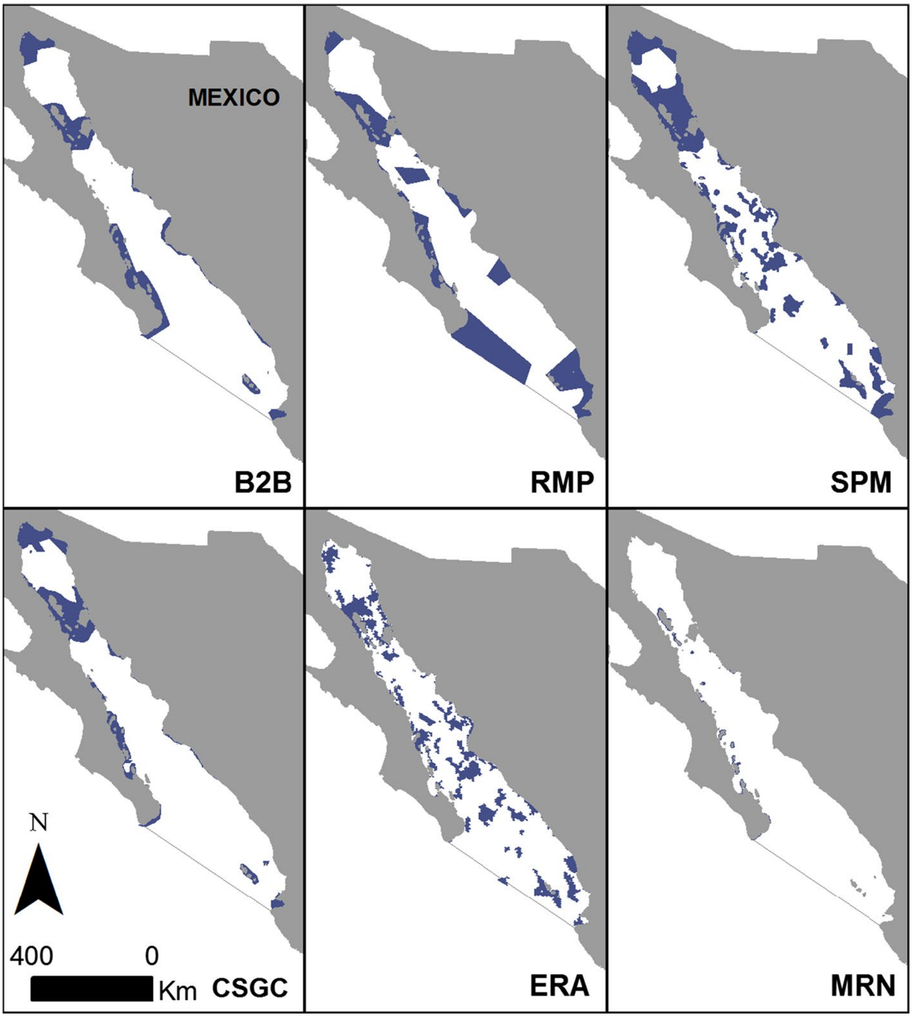

Fig. 2 Priority conservation areas identified by systematic conservation planning in the Gulf of California, Mexico. Acronyms and area characteristics are in Table 2 (Colour figure online)

from −1 (no agreement) to 1 (perfect agreement between maps); a Kappa value of 0 indicates random agreement. We used the Map Comparison Kit software (Visser and De Nijs 2006) to calculate Kappa. Kappa values express strength of agreement as low (−1 to 0.2), medium-low (0.2–0.4), medium (0.4–0.6), high (0.6–0.8), and almost perfect (0.8–1) (Ackers et al. 2015).

Table 1 Systematic conservation prioritization exercises in the Gulf of California and main characteristics

Acronym	Name	Extent (km^2)	Goals	Area selection
B2B	Baja to Bering (Morgan 2005)	Sub-continental 7,165,359	1–3	Spatial overlap of priority areas
RMP	Marine Priority Regions (Arriaga Cabrera et al. 1998)	National 3,290,584	1–3	Prioritization software
SPM	Marine Priority Sites (CONABIO 2007)	National 3,152,985	1,2	Spatial overlap of priority areas
CSGC	Coalition for the Sustainability of the Gulf of California (Enriquez-Andrade et al. 2005)	Regional 902,225	1	Spatial overlap of priority areas
ERA	Ecoregional Assessment (Ulloa et al. 2006)	Regional 361,375	1,2	Prioritization software
MRN	Marine Reserves Network (Sala et al. 2002)	Sub-regional 132,176	1,2	Prioritization software

Indicates main goals in each exercise: 1. Biodiversity conservation; 2. Natural resource management; and 3. Research priorities. Modified from (Álvarez-Romero et al. 2013)

Results

Species records

We produced a comprehensive database of recorded species in the Gulf of California. We identified biodiversity hotspots based on 286,533 occurrence records of 12,105 unique species across the Gulf. These species records were concentrated in coastal areas (Fig. 3). A summary of taxonomic classification of the occurrence database (Table S5) shows most occurrence records belonged to the kingdoms Animalia and Chromista whereas most species belonged to the kingdoms Animalia and Plantae. Thirty species comprised 10% of

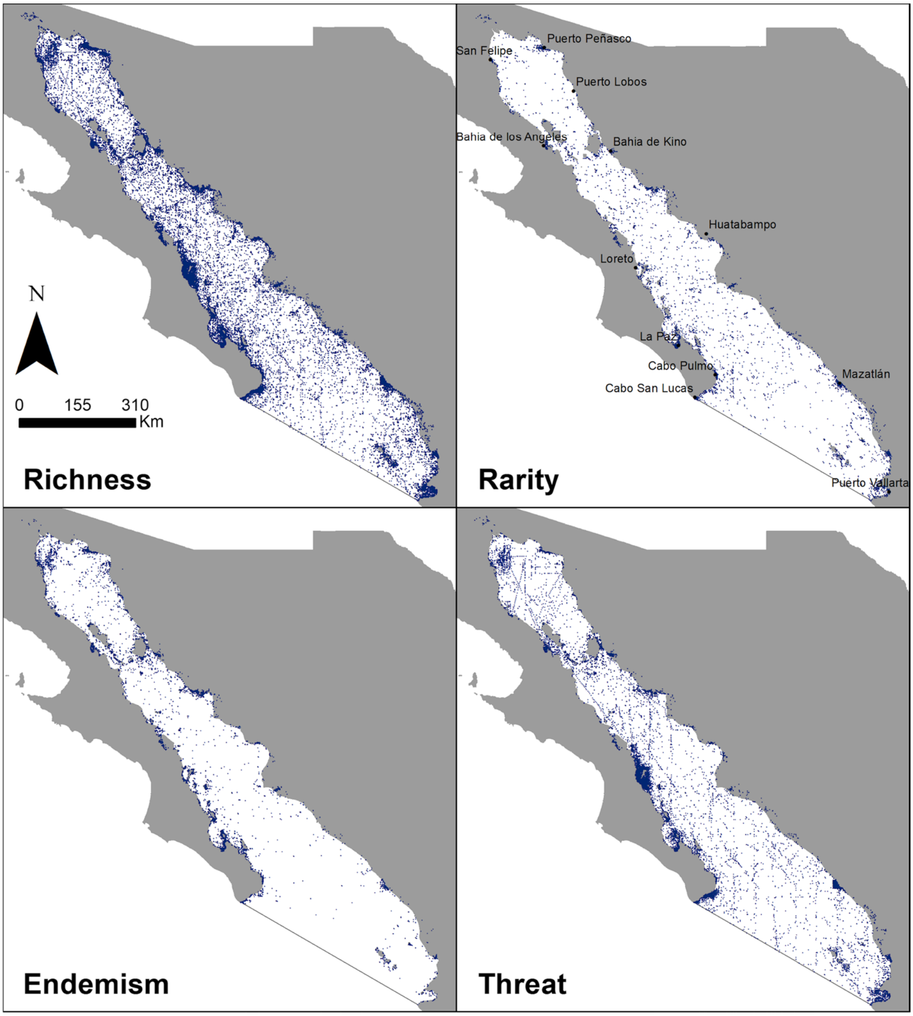

Fig. 3 Species occurrence records identified in marine and coastal areas of the Gulf of California, Mexico. Records were drawn from drawn from global databases, regional and local studies, and used to derive biodiversity hotspots (Colour figure online)

the cumulative frequency of occurrence (Table S6). Fifty-two percent of the total species (6388) were found in five or fewer grid points in spatial proximity, or 45 km^2, and were designated as rare, for a total of 12,250 occurrence records. Three hundred and eighty six species were classified as threatened, including 27,962 occurrence records; these represent only 9.8% of total species. We found occurrence records in existing databases for less than 50% of the reported endemic species for the marine and coastal areas of the Gulf of California (1400 reported endemic species; Table S4). These 642 endemic species represented 18,271 occurrence records or 6.4% of total records. In the map of occurrence records (Fig. 3), it is possible to see continuous lines of points, indicating sampling transects; these focused sampling efforts underscore the need for the statistical approach applied here to derive hotspots while accounting for heterogeneous sampling effort (Raedig et al. 2010).

Biodiversity hotspots

The point-to-grid maps (Fig. 4) show a maximum of 2094 species per 9 km^2 grid cell when considering total species richness, and maximums of 366 rare, 66 endemic, and 105 threatened species per 9 km^2 grid cell. High richness cells are concentrated near population centers, such as La Paz (Baja California Sur), Puerto Vallarta (Jalisco), Mazatlán (Sinaloa), and Puerto Peñasco (Sonora). A similar pattern is found for rare species, while high endemism and threat are found along the coasts and in the Midriff Islands, between Bahía de los Ángeles and Bahía de Kino. The Spearman rank correlation ($\boldsymbol{r_s}$) for point-to-point grid maps show high values between total species richness and endemism (Figure S1). Total richness and endemism show clusters where these datasets are negatively correlated. There is also a negative correlation between rare and threatened species occurrences.

Figure 5 shows the interpolated species richness models that adjust for distance and sampling effort. In general, these models show that the southern Gulf, along the Baja California Peninsula, is an important biodiversity hotspot. These maps were used to delineate biodiversity hotspots based on the 90% quantile of interpolated richness. The values for mean species richness by biodiversity hotspots are in Table 2. The mean point-to-grid richness was lowest for endemic species and highest for total richness (mean 29.0, 48.4 SD, species per 9 km^2 grid cell, Table 2).

We identified biodiversity hotspots based on rarity in Bahía de los Ángeles, in the central Gulf, and in Bahía de La Paz, and along the Baja California Peninsula south towards Cabo San Lucas. These areas include Cabo Pulmo, the only structural coral reef in the Gulf of California, and the northernmost in the Eastern Pacific (Alvarez-Filip et al. 2006). We also identified rarity hotspots south of Mazatlán (Sinaloa) and in Puerto Peñasco (Sonora), along the mainland. Biodiversity hotspots based on endemism are similarly found in the Midriff Islands, between Bahía de los Ángeles and Bahía de Kino, and south along the Baja California Peninsula including the islands of La Bahía de La Paz. Biodiversity hotspots based on threatened species are concentrated in the Midriff Islands, the central Gulf, Bahia de La Paz, and Bahia de Banderas, along the coast of Puerto Vallarta, in the state of Jalisco. The mean adjusted richness was lowest for rare species (mean 50.1, 23.6 SD, species per 9 km^2 grid cell) and highest for total richness (mean 1745.0, 60.0 SD, species per 9 km^2 grid cell, Table 2).

The robustness (Figure S2) values reflect the spatial distribution of the species occurrences and indicate how heavily the model relies on information from single points. Across biodiversity hotspots, higher robustness values were found towards the Upper Gulf and in areas more heavily sampled; these areas have a higher proportion of more uniformly

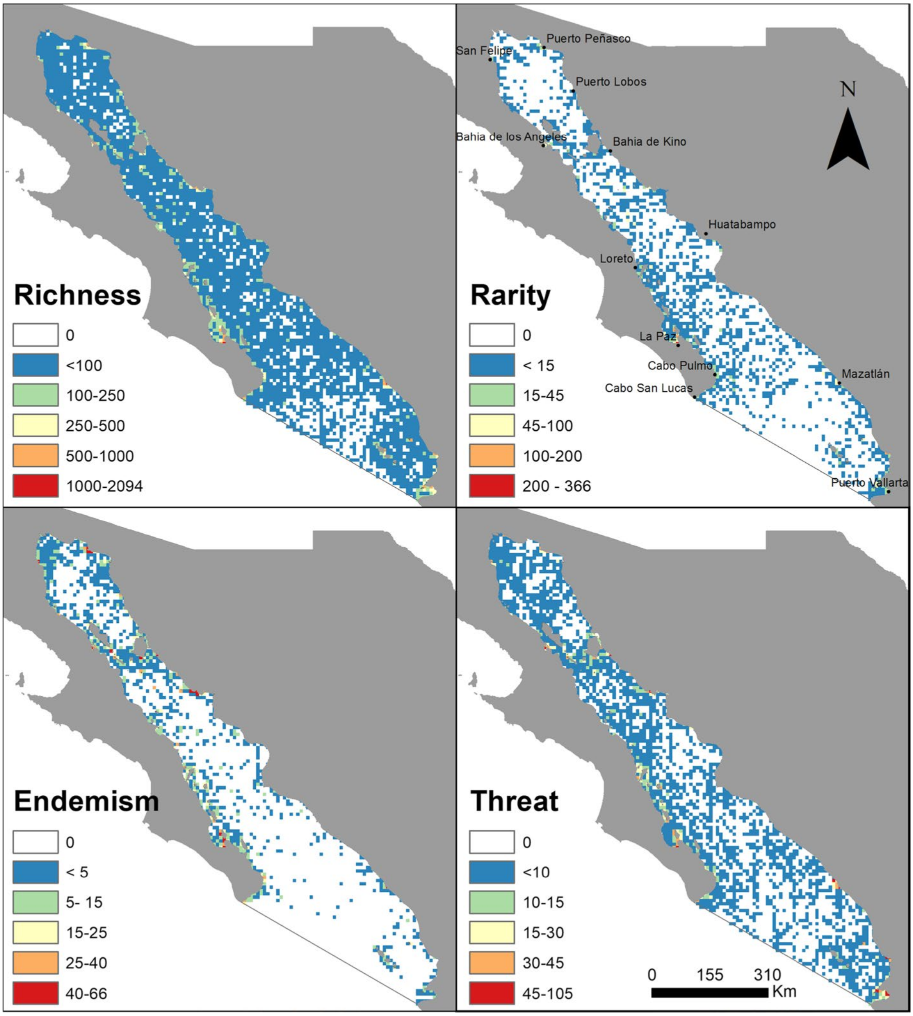

Fig. 4 Point-to-grid maps for data used to derive biodiversity hotspots in the Gulf of California. Number of species per 9 km^2 grid cell, based on species occurrence records in Fig. 3 (Colour figure online)

distributed species with a higher number of occurrences and a smaller number of clustered species with few occurrences (Raedig et al. 2010). The mean robustness per 9 km^2 grid cell ranged between 0.8 ± 0.04 and 26.6 ± 7.5, with highest values for the rarity biodiversity hotspot (Table 2).

Overlap analysis

Overlap between hotspots and the existing network of marine and coastal protected areas was low (Kappa < 0.2). This level of agreement was consistent across types of hotspots. Agreement between biodiversity hotspots and priority areas varied from low and medium-low (Kappa 0.2–0.4), with most values considered low (Table 3). Priority

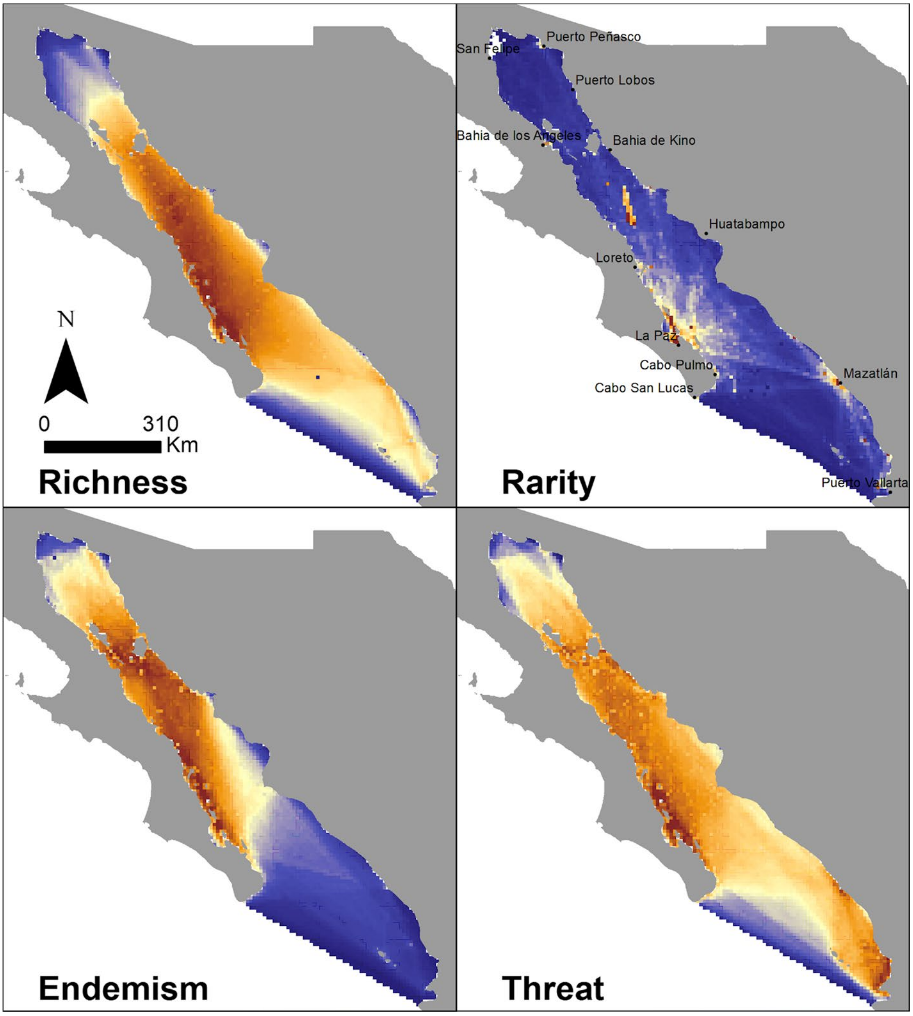

Fig. 5 Interpolated species richness models adjusted for distance and sampling effort in the Gulf of California. Values are normalized for each model (Colour figure online)

areas derived from the Baja to Bering exercises (Morgan 2005) and the Marine Priority Regions initiative (Arriaga Cabrera et al. 1998) had moderate agreement, with endemism and threatened species hotspots. Spatial coincidence between priority areas and hotspots was generally higher in the Midriff Islands, central Gulf, and in Bahía de La Paz, along the southeast coast of the Baja California Peninsula (Figure S3).

Spatial agreement amongst the different types of hotspots ranged from low to medium (Kappa 0.4–0.6; Table 4). Richness hotspots had medium agreement with all other hotspots, since this hotspot covers a larger area. Overlap between the rarity and endemic hotspots was low, and overlap between rarity and threat hotspots was medium. The endemic hotspots had medium agreement with threatened species hotspots.

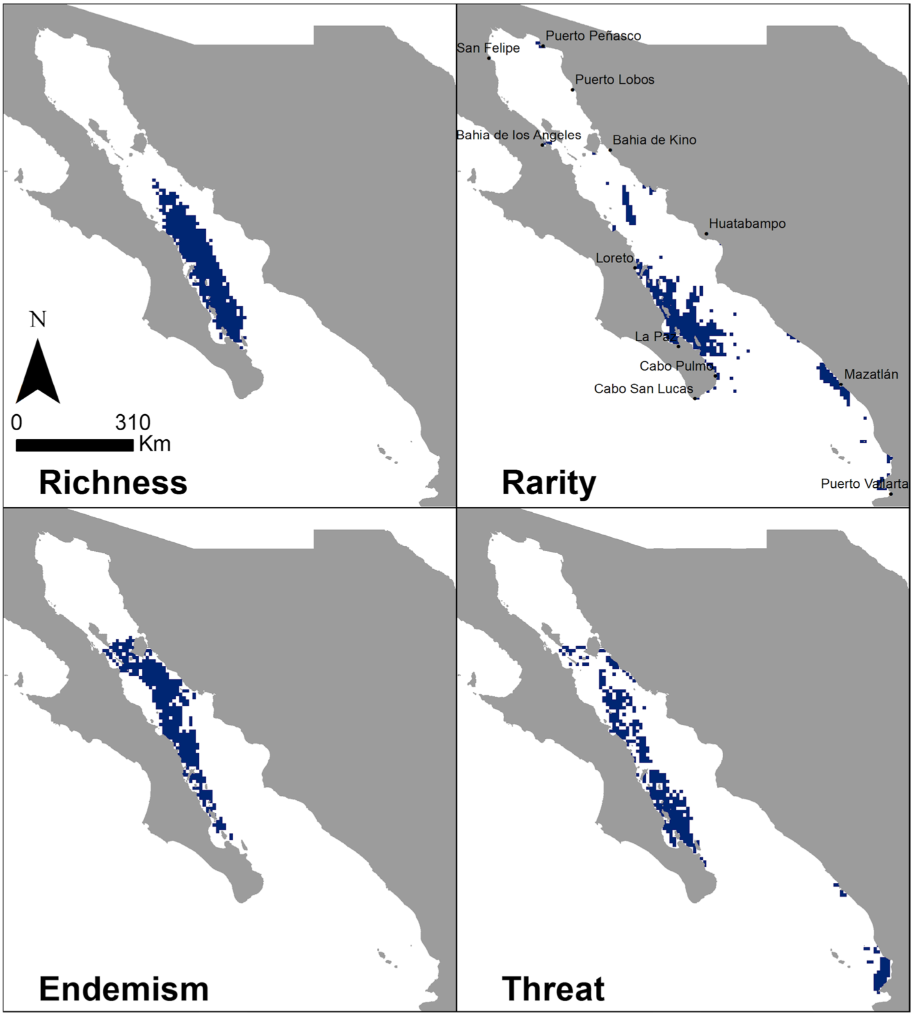

Fig. 6 Biodiversity hotspots in the Gulf of California, defined based on the 90% quantile of interpolated species richness models (Colour figure online)

Table 2 Mean and standard deviation values (in parenthesis) of species richness in the biodiversity hotspots identified in Fig. 6, for the original point-to-grid map and for adjusted species richness

Biodiversity hotspot	No. Grid cells	Point-to-grid species richness	Adjusted species richness	Robustness
Richness	381	28.99 (48.43)	1745.04 (60)	0.78 (0.04)
Rarity	374	16.037 (29.15)	50.09 (23.58)	26.62 (7.49)
Endemism	381	2.19 (2.05)	99.68 (4.34)	12.93 (1.17)
Threat	381	5.16 (9.31)	76.20 (5.14)	16.69 (2.62)

Table also includes robustness values

Table 3 Kappa statistic of overlap between biodiversity hotspots, current protected areas, and priority areas

Area	Biodiversity hotspot			
	Richness	Rarity	Endemism	Threat
Current network	0.041	0.089	0.056	0.038
B2B	0.136	**0.301**	**0.242**	**0.226**
CSGC	0.09	0.178	0.153	0.145
ERA	0.097	0.13	0.127	0.111
MRN	0.075	0.186	0.04	0.066
RMP	0.127	0.155	**0.219**	**0.226**
SPM	0.088	0.126	0.181	0.14

Acronyms for conservation prioritization exercises are in Table 2. Kappa values express strength of agreement as low (−1 to 0.2), medium-low (0.2–0.4; in bold) (Ackers et al. 2015)

Table 4 Kappa statistic of overlap between biodiversity hotspots

Biodiversity hotspot	Richness	Rarity	Endemism
Rarity	**0.377**		
Endemism	***0.469***	0.152	
Threat	***0.553***	**0.347**	***0.494***

Kappa values express strength of agreement as low (−1 to 0.2), medium-low, bold, (0.2–0.4), and medium, bold italic, (0.4–0.6) (Ackers et al. 2015)

Discussion

We identified biodiversity hotspots based on different criteria, including species richness, endemism, rarity, and threat in the Gulf of California. Our approach advances previous qualitative and quantitative efforts to determine biologically important areas in marine and coastal regions in the Gulf. Overall, we found slight overlap between these biodiversity hotspots and the current network of marine and coastal protected areas and priority areas, and low to high spatial agreement between biodiversity hotspots based on different criteria. Our results underscore the need for systematic conservation planning that maximizes the representation of species, particularly rare, endemic, and threatened species, while implementing a process that assures stakeholder participation and provides proper resources, planning, and governance mechanisms (Nava and Ramírez-Herrera 2011). We discuss each our findings in the following paragraphs.

We found both negative and positive correlations between point-grid maps for different biodiversity hotspots. Two hotspots, for example species richness and rarity, may be positively related when cells occupied by rare species are also species-rich and represent a subset of cells occupied by common species (Villalobos et al. 2013). This relationship is supported by previous studies (Grenyer et al. 2006; Lamoreux et al. 2006) and could facilitate spatial prioritization processes, since protection of only the richest cells would guarantee protection of other aspects of biodiversity, such as rarity and endemism (Villalobos et al. 2013).

Overlap between biodiversity hotspots and priority areas selected through previous systematic conservation planning exercises ranged from low to medium. Together, the priority areas identified by the extant systematic planning exercises included in this study cover ~100,000 km^2, but show little overlap among exercises as they were designed with different objectives and base data (see Álvarez-Romero et al. 2013 for further discussion). Other studies have found that areas prioritized through hotspots had different spatial configuration compared to more complex spatial prioritization methods (Schröter and Remme 2016). The Marine Reserves Network and Baja to Bering analyses had the highest spatial agreement with biodiversity hotspots; both exercises focused on a few species and key habitats (Álvarez-Romero et al. 2013). The Marine Reserves Network exercise prioritized the protection of fish and selected a few, small priority areas aimed at establishing a network of no-take zones (Sala et al. 2002). Meanwhile, Baja to Bering focused on species of conservation concern throughout North America and considered processes operating over large geographic extents (Morgan 2005). Biodiversity hotspots based on different criteria were composed of a similar number of grid cells, such that the degree of overlap is not a function of the size of the hotspots.

Spatial agreement amongst biodiversity hotspots based on different criteria ranged from low to high. The level of congruence among hotspot types has implications for the use of hotspots in reserve selection; when congruence among types of hotspots is high, it may not matter which hotspot is used to guide conservation policy (Orme et al. 2005). However, when spatial congruence is low, different types of hotspots cannot be used as surrogates of one another. Our results suggest that different types of biodiversity hotspots might be governed by distinct ecological, evolutionary, and anthropogenic processes (Orme et al. 2005). Previously, spatial congruence between different types of hotspots was shown to be scale-dependent, to vary across taxonomic groups, and to demonstrate distinct capacity in identifying areas of high biodiversity (Orme et al. 2005; Xu et al. 2008). Additionally, researchers comparing performance of different types of hotspots have reached different conclusions about their effectiveness; this variation in results is likely driven by differences in the type of hotspot tested, the scales of the analyses, the methods used to test the indices, the patterns of species distribution, and the areas in which the studies were conducted (Lawler et al. 2003). In this study, biodiversity hotspots based on species richness, rarity, endemism, and threatened species showed agreement on the importance of Bahía de La Paz, in the southern Gulf (Fig. 5).

We took advantage of the growth of global biogeographic databases, that have made more datasets available for analyses of species richness and hotspots (Coro et al. 2016; De Pooter et al. 2017), to compile the largest species occurrence data set to date for the Gulf of California's marine and coastal habitats. Comprehensive species censuses are the best method to identify hotspots; but these analyses require extensive resources and using available data as a surrogate is in many cases the only option (Shriner et al. 2006). Our dataset can be further applied to investigate taxa-specific hypotheses. This database included records collected through time, providing a description of the "biological state" of the species/region; considering that average generation time of many species of concern (e.g. reef fish, large mammals) is often between 20 and 100 years, these records may barely cover one generation (Willis et al. 2007).

The programmatic approach we applied ensures that the process we used is repeatable, testable, and transparent. However, the development of our synthetic database is not without caveats because the use of aggregated datasets can propagate errors at the point of data collection (Poisot et al. 2016). All observational studies will be limited in space and time and all sampling methods are biased; as a result, sampled richness is a subestimate of actual species richness, because assessments are commonly skewed towards common species in easily accessed habitats and some species will always be missed from inventories (Costello and Berghe 2006; Poisot et al. 2016). We used a geometric interpolation approach (Raedig et al. 2010) to derive reliable distribution patterns that can address the issues present in large-scale datasets, of data scarcity, poor data quality, and lack of knowledge of the environmental correlates of species. Although this approach was developed for terrestrial systems, the issues it addresses are equivalent in marine systems, namely that widespread species dominate distribution patterns and that spatial sampling effort is heterogeneous; this approach had been previously applied for other marine datasets (Kuhn et al. 2011). Another issue in aggregated datasets, that systematic inaccuracy may inflate species richness and lead to distorted distributional patterns (Boyle et al. 2013) was addressed through the use of taxonomic name resolution querying which helped correct and standardize species names. Additionally, our database likely considers both larvae and adults in the occurrence records, such that distributional patterns might reflect the drift and dispersal of larvae outside the adult range (Dambach and Rödder 2011).

The most abundant species in the occurrence database reflect intensive monitoring efforts focused on important fishery species such as the bivalve geoduck (*Panopea generosa*) and on megafauna of conservation importance such as fin whale (*Balaenoptera physalus*) and blue whale (*Balaenoptera musculus*), as well as common marine and coastal species such as the yellow-footed gull (*Larus livens*) and the bullseye puffer (*Sphoeroides annulatus*). Species records are likely still lacking from many taxa in the Gulf that have been poorly studied (Brusca et al. 2005), and from environments such as deep-water habitats and seamounts that are poorly sampled (Sala et al. 2003). Future work is needed such that collected data in the Gulf of California are made available as they are published, and to create a central repository of data sources for conservation efforts. A metadata archive to inventory monitoring efforts already exists, http://monitoreonoroeste.mx/faq.php, but a centralized geodatabase would facilitate research efforts.

Further work should be carried out to determine if existing marine and coastal protected areas are protecting key habitats and ecosystem services (see Munguia-Vega et al. 2018). Effective conservation landscapes should include areas of high biodiversity and the key habitats that sustain them (Struebig et al. 2009). However, many marine and coastal protected areas, including areas in the Gulf of California, have been established opportunistically based on narrow criteria that do not consider ecosystem processes nor human uses, and did not follow a committed conservation planning process (Roberts et al. 2003; Munguia-Vega et al. 2018). With some exceptions such as Cabo Pulmo, in the southern Gulf (Aburto-Oropeza et al. 2011), many marine protected areas in Mexico have not met conservation or sustainability goals (Rife et al. 2013).

The performance of extant marine reserves can be assessed by comparing them to the minimum number of sites needed to represent all diversity, even when this was not the original goal of the reserve design (Cabeza and Moilanen 2001). Other surrogates that can be used to assess the effectiveness of protected areas include maintaining phylogenetic diversity (Pérez-Losada and Crandall 2003), preserving key ecosystem functions such as marine productivity (Valavanis et al. 2004; Lascelles et al. 2012; Selig et al. 2014), or environmental features (Hyrenbach et al. 2000). Even if well-planned, marine and coastal protected areas only contribute to conserving marine biodiversity if effectively managed (Aburto-Oropeza et al. 2011).

The comprehensive hotspot models we developed are not alone sufficient to identify and place conservation areas. Establishment of new protected areas should consider other criteria not considered in this analysis, including marine connectivity, the socioeconomic costs of implementation, and habitat representation by applying site-selection algorithms that maximize the representation of species and habitat diversity while considering limits on cost or area (Green et al. 2014; Munguia-Vega et al. 2018); and should incorporate stakeholder knowledge and buy-in, within the context of integrated coastal zone management (Roberts et al. 2003). However, the biodiversity hotspots we identified can serve as a starting point for reserve selection and inform marine conservation planning processes to maximize representation of biodiversity in networks of conservation areas (Shriner et al. 2006; Magris et al. 2014). The species richness hotspots identified here have already been applied to support a Coastal and Marine Spatial Planning process along the coast of the state of Sonora, in the Northern Gulf, that is proposing fishery management tools such as fishery refuges and exclusive-use areas (Turk-Boyer et al. 2014; Morzaria-Luna, et al. unpublished data), to inform general placement rules for marine protected areas in the Gulf of California (Munguia-Vega et al. 2018), and in a prioritization exercise to identify potential fishery refuges (The Nature Conservancy 2016).

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Supplementary Information

Biodiversity hotspots are not congruent with conservation areas in the Gulf of California

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Figure S1. Spearman rank correlation (r_s) between pairs of point-to-grid maps for observed species occurrence.

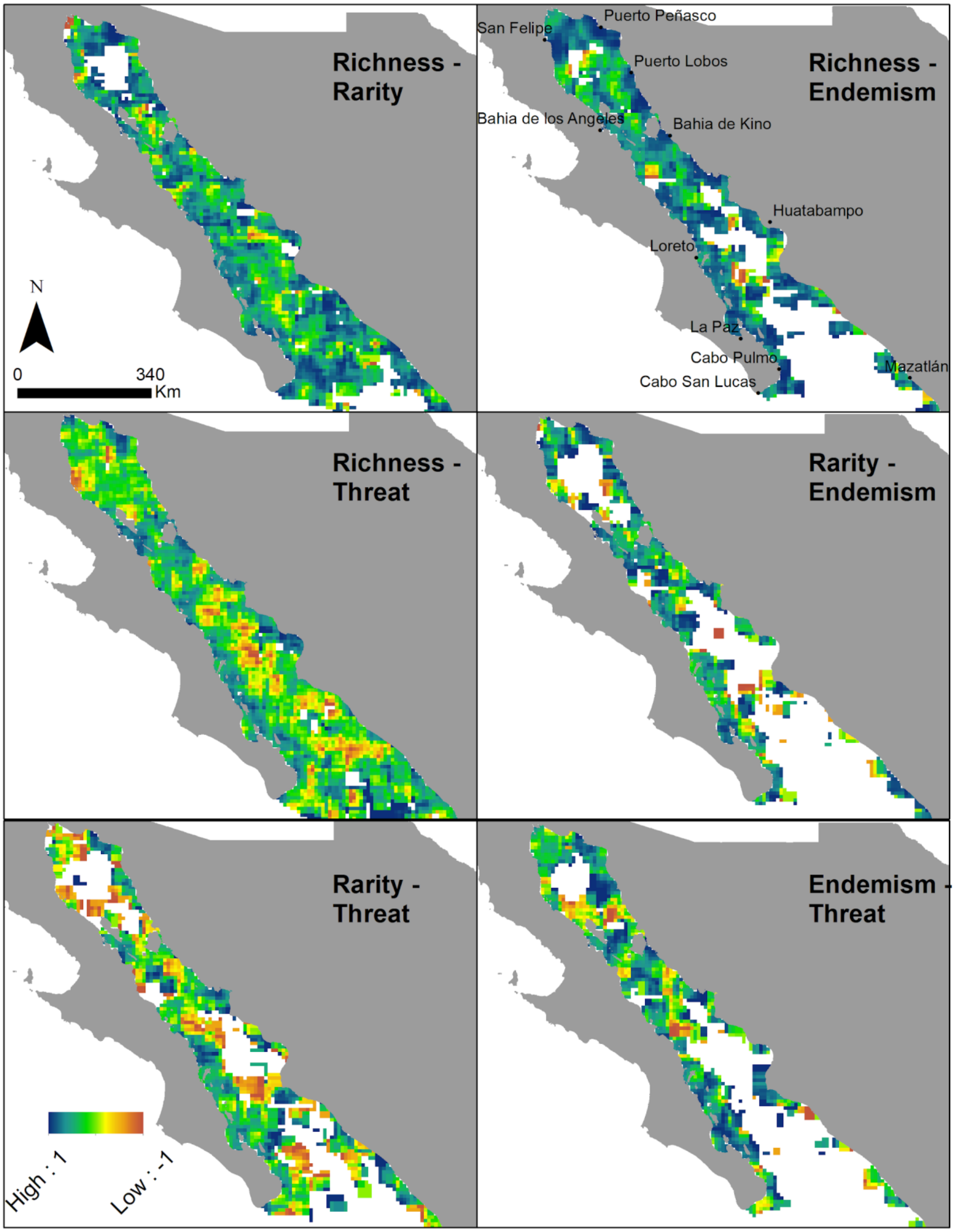
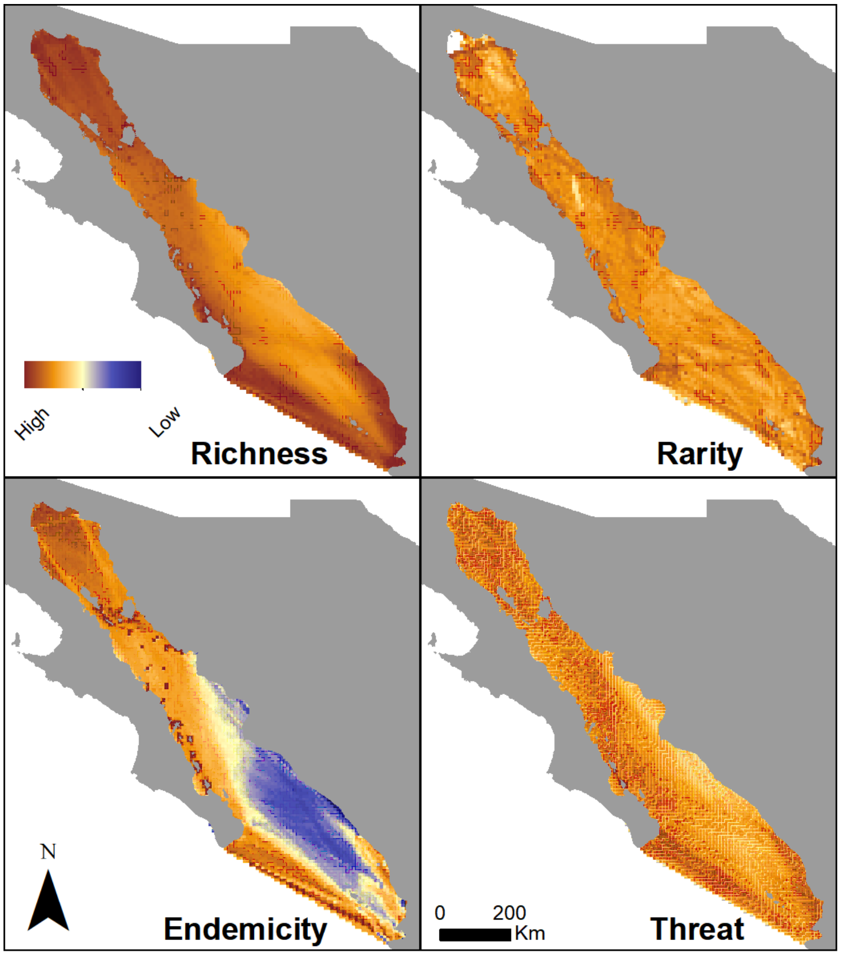


Figure S2 Robustness of interpolated species richness models in the Gulf of California



High
Low
Richness
Rarity
N
Endemicity
0
200
Km
Threat

Figure S3 Spatial coincidence between the existing the existing network of Marine and Coastal Marine Protected Areas, priority areas, and biodiversity hotspots in the Gulf of California. Hotspots delineated based on interpolated species richness adjusted for unequal sampling

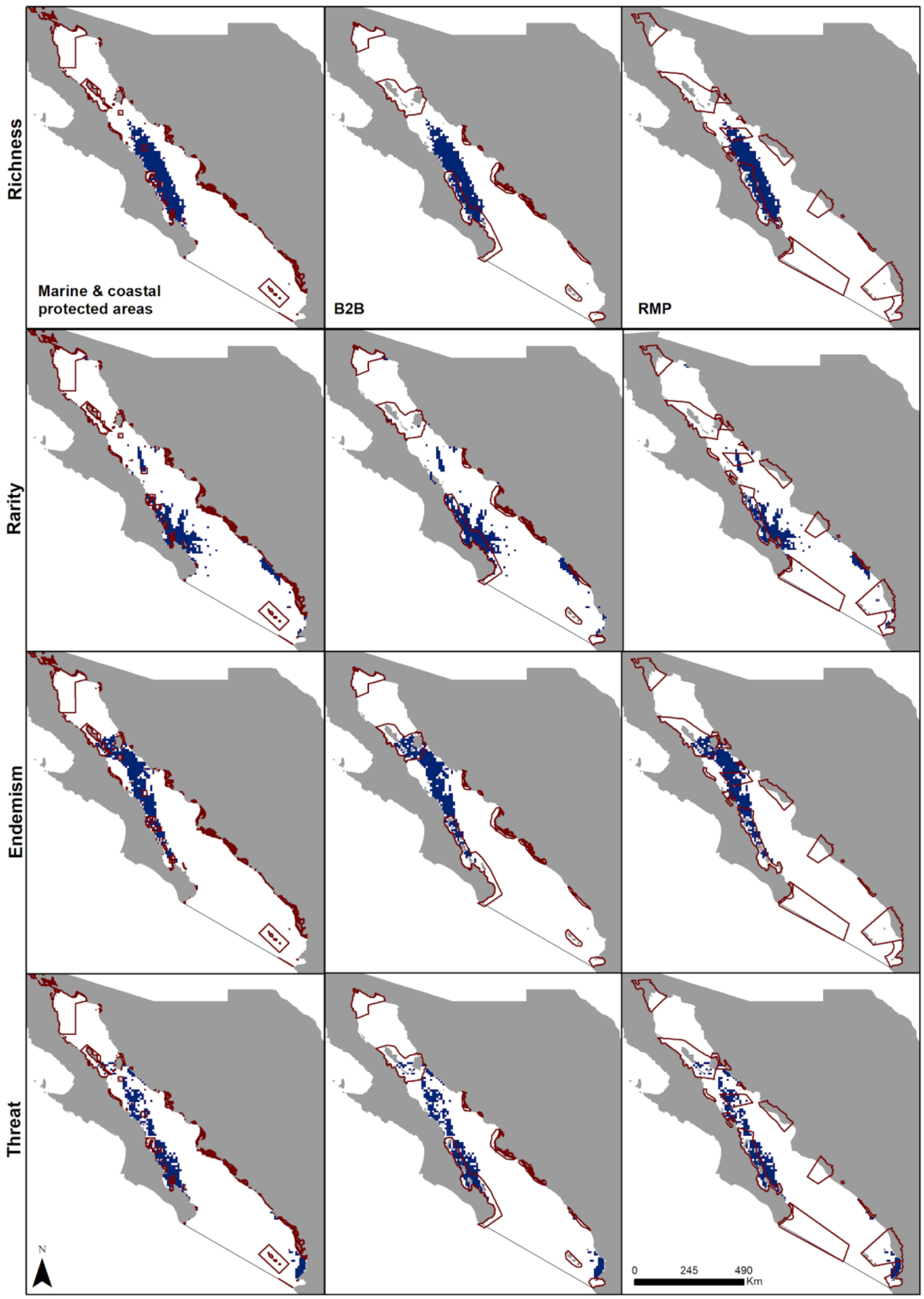


Figure S1 (cont.)

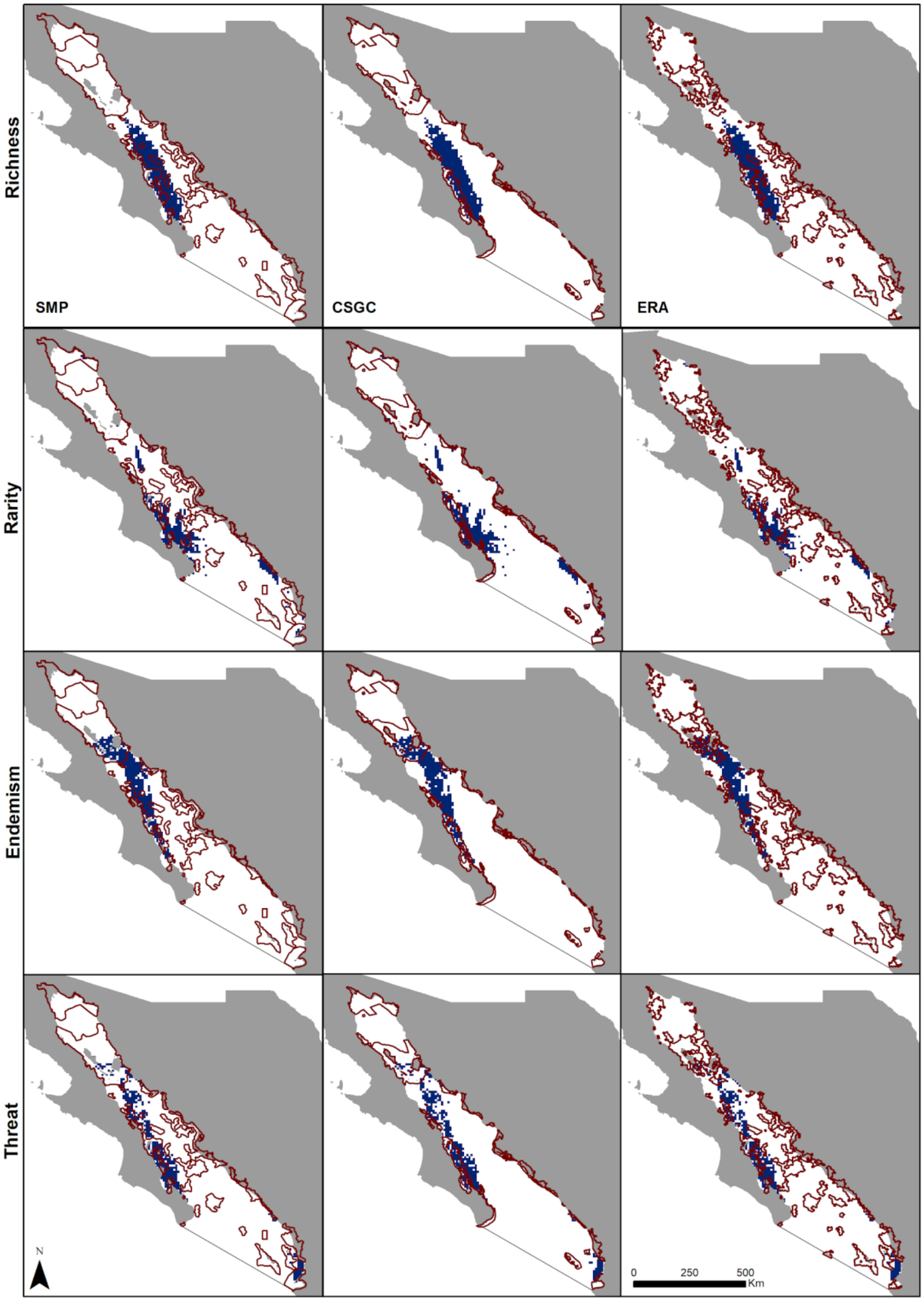

Richness
Rarity
Endemism
Threat
SMP
CSGC
ERA
N
0
250
500
Km

Figure S1 (cont.)

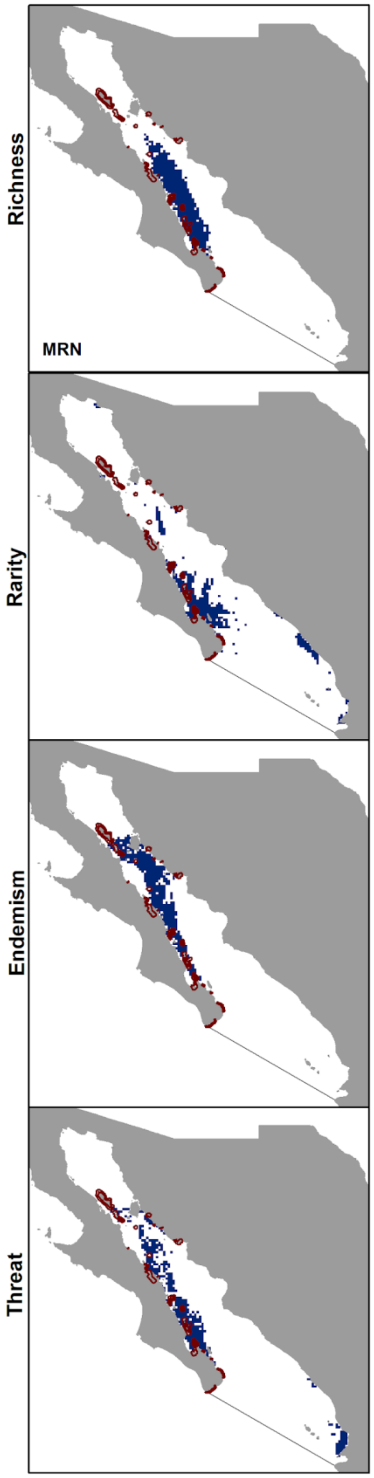


Table S1. R software framework packages used in data retrieval, analysis, and visualization.

Packages/ functions	Application	Reference
rvertnet	Retrieval of species occurrence records	Chamberlain et al., 2015
rbison		Chamberlain, 2015
rebird		Maia et al., 2015
ridigbio		Michonneau and Collins, 2016
ecoengine		Ram, 2016
taxize	Validate species taxonomy and obtain classification	Chamberlain and Szöcs, 2013
taxizesoap		Chamberlain et al., 2014
tidyverse	Data analysis and management	
sperich	Derive the hotspot models	Lange et al., 2015
ggmap	Results visualization	Kahle and Wickham, 2013
cowplot		Wilke, 2015
ggplot2		Wickham, 2009
doSNOW	Parallel computing	Analytics and Weston, 2014
gdal_polygonizeR	Raster to polygon	https://johnbaumgartner.wordpress.com/2012/07/26/getting-rasters-into-shape-from-r/
RobustI.R	Measures of spatial autocorrelation	http://www.colby.edu/~mgimond/R/RobustI.R

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Table S2. Marine and Coastal Protected Areas in the Gulf of California. Areas are divided by management categories. Table includes total site area, no-take area, and area in marine and coastal habitats, considered in this study. Note some areas have two designations that overlap totally or partially. Figure 1 shows the total area covered by these Marine and Coastal Protected Areas.

No	Marine and Coastal Protected Area	Year decreed	Area (ha)	No-take area (ha)	Marine and coastal area (ha)
	Areas for Protection of Flora and Fauna				
1	Balandra	2012	2,512.7	262.1	1,127.31
2	Islas del Golfo de California	1986	423,177.9	0.0	40,253.14
3	Valle de Los Cirios	2000	2,518,288.0	0.0	569.76
4	Cabo San Lucas	1973	3,996.04	0.0	3665.08
5	Meseta de Cacaxtla	2000	50,862.31	0.0	396.58
	Biosphere reserves				
6	Alto Golfo de California y Delta del Río Colorado	2003	1,107,634.9	2,552.9	544,471.12
7	Zona marina Bahía de los Ángeles, Canales de Ballenas y Salsipuedes	2007	388,956.3	6.9	373,208.80
8	Isla San Pedro Martir	2002	29,763.1	8.3	29,944.82
9	Islas Marias	2000	612,056.5	0.0	611,076.03
10	El Vizcaino	1988	2,546,790.2	0.0	48,648.57
11	Marismas Nacionales Nayarit	2010	133,854.4	0.0	0.12
12	Pacífico Mexicano Profundo	2016	57,786,214.9	18,777,103.9	5,571.75
	National Parks				
13	Zona marina del Archipiélago de San Lorenzo	2005	58,467.8	88.2	57,164.41

14	Bahia de Loreto	1996	185,039.6	0.0	184,749.49
15	Cabo Pulmo	1995	7,000.0	7,000.0	6,541.99
16	Islas Marietas	2005	1,446.1	0.0	1,051.34
17	Isla Isabel	1980	194.17	0.0	79.01
18	Zona Marina del Archipielago de Espíritu Santo	2007	47,392.3	0.0	46,926.14
	Ramsar Wetlands of International Importance				
19	Balandra	2008	448.7	262.1	1,127.31
20	Canal del Infiernillo y esteros del territorio Comcaac (Xepe Coosot)	2009	29,700.0	0.0	26,826.45
21	Complejo Lagunar Bahía Guásimas - Estero Lobos	2008	135,197.5	0.0	24,548.35
22	Corredor Costero La Asamblea - San Francisquito	2005	44,303.8	0.0	41,436.78
23	Ensenada de Pabellones	2008	40,638.7	0.0	26,275.77
24	Estero El Soldado	2011	349.9	0.0	199.54
25	Humedales de Bahía Adair	2009	42,429.8	0.0	8,578.11
26	Humedales de Bahía San Jorge	2010	12,197.8	0.0	1,490.50
27	Humedales de la Laguna la Cruz	2013	6,665.1	0.0	2,797.03
28	Humedales de Yavaros - Moroncarit	2009	13,627.2	0.0	6,477.93
29	Humedales del Delta del Río Colorado (Sonora y Baja California)	1996	250,000.0	0.0	86,470.90
30	Humedales El Mogote - Ensenada de La Paz	2008	9,184.1	0.0	86,470.90
31	Isla Rasa	2006	66.0	0.0	67.01
32	La Tovara	2008	5,733.0	0.0	9.36
33	Laguna Huizache-Caimanero	2007	48,282.7	0.0	5,243.49
34	Laguna Playa Colorada - Santa María La Reforma	2004	53,140.0	0.0	61,696.47
35	Lagunas de Santa María-Topolobampo-Ohuira	2009	22,500.0	0.0	26,314.22
36	Marismas Nacionales	1995	200,000.0	0.0	654.04
37	Oasis Sierra de La Giganta	2008	41,181.4	0.0	17.58
38	Parque Nacional Bahía de Loreto	2004	206,580.8	0.0	184,897.25
39	Parque Nacional Cabo Pulmo	2008	7,100.2	7,100.2	6,599.47
40	Parque Nacional Isla Isabel	2003	93.7	0.0	79.01
41	Parque Nacional Islas Marietas	2004	1,357.3	0.0	18.67

42	Playa Tortuguera El Verde Camacho	2004	6,454.3	0.0	103.18
43	Reserva de la Biosfera Isla San Pedro Mártir	2004	30,165.0	0.0	29,945.43
44	Sistema de Humedales Remanentes del Delta del Río Colorado	2008	127,614.0	0.0	86,470.90
45	Sistema Lagunar Agiabampo - Bacorehuis - Río Fuerte Antiguo	2008	90,804.4	0.0	2,059.26
46	Sistema Lagunar Ceuta	2008	1,497.0	0.0	435.46
47	Sistema Lagunar San Ignacio - Navachiste - Macapule	2008	79,872.9	0.0	31,579.69
48	Sistema Ripario de la Cuenca y Estero de San José del Cabo	2008	124,219.0	0.0	9.20
	Fishery refuges				
49	El Pardito	2012	63.6	63.6	27.08
50	Estero San José	2012	94.1	94.1	0.70
51	Estero Tembabiche	2012	57.0	57.0	36.15
52	La Habana	2012	69.6	69.6	60.06
53	La Morena 3	2012	32.8	32.8	32.70
54	Norte San Francisquito	2012	59.3	59.3	16.82
55	Punta Botella	2012	86.2	86.2	76.22
56	Punta Coyote	2012	74.0	74.0	73.74
57	San Diego	2012	138.2	138.2	138.23
59	San Marcial	2012	587.3	587.3	587.27
59	San Mateo	2012	61.3	61.3	48.19
	Decrees				
60	Acuerdo por el que se suspende la pesca mediante el uso de redes de enmalle, cimbras y/o palangres en el Norte del Golfo de California	2015	11,730.3	0.0	1,169,902.50
61	Área de Refugio para la Protección de la Vaquita	2005	1,263.9	1,263.9	48.19

Table S3. Data portals queried for species occurrence records. Other data sources are specified in the text.

Name	Taxa	Website
Ocean Biogeographic information System - OBIS	Marine species	www.iobis.org
speciesLink	General	splink.cria.org.br
Global Biodiversity Information Facility - GBIF	General	www.gbif.org
HOLOS Ecoinformatics Engine – Ecoengine	General	holos.berkeley.edu
iDigBio	General	www.idigbio.org
Biodiversity Information Serving Our Nation – Bison	General	bison.usgs.ornl.gov
VertNet	Vertebrates	www.vertnet.org
Ebird	Birds	ebird.org
FishBase	Fish	www.fishbase.org
SEINet	Plants	swbiodiversity.org/seinet

Table S4. Sources reviewed to create the list of endemic species.

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Table S5. Summary of the taxonomic composition of taxa in the species occurrence database. Table shows number of records by kingdom, as well as number of infra-taxa by kingdom.

Kingdom	No. records	No. species	No. families	No. orders	No. classes
Animalia	224747	7873	1354	277	55
Archaea	3	2	1	1	1
Bacteria	184	46	13	10	5
Chromista	42714	1512	181	67	12
Fungi	299	174	33	18	8
Plantae	18527	2486	223	82	20
Protozoa	8	5	3	2	2
Incertae sedis	46	7	2	2	2

Table S6. Species comprising 10% of cumulative frequency species occurrence in the species occurrence database used to generate hotspot models.

Kingdom	Class	Order	Family	Species	%
Animalia	Bivalvia	Myoida	Hiatellidae	*Panopea generosa*	0.6
Animalia	Aves	Pelecaniformes	Pelecanidae	*Pelecanus occidentalis*	1.2
Animalia	Aves	Suliformes	Fregatidae	*Fregata magnificens*	1.6
Animalia	Aves	Charadriiformes	Laridae	*Larus heermanni*	2.1
Animalia	Mammalia	Cetacea	Balaenopteridae	*Balaenoptera physalus*	2.5
Animalia	Mammalia	Cetacea	Balaenopteridae	*Balaenoptera musculus*	2.9
Animalia	Aves	Suliformes	Sulidae	*Sula leucogaster*	3.3
Animalia	Actinopterygii	Tetraodontiformes	Balistidae	*Balistes polylepis*	3.7
Animalia	Aves	Suliformes	Sulidae	*Sula nebouxii*	4.1
Animalia	Mammalia	Cetacea	Delphinidae	*Tursiops truncatus*	4.4
Animalia	Aves	Charadriiformes	Laridae	*Larus livens*	4.8
Animalia	Actinopterygii	Perciformes	Serranidae	*Paralabrax maculatofasciatus*	5.2
Animalia	Actinopterygii	Perciformes	Pomacentridae	*Abudefduf troschelii*	5.5
Animalia	Actinopterygii	Perciformes	Apogonidae	*Apogon retrosella*	5.8
Animalia	Actinopterygii	Tetraodontiformes	Tetraodontidae	*Sphoeroides annulatus*	6.2
Animalia	Aves	Charadriiformes	Scolopacidae	*Tringa semipalmata*	6.5
Animalia	Actinopterygii	Perciformes	Pomacentridae	*Stegastes rectifraenum*	6.8
Animalia	Aves	Suliformes	Phalacrocoracidae	*Phalacrocorax auritus*	7.0
Animalia	Actinopterygii	Perciformes	Labridae	*Thalassoma lucasanum*	7.3
Animalia	Actinopterygii	Pleuronectiformes	Paralichthyidae	*Syacium ovale*	7.6

Animalia	Actinopterygii	Perciformes	Blenniidae	*Ophioblennius steindachneri*	7.9
Animalia	Actinopterygii	Perciformes	Serranidae	*Epinephelus labriformis*	8.1
Animalia	Actinopterygii	Perciformes	Lutjanidae	*Lutjanus argentiventris*	8.4
Animalia	Aves	Charadriiformes	Laridae	*Thalasseus maximus*	8.7
Animalia	Actinopterygii	Perciformes	Serranidae	*Mycteroperca rosacea*	8.9
Animalia	Actinopterygii	Perciformes	Labridae	*Bodianus diplotaenia*	9.2
Animalia	Actinopterygii	Perciformes	Haemulidae	*Haemulon sexfasciatum*	9.4
Animalia	Actinopterygii	Mugiliformes	Mugilidae	*Mugil curema*	9.7
Animalia	Actinopterygii	Perciformes	Pomacanthidae	*Holacanthus passer*	9.9