Assessing best practice for selecting surrogates and target–setting methods in a megadiverse country

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Abstract
Assessing best practice for selecting surrogates and target–setting methods in a megadiverse country. Systematic conservation planning provides a framework to identify representative areas of biodiversity, but its effectiveness depends on the choice of surrogates and targets. Mexico has conducted participatory and comprehensive gap analyses. We present the results of two independent surrogate assessments to test the criteria used in Mexico's spatial conservation prioritization. We tested the surrogate efficiency of range restricted, endemic, and threatened mammals and the influence of target–setting on the spatial configuration of the conservation network, as well as the performance of taxonomic–based surrogates. Results show that target–setting heavily influences the spatial configuration and irreplaceability values of the conservation area network. Representation effectiveness and coverage of species distribution was sensitive to surrogate selection but not to target–setting. Threatened and rare species were poorly represented when other surrogate species were used, while threatened mammals represented 90 % of all species. The effectiveness of networks designed for a single vertebrate taxon varied greatly; reptiles and amphibians performed better than random achieving high species representation.

Key words: Systematic conservation planning, Surrogate species, Target setting, Endemic species, Threatened species, Megadiverse country

Resumen
Evaluación de las mejores prácticas para seleccionar sustitutos y métodos para establecer metas de conservación en un país megadiverso. La planificación sistemática de la conservación proporciona un marco para identificar áreas representativas de la biodiversidad, pero su eficacia depende de la elección de sustitutos y de las metas de conservación. México ha realizado análisis integrales y participativos de vacíos y omisiones en conservación. En este trabajo presentamos los resultados de dos evaluaciones independientes sobre sustitutos de la biodiversidad a fin de poner a prueba los criterios utilizados en México para identificar las prioridades espaciales de conservación. Se probó el efecto sombrilla de los mamíferos de distribución restringida, endémicos y amenazados, y la influencia del establecimiento de las metas en la configuración espacial de la red de áreas de conservación, así como el desempeño de sustitutos taxonómicos. Los resultados muestran que el establecimiento de metas influye mucho en la configuración espacial y en los valores de irremplazabilidad de la red. La eficacia de la representación y la cobertura de las áreas de distribución de las especies variaron con la selección de los sustitutos, pero no con el establecimiento de las metas. Las especies amenazadas y las raras no estuvieron suficientemente representadas cuando se usaron otras especies como sustitutos, mientras que los mamíferos amenazados representaron el 90% de todas las especies. La eficacia de las redes diseñadas para un solo taxón de vertebrados varió mucho; los reptiles y anfibios obtuvieron mejores resultados que los obtenidos al azar, y lograron una alta representación de otros grupos taxonómicos en la red diseñada para dichos taxones.

Palabras clave: Planificación sistemática de la conservación, Especies sustitutas, Metas de conservación, Especies endémicas, Especies amenazadas, País megadiverso

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Introduction

Conserving biological diversity in the face of an irrefutable environmental crisis remains a serious challenge as governments and societies have largely failed to keep up with the anthropogenic pace of change (Stafford–Smith et al., 2012). To minimize biodiversity loss, there is a central and urgent need to concentrate the scarce conservation resources and efforts on effective conservation area systems in regions of high biological value (Chape et al., 2005; Rands et al., 2010). Assuring adequate representation and long–term maintenance of biodiversity lies at the heart of an effective protected area (PA) network (Gaston et al., 2008). Systematic conservation planning (SCP) provides a framework to select complementary conservation areas that represent the biodiversity of the planning region (Sarkar et al., 2006). Core to the process of spatial conservation prioritizaition within the SCP framework is the selection of biological and environmental data to represent biodiversity and the treatment of socioeconomic data to consider budgetary and sociopolitical constraints for maximizing implementation efficiency (Sarkar et al., 2006; Kukkala and Moilanen, 2013). Practitioners therefore face difficult decisions when determining key aspects of their conservation plan. They have to decide, first, which datasets are sufficiently reliable to serve as surrogates for biodiversity, second, how to assign conservation targets for species, vegetation types or other features used as surrogates; and third, (3) how to avoid selecting unsuitable areas for conservation action.

The field of SCP has been useful in advancing concepts and designing reserve selection tools. One of the objectives of peer–reviewed studies has been to test biological data and establish limitations (Knight and Cowling, 2007). Nonetheless, conservation planning must often be conducted in the absence of comprehensive biodiversity datasets, and the adequacy of results and decisions in real–world circumstances has rarely been tested. These challenges highlight the need to test the choice of biodiversity data, and validate their robustness using various analytical approaches in order to promote an efficient network of conservation areas.

More than ten years ago, the Programme of Work on Protected Areas of the Convention on Biological Diversity (CBD) encouraged the Parties to increase representativeness and coverage of biodiversity within national PA systems. Mexico was one of the first countries to conduct comprehensive conservation gap analyses for the terrestrial, marine and freshwater environments (Koleff et al., 2009; Lira–Noriega et al., 2015). The process involved over 260 experts from numerous academic and research institutions, civil society organizations, and governmental agencies. The purpose was to conduct a spatial conservation prioritization to assess the effectiveness of PAs to adequately represent Mexico's biodiversity, and to guide the implementation of area–based conservation measures.

The aim of this paper was, first, to test the criteria used in Mexico's spatial conservation prioritization to select biodiversity surrogates and set conservation targets through two independent surrogate assessments, and second, to frame our findings as lessons learned in the context of a megadiverse country. In the first surrogate assessment we explored questions regarding the appropriateness of using range restricted (hereafter referred as rare species), endemic and threatened species as surrogates for other species not previously considered. We also examined the influence of target–setting on the spatial configuration of the conservation network. In the second surrogate assessment we analyzed the performance of selected taxonomic groups as surrogates for other known species groups.

We first provide a brief overview of the core methodological decisions of Mexico's spatial conservation prioritization analyses in terrestrial environments (hereafter, gap analysis) and the overall results (described in detail in Urquiza–Haas et al., 2009). We then present and update the results of the independent surrogate assessments based on the methods of gap analysis (Koleff et al., 2011). Finally, in view of these results and the relevant and recent SCP literature we discuss whether methodological decisions were appropriate to ensure a conservation network representative of Mexico's megadiversity.

The lessons learned from the surrogate assessments in the context of the Mexican gap analysis project may be useful to guide decision makers, planners and managers in other countries in the selection of conservation targets and surrogates,. This is of foremost relevance in megadiverse developing countries that need to develop a clear spatial guide towards meeting Aichi target 11 for effectively conserving 17 % of terrestrial and inland water areas of particular importance to biodiversity, especially when spatial patterns of biodiversity are complex and represent major challenges to fulfill criteria expressed theoretically in SCP.

SCP for biodiversity conservation in Mexico

The most common obstacle for conducting high–resolution systematic conservation assessments is having limited data or access to data on species distributions (Kremen et al., 2008). Commission and omission errors inherent to species occurrence data can affect the comprehensiveness, representativeness, efficiency and adequacy of reserve networks in different ways (Rondinini et al., 2006). The challenge of acquiring good quality information on species distributions for the spatial conservation prioritization was overcome in Mexico with the collaboration of government agencies and numerous researchers (see Koleff et al., 2009). Species distribution modeling (hereafter, SDM) with explicit considerations on the use of reliable taxonomic determination, precise georeferencing (Soberón and Peterson, 2004) and a post–processing step after modelling that minimizes commission errors was considered the best tool to deal with scarce and biased occurrence data (despite efforts of the National Biodiversity Information System, SNIB, and worldwide of the Global Biodiversity Information Facility, GBIF). The National Commission for the Knowledge and Use of Biodiversity (CONABIO) commissioned expert–lead–technical groups (see references and methods in Koleff et al., 2009) to generate SDMs using niche modelling techniques from species records reviewed and curated by experts belonging mainly to the SNIB and available through GBIF. This effort corresponded to about 2,412,000 records to generate distribution maps for 2,408 species, including a broad span of taxonomic groups, mainly vascular plants and terrestrial vertebrates. The SDMs database for vertebrates was by far the most complete as it represented 86% of the vertebrate species in Mexico.

The use of several types of surrogates representing different levels of biological organization and targets assigned to each based on biological knowledge and socio–ecological context are considered best practice in SCP (Groves et al., 2002; Carwardine et al., 2009; Polak et al., 2015). To accomplish this, a working group consisting of members from CONABIO, the National Protected Areas Commission (CONANP), several national and international NGOs and academic institutions discussed the criteria for conducting a spatial conservation prioritization within the SCP framework in five workshops that took place during 2005 and 2006. The final biodiversity dataset comprised 1,450 plant and vertebrate SDMs, 68 vegetation type maps, nine species richness maps (overall and endemic) and 12 *ad hoc* richness and endemism indices to represent flowering plant diversity (in particular of four families, and two genera; Koleff et al., 2009). Target–setting for species, which ranged from 5–40 % of their distribution area, were based on weights given to different criteria, such as the degree of rarity, in terms of geographic distribution area, country endemism, extinction risk status in the Mexican red list (NOM–059–SEMARNAT–2001) and in the international red list (IUCN), and status in CITES appendices (I and II) as a proxy of species that need conservation actions because of overexploitation and illegal trade (detailed in Urquiza–Haas et al., 2009).

Integration of conservation costs was considered a key aspect in order to come up with a potentially more amenable network for long term persistence of biodiversity and viable in terms of management costs (Luck et al., 2004; Chan et al., 2006). Threats to biodiversity were used to define a suitability layer (i.e. costs) to orient priorities to sites where impediments to conservation are lower and to minimize the selection of areas that have likely lost their biodiversity value. Weights were assigned to each of the 19 threat layers selected based on data availability and known impact on species and ecosystems to obtain a final integrated cost value for each planning unit (detailed in Urquiza–Haas et al., 2009). We used Marxan software (Ball and Possingham, 2000) to identify a set of planning units (out of 8,045 hexagons of 256 km^2) that meet the representation targets for biodiversity surrogates while minimizing the area and the costs of the conservation network. Marxan uses a simulated annealing algorithm to find multiple alternative good solutions to the minimum set problem; it does so with an iterative improvement method that incorporates occasional backward steps. Marxan produces a best solution that represents the reserve network with the lowest score from all the reserve networks generated and also provides the selection frequency of sites (Ball et al., 2009). Marxan was run for Mexico's spatial prioritization analysis with 10,000 runs and 1,000,000 iterations. PAs were not considered *a priori* in the selection of priority conservation sites because not all PAs in the network have proven effective in terms of reducing or halting ecosystem degradation. Furthermore, as part of the gap analysis, all participants and stakeholders agreed to evaluate the performance of PA to represent species and other biodiversity elements efficiently (results not shown here).

This algorithmic process allowed the selection of terrestrial priority sites (TPS) for conservation. These sites cover 594,894 km^2 (30.6 % of the country's continental territory) and include a subset of the best solution sites (43 % of the country) with the highest selection frequency scores that met most of the biodiversity surrogate targets (90.5 %). Irreplaceable sites, i.e. essential sites to meet conservation targets or sites where unique biodiversity elements are distributed, cover 16.6 % of the territory and accomplished conservation targets for 81 % of all biodiversity surrogates. As Mexico continues to reinforce efforts for conservation, the percentage of coverage of TPS under protected areas (federal, state, municipal and private PA) has increased 1,316,927 ha (2.1 %) in the last 10 years (CONABIO, 2015; CONANP, 2017). The PA network covered a total of 244,539 km^2 (or 12.54 % of the continental surface) by the end of 2016 (Sarukhán et al., 2017).

Surrogate assessments

Effectiveness of biodiversity surrogates: influence of target–setting methods and selection criteria

Methods

We determined whether a system of priority sites for conservation based on mammal species of conservation concern (i.e. endemic, rare and threatened) was appropriate in terms of the representation of other species of this taxonomic group. Mammals were chosen for this assessment as Mexico holds the second largest number of mammal diversity worldwide (564 described taxa, including 169 endemic terrestrial species and 50 marine species). Besides, species have relatively well–known distributional data, and at least half of the taxa (291) are threatened according to the Mexican legal list of endangered species (NOM–059–SEMARNAT–2001), circumstances that explain the interest to assess whether species of conservation concern of this group deliver efficient outcomes as surrogates of other mammal and vertebrate species (cf. Di Minin et al., 2016).

We used SDMs (Ceballos et al., 2006) described in Koleff et al., 2009) of 354 mammal species of 10 orders. Data available were insufficient to produce SDMs for a further 113 mammals whose distributions are highly restricted, so we used maps from occurrence records. In total, our dataset on mammal distribution covered 96 % of all terrestrial mammal species in Mexico. Species only occurring on islands were excluded from the analysis as island inventory was incomplete. Most of the insular territory in Mexico (84.8 %) today is already protected by the PA system, which is very relevant because of the elevated number of insular endemics and threatened species (Sarukhán et al., 2017). We used this dataset to identify ten conservation area networks based on the best solution (hereafter, CAN) using four surrogate groups and different conservation targets running Marxan (1,000,000 iterations and 10,000 runs). Surrogate groups were as follows: [1] Threatened species (TS; n = 104); species listed as critically endangered (CR), endangered (E), or vulnerable (VU) in the IUCN red list, or listed as possibly extinct in the wild (E), at risk of extinction (P), or threatened (A) in the Mexican list of endangered species (NOM–059–SEMARNAT–2001). [2] All species of conservation concern (SCC; n = 241); species that fulfill any of the following criteria: (a) endemic to the country; (b) of restricted distribution (using as a threshold the last quartile of the geographic distribution range of all mammal species, hereafter referred as rare species); (c) listed as E, P or A in the Mexican list of endangered species; (d) listed as CR, E or VU in the IUCN Red List; (e) listed in CITES Appendices I or II. [3] Other species, i.e. those that did not fulfil any of the above mentioned criteria and are usually not considered of conservation concern (OS; n = 204). and [4] All mammal species (AS; n = 445).

We set targets at 10 % and 20 % of the species distribution area (OS and AS), and also used variable target levels (5–40 %) for species of conservation concern (TS and SCC), by applying the target–setting methods used for the Gap Analysis, i.e. assigning values to each criteria above mentioned and summing them to obtain the final percentage. Threatened, endemic and rare species thus had the highest conservation targets (Supplementary Material, see Urquiza–Haas et al., 2009). We used the same costs layer as in the Gap Analysis (see Urquiza–Haas et al., 2009) to consider the degree of impediments to conservation success at the beginning of the planning process. We further tested whether sites selected randomly were as efficient as sites selected using surrogate groups with SCP tools. We generated 100 random solutions to obtain average values of species representation and proportion of species distribution area achieved by the random CANs. We considered 799 and 1,579 planning units for analysis (scenarios R–799 and R–1579, respectively), corresponding to the average number of planning units of scenarios using 10 % and 20 % variable target values, respectively.

Results

The solutions of the ten different scenarios based on four indicator groups and three alternative conservation target–settings differed in total area, spatial distribution, selection frequency of planning units', and representation of mammal species (table 1). As expected, the size of the CAN was strongly influenced by the targets assigned. It doubled from *circa* 10 to 20 % of the country's continental surface, as targets were doubled from 10 to 20 % of the total species' distribution area, irrespective of the indicator group used. Scenarios with conservation targets of 20 % had CAN with more planning units of higher selection frequencies (i.e. irreplaceable sites) in comparison with scenarios where conservation targets were set at 10 %. CANs were similar in size for scenarios using variable target levels (TS–V; SCC–V) and target levels of 10 % (TS–10; SCC–10; AS–10; OS–10) (table 1). An important difference between scenarios of variable target levels and targets of 10% was in respect to the selection frequency and the spatial distribution of planning units, as well as in the levels of species representation. Solutions of scenarios with variable target levels (TS–V; SCC–V) were more spatially compact and had a higher number of irreplaceable units (fig. 1). For instance, the number of clusters, i.e. adjacent and connected planning units of larger size (> 2,560 km^2), was higher for the scenario designed for species of conservation concern using variable targets than for the scenario with 10 % targets (11 *vs.* 4 clusters, respectively). The frequency distribution of clusters differed significantly between these scenarios (one–tailed Mann–Whitney test U = 169; p = 0.04). Also, scenario SCC–V had more planning units with selection frequencies higher than 80 % (n = 819) than the scenario SCC–10 which only had 136 planning units. Considering a selection frequency of more than 90 %, the numbers decreased to 136 and 79 planning units, respectively). In scenarios TS–V and SCC–V, selected planning units with high irreplaceability scores were concentrated in several geographical areas across the country: the northern part of the Mexican plateau, the Pacific coast (along the states of Michoacan and Guerrero), and southern Mexico (Chimapalas, Lacandon Forest, Maya Forest). Many of these areas coincide with areas of high conservation importance identified in other planning exercises based on patterns of mammal species richness and the concentration of endemic and threatened species (Ceballos et al., 1998).

Representation values (i.e. proportion of species in the CAN) for all mammal species was high (81.8–100 %) irrespective of the indicator group or target levels used to design the CAN. A sample of randomly chosen planning units of *ca.* 10 % and 20 % of the continental surface also achieved high representation values (83.4 and 87.5 %, respectively). Nonetheless, representation values for several non–target groups varied considerably. For instance, in scenarios using species of less concern (OS–10 and OS–20), representation values varied from 23.6 % for rare species to 84.5 % for all mammal species. Rare species had a poor representation (23.6–34.9 %) in scenarios that did not explicitly consider these species in the planning process (OS–10, OS–20), attaining higher representation in scenarios designed for threatened species (66–73.6 %; table 1). Scenarios designed for non–conservation concern species (OS–10, OS–20) performed slightly worse than randomly chosen planning units of similar area (R–799, R–1579), in particular for rare species (table 1).

Scenarios performed differently with regards to the average proportion of species distribution area achieved by CANs, with increments in accordance with representation targets. CANs designed for threatened species and species of conservation concern using variable and 10 % targets captured an average of 18–24 % of the species' distribution area, whereas scenarios for all indicator groups with 20 % targets captured an average of 24–31 % of the species' distribution area. The scenario designed for species of less conservation concern using 10 % targets (OS–10) was outperformed by almost all others (fig. 2), and was very similar to the scenario of randomly chosen planning units of equivalent total area (R–799: 11.9, 95 % CI = 10.8–13.0). OS–10 covered on average 12 % of the species distribution, while the scenario designed for threatened species with 10 % target (TS–10) covered on average 18 %; nonetheless these scenarios did not differ statistically from each other (fig. 2). The scenario designed for species of conservation concern with 10 % and variable target levels performed as well as scenarios designed for all species using a 10 % target; they had the highest species' distribution area average, significantly different from all other scenarios using a 10 % target level. Less than 2 % of rare species had more than 60 % of their distribution area covered by the CAN in scenario OS–10, in comparison to 25 % of rare species in scenario TS–10. On the other hand, only 5 % of rare species had less than 10 % of their distribution area covered by CANs designed for threatened species and for species of conservation concern using variable targets (TS–V and SCC–V; fig. 3) in comparison to scenario OS–10, in which 8.5 % of the rare species had less than 10 % of their distribution covered.

Overall threatened species performed well as surrogates based on the high representation achieved for non–target species. When endemic and rare species were also considered as surrogates (i.e. all species of conservation concern), it was possible to represent all mammal species, including those of less concern. Moreover, CANs designed for species of conservation concern using variable target levels as in the Mexican Gap Analysis were more area efficient and more compact (i.e. CAN is more connected and its perimeter is minimized) than that of the CAN designed for all mammal species using a 10 % representation target.

Testing the effectiveness of taxonomic groups as biodiversity surrogates

Methods

In this assessment, we explored whether a CAN designed for a given vertebrate taxon can appropriately represent all vertebrates. We used the same database and criteria used in the Mexican Gap Analysis described beforehand (i.e. size of planning units, spatial prioritization algorithm, cost and target–setting methods) and compared the performance of mammals, resident birds (hereafter referred as birds), reptiles and amphibians as taxonomic surrogates. A total of 1,146 species were selected following target–setting methods to focus on species of conservation concern (i.e. endemic, rare, and threatened) (208 amphibians, 424 reptiles, 273 birds, 241 mammals).

Surrogate performance was measured in terms of the effectiveness of CAN designed for each indicator group to represent non–target species from other taxa. We standardized our analyses to a subset of planning units from the best solutions. From these units we calculated species accumulation curves in EstimateS (Colwell, 2006), first, to predict the number of species represented in a given number of planning units and second, to statistically compare the performance of indicator groups based on 95 % confidence intervals. We further tested whether sites selected for indicator taxa using SCP tools were more or less efficient than sites selected randomly. We generated 100 random solutions (considering 477 and 1,510 planning units) to obtain averaged accumulation curves.

Results

CANs selected for full coverage of indicator taxa included between 753 and 875 of all non–target species, while the number of planning units ranged from 477 for amphibians to 1,510 for birds (table 2; fig. 4). CANs designed for amphibians, reptiles and mammals did not differ significantly in their effectiveness as indicators (as measured by overlapping confidence intervals; fig. 5). On average, CANs designed for amphibians and reptiles represented the highest proportion of non–target species (on average, 80.1 % and 85.7 %, respectively), while CAN designed for birds represented the lowest number of species (74 %) over an area three times that of amphibians (table 2). With the CAN size being equal (477 planning units), amphibians were the most effective surrogate, representing on average of 80.1 % of non–target species, and 83.9 % of species from all four vertebrate groups examined, followed by the CAN designed for reptiles (78.4 % and 87.3 %, respectively; table 3). CAN designed for birds was the least effective (60.9 % and 71.1 %). In contrast, birds were represented almost entirely (on average 97.3 %) by the CAN designed for other taxa, while amphibians and mammals had the poorest average representation within CAN designed for other taxa (59.8 % and 65.5 %, respectively). Differences in the degree of effectiveness of indicator groups were more evident when the number of species that accomplished their conservation targets was measured. CAN designed for reptiles accomplished or surpassed the targets for 958 species of all four taxa (on average 73.5 %), in contrast with the CAN designed for amphibians that accomplished or surpassed the targets for only 748 species (56.1 % on average). However, the CAN for reptiles was almost twice as large as that for amphibians, and managed to increase the total number of species that accomplished their conservation targets by 18.3 %. In contrast, the CAN designed for birds only increased the number of species that accomplished their target by 7.6 % with respect to the CAN designed for amphibians, but in an area 3.2 times larger.

Using the same number of planning units as the best solutions for amphibians (n = 477) and birds (n = 1,510), we found that a random selection of sites represented 71.9 % and 82.9 % of all species, respectively. Randomly selected planning units outperformed

Table 1. Comparison of conservation scenarios for the protection of Mexican terrestrial mammals resulting from varying subsets of mammal species and conservation targets: TS–10, threatened species, 10 % conservation targets; TS–V, threatened species, variable (5–40 %) conservation targets; SCC–10, species of conservation concern, 10 % conservation targets; SCC–V, species of conservation concern, variable (5–40 %) conservation targets; OS–10, other species, i.e. of non–conservation concern, 10 % conservation targets; AS–10, all species, 10 % conservation targets; R–799, 100 random solutions, each 799 planning units, mean (SD); TS–20, threatened species, 20% conservation targets; SCC–20, species of conservation concern, 20 % conservation targets; OS–20, other species, i.e. of non–conservation concern, 20 % conservation targets; AS–20, all species, 20 % conservation targets; R–1579, 100 random solutions, each 1,579 planning units, mean (SD).

Tabla 1. Comparación de los escenarios de conservación para la protección de mamíferos terrestres en México derivados de distintos subconjuntos de especies de mamíferos y metas de conservación: TS–10, especies amenazadas, metas de conservación del 10 %; TS–V, especies amenazadas, metas de conservación variables (5–40 %); SCC–10, especies de interés para la conservación, metas de conservación del 10 %; SCC–V, especies de interés para la conservación, metas de conservación variables (5–40 %); OS–10, otras especies, es decir, de poco interés para la conservación, metas de conservación del 10 %; AS–10, todas las especies, metas de conservación del 10 %; R–799, 100 soluciones aleatorias, considerando 799 unidades de planificación, media (DE); TS–20, especies amenazadas, metas de conservación del 20 %; SCC–20, especies de interés para la conservación, metas de conservación del 20 %; OS–20, otras especies de poco interés para la conservación, metas de conservación del 20 %; AS–20, todas las especies, metas de conservación del 20 %; R–1579, 100 soluciones aleatorias, considerando 1.579 unidades de planificación, media (DE).

Scenario	Planning units (#)	All species (%) n = 445	Threatened species (%) n = 104	Species of conservation concern (%) n = 241	Endemic species (%) n = 128	Rare species (%) n = 106
TS–10	785	91.9	100	85.1	89.1	66.0
TS–V	767	91.5	100	84.23	87.50	66.0
SCC–10	780	100	100	100	100	100
SCC– V	819	100	100	100	100	100
OS–10	826	81.8	67.3	66.4	74.2	23.6
AS–10	819	100	100	100	100	100
R–799	799	83.4 (1.3)	70.2 (3.1)	69.6 (2.4)	77.0 (2.5)	30.0 (5.3)
TS–20	1,560	93.7	100	88.4	93.0	73.6
SCC–20	1,571	100	100	100	100	100
OS–20	1,599	84.5	69.2	71.1	77.3	34.9
AS–20	1,588	100	100	100	100	100
R–1579	1,579	87.5 (1.1)	77.1 (3.1)	77.1 (2.1)	83.2 (2.4)	47.2 (4.7)

those achieved by CAN designed for birds by 7.6 %. Likewise, the confidence intervals of CAN designed for mammals overlapped those of the random selections of sites. However, the CAN for amphibians and reptiles outperformed the random solutions (fig. 5).

As the effect of using costs in the performance of indicator groups was not accounted for when compared with sites selected at random, we explored their influence on the efficiency of indicator groups by comparing the random selected sites with the CAN designed for indicator groups without using cost information in the algorithm selection process. Results (not presented here) showed the same tendency as described for the CANs designed for each taxon. In general, however, they represented around 1 % more species than CANs that included costs.

The minimum set of planning units (1,824, representing 23.3 % of the country's continental surface) required to achieve all targets for vertebrate species of conservation concern was almost as large as the CAN designed for birds, and four times as large as the CAN designed for amphibians (fig. 4). Integration of CANs designed individually for each of the indicator groups consisted of 2,582 planning units (32.9 % of

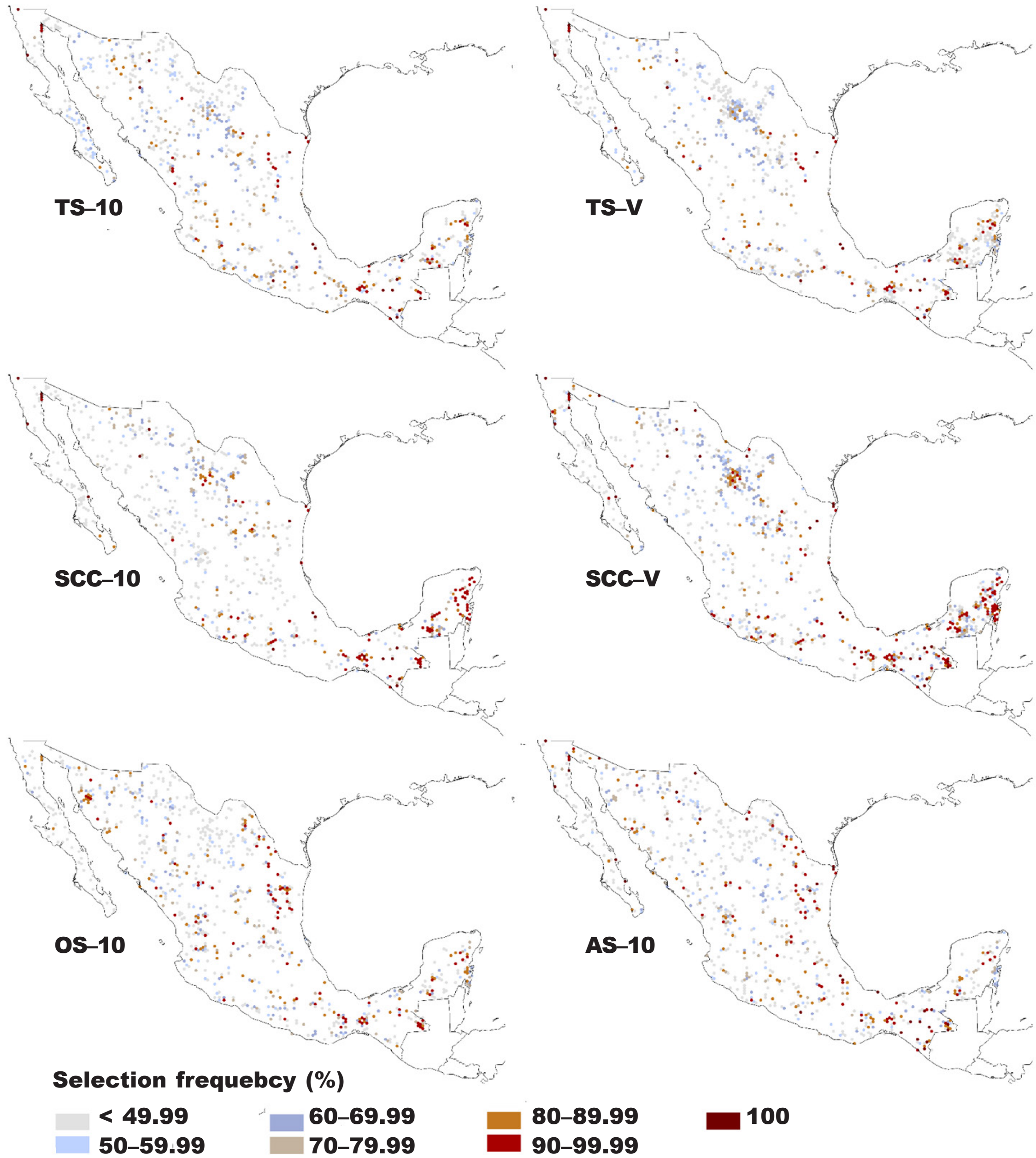


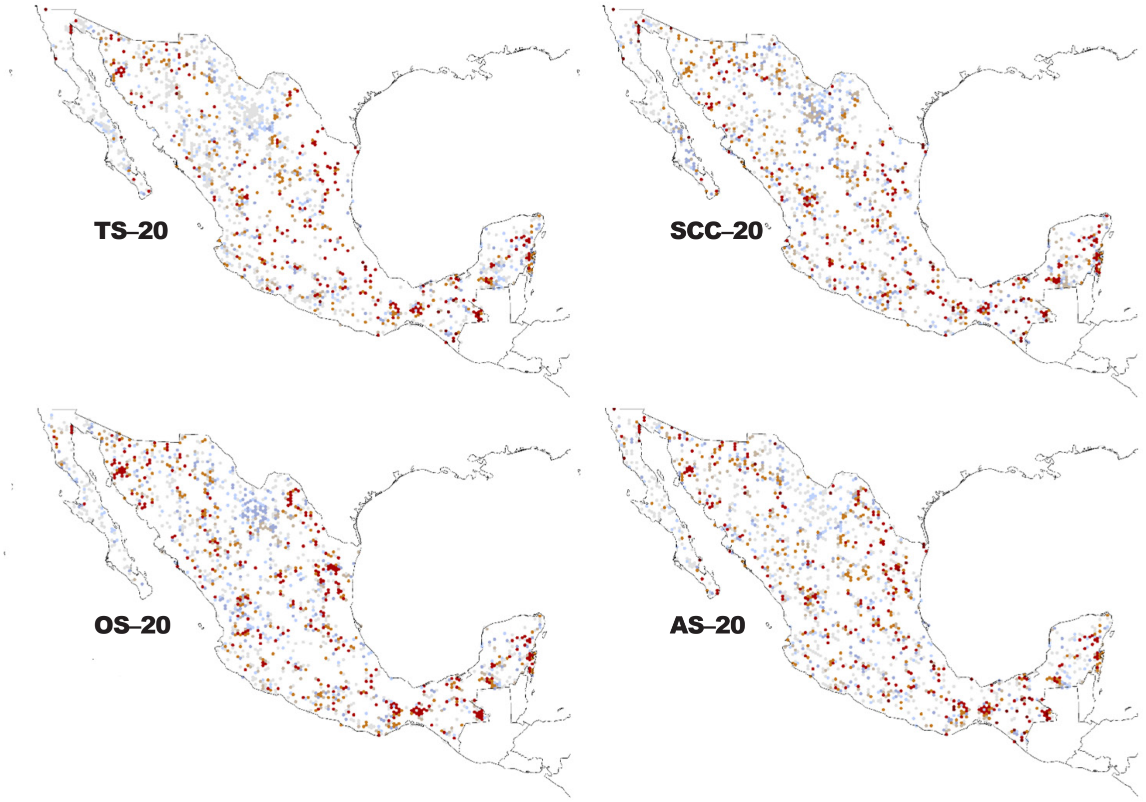
Fig. 1. Conservation area networks designed with varying target levels for different subgroups of Mexican mammal species (i.e. scenarios, see abbreviations in table 1). Planning units of Marxan best solutions are shown by selection frequency intervals (degree of irreplaceability).

Fig. 1. Redes de áreas de conservación diseñadas con diferentes valores de metas de conservación para distintos subgrupos de especies de mamíferos en México (es decir, escenarios; véanse las abreviaciones en la tabla 1). Las unidades de planificación de las mejores soluciones de Marxan se muestran por intervalos de sus frecuencias de selección (grado de irremplazabilidad).

the continental surface), while only about a third of the planning units were spatially congruent between two or more CANs (i.e. 47; 221 and 606 units were spatially coincident for four, three, and two of the CANs designed for indicator groups, respectively).

Discussion

Endangered species and endemic and rare species have commonly been used or proposed as surrogates in SCP exercises (e.g. Brooks et al., 2004; Diniz et al.,



2017). However, questions have arisen as to whether they are adequate indicators to guide the implementation of cost–efficient conservation approaches (see references in Drummond et al., 2010). This issue has been poorly explored with large datasets in the context of a real–world conservation planning process. Our assessment using a comprehensive terrestrial vertebrate dataset showed that threatened species provided coverage for 92 % of all mammal species examined, even though they constitute only 24 % of all species examined. Furthermore, nearly 30 % of all threatened species were missing in CANs not designed for these species. Very similar results were found by Drummond et al. (2010) for mammal species in Indonesia, another megadiverse country. Likewise, Lawler et al. (2003) in the Middle Atlantic region of the United States found that threatened species from several taxa performed well as surrogates as they covered on average of 84 % of all species examined, while threatened species were poorly represented (15–58 %) in CANs designed for other species. Even when using a limited number of species, rare and threatened species had the best surrogacy performance (Jones et al., 2016). The results of these studies and our own are similar even though the planning units differed widely in size(1–650 km^2), which is not expected because larger planning units are more likely to represent more species. At the subcontinental scale, Tognelli (2005) also showed the effectiveness of threatened terrestrial mammal species but specifically noted that of geographically rare species as indicator groups for other South American mammal species.

In the present work we highlight the ability of the set of threatened, endemic and rare species to act as effective surrogates in megadiverse Mexico for the coverage of all other species. The use of threatened species alone was not as adequate as it missed a large proportion of rare species. This is of particular relevance for conservation in a country with a high proportion of endemic and range restricted species (Llorente–Bousquets and Ocegueda, 2008). Like studies in other biogeographic regions (e.g. Lawler et al., 2003; Larsen et al., 2007; Jones et al., 2016), our findings illustrate that the efficacy of a surrogate group is related to a greater proportion of threatened and rare species regardless of the taxonomic group used, in particular when trying to cover other threatened and rare species. Nonetheless, this may not be always the case. Franco et al. (2009) found that threatened butterflies were not adequate to represent the non–threatened species of butterflies.

The usefulness of taxonomic groups to act as surrogates in SCP is still an unresolved issue (see Rodrigues and Brooks, 2007). In particular, in high beta diversity countries, like Mexico, Koleff et al. (2008) anticipated that no vertebrate taxonomic group could be used to set priorities for other groups based on the general weak congruence of their diversity patterns. The results of the taxonomic surrogate assessment shown here indicate that at least half of the species in other taxonomic groups were covered by a single taxonomic group. Similar conclusions are found elsewhere (Lawler et al., 2003; Moore et al., 2003; Rondinini and Boitani, 2006; Larsen et al., 2009). While no conservation area system designed for a

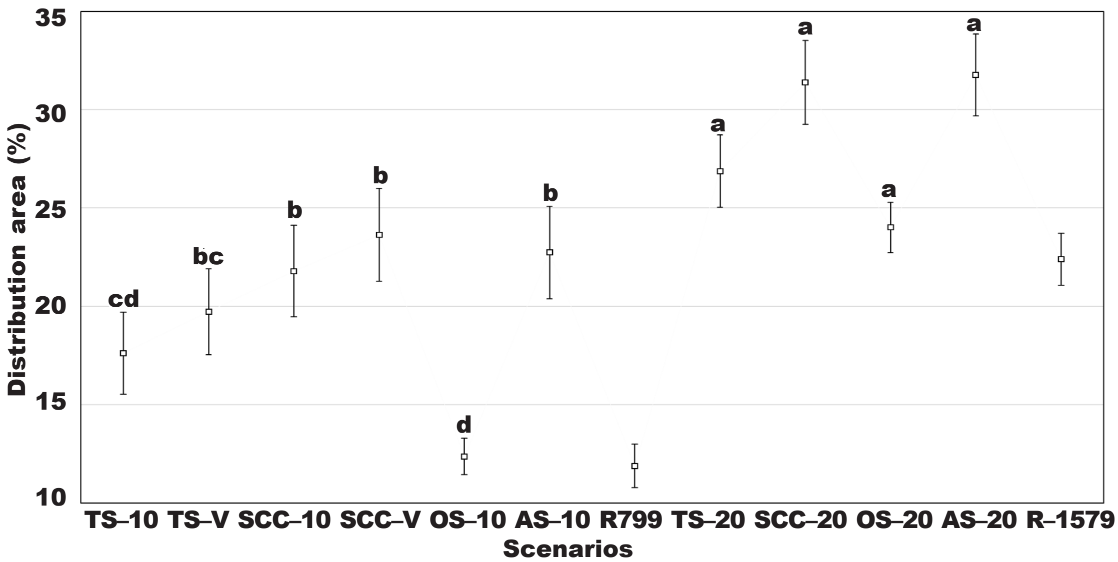


Fig. 2. Percentage of species distribution area covered by conservation area networks designed for different subsets of mammal species (i.e. scenarios; see table 1 for abbreviations). The letters indicate significant differences between scenarios (Kruskal–Wallis, n = 4,184, $p < 0.001$, K–W H test and pairwise comparisons conducted in SPSS® Statistics 19; highest significant pairwise p–value = 0.021).

Fig. 2. Porcentaje de las áreas de distribución de las especies cubierta por redes de áreas de conservación diseñadas para diferentes subconjuntos de especies de mamíferos (es decir, escenarios; véanse las abreviaciones en la tabla 1). Las letras indican diferencias significativas entre los escenarios (Kruskal–Wallis, n = 4.184, p *< 0,001, prueba K–W y comparaciones por pares realizadas en SPSS® Statistics 19; valor del par más significativo* p *= 0,021).*

single taxon is able to represent all species of other taxonomic groups, the reptiles and amphibians were the most effective surrogates because they represented a very high percentage of non–target species, and performed better than expected at random.

The efficacy of a surrogate group might vary between regions and taxonomic groups due to scale dependence in spatial patterns of species richness and species turnover (Hess et al., 2006; Franco et al., 2009). However, distributional congruence (Koleff et al., 2008) did not serve as predictor of the performance of indicators groups or of overall priorities for terrestrial vertebrate conservation. The number of species within an indicator group might influence their effectiveness (Larsen et al., 2012). In this case, however, it did not appear to be important, as 208 species of amphibians used as surrogates were as effective as 424 reptile species for the representation of other vertebrate species. On average, Mexican amphibians and reptiles, which were more effective surrogates, have smaller range sizes and higher species turnover rates than birds. Thus, efficacy of a surrogate group at this national scale of analysis appears to be related to the use of indicator species that have relatively non–overlapping ranges, collectively covering many environments (Lawler et al., 2003; Lewandowski et al., 2010). Moreover, taxa that contain many species with restricted ranges are less likely to be captured by CAN designed for other taxa with widespread distributions (Brooks et al., 2001; Moore et al., 2003). Likewise, ecological surrogates might be less effective for threatened taxa or of species of conservation concern than more widely distributed features (Grantham et al., 2010). A better insight could be gained by testing random species, and by controlling their distributional characteristics (e.g. widespread or restricted distributions, fragmented or continuous; see Sánchez–Fernández and Abellán, 2015).

Concerns have arisen about the apparent arbitrariness of target–setting, and the often too low target values (Carwardine et al., 2009; Di Minin and Moilanen, 2012). For the gap analysis, a method was developed to establish species targets more objectively with the aid of expert input and easily measured characteristics related to the conservation status and the distribution of species (see Supplementary material). Here we did not try to thoroughly evaluate the influence of this target–setting method on species persistence *per se*, but rather to evaluate the appropriateness of this method in view of indicator effectiveness, and on the configuration of the CAN, which might ultimately influence species persistence. Results of the independent assessment indicate that variable target–setting, giving more weight to species

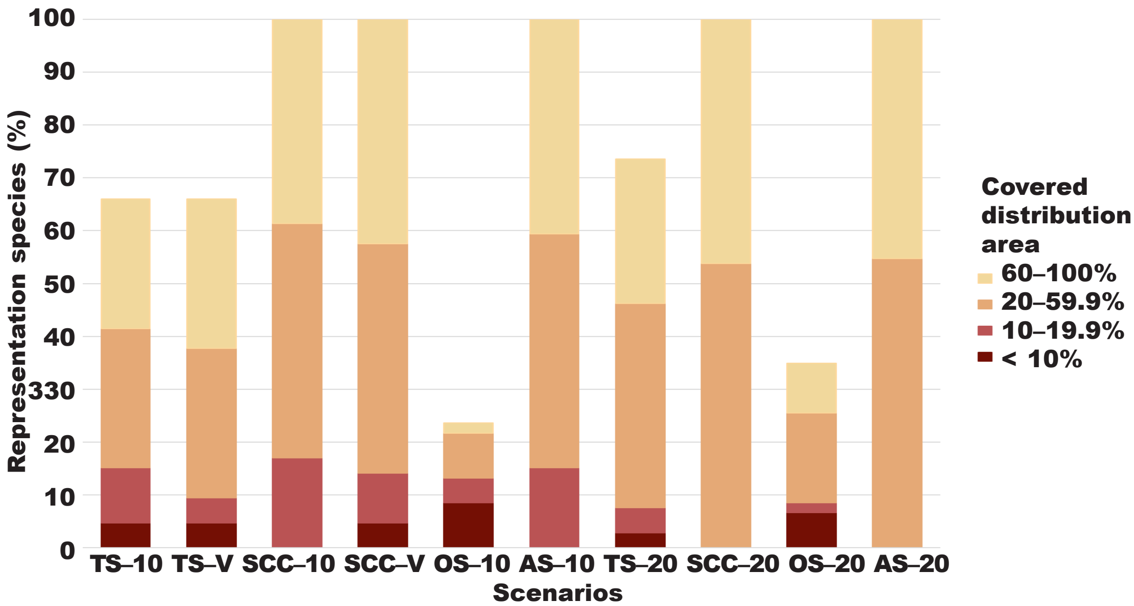


Fig. 3. Percentage of rare Mexican mammal species represented in each scenario shown by the percentage of their distribution area covered by conservation area networks designed for different subgroups of mammal species (i.e. scenario, see table 1 for abbreviations).

Fig. 3. Porcentaje de especies raras de mamíferos de México representadas en cada escenario según el porcentaje de su área de distribución cubierta por las redes de áreas de conservación diseñadas para diferentes subgrupos de especies de mamíferos (es decir, escenarios; véanse las abreviaciones en la tabla 1).

of mammals of conservation concern (i.e. set of threatened, endemic and rare species) than to conventional fixed targets of 10 % for all species (e.g. Urbina–Cardona and Flores–Villela, 2010), did not significantly influence the number of represented species and average species distribution area covered by the CAN. However, it did generate a more compact, connected and more area efficient CAN with a higher number of

Table 2. Representation percentage of Mexican vertebrate species of conservation concern by taxonomic group (rows) in the conservation area network designed for amphibians, reptiles, birds, and mammals (columns): [1] average for non–target species.

Tabla 2. Porcentaje de representación de especies de vertebrados de interés para la conservación por grupo taxonómico (filas) en la red de áreas de conservación diseñada para anfibios, reptiles, aves y mamíferos (columnas), en México: [1] promedio de las especies no objetivo.

	Amphibians (n = 208)	Reptiles (n = 424)	Birds (n = 273)	Mammals (n = 241)	Average[1]
# of units	477	967	1,510	795	
Amphibians	100	82.7	75	63	73.5
Reptiles	78.1	100	77.8	74.5	76.8
Birds	95.6	99.3	100	98.5	97.8
Mammals	66.8	75.1	69.3	100	70.4
Total	83.9	91.5	80.8	83.5	
Average[1]	80.1	85.7	74.0	78.7	

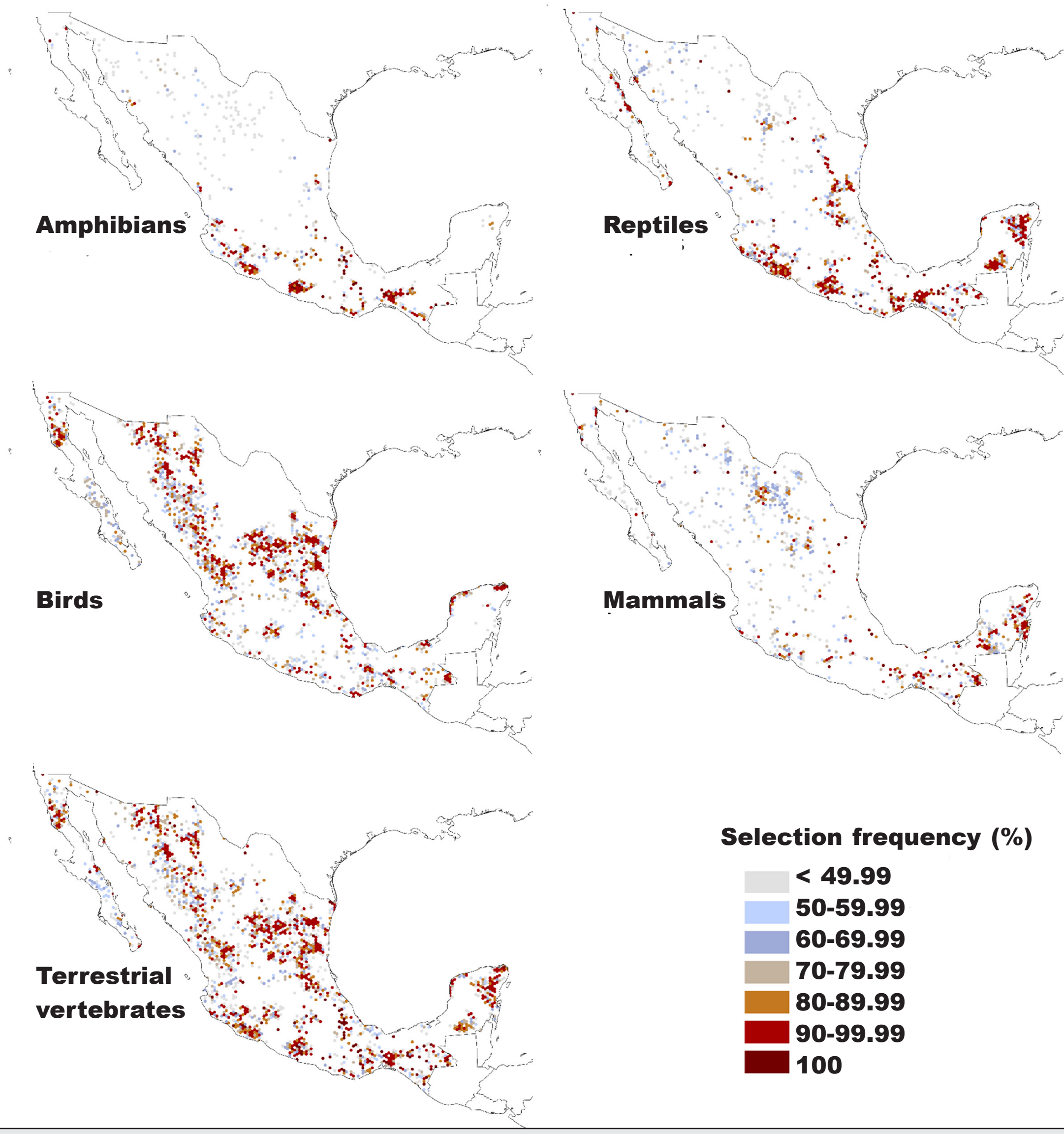


Fig. 4. Conservation area networks designed for indicator species groups individually and collectively. Planning units of Marxan best solutions are shown by selection frequency intervals (degree of irreplaceability).

Fig. 4. Redes de áreas de conservación diseñadas para grupos de especies indicadoras y en su conjunto. Las unidades de planificación de las mejores soluciones de Marxan se muestran por intervalos de sus frecuencias de selección (grado de irremplazabilidad).

irreplaceable sites, in contrast with expectations that more area is needed to meet higher targets (Justus et al., 2008), in particular in high beta diverse regions. Our results support the use of threat classifications and proxies for vulnerability to set larger targets for more threatened and vulnerable species (Lombard et al., 2003; Moore et al., 2003). The methods to select surrogate species in the gap analysis maximized species representation, and can be easily applied to other megadiverse regions and countries when faced with limited information about habitat requirements and minimum viable population sizes. Nonetheless, we also recommend adjustments to target–setting in order to assign higher target levels to rare species. On the other hand, other considerations should be included to guarantee that the CAN selects peak abundance locations where species are presumably more viable (Bonn et al., 2002). Furthermore, when very few areas are identified as irreplaceable, the conservation network is considered poorly defined

Table 3. Estimation of the representation percentage of Mexican vertebrate species of conservation concern by taxonomic group (rows) in the conservation area network designed for amphibians, reptiles, birds and mammals (columns) considering an equal number of planning units (477): [1] average for non–target species.

Tabla 3. Estimación del porcentaje de representación de las especies de vertebrados de interés para la conservación por grupo taxonómico (filas) en la red de áreas de conservación diseñada para anfibios, reptiles, aves y mamíferos (columnas), en México, considerando el mismo número de unidades de planificación (477): [1] promedio de las especies no objetivo.

	Amphibians (n = 208)	Reptiles (n = 424)	Birds (n = 273)	Mammals (n = 241)	Average[1]
Amphibians	100	68.8	55.3	55.3	59.8
Reptiles	78.1	100	65.3	68.4	70.7
Birds	95.6	98.9	100	97.8	97.3
Mammals	66.8	67.6	62.2	100	65.6
Total	83.9	87.3	71.1	79.7	
Average[1]	80.1	78.4	60.9	73.8	

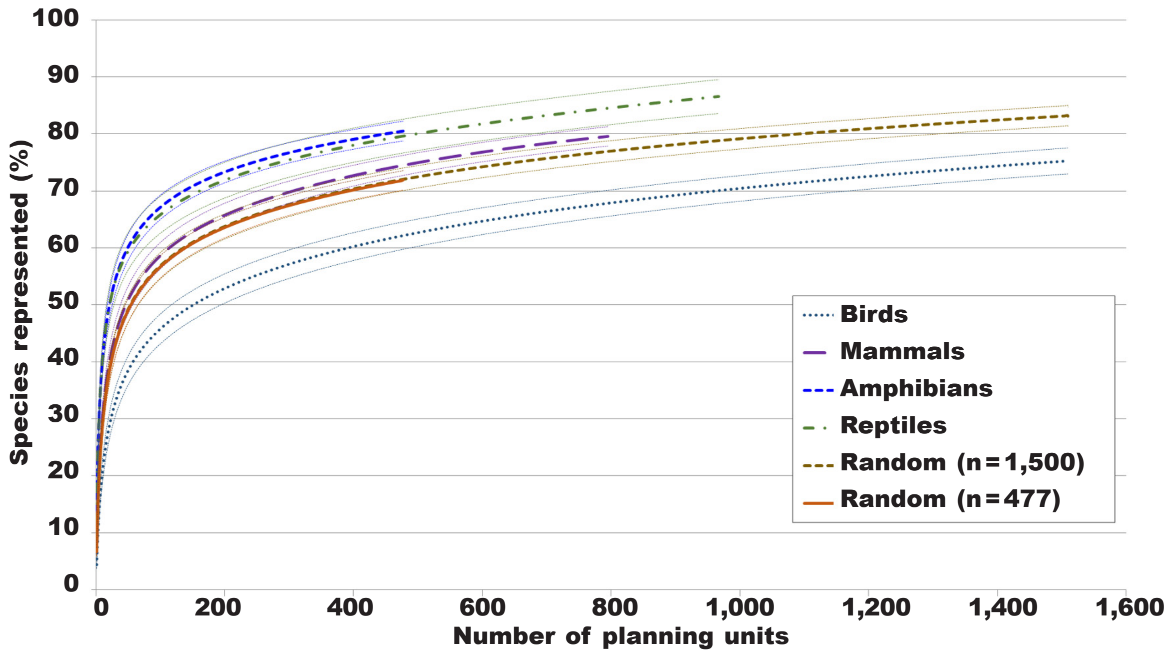


Fig. 5. Cumulative percentage of all non–target species represented in the conservation area network designed for Mexican amphibians, reptiles, birds and mammals, compared against random selected sites (n = 477 and n = 1,500). Dotted lines denote 95% confidence intervals.

Fig. 5. Porcentaje acumulado de todas las especies de otros grupos representadas en la red de áreas de conservación diseñada para los anfibios, reptiles, aves y mamíferos en México, comparado con sitios seleccionados aleatoriamente (n = 477 y n = 1.500). Las líneas discontinuas denotan intervalos de confianza del 95%.

and difficult to implement in real–world settings. As the opposite is also true when too many irreplaceable sites are identified. Levin et al. (2015) recommended performing a sensitivity analysis and provided a general guideline (i.e. 10–20 % of the study areas with sites of selection frequency values over 90 %) for a flexible conservation area network that could be more useful for managers and decision makers.

Areas of high irreplaceability (90–100 % selection frequency, 16.6 % of the CAN) identified for all vertebrate species of conservation concern did not coincide with most conservation areas detected by Sarkar et al. (2009) in Mesoamerica for plant and vertebrate species at risk of extinction using a systematic approach —with targets set at 10 % and 20 % of species potential distribution area. This is most likely because the latter study did not include 'cost' information as it identifies large areas of transformed land (e.g. induced pasturelands in Veracruz) as important for protection. This highlights the need to incorporate information on the human impact at the beginning of the planning process —especially in the absence of species distribution maps that account for current habitat conditions— in order to come up with a more viable CAN for conservation action.

Conclusions

Designing conservation networks to guide biodiversity conservation actions is a particularly challenging task for governments and conservation practitioners in megadiverse countries. The available choice of data, biodiversity surrogates, and target–setting methods, for example, affect the accuracy of the desired conservation plan outcome (Rondinini et al., 2006). As such, the Mexican gap analysis project calls for the active participation and engagement of biodiversity scientists and national–level stakeholders. In this work, we contribute to the debate around the usefulness of surrogates for representing biodiversity at the species level. We also test the decisions taken with respect to the choice of surrogates and target setting methods used in the Mexican gap analysis project by means of two independent assessments. Chosen criteria were appropriate to select surrogates that maximized overall vertebrate species representation in a mega and high beta–diverse country such as Mexico (Koleff et al., 2008). This was a key step in the process, especially for stakeholders that wanted to know about the robustness of choice of surrogates. The use of a comprehensive dataset guards against bias and is of particular importance when implementating conservation action in real–world circumstances.

In view of our results, we outline some practical recommendations to planners when selecting species–level surrogates: 1) conservation planning should include comprehensive suites of complementary measures of biodiversity, including as many species as possible from taxonomically diverse groups for which reasonable good quality distribution information is available; 2) surrogate species groups should be comprised a great number of rare species distributed across broad environmental gradients because as many of them are sensitive to environmental changes they might be good indicators for other species; 3) rare and threatened species need to be included in the planning process as they are most likely to be missed by other environmental or species indicators; and 4) there is a need for a better understanding of the distribution of rare, threatened and understudied species and their sensitivity to human impacts for dynamic conservation planning.

The challenge in mega and beta diverse countries like Mexico with pressing environmental problems (Bradshaw et al., 2010) implies the need for urgent and effective conservation action. Mexico has partly paved the way by identifying areas where a significant proportion of its biodiversity can be maintained.

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