Representation of Threatened Biodiversity in Protected Areas and Identification of Complementary Areas for Their Conservation: Plethodontid Salamanders in Mexico

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Abstract

Protected areas (PAs) have been the most important conservation instrument worldwide and are reaching the coverage percentage suggested internationally (17%), but with the risk of not being ecologically representative, which is particularly concerning for threatened species. Using a database of records from museums, literature, and our fieldwork, we evaluated the representation of 132 plethodontid salamander species, a highly threatened group, in the PAs of Mexico. We assessed the importance of PAs, according to the type of governance, to represent the salamander species diversity, estimating the proportion of suitable habitat within PAs where salamanders occur and detecting potential areas to protect threatened species that are outside of PAs. Approximately 40% of plethodontid species, including threatened species, have not been recorded in PAs. A set of federal PAs harbor the greatest number of species, while state, community, and private PAs have different species composition and a high complementariness to federal areas. In 82% of PAs with plethodontid records, suitable habitat covers more than half of their extent. To protect the 36 threatened plethodontid species that have not been recorded in any PA, we detected 26 potential sites, as well as 12 close and suitable established PAs, to complement the protection of threatened species. Different types of governance of PAs are highly complementary to protect threatened species, but not all PAs seem to have the proper conditions for their survival.

Keywords

amphibians, complementariness, threatened species, protected areas governance, representativeness, suitable habitat

Introduction

Protected areas (PAs) have long been the most important instrument at the global level to counteract the loss of biodiversity and the ecological integrity of ecosystems (Gaston, Jackson, Cantú-Salazar, & Cruz-Piñón, 2008; Pimm et al., 2014; Rodrigues et al., 2004). They have ecological or cultural features of high value to society (Juffe-Bignoli et al., 2014) and can be distinguished or classified according to different criteria. For example, depending on the level of allowed human intervention, there are highly protected sites (e.g., Strict Nature Reserve), parks where visitors are received (e.g., National Park), and sites where resource extraction is allowed in a limited and sustainable manner (e.g., Protected Area with Sustainable Use of Natural Resources), among others (Dudley, 2008). In relation

to their importance or interest, the PAs can be international (e.g., RAMSAR sites or Biosphere Reserves), national (e.g., National Parks), or local (e.g., state,

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municipal or community parks). Another criterion for differentiating PAs is the type of administration (governmental or nongovernmental), also called governance (Borrini-Feyerabend, Johnson, & Pansky, 2006; Deguignet et al., 2014; Juffe-Bignoli et al., 2014).

The effectiveness at protecting biodiversity of each governance type of PA is a relevant issue in the field of biological conservation. For example, the type of governance seems to be a factor that influences the effectiveness of PAs (Ellis & Porter-Bolland, 2008; Porter-Bolland et al., 2012), since it is closely related to management strategies and intervention levels of the local inhabitants (Hayes, 2006). In this regard, community reserves are apparently better preserved due to the knowledge and care of the local inhabitants of their territory (Holdgate & Phillips, 1999). However, it is also argued that there is not a single type of governance of PA that can be considered the best to protect biodiversity; instead, they should be considered as complementary (Smith, 2013), because species composition represented in PAs may differ between governance types of PA (L. Ochoa-Ochoa, Urbina-Cardona, Vázquez, Flores-Villela, & Bezaury-Creel, 2009).

Recently, the Convention on Biological Diversity (CBD) reported that there are 197,368 PAs, distributed in 124 countries, among which 15.4% of the surface area of the terrestrial and continental waters of the planet is covered. The CBD also highlighted the possibility of reaching Aichi Biodiversity Target 11 to protect 17% by 2020, although at the risk of not being ecologically representative; PAs may not adequately cover all the terrestrial ecoregions, biomes, and realms of the world or be efficient in the conservation of biological diversity (CBD, 2014; Juffe-Bignoli et al., 2014).

One way to evaluate the effectiveness of PAs has been to analyze the habitat conditions within them. For example, it is possible to evaluate whether rates of deforestation within PAs are lower than in their surroundings (Mas, 2005), if the declaration of a PA actually reduces deforestation (Andam, Ferraro, Pfaff, Sanchez-Azofeifa, & Robalino, 2008), or if the probability of fires in PAs managed by local inhabitants decreases in relation to surrounding areas (Nelson & Chomitz, 2011). On the other hand, the fact that a site is officially protected by a government or by social groups does not necessarily imply that the entire area of the PA is conserved. This could adversely affect several of the species that inhabit the PA, especially those most sensitive to environmental changes, and therefore its effectiveness to protect biodiversity could be compromised.

Another way to evaluate the effectiveness of PAs has been through the analysis of their species representation. Rodrigues et al. (2004) found that the distribution of PAs in the world does not match with patterns of species diversity and that groups of vertebrates with high levels of endemism are poorly represented. In addition to considering how well represented are species within PAs in general, it is necessary to evaluate in particular how well represented are threatened species, since it is possible that a significant portion of these species are not present in any PA (Nori et al., 2015). In this sense, it is necessary to detect and protect spaces inhabited by those threatened species not represented in PAs, in order to complement their inclusion.

Amphibians are the most globally threatened group of terrestrial vertebrates (Secretariat of the Convention on Biological Diversity, 2010; Stuart et al., 2008). It is estimated that one out of every three amphibian species is threatened with extinction, one in four species does not have enough data to estimate their level of risk (International Union for Conservation of Nature [IUCN], 2017), and 16% of the 7,958 known species (Frost, 2019) have not yet been evaluated. On the other hand, amphibians are not sufficiently represented in the World Database on Protected Areas, since it is estimated that 17% of the current species are not present within any PA (Rodrigues et al., 2004; Venter et al., 2014) and 38% of these species not represented in PAs are threatened (Nori et al., 2015).

The family Plethodontidae, with 476 described species, is the most globally diverse family of salamanders (66% of the salamanders in the world are plethodontids) and the fifth among all amphibians (Frost, 2019). Most plethodontid species have small ranges, exhibit very specific micro-habitat requirements (Wake, 1987; Wake & Lynch, 1976) and one out of every two plethodontid species is threatened (IUCN, 2017), a higher proportion than that of amphibians in general. Mexico is the second richest country for plethodontid species, with 132 described species, 81% of which are endemic to the country (Frost, 2019; Parra-Olea, Flores-Villela, & Mendoza-Almeralla, 2014) and 72% of the species (95 species) are threatened with extinction (IUCN, 2017), a proportion more than double that of globally threatened amphibians. Actually, Mexico is by far the country with the highest number of threatened plethodontid species, followed by the United States (36 species), Guatemala (27 species), and Costa Rica (26 species), respectively (IUCN, 2017). Within family Plethodontidae, some genera in Mexico face critical conservation problems as indicated by their high proportions of threatened species: *Thorius* (96%), *Chiropterotriton* (83%), and *Pseudoeurycea* (78%) (Frías-Álvarez, Zúñiga-Vega, & Flores-Villela, 2010). Declines of several Mexican plethodontid salamanders have been documented in the last two decades, and habitat transformation is recognized as the main threat that has caused such declines (Parra-Olea, García-París, & Wake, 1999; Rovito, Parra-Olea, Vásquez-Almazán, Papenfuss, & Wake,

2009). In fact, it is estimated that 111 Mexican pletho-dontids are negatively affected by habitat transformation (Frías-Alvarez et al., 2010), which is caused by human activities such as agriculture, cattle breeding, logging, and urban development, that modify natural terrestrial ecosystems of the country (Sánchez, Flores, Cruz-Leyva, & Velázquez, 2009).

In México, there are about 1,200 PAs of different governance types, which together cover 14.4% of the almost 2 million km^2 of land surface and inland waters (Comisión Nacional de Áreas Naturales Protegidas [CONANP], 2018), a percentage slightly lower than suggested worldwide and close to Aichi Biodiversity Target 11. The spatial location of PAs in Mexico, however, does not necessarily represent the variety of the country's ecosystems and biodiversity (CONANP, 2011; Halffter, 2007). About PAs and Mexican amphibian fauna, García (2006) found that no protected area coincides with the location of hotspots of amphibian richness and endemism in central western Mexico, particularly in the states of Jalisco, Colima, Guerrero, center of Michoacán, and center and south of Oaxaca. Some of these sites still maintain extensions of conserved vegetation that urgently need protection (Urbina-Cardona & Flores-Villela, 2010). Likewise, Urbina-Cardona and Loyola (2008) found that potential distribution of some species of hylid frogs are not represented within the PAs of Mexico. Ochoa-Ochoa, Vázquez, Urbina-Cardona, & Flores-Villela (2011), based on the results of three algorithms, detected 53 high-priority sites for amphibian conservation and 19 of those sites do not occur in any protected area. Finally, Juárez-Ramírez, Aguilar-López, & Pineda (2016), based on fieldwork, found that a set of small protected areas in the mountainous region of Veracruz can act in a complementary way to protect a high number of threatened frogs and salamanders.

Given the high number of threatened plethodontid species and PAs in Mexico, it is of particular interest to evaluate how effective these PAs at representing these threatened species as well as to quantify amount of suitable habitat that exists in PAs where threatened species live. We evaluate the representation of plethodontid salamanders in PAs of Mexico, with particular attention to threatened species. We examine the spatial distribution of species richness, assess the number of salamander species recorded in PAs, evaluate the importance of each governance type of PA through complementariness to represent salamander species, and estimate the proportion of suitable habitat within PAs where salamanders have been recorded. In addition, we identify potential areas to conserve threatened species of salamanders that are not present in established PAs.

Methods

Data of Plethodontid Salamanders

Records of observations and collections of all species of plethodontid salamanders (hereafter "salamanders") known from Mexico were obtained from seven main sources: (a) database of the Mexican Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO); (b) database of the Global Biodiversity Information Facility (www.gbif.org); (c) VertNet database (www.vertnet.org); (d) database of the Colección de Anfibios y Reptiles del Instituto de Ecología, A.C. (CARIE); (e) Colección Herpetológica-Unidad San Cristóbal of El Colegio de la Frontera Sur (ECOSUR); (f) specialized literature (Appendix S1 Supplementary Material); and (g) fieldwork of our research group between 2010–2017 in the central and southern region of Veracruz. Records we used in this study met at least the following criteria: (a) species name; (b) latitude and longitude data, or precise description of the locality; and (c) an identifier or key of the database of origin (e.g., catalog or collection number). The data set was taxonomically standardized according to Frost (2019). Geo-locations and species nomenclature were verified projecting spatially all record of each species, using ArcGis software version 10.2.2 for Desktop (Environmental Systems Resource Institute [ESRI], 2014) and Google Earth Pro (2015) version 7.1.5.1557. All dubious and duplicate records were eliminated. The final database consisted of 21,609 records of the 132 plethodontid species in Mexico, ranging from 1 to 2,326 records per species (mean = 164 records, median = 43 and standard deviation [SD] = 333).

The current conservation status of each species was compiled using the IUCN (2017) categories, considering as Threatened Species those Critically Endangered (CR), Endangered (EN), and Vulnerable (VU) species, while the Near Threatened (NT) and Least Concern (LC) species were considered as Not Threatened. Given that the level of threat of the species in Data Deficient category and those that have not yet been evaluated is unknown, the conservation status of these species was considered Uncertain.

Data for Protected Areas

The layers of terrestrial protected areas of Mexico that we used in this study were from the Comisión Nacional de Áreas Naturales Protegidas (CONANP, 2016, 2017), CONABIO, (2015) and the layers generated by Bezaury-Creel et al. (Bezaury-Creel, Torres-Origel, Ochoa-Ochoa, Castro-Campos, & Moreno-Díaz, 2009; Bezaury-Creel, Ochoa-Ochoa, Rodriguez-Ramirez, et al., 2012; Bezaury-Creel, Ochoa-Ochoa, & Torres-

Origel, 2012; Bezaury-Creel, Torres-Origel, Ochoa-Ochoa, Castro-Campos, & Moreno-Díaz, 2012). We classified the PAs according to their type of governance in Federal (federal reserves and RAMSAR sites), State, Municipal, Community (conserved areas declared and run by local communities), and Private (private areas and areas voluntarily conserved). The total number of protected areas considered in this study was 1,214, where 269 were federal (236,179 km^2 of coverage), 315 state (36,626 km^2), 112 municipal (1,757 km^2), 167 community (3,733 km^2), and 351 private (6,824 km^2) (Figure S1 Supplementary Material). To avoid double counting of the protected area in the sites with overlapping decrees, we did not consider the overlapped area of the lower governmental hierarchy PAs. Federal PAs have a higher hierarchy than state PAs and, in turn, state PAs prevailed over municipal ones. Likewise, only community and private land protection initiatives occurring outside governmental reserves were considered. There was no overlapping of nongovernmental PAs.

Analyzing Species Richness Distribution, Representativeness, Complementariness, and Suitable Habitat

To examine the distribution of salamander species richness, we initially used ArcGis software version 10.2.2 for Desktop (ESRI, 2014) to create a grid of 30 × 30 km that covered the whole of Mexico, later we projected all records on the grid, and finally we calculated the number of species occurring in each cell of 30 × 30 km. To determine which salamander species have been registered within PAs, we compared the spatial distribution of salamander records with the distribution of protected areas in Mexico. Following the nomenclature of Rodrigues et al. (2004), we considered as "covered species" those species with at least one record within a PA and as "gap species" those that do not have any record within a PA. A locality was considered as a site with a unique latitude–longitude combination, in which one or more plethodontid species have been recorded.

To evaluate the importance both individually and jointly of PAs in the representation of salamanders, we used a complementariness approach (when two or more things combining in such a way as to form a complete whole). In this study, we considered the most relevant PA as the one that included the largest number of species, the second most important as that which complemented with the greatest number of species to the first, the third most relevant PA was that which complemented with the greatest number of species the first two PAs and so on, until reaching the maximum accumulated number of species. Subsequently, the importance of the remaining PAs was established based on the highest number of threatened species present, species

richness, and extension, respectively. PAs with the greatest values of this attributes were considered more relevant. Complementariness approach was carried out with all covered species, as well as only with threatened covered species. With the resulting information, species accumulation curves were generated considering the type of governance.

We considered the vegetation type (both primary and secondary forest) where each species has been recorded as suitable habitat within PAs. We considered secondary forest because some salamander species, including threatened species, can live in these types of forests (Díaz-García, Pineda, López-Barrera, & Moreno, 2017; Juárez-Ramírez et al., 2016; Raffaëlli, 2013; Russildi, Arroyo-Rodríguez, Hernández-Ordóñez, Pineda, & Reynoso, 2016; Sandoval-Comte, Pineda, & Aguilar-López, 2012). To estimate the proportion of suitable habitat within the protected areas greater than 25 ha, we used the layer Land Use and Vegetation Types (Serie VI of Instituto Nacional de Estadística y Geografía [INEGI], 2016). For reserves less than or equal to 25 ha, we used aerial images of Google Earth Pro (Google LLC, 2015) version 7.1.5.1557 because the size of the minimum mapping unit (4 mm^2) and the scale (1: 250 000) of the Land Use and Vegetation Types layer do not permit proper mapping of polygons smaller than 25 ha. To examine the association between the size and proportion of suitable habitat of the PAs with salamander records, we used Pearson Correlation tests, following arcsine transformation because suitable habitat was calculated as proportions (Zar, 1999). Correlation tests were carried out for the set of PAs with species records, and for each governance type of PAs, except for the municipal PA due it was a single case.

Detecting Potential Areas to Protect Threatened Gap Species

To detect potential spaces for protection of threatened gap species, we followed two strategies: (a) locate sites with favorable conditions where threatened gap species have been recorded and (b) identify the established PAs closest to the localities with records of threatened gap species that have potentially favorable conditions for their occurrence.

The first strategy consisted of determining the amount of suitable habitat (primary and secondary forest) for the salamanders within a 2.5 km radius (buffer) of occurrence records for threatened gap species, which we have called "complementary sites." This buffer size allowed us to estimate the amount of both transformed and suitable habitat in the landscape where the threatened gap salamander was found. Initially, we detected threatened gap species with only one known locality, or those whose known localities were so close that occurred within a

single buffer. Subsequently, we examined by hand which other threatened gap species had been recorded in these same sites, so that with the minimum number of complementary sites the greatest number of threatened gap species could be protected. Then, we located the sites where the CR gap species were registered and from those sites, we chose the one that included, in order of importance: (a) the greatest number of localities and records of the focal species; (b) localities of other threatened gap species; and (c) the highest proportion of suitable habitat. We repeated this procedure with the EN and VU gap species, respectively, until all the threatened gap species had at least one locality within the complementary sites. To estimate the proportion of suitable habitat within the buffers, we used the layer Land Use and Vegetation Types (Serie VI of INEGI, 2016). The spatial analysis was performed using ArcGis software version 10.2.2 for Desktop. Finally, we ordered the complementary sites according to their conservation priority based on the number of threatened species and the percentage of suitable habitat.

For the second strategy, we identified by hand the closest PA for each threatened gap species that also included suitable habitat (both primary and secondary forest), which we have called "close and suitable protected area" (hereafter CSPA). We considered 30 km as the maximum distance at which a PA can be considered close, because most of the threatened species are microendemic. In addition, we calculated the proportion of suitable habitat within CSPAs using the layer Land Use and Vegetation Types (Serie VI of INEGI, 2016) and ArcGis software version 10.2.2 for Desktop.

Results

Salamander Species Richness Distribution

The localities with salamander records were distributed mainly in the Sierra Madre Oriental, the Trans-Mexican Volcanic Belt, the Sierra Madre del Sur (mainly in Oaxaca), the state of Chiapas and to a lesser extent in the Yucatan Peninsula, the northern portion of the Baja California peninsula, and the center-west and northeast of Mexico (Figure 1(a)). The species richness was distributed heterogeneously; of the 2,476 cells of 30×30 km that covered Mexico, only 256 (10.3%) had records of salamanders. Species richness within spaces of 900 km^2 varied between 1 and 16 species (mean = 2.2, $SD = 2.0$ species). Of the total cells with species records, 210 (82%) had between 1 and 3 species, 28 (11%) between 4 and 5 species, 12 (4%) between 5 and 6 species, 4 (2%) had between 8 and 9 species and only 2 cells (1%) had 14 or 16 species. The two richest cells were located in the mountainous region of central Veracruz and in Sierra de Juarez, in northern Oaxaca (Figure 1(b)).

Salamanders in Protected Areas

Of the 132 plethodontid species recorded in Mexico, 82 species (62% of the total) have been recorded in PAs, while of the 95 threatened species of the country, 59 species (62% of the total) have been detected in PAs (Table S1 Supplementary Material). In addition, seven uncertain species have been registered within PAs. With respect to the spatial distribution of threatened covered species, 15 species had fewer than a quarter of their known localities within PAs, 24 species had between 25% and 50%, 6 species had between 51% and 75%, and 14 species had between 76% and 100% of their localities in PAs, including nine species (*Chiropterotriton cracens, Chiropterotriton mosaueri, Dendrotriton megarhinus, Dendrotriton xolocalcae, Pseudoeurycea longicauda, Pseudoeurycea orchimelas, Pseudoeurycea tlilicxitl, Pseudoeurycea unguidentis,* and *Thorius narismagnus*) that have been registered exclusively within a PA.

Of the 1,214 PAs considered in this study, only 83 reserves (6.7%) had salamander records: 44 federal PAs (16% of all federal PAs), 24 state PAs (7.6%), 1 municipal (0.9%), 5 community PAs (3%), and 9 private (2.6%) (Figure 2, Table S2 Supplementary Material). In all governance types of PA, the largest proportion of the species that make up the salamander fauna were threatened species, including species in the highest risk category (CR). The set of federal PAs had the largest number of species (52), ranging from 1 to 12 species per PA (mean = 2.7, $SD = 2.0$), as well as the highest number of threatened species (38). State PAs had the second highest number of species (33), ranging from 1 to 6 species per PA (mean = 2.6, $SD = 1.9$), and a total of 20 threatened species. Within the community PAs, 13 species have been detected, ranging from 1 to 7 species per PA (mean = 3.0, $SD = 2.3$), and 11 threatened species in total. In private PAs, 13 species have been recorded, ranging from 1 to 5 per PA (mean = 1.6, $SD = 1.3$) and 8 species in total were considered threatened. Finally, within the single municipal PA, six species have been detected, three of which were threatened (Figure 3).

Protected Areas Complementariness

Of the 83 PAs that include salamander localities, 31 were needed to contain the 82 covered species. The 31 PAs included all five types of governance: 17 federal, 7 state, 4 private, 2 community, and 1 municipal PA. On the other hand, 26 PAs were the minimum number needed to harbor the 59 threatened covered species. Within this set of PAs, there were 14 federal, 5 state, 4 private, 2 community, and 1 municipal PA (Figure 4(a)). Accumulation of protected area, following the order of
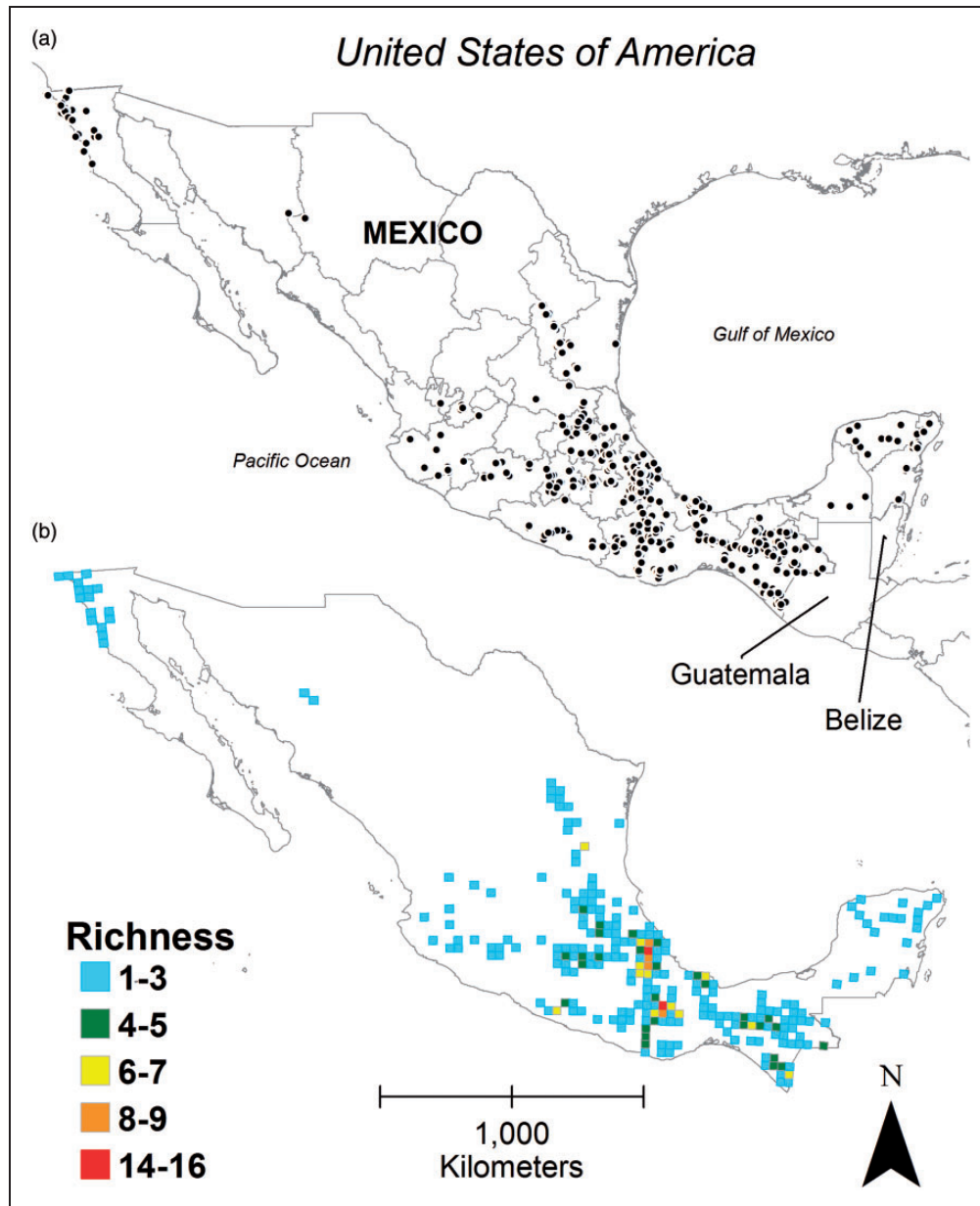
Figure 1. Distribution of localities where salamanders have been recorded in Mexico (a) and distribution of species richness in cells of 900 km² (b).

the reserves according to its priority, has a staggered and irregular form (Figure 4(a)).

Suitable Habitat Within Protected Areas

The proportion of suitable habitat in PAs with salamander records ranged from 0.03% to 100%, where 82% of PAs had suitable habitat in more than half of their extent. Both in federal (the largest areas) and state reserves, the proportion of suitable habitat varied from 0.03% to 100%, while in almost all nongovernmental

reserves (except four private), more than 90% of their extent was covered by suitable habitat. The single municipal PA, one of the smallest reserves (ca 100 ha), had slightly more than half its area with suitable habitat (Figure 4(b)). Considering all PAs with species records, there was no correlation between the area of PAs and their proportion of suitable habitat ($r = -.078$, $p = .5$) but when analyses were performed by type of governance, we only found correlation between the extension of PAs and the percentage of suitable habitat of community PAs ($r = .769$, $p = .01$).
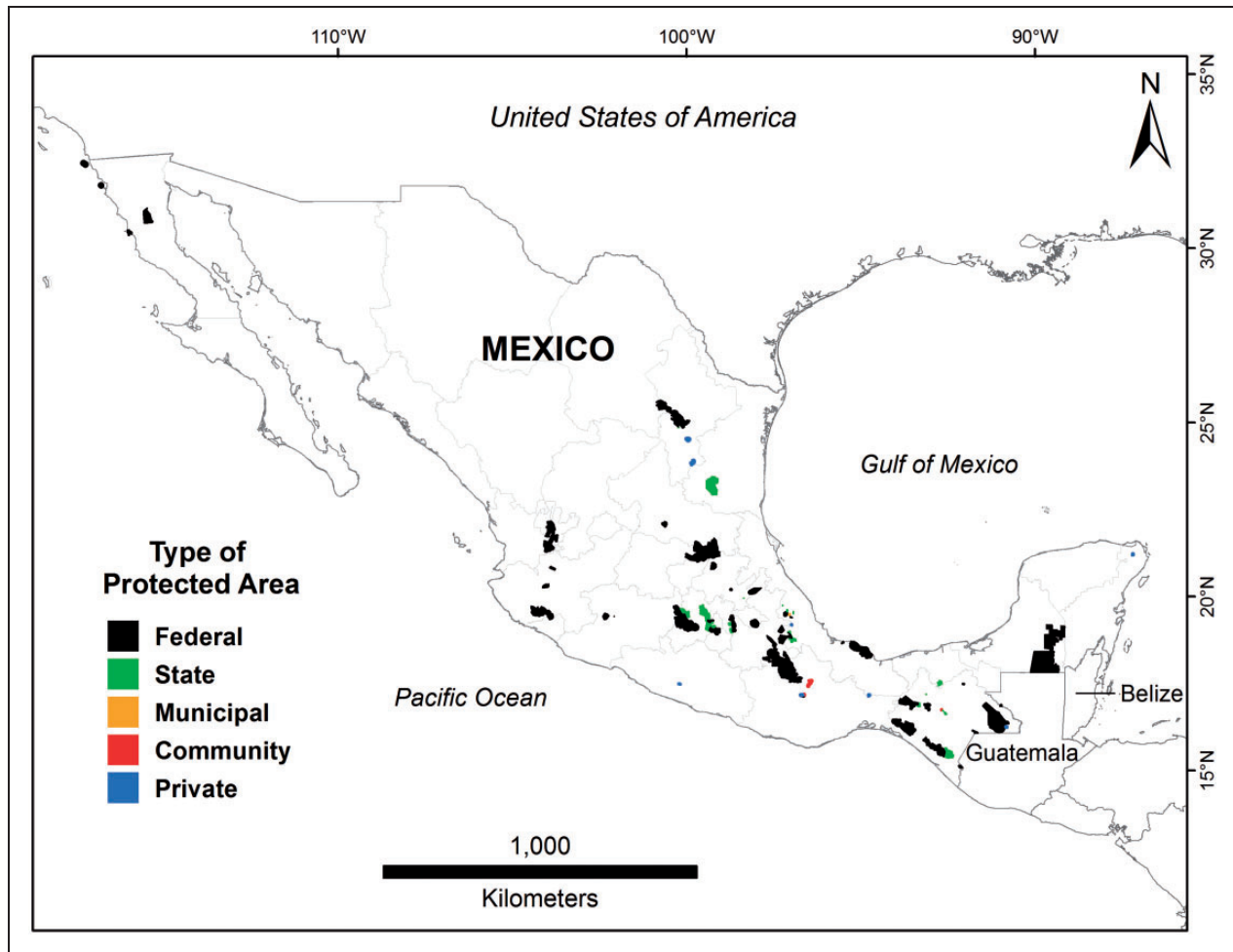
Figure 2. Location of protected areas with salamander records distinguished by governance types.

Potential Areas to Fully Represent the Threatened Species in Protected Areas

To protect the 36 threatened gap species, we detected 26 complementary sites (Table 1), which were located mainly south of the Sierra Madre Oriental, Sierra Madre del Sur, Sierra Norte of Oaxaca, and the highlands of Chiapas, six of them very near established PAs (Figure 5). In addition to the 36 threatened gap species, the complementary sites included another 16 threatened covered species. In 21 of the 26 complementary sites, the suitable habitat varied between 50% and 100%, while in the 5 remaining sites, suitable habitat ranged from 21% to 47% (Table 1).

With respect to PAs close to localities of threatened gap species, we detected 12 CSPAs that could harbor 15 threatened gap species (Table 2). These CSPAs (five private, three federal, two state, and two community) were located mainly in the southern portion of the Sierra Madre Oriental, in the Trans-Mexican Volcanic Belt and to a lesser extent in Oaxaca. In addition, six of these 12 PAs had records of seven threatened covered species. The proportion of suitable habitat in 9 of the 12 CSPAs ranged from 50% to 100%, while in the 3 remaining areas, the suitable habitat ranged from 20% to 36% (Table 2).

Discussion

Our results show that the current set of PAs included in our analysis does not protect all the threatened salamander species occurring in Mexico, almost two out of five threatened species do not inhabit any protected area. The need to have PAs of all governance types to represent 62% of threatened species highlights the complementariness of different types of governance to protect threatened biodiversity. On the other hand, given that in one of every five PAs that harbor threatened salamanders had less than half of suitable habitat, it should not be assumed that the entire PA represents a space with adequate conditions for the survival of the threatened species. Finally, the 26 sites detected in this study as complementary areas to protect the threatened gap
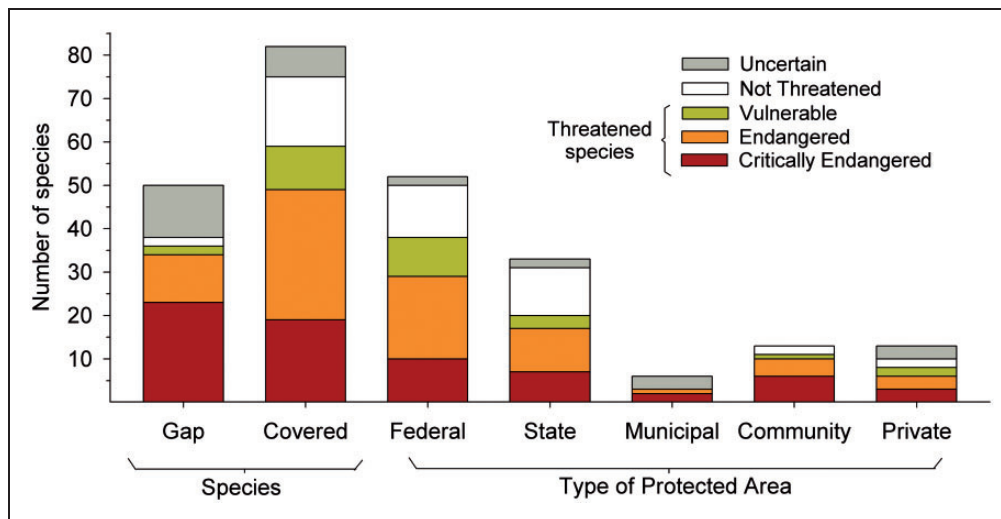
Figure 3. Number of gap species, total covered species, and covered species within the different governance types of protected areas. The threatened species are classified by their IUCN risk category.

species, as well as 12 CSPAs, could function as strategic areas for the conservation of threatened amphibians. However, it is necessary to verify the current existence of populations of threatened gap species, the environmental conditions, and threats.

Despite the fact that the terrestrial protected area in the country currently approaches 17%, as internationally suggested in the Aichi Target 11 (Juffe-Bignoli et al., 2014), only three out of five threatened salamander species occurred within protected sites. This level of representation reflects a partial dissimilarity between the distribution of PAs and the spatial distribution of the plethodontid salamanders. This shows that current conservation efforts based only on percentage goals do not guarantee the inclusion of biodiversity at risk, since they do not take into account the differences between biomes, environmental and species susceptibility, species richness values, and endemism (Brooks et al., 2004; Pimm et al., 2014).

The proportion of gap species reported in our study (38%) was higher than the proportion estimated globally for all amphibians (25%, Nori et al., 2015); the same is true with only the threatened species. Despite the level of representation of threatened amphibians, this scenario varies by countries. For example, in Australia, the distribution of all threatened amphibian species (24 spp.; according to the Australia's Environment Protection and Biodiversity Conservation Act criteria) coincides, at least in some portion of the distribution, with the PAs (Watson et al., 2011). This suggests that challenges to reach a total representation of threatened species differ between countries or regions.

The distribution of PAs that contain threatened species, as well as complementary sites with threatened gap species, coincided mostly with the mountainous regions where the plethodontids have diversified in Mexico (Rovito & Parra-Olea, 2016; Rovito, Parra-Olea, Hanken, Bonett, & Wake, 2013; Rovito, Parra-Olea, Recuero, & Wake, 2015; Wake, 1987), mainly in the Sierra Madre Oriental, the Sierra Madre del Sur, and the Trans-Mexican Volcanic Belt, where the highest values of amphibian diversity are observed (Rovito et al., 2013, 2015; Vieites, Min, & Wake, 2007; Wiens, Parra-Olea, García-París, & Wake, 2007), mainly beta diversity (Ochoa-Ochoa et al., 2014). In particular, the distribution of complementary sites to protect the threatened gap species that we detected in this study coincided with 13 sites proposed by the Alliance for Zero Extinction (AZE, 2017) to protect 22 salamander species in imminent risk of extinction, while 29 more species with these characteristics have already been recorded in some PA. In addition, within the complementary sites to protect threatened gap species that we proposed here, there were six species considered among the world's most Evolutionary Distinct and Globally Endangered species by the initiative Evolutionary Distinct and Globally Endangered of Existence Programme, which are threatened species that represent a significant amount of unique evolutionary history (Zoological Society of London [ZSL], 2018). The complementary sites we detected in this study coincided with 10 of the 53 high priority sites proposed by Ochoa-Ochoa et al. (2011) to protect amphibians in Mexico: in central Guerrero, throughout Oaxaca, in the mountainous region of Chiapas, Puebla and the center of Veracruz. It should be noted that although 22% of the gap species have not been evaluated with respect to their extinction risk due to insufficient data or because they were
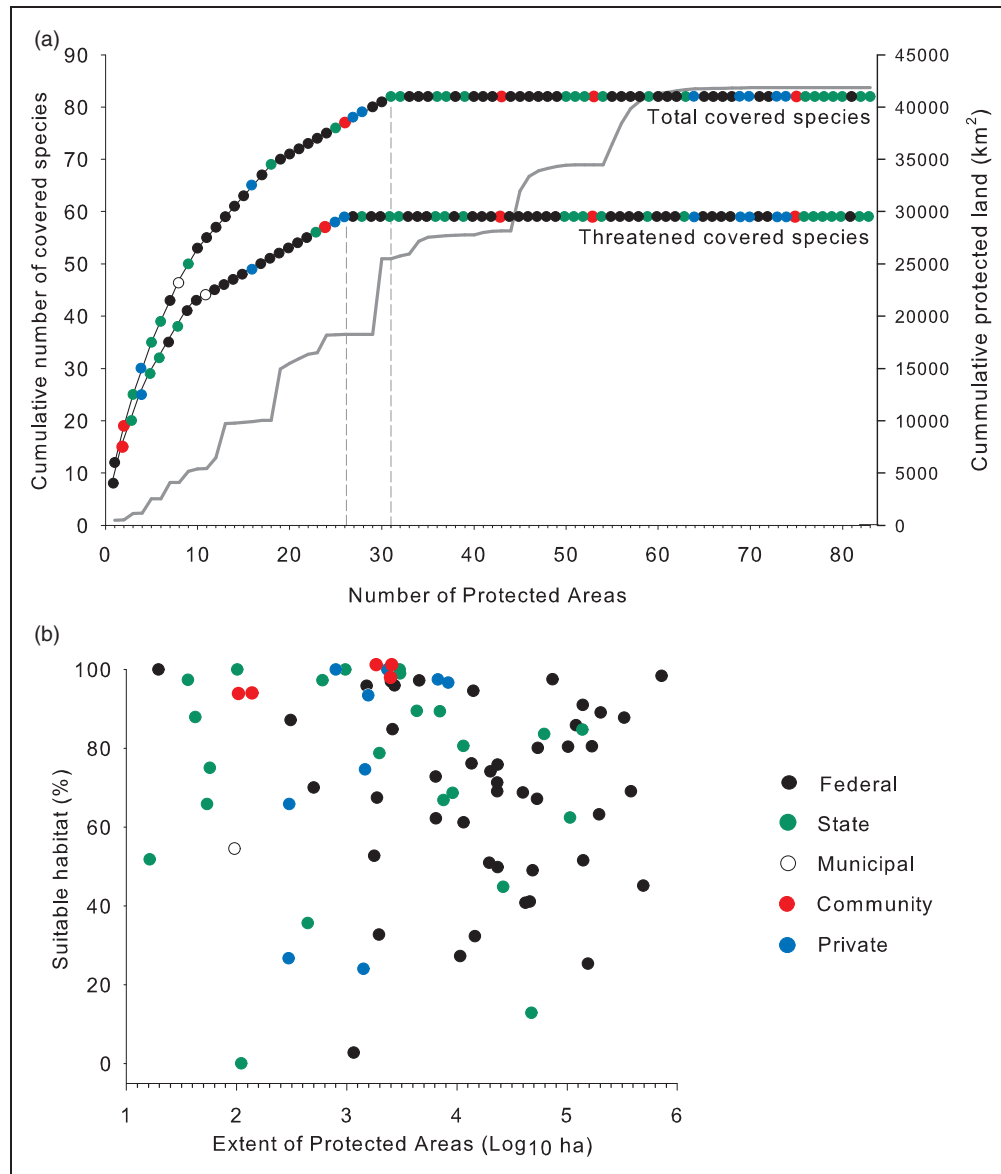
Figure 4. Accumulation curves of total covered species and threatened covered species and accumulation of protected land (grey line) by each PA (a). The dotted lines highlight the minimum number of PAs needed to contain the maximum of covered species. Relationship between the total extent of protected areas with salamander records and their proportion of suitable habitat (b).

described recently, it is possible that these species are at high risk of extinction, as is commonly the case with newly described species whose distribution is very restricted (Howard & Bickford, 2014; Pimm et al., 2014).

All governance types of PAs play an important role for in situ conservation of threatened salamanders, as has been pointed out globally for biodiversity in general (Chape, Harrison, Spalding, & Lysenko, 2005). However, not all governance types of PAs necessarily play the same role in conservation; in fact, they seem to play different roles and are highly complementary. Federal PAs were among the largest reserves and, due to their size, could harbor a greater number of species

(located in the first places of the species accumulation curve, Figure 4(a)), compared with smaller reserves. However, among the large reserves, there seemed to be a high redundancy of species (i.e., low complementariness) derived from sharing mainly widely distributed species. As shown by Juárez-Ramírez et al. (2016), small areas may present high complementariness for the protection of species and even more when we analyze the representation of a group such as plethodontid salamanders characterized by restricted distribution. Another factor that may be influencing the prevalence of federal PAs for the representation of plethodontid salamanders is their recognition and promotion.
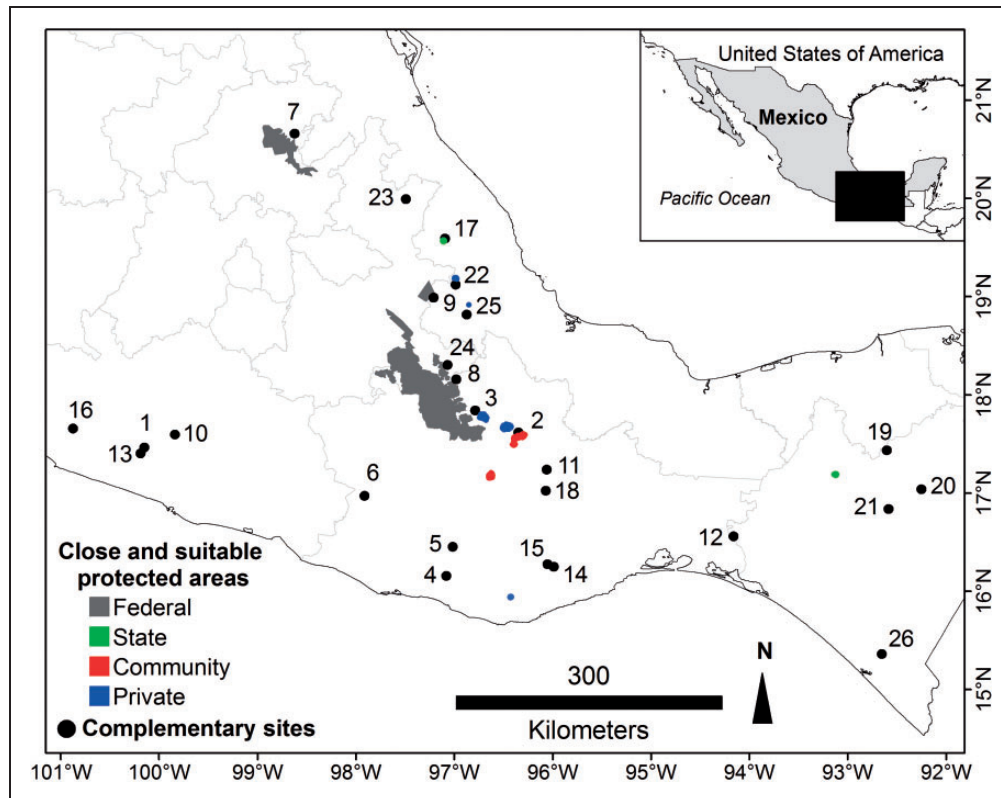
Figure 5. Distribution of potential areas to represent all threatened gap species in Mexico. The CSPAs are distinguished by governance type. The numbers refer to the priority rank of the complementary sites.

In addition to being the oldest governance type of PA, federal reserves have the highest recognition and, therefore, generally concentrate and attract greater interest to study them (Lockwood, 2010).

State PAs, generally with an intermediate size, showed high complementariness values among all the studied PAs, which could be due to a combination of intermediate values of species richness and a singular or different composition. With respect to nongovernmental reserves, which were generally the smallest but with a high proportion of suitable habitat, they typically did not harbor a high number of species, but did have a particular composition, which would support the high complementariness value observed in this study. In Mexico, nongovernmental PAs have been considered as crucial for endemic and microendemic amphibians (Ochoa-Ochoa et al., 2009). We found that 11 threatened species and one uncertain species are found exclusively in nongovernmental PAs. Furthermore, nongovernmental PAs are the most common type among CSPAs to harbor threatened gap species, and all (except two) are located in Oaxaca. Ellis and Porter-Bolland (2008) found that the type of governance is related to land management and management strategies and, especially in community reserves, forest management is more

effective than in reserves of other governance types due to knowledge and planning by the local inhabitants.

The results of this work are based on the analysis of specific localities where salamanders have been recorded, which increased the level of certainty regarding the presence of the species studied in the PAs and in the potential areas to protect the threatened gap species. However, despite the fact that the data were carefully checked, it is possible that there are commission errors. Some records date from several decades ago and the species may not currently be present at the recorded locality, the locality description may be imprecise and its subsequent georeferencing therefore not accurate or taxonomic identification could be incorrect. In any case, current fieldwork would help to confirm the current presence of the species, particularly the threatened species, as well as the conditions of their habitat.

With respect to the level of knowledge about the geographical distribution of highly threatened species such as those studied in this work, it is highly probable that there are localities where the species are present but have not yet been recorded. Thus, it is necessary to continue with field searches to have more precise information about distribution of species and generate more robust results. The use of distribution models to reach the objectives of

Table 1. Attributes of Complementary Sites for Protection of Threatened Gap Salamander Species in Mexico, Ordered by Priority Rank.

| Priority rank | Threatened gap species | | Suitable habitat (%) | Primary and secondary vegetation (km^2) |
	Number	Scientific name		
1	3	*Pseudoeurycea ahuitzotl, P. teotepec, P. tlacuiloh*	91	13 and 5
2	3	*Pseudoeurycea orchileucos, Thorius smithi, T. insperatus*	57	11 and 0
3	2	*Pseudoeurycea aurantia, Thorius papaloae*	90	7 and 10
4	2	*Isthmura maxima, Pseudoeurycea anitae*	78	0 and 15
5	2	*Pseudoeurycea cochranae, P. conanti*	71	0 and 14
6	2	*Bolitoglossa riletti, Isthmura maxima*	54	0 and 11
7	2	*Chiropterotriton arboreus, C. terrestris*	47	9 and 0.5
8	2	*Pseudoeurycea obesa, P. ruficauda*	43	8 and 0.5
9	2	*Thorius lunaris, T. spilogaster*	38	7 and 0.5
10	1	*Pseudoeurycea tenchalli*	100	12 and 8
11	1	*Ixalotriton parvus*	100	1 and 19
12	1	*Pseudoeurycea aquatica*	100	0 and 20
13	1	*Thorius infernalis*	96	18 and 1
14	1	*Thorius minutissimus*	96	8 and 11
15	1	*Bolitoglossa zapoteca*	95	0 and 19
16	1	*Pseudoeurycea kuautli*	82	16 and 0
17	1	*Isthmura naucampatepetl*	78	15 and 0
18	1	*Pseudoeurycea mystax*	77	0 and 15
19	1	*Bradytriton silus*	72	11 and 3
20	1	*Cryptotriton alvarezdeltoroi*	68	1 and 12
21	1	*Bolitoglossa rostrata*	59	0.5 and 11
22	1	*Chiropterotriton chiropterus*	55	9 and 1
23	1	*Thorius schmidti*	50	10 and 0.5
24	1	*Aquiloeurycea quetzalanensis*	50	0 and 10
25	1	*Aquiloeurycea praecellens*[a]	39	0 and 8
26	1	*Bolitoglossa flaviventris*	21	0 and 4

[a]Species known from a single locality currently surrounded by transformed habitat. Due to this, we located a complementary site close to the locality, with favorable conditions for the species to occur.

this study does not seem the most appropriate at this moment (60% of the salamanders studied have less than ten known localities), since this could generate both commission and omission errors that could lead to inaccurate results with a high risk in a conservation context (Pineda & Lobo, 2009; Rondinini, Wilson, Boitani, Grantham, & Possingham, 2006). Cantú-Salazar and Gaston (2013) found that in the case of the amphibians of the New World (where the greatest diversity of amphibians is found globally), the representation within the protected areas (evaluated through distribution maps and compared with lists of species) is overestimated, especially in protected areas with greater species richness, and underestimated in reserves with lower species richness. Likewise, Urbina-Cardona and Loyola (2008) found that some species of Neotropical frogs threatened of extinction only possess a quarter of their potential distribution protected, mostly the peripheral distribution.

Although our results showed that 62% of the species have at least one locality within a PA, it does not necessarily imply that these species are fully protected, since only a portion of their distribution is in protected areas (e.g., two thirds of these species own less than half of their locations in a PA). Also, the permanence of the species depends on the viability of their populations and the habitat conditions within the PAs, so not all PAs have been really effective in protecting species (Rodrigues et al., 2004).

Implications for Conservation

In a highly biodiverse and environmentally heterogeneous country like Mexico, the number, extent, and current location of protected areas are not sufficient for harboring all threatened plethodontid salamander species. Despite the proportion of protected space is close to international suggestions, almost 40% of threatened species do not occur in protected areas. The design of a reserve system should consider as a priority criterion to include the occurrence of all those species that need immediate attention for their protection, specifically

Table 2. Attributes of Established CSPAs That Could Harbor Threatened Gap Species.

Name and governance type	State	Suitable habitat (%)	Total extent (km^2)	Threatened gap species with potential occurrence	
				Number	Scientific name
Tehuacán-Cuicatlán[F]	PUE-OAX	20	4900	1	*Thorius papaloae* (17)
Pico de Orizaba[F]	PUE-VER	51	197	2	*Thorius spilogaster* (30), *T. lunaris* (4)
Barranca de Metztitlán[F]	HGO	29	953	1	*Chiropterotriton arboreus* (2)
Tzama Cun Pümy[S]	CHI	100	1	1	*Cryptotriton alvarezdeltoroi* (2)
San Pedro del Monte[S]	VER	36	4	1	*Isthmura naucampatepetl* (2)
Ixtlán de Juárez[C]	OAX	100	38	2	*Pseudoeurycea orchileucos* (4), *Thorius insperatus* (5)
Santa Catarina Ixtepeji[C]	OAX	99	18	1	*Pseudoeurycea cochranae* (1)
Zona de Restauración Ecológica Comunitaria de San Juan Teponaxtla[P]	OAX	97	31	2	*Pseudoeurycea aurantia* (21), *P. ruficauda* (27)
Área de Conservación Nopalera del Rosario[P]	OAX	100	41	1	*Thorius smithi* (4)
Reserva Ecológica Natural Cuenca Alta del Rio Atoyac[P]	VER	100	0.1	1	*Aquiloeurycea praecellens* (7)
La Reforma[P]	OAX	100	0.1	1	*Pseudoeurycea conanti* (2)
Las Cañadas[P]	VER	82	3	1	*Chiropterotriton chiropterus* (2)

Note. The distance in km to the CSPAs is referred to within parentheses after the name of each species. Governance type is referred in superscript at the end of the name of each PA: C = community; F = federal; P = private; S = State. Mexican states where the CSPAs are located: CHI = Chiapas; HGO = Hidalgo; OAX = Oaxaca; PUE = Puebla; VER = Veracruz; CSPAs = close and suitable protected areas.

those species threatened by habitat transformation. Areas that contain threatened gap species, not only of salamander species but of other threatened species, could serve as a guide for the creation of new protected areas and strengthen the existing reserve system. The set of new areas that would help to protect threatened species can be a combination of different types of governance, where federal, state, and municipal governments, as well as community and private sectors can be involved in the protection of threatened biodiversity.

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