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Representativeness, Complementarity, and Degree of Local Extirpation Risk for *Thamnophis* Species Inside and Outside of Protected Areas of Mexico

Crystian Sadiel Venegas-Barrera [1], Javier Manjarrez [2,*], Ángel Rodríguez-Moreno [3], Yeimi Alexandra Mendoza-Walle [1], Jorge Víctor Horta-Vega [1], Itzel R. Rodríguez-deLeón [1], Armando Sunny [4] and Ausencio Azuara Domínguez [1]

1 Instituto Tecnológico de Ciudad Victoria, Tecnológico Nacional de México, Ciudad Victoria P.C. 87010, Mexico; crystian.vb@cdvictoria.tecnm.mx (C.S.V.-B.); ale_walle98@hotmail.com (Y.A.M.-W.); jorge.hv@cdvictoria.tecnm.mx (J.V.H.-V.); itzel.rd@cdvictoria.tecnm.mx (I.R.R.-d.); ausencio.ad@cdvictoria.tecnm.mx (A.A.D.)
2 Centro de Investigación en Recursos Bióticos, Universidad Autónoma del Estado de México, Toluca P.C. 50000, Mexico
3 Instituto de Biología, UNAM, Coyoacán, Ciudad de México P.C. 04510, Mexico; tanicandil@hotmail.com
4 Centro de Investigación en Ciencias Biológicas Aplicadas, Facultad de Ciencias, Universidad Autónoma del Estado de México, Toluca P.C. 50000, Mexico; sunny.biologia@gmail.com
* Correspondence: jsilva@uaemex.mx

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Abstract: Protected areas (PAs) are geographical spaces intended to conserve populations, communities, and ecosystems, in which species richness must be maximized, the conserved area must be minimized, and anthropogenic pressure must be reduced. The present study analyzed the representativeness, complementarity, and degree of risk of 25 garter snake species of the genus *Thamnophis* in the PAs of Mexico. This study proposes that at least 17% of the potential geographic distribution (PGD) of species will be found inside PAs and in areas (Aichi Target 11) with a low human footprint (HF). The PGD of species was associated with the PAs and HF layers to identify where and which species could be at local extirpation risk by human activities. The results indicate that the federal PAs contain 85.2% of the species, while the state PAs contain 77.7% of the species. An average of 13.4% of the PGD of these species is found inside PAs, and two species are found outside. In 13 federal PAs and 10 state PAs, the *Thamnophis* species present high local extirpation risk from human activities. In total, 37% of species are found in PAs with a medium to very high human footprint; therefore, their persistence could be at local extirpation risk. Compared to other taxa, species of the genus *Thamnophis* are well represented. However, the PDG of more than half of the species achieves Aichi Target 11.

Keywords: human footprint; multivariate analysis; geographic distribution

1. Introduction

Estimations of diversity loss propose that nearly 37% of species might be threatened or driven to extinction by 2100 [1]. In this regard, protected areas (PA) represent geographic spaces to conserve populations, communities, and ecosystems [2]. The International Union for the Conservation of Nature defines PA as "A clearly defined geographical space, recognized, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values" [3]. The Convention on Biological Diversity, in Target 11, proposes that at least 17% of the terrestrial and continental water of signatory countries will be protected areas by 2020 [4]. The importance of maintaining conservation efforts is that approximately 25% of species with some categories of risk are estimated to be out of these lists [1]. However, one-third of the world PAs are under intense human pressure [5] or do not represent regional biodiversity because there is a bias toward areas of higher elevation [6], steeper slopes, and greater distances from roads and cities [7,8]; human pressures have increased inside them [9], and a total of 13% of PAs have been inadequately managed [10]. Inclusion within PAs confers limited benefits to species if those parks are poorly protected [11] because extinction risk is related to the extent of high human pressure within species ranges and the change in this extent over time [12]. In addition, the creation of PAs does not guarantee that they contain regional diversity (representativity) and reduce anthropic pressure (effectiveness). Of particular importance are areas located in diverse regions and under anthropic pressure [13,14].

Mexico is located between the Neotropical and Nearctic biological regions and contains 11% of the world's hotspots; over half of the country still maintains native vegetation cover in reasonably good environmental conditions [15], its elevational range is from 0 to 5600 m a.s.l., and it is affected by two oceans, all of which together lead to high biodiversity [16]. In terms of conservation, 13.25% of the terrestrial surface and insular area of Mexico has been given the PA designation [17], and 92% of PAs are private property [18]. However, Mexico's rates of annual deforestation between 1973 and 2000 were 0.25% for temperate forest, 0.76% for tropical forest, and 0.33% for scrubland [19]. Additionally, in 13 Mexican PAs, agricultural and urban frontiers increased in both buffer zones and core zones [20–22]. However, during nine years (1993–2002), 13 of the 42 PAs presented a significant reduction in their original vegetation [23]. Additionally, Sánchez-Cordero and Figueroa [24] reported that six biosphere reserves were ineffective in reducing the loss of natural land cover. On 14 biospheres reserves of Mesoamerican Biodiversity Hotspot, it was reported that high human population density and low nonfarming occupation were identified as the main underlying drivers of biodiversity change [25]. Therefore, given changes within PA, it is necessary to estimate the representativeness and degree of anthropogenic impact on species that are distributed in PAs in Mexico, specifically those that are susceptible to environmental changes. Such is the case for the species of the genus *Thamnophis*, which are semiaquatic snake species with a medium to high dependence on water bodies, vegetation, and specific diets [26]. In addition, 15 species of this genus are under threat, and one is under special protection by the Mexican government (Table 1).

Garter snakes are diurnal species, distributed from Canada to Costa Rica [26–28], associated with aquatic systems and mesic environments, with a very variable diet, where certain species specialize in slugs, fish, amphibians, etc., or they are generalists in the type of prey [26,29], and much of the literature on *Thamnophis* focuses on the proximate and ultimate mechanisms of this variation in feeding ecology e.g., refs. [30–34]. Their populations can be locally abundant [26,35], allowing their relative ease of study both in natural conditions and in captivity. Despite its relatively high abundance and wide distribution compared to other reptiles, this group has suffered critical declines in the last 10 years [36], although there are no field studies that indicate populations with low densities are at greater risk of local extinction.

In addition to its feeding plasticity, *Thamnophis* presents great morphological, physiological, behavioral, and ecological variation, even at the microgeographic level, e.g., refs. [27,32,37–39]. *Thamnophis* is a monophyletic group that originated in the Mexican highlands during the mid-Miocene ~5–6 million years ago, and its divergence as a genus occurred possibly two million years ago in Mexico [27,35,40]. This group constitutes a clade relatively rich in species present in a wide variety of communities and ecoregions in North and Central America. Many *Thamnophis* species occupy biodiversity hotspots such as biogeographic boundaries [26], such as the Mexican Transition Zone or the California Floristic Province [41,42]. The Garter snakes are susceptible to environmental changes due to anthropogenic activity, such as land cover change (48–50) or climate change [36]. However, we lack information on the ecology and current conservation status of most *Thamnophis* species that are endemic to, or primarily distributed in Mexico [36].

Table 1. Percent of distribution of *Thamnophis* species in Mexico and protected areas (federal and state).

Species	Species Abbreviation	Number PA	Percent Distribution			
			Mexico	All PA	Federal	State
T. bogerti	bog	1	0.12	4.7	4.7	0.0
T. chrysocephalus T	chr	6	3.45	6.7	5.7	1.0
T. conanti	con	2	0.08	26.4	26.3	0.2
T. cyrtopsis T	cyr	49	55.49	10.7	8.4	2.3
T. elegans T	ele	1	0.15	24.7	24.7	0.0
T. eques T	equ	38	28.39	11.7	8.8	2.9
T. errans	err	3	5.98	15.1	14.7	0.3
T. exsul T	exs	8	0.21	21.2	17.7	3.5
T. fulvus	ful	5	0.46	17.5	11.8	5.7
T. godmani T	god	0	0.01	0.0	0.0	0.0
T. hammondii T	ham	5	1.81	18.2	18.2	0.0
T. lineri	lin	0	0.06	2.5	2.4	0.1
T. marcianus T	mar	71	21.62	9.9	8.9	1.0
T. melanogaster T	mel	16	13.41	13.0	7.8	5.2
T. mendax T	men	1	0.18	19.0	0.0	19.0
T. nigronuchalis	nig	0	0.95	13.9	13.7	0.1
T. postremus	pos	0	0.29	26.0	23.8	2.2
T. proximus	pro	23	14.79	11.0	8.4	2.6
T. pulcrilatus SP	pul	11	2.64	22.9	11.6	11.4
T. rufipunctatus	ruf	3	7.02	8.7	8.5	0.2
T. scalaris T	scala	19	2.99	20.4	9.6	10.8
T. scaliger T	scali	7	0.80	28.9	8.5	20.4
T. sirtalis T	sir	0	0.09	0.7	0.7	0.0
T. sumichasti T	sum	4	0.42	20.5	17.2	3.3
T. valida	val	3	4.39	5.3	4.7	0.6
All species			76.70	13.0	10.8	2.2

Number PA = Number of PAs with almost on-field record. **Mexico** = Percent of PDG of *Thamnophis* species in Mexico. **All PAs** = Percent of PDG inside Mexico Pas. **Federal** = Percent of PDG inside federal Pas. **State** = Percent of PDG inside state PAS. **T** = Threatened. Those that could be in danger of disappearing in the short or medium term, if the factors that negatively affect their viability continue to operate by causing the deterioration or modification of their habitat or directly reducing the size of their populations. **SP** = Subject to special protection. Those that could be threatened by factors that negatively affect their viability, so the need to promote their recovery and conservation or the recovery and conservation of the populations of the associated species is determined [29].

The present study analyzed the potential geographic distribution of 25 garter snakes (genus *Thamnophis*) in 152 federal PAs and 389 state PAs, which corresponds to two of the three levels of governmental and political organization in Mexico: a federal central government, state governments, and municipal (substate) governments. This is in order to perform the following: (1) estimate the distribution of these species in PAs (National and state) and Mexico to identify species poorly represented in PAs as well as PAs that contain most species; (2) identify federal and state PAs that contain the maximum number of species in a minimum number of Pas; (3) associate the distribution of species with the human footprint at the country scale to identify the species with higher risk from anthropogenic pressure; and (4) associate the distribution of species, the human footprint, and PAs to identify the PAs where species may be most at risk. We propose that at least 17% of the PGD of species will be found inside PAs (as proposed in the Convention on Biological Diversity, Target 11) and in areas with a smaller human footprint. The results can be used to generate and update management plans for federal and state PAs.

2. Materials and Methods

The potential geographic distribution (PGD) of the 25 species of the *Thamnophis* genus present in Mexico was associated with protected areas (PAs) and human footprint layersto identify where and which species could be at risk of local extirpation by human activities in Mexico and their PAs.

The LA federal analysis was conducted separately from the PA state analysis (Figure 1). In this sense, areas with high and very high human footprints are associated with a reduction in native conditions that permit the occurrence of viable populations. The layers of federal and state PAs as well as Mexico polygons were obtained from the Portal de GeoInformación of CONABIO (http://www.conabio.gob.mx/informacion/gis/, accessed on 3 June 2024).

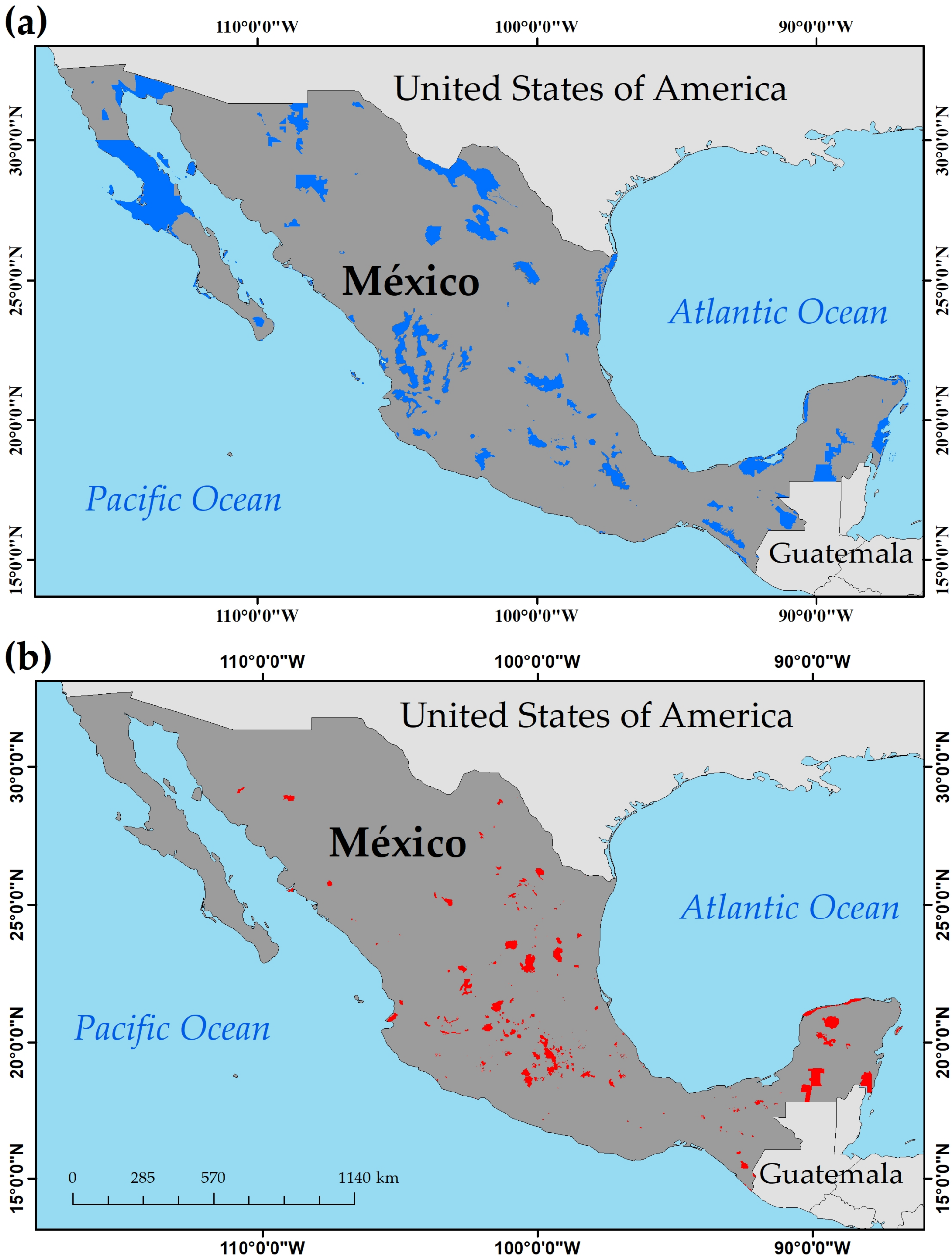

Figure 1. (**a**) Geographic distribution of federal (blue) and (**b**) state (red) protected areas of Mexico.

2.1. Study Area

The prediction of geographic distribution was generated from 11° to 57° latitude and from 64° to −127° longitude to include the total distribution of *Thamnophis* genus in America [26]; however, we analyzed only the presence and absence of species in Mexico. The PAs are managed by federal, State, and municipal (substate) governmental dependences, where the federal PA represents 10.7% of terrestrial territory with 184 PAs [43], 334 state PAs that protect 2.2%, and 51 municipal PAs that occupies nearly 0.1% of the territory [44]. In this study, we analyzed both the state and municipal PAs and named them state PAs (Figure 1). The study was restricted to terrestrial PAs that contain information on the human footprint layer proposed by González-Abraham et al. [15]. Therefore, we analyzed 180 federal PAs and 389 state PAs.

2.2. Geographic Potential Distribution (GPD)

The species PGD were generated with the Maximum Entropy algorithm ver. 3.4.0 [45]. The algorithm searches for a combination of variables with maximum entropy and estimates the importance of each in the distribution of species with respect to the sites where they were recorded [46]. The algorithm consists of comparing a set of environmental variables with the records of species presence and estimating their potential distribution, i.e., predicting in which other areas the species may be found [45–47]. The models were generated with 75% for records and the remaining 25% for validation, where the selection of this sample was random. Therefore, each model presents variations, and to reduce this random effect, we generate 20 models of species with more than 20 field records (Table 1). In contrast, the predictions for species with 8 to 20 records were generated with the Jackknife or "leave-one-out" method. The Jackknife procedure corrects for estimation bias and evaluates predictive performance based on the ability of each model to predict the single excluded locality in the training data [48]. This method consisted of generating several models equal to the number of records, where in each model one record was excluded, and the probability of the excluded record was extracted by elaborating a matrix containing each of the models generated and the presence and absence of the species.

2.2.1. Field Records

The field records were obtained from the Global Diversity Information Facility (GBIF, https://www.GBIF.org/, accessed on 5 April 2024); this base contains field verified records reported by CONABIO (Sistema Nacional de Información sobre Biodiversidad). The over-representation of environmental conditions and spatial autocorrelation, due to over-sampling, was reduced with a spatial rarified routine implemented in SDM Tools [49] at a 3 km distance. The species *T. godmani* is composed by independently evolving lineages [50]. Therefore, field records of *T. godmani* were reassigned to five species in function of their geographic location. *Thamnophis godmani* occurs in pine-oak forests and cloud forests in the Sierra Madre del Sur of Guerrero; *T. bogerti* occurs in oak woodland, pine-oak forests, and pine-oak-madroño forests in the Mesa del Sur in Oaxaca, exclusive to the Sierra de Juárez; *T. lineri* occurs in pine-oak forests and pine-oak-madroño forests in the Sierra de Juárez portion of Mesa del Sur in Oaxaca, and; *T. conanti* occurs at the southern interface of the Mesa Central and Sierra Madre Oriental near the Puebla-Veracruz state line [26]. *Thamnophis elegans* was the species with the most field records, while *T. conanti*, *T. exsul*, *T. pulchrilatus*, *T. nigronuchalis*, *T. lineri*, and *T. godmani* were the species with fewer than 20 records (Tables 1 and S1).

2.2.2. Predictor Variables

The snakes, given their ectothermic condition and their low dispersal rate, are often found to be in disequilibrium with the climate and absent in climatically suitable areas. Therefore, the present study used three categorical variables that reflect the geographic barriers (watersheds), biogeography (ecoregions), and biome types that determine their distribution, as well as other continuous variables that describe climate, land cover, and topography to reduce the overpredictions of the geographic distribution of species. We use 34 environmental continuous variables to predict the PGD of the *Thamnophis* species. The 34 variables were associated with primary productivity (temperature, precipitation, climatic moisture index, and solar radiation), local conditions related to land cover (water, scrubs, deciduous broadleaf trees, herbaceous, and regularly flooded vegetation as well as canopy height), indirect factors possibly associated with other variables that are not included in the prediction (topography), and categorical factors that could restrict species distribution (basins, biomes, and ecoregions). However, this number was reduced to 18 variables to exclude redundant variation among variables (Table 2). In the first step, we performed a principal component analysis (PCA) with the 34 continuous variables to identify variables with similar factor structure values in the first two components, and from this subset. The second step was calculating the variance inflation factor (VIF = $1/(1 - r^2)$) to obtain the final set of variables. The VIF was obtained by multiple regression using the variable with the highest correlation coefficient as a predictor variable and the others as independent variables. We excluded the dependent variable if the VIF was greater than 5.0 because its variation was contained in the other independent variables [51]. The spatial resolution of the predictor variables was 30 arc seconds (near 1 km^2). The final group of predictor variables includes solar radiation, which is the power per unit area received from the sun, energy that is used for plants to photosynthesize. The temperature determines the regulated interactions of species with environments, especially in species whose internal temperature depends on external sources. The annual precipitation is the total rainfall that precipitates and determines the water available to species. The climatic moisture index measures the moisture conditions in a region by comparing annual precipitation to potential evapotranspiration. The land cover was determined with a MODIS sensor, which expressed the percentage of water, scrubs, deciduous broadleaf trees, herbaceous, and regularly flooded vegetation in a km^2, which are related to the presence of species. The categorical variables include hydrological basin (higher elevation is a geographic barrier to the dispersal of species), biome types (species occurring in environments), and ecoregions ("relatively large units of land containing a distinct assemblage of natural communities sharing a large majority of species, dynamics, and environmental conditions").

Table 2. Environmental variables were used to predict geographical distribution of *Thamnophis* species.

Environmental Variable	Type	Units	Source
Water	Continuous	Percent	[52]
Canopy height	Continuous	Meters	[53]
Scrubs	Continuous	Percent	[52]
Biomes	Categorical		[54]
Basins	Categorical		[55]
Ecoregions	Categorical		[54]
Deciduous broadleaf trees	Continuous	Percent	[52]
Elevation	Continuous	masl	[56]
Evergreen/Deciduous needleleaf trees	Continuous	Percent	[52]
Herbaceous vegetation	Continuous	Percent	[52]
Climatic moisture index	Continuous		[57]
Maximum temperature, coldest quarter	Continuous	°C	[56]
Annual precipitation	Continuous	mm	[56]
Solar radiation, June	Continuous	kJ m^{-2} day^{-1}	[58]
Solar radiation, September	Continuous	kJ m^{-2} day^{-1}	[58]
Annual average temperature (°C)	Continuous	°C	[35]
Regularly flooded vegetation (%)	Continuous	Percent	[31]

2.2.3. Validation

The performance of the model for species with more than 20 field records was assessed using the partial receiver operating characteristic (ROC) curve, which was calculated with NicheToolBox on https://species.conabio.gob.mx/geoportal_v0.1.html, (accessed on 5 April 2024) using individual predictions. We used partial ROC curve parameters with a proportion of omission of 0.05, 20% of random points, and 1000 replicates for the bootstrap. In contrast, for species with fewer than 20 field records, "pValueCompute" software version 2/20/06 was used, which evaluates the predictability of species models with small samples [59]. The algorithm displays values from 0 to 1 indicating the presence or absence of the species as a function of the reciprocal probability value. The value resulting from the analysis indicates the probability of success under randomization. The null hypothesis is that the presence of the species is not related to the probability of occurrence. This method allowed us to identify the relationship between sample size and the lowest presence threshold.

2.2.4. Binary Maps

The PGD was obtained from the consensus of 20 replicates per species because it is a random process since each model is different. The consensus map was obtained with the weighted mean method [Marmion], which consisted of multiplying the area under the curve (AUC) of the MDP validation by its corresponding replicate. The AUC provides a single measure of model performance, independent of any choice of threshold. The AUC reflects the accuracy of the performed model, where values close to 1 indicate prediction capacity, while values close to 0.0 correspond to models with low accuracy. The consensus was performed in QGIS software (v 3.22.8). The maps generated presented a value ranging from 0 to 1; therefore, we converted them to a binary map of presence–absence. The presence or absence of the species was estimated by using a fixed threshold value of 10% generated by MaxEnt. The binary map was obtained by reclassifying the consensus map, where pixels that had a value lower than the average of the fixed cumulative threshold for the 10% probability of occurrence were considered as having an absence of the species, while at values above this threshold, the species was considered present [60].

2.3. Analysis

2.3.1. Representativity

The representativity was measured as the similitude of species inside PAs with respect to a species pool that occurs in a region. We categorized PAs in the function of a weighted Sorensen-Dice index, where categories obtained were associated with *Thamnophis* species presence in PAs to identify which species tend to occur in higher and lower representativity in PAs. In this study, we used biological provinces as region to measure the species pool that potentially can occur in each PA. The biogeographic provinces were defined as areas with similar biogeographic characteristics (vascular plants, amphibians and reptiles, and mammals) and morphotectonic features. The Sorensen-Dice index was used to measure similitudes among PAs and biological provinces, due to assuming an imperfect sampling. The index varies from 0.0 to 1.0, where values equal to 0.0 occur when no species were shared among PAs and the region to which it belongs, and when the value is 1.0 all species were shared; the value was estimated with Equation (1).

$$S - Di = (2 * a)/(2 * a + b + c) \quad (1)$$

where $S - Di$ is the Sorensen-Dice index, a is the number of species that share a region in PAs, b is the number of species that only occur in Pas, and c = the number of species that occur only in biological provinces.

The PAs can occur in more than one biological province; therefore, we estimated a Sorensen-Dice similarity index for separate provinces and weighted the proportion of area occupied by PAs in the biogeographic province to which it belongs with Equation (2).

$$S - D_w = \sum_i^n (S - D_i * p_i) \quad (2)$$

where $S - D_w$ is the Sorensen-Dice index weighted, $S - D_i$ is the Sorensen-Dice index of the fraction of the PA in i biogeographic province, and p_i is the proportion of the PA in I biogeographic province. The PAs were categorized in five categories of the Sorensen-Dice index weighted with a class width constant of 0.176 $S - D_w$ for federal and state PAs.

The five classes of PAs were associated with the presence of 25 *Thamnophis* species with simple correspondence analyses (SCA). The SCA is a modification of the Chi square (X^2)

test and is used to analyze contingency tables and create a Cartesian diagram. The analysis is used to represent the level of association between the categories of each variable [61]. The analyses were performed for federal and state PAs. We report the X^2, degree of freedom, the probability that the hypothesis is true, and a bidimensional graphic of the scores of SCA.

The representatives of each species in federal and state PAs were estimated by the intersection of the individual layer of species presence in Mexico [CONABIO. Áreas geoestadísticas estatales, escala: 1:250,000. edición], federal PAs [43], and state PAs [44] polygons. The representations were obtained by dividing the ha where species could be present by the total ha in PAs and multiplying the result by 100. The same procedure was performed for richness. The layer was reprojected to the Lambert conical conformal to calculate areas.

2.3.2. Complementarity

Complementarity was obtained by Humphries et al. [62] method to identify the smallest number of PAs that contained the highest richness. The procedure consisted of choosing the two PAs that together had the greatest number of species; the first was the one with the greatest species richness, and the second had the greatest number of additional species, i.e., those that were not represented in the first PA. The third PA was the one that contained the greatest number of species not considered in the first two PAs with the greatest richness; the same criterion was used iteratively until the smallest number of PAs contained the 25 species of the genus *Thamnophis*. The complementarity was obtained for federal and state PAs.

2.3.3. Risk of Local Extirpation

The human footprint is related to local extinction risk [12]; therefore, we associated species distribution, human footprint, and PAs to identify where and which species could occur in areas with more anthropogenic pressure. The human footprint is defined as the ability of humans to transform the face of the Earth through land use and development of energy infrastructure. We used the human footprint map for Mexico proposed by González-Abraham et al. [15], which obtained a human footprint index (HFI) as a function of land use and land cover, land communication routes, urban settlements, agriculture, aquaculture, forestry plantations, and cultivated grassland areas. The HFI was classified into areas with very low human footprint (HF = 0, untransformed) and low footprint (HF = 0.5–1), medium footprint (10.6% of Mexico, HF = 2–3), and high (HF = 4–6) and very high ($HF \geq 7$) footprint [15]. The individual species layers of the PGD were spatially intersected with the human footprint and the federal and state PAs polygons to identify the species that are at risk at the country level.

The association of 25 species in five human footprint categories and PAs (152 federal and 334 state) was performed with simple (SCA) and multiple (MCA) correspondence analysis. The SCA was used to associate species with human footprint categories in Mexico. The SCA is a modification of the Chi square (X^2) test and is used to analyze contingency tables and create a Cartesian diagram. The analysis is used to represent the level of association between the categories of each variable [61]. In this analysis, we grouped species as a function of the percent of their distribution in each human footprint category with generalized k-means analysis. This analysis searches for a combination of sites that maximize differences between groups and minimize variations within groups based on ANOVA. The null hypothesis was that variations between and within groups are similar. The final aggregation was graphically represented using SCA. The association of species, human footprint, and PA was performed with MCA, which is an extension of SCA, where the nature of the association between more than two categorical variables can be visually studied [63]. MCA is a multivariate statistical technique used in large complex datasets to analyze and graphically represent multivariate categorical data. The positions of the categories of different variables reflected the degree of association between them. The analyses were performed for Mexico, federal PAs, and state PAs in Statistica software v. 13, and maps were created using the free and open source QGIS.

3. Results

3.1. Representativiness

The species of the genus *Thamnophis* can potentially be distributed in 76.7% of Mexico, and from one to three species can occur in nearly 65.7% of the country (Figure 2). The highest richness occurs in central and western Mexico. The GPD of 12% of the species were distributed in more than 17% of Mexico, where *T. cyrtopsis* presented the highest percent distribution in Mexico (Table 1). The 44% *Thamnophis* species complied with Aichi Target 11 (more than 17% of DGP inside federal or state PAs (Table 1); considering only federal Pas, the 24% of *Thamnophis* complied with Aichi Target 11; and 8% of DGP in state PAs meet this criterion (Table 1) (Figure 3c,d). The 87.7% of federal PAs potentially contain more than one *Thamnophis* species (Figure 3a,b), where the more frequent richness in PAs was 2–3 species. The 95.1% of state PAs potentially contain more than one *Thamnophis* species (Figure 3c,d), where only *T. mendax and T. scaliger* complied with Aichi Target 11 (Table 1). *Thamnophis godmani* was absent in federal and state PAs. *Thamnophis mendax* and *T. postremus* were absent from federal PAs, while *T. elegans*, *T. hammondii*, and *T. sirtalis* were absent from state PAs (Tables 1 and S1).

Figure 2. Richness of genus *Thamnophis* in Mexico (percent of richness).

The association of the frequency of the occurrence of 23 *Thamnophis* species with five categories of the Sorensen-Dice index weighted federal PAs was statistically significative ($X^2_{d.f.=88} = 1392$, $p < 0.001$), where the first two dimensions extract 76.0% of the variation in data. The median of the Sorensen-Dice index weighted on PAs was 0.5. The 23 *Thamnophis* species predicted to occur in federal PAs were clustered in three groups. The first group cluster was *T. conanti*, *T. chrysocephalus*, *T. fulvus*, *T. nigricaudis*, *T. postremus*, and *T. sumichasti*, which more frequently occur in PAs with medium to high regional representativity (Figure 4a,b, from 0.47 to 0.82, Table S2). The second group cluster was *Thamnophis marcianus*, *T. proximus*, and *T. validus*, which more frequently occurred in federal PAs with a very high representativity (Figure 4a,b, 0.82 to 1.0), or a very low representativity (0.11 to 0.29). The last group includes the rest of the species that tend to occur in PAs with low representativity (Figure 4a,b. from 0.29 to 0.47).

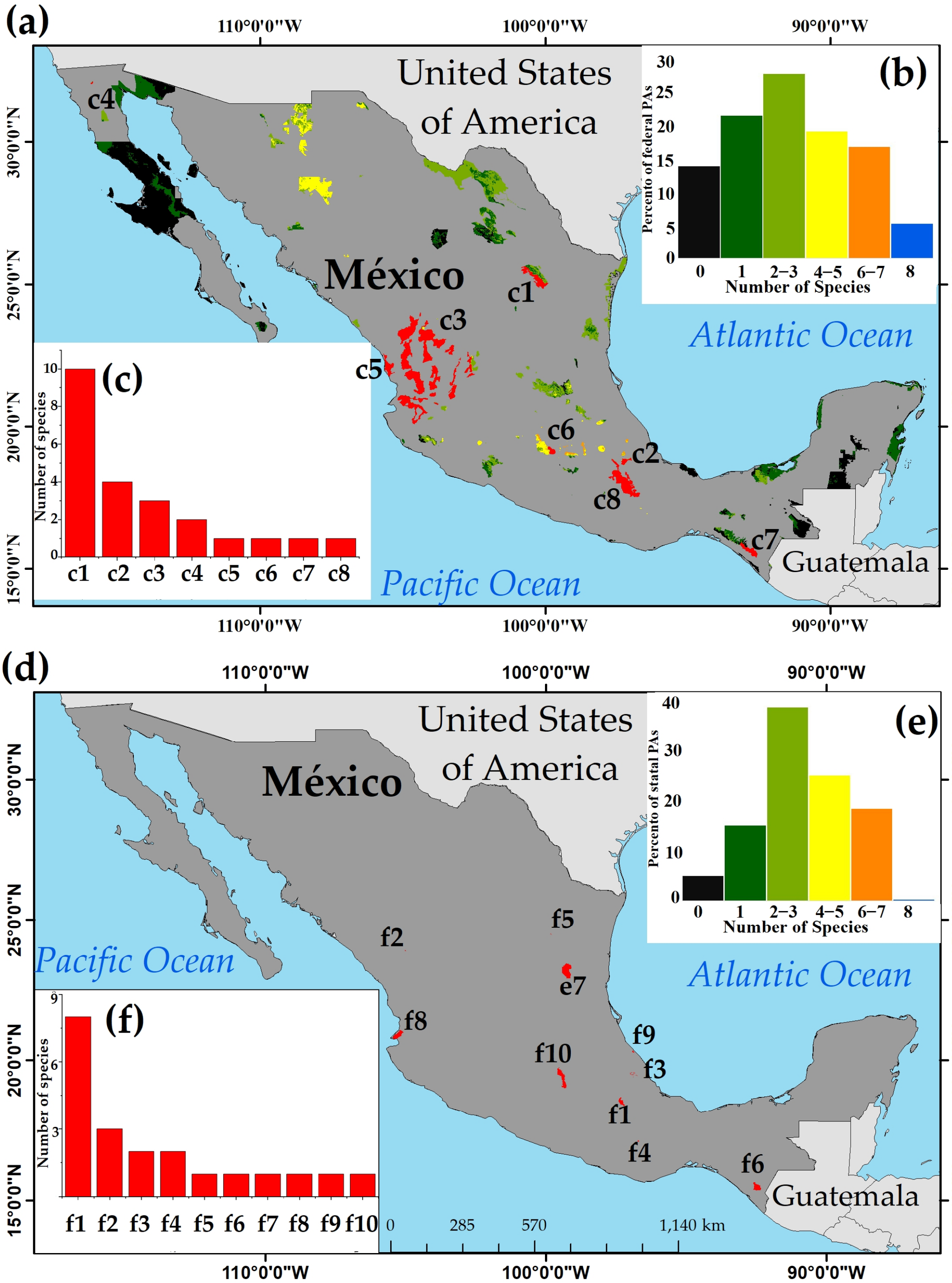

Figure 3. (**a**) Richness of the genus *Thamnophis* in federal PAs. (**b**) Percentage of federal PAs by number of species (red polygon). (**c**) Federal PAs that potentially concentrate the maximum complementarity of the *Thamnophis* species, where c1 = C.A.D.N.R. 026 Bajo Río San Juan, c2 = Cañon del Río Blanco, c3 = C.A.D.N.R. 043 Estado de Nayarit, c4 = Constitución de 1857, c5 = Marismas Nacionales Nayarit, c6 = Nevado de Toluca, c7 = El Triunfo, and c8 = Tehuacán-Cuicatlán. (**d**) Richness of the genus *Thamnophis* in state PAs. (**e**) Percentage of state PAs by the number of species. (**f**) State PAs that potentially concentrate the maximum complementarity of *Thamnophis* species (red polygon), where f1 = Cerro Colorado, f2 = El Tecuán, f3 = Archipiélago de Bosques y Selvas de la Región Capital del Estado de Veracruz, f4 = Zona de Reserva Ecológica El Fortín, Cruz Blanca y Cerro del Crestón, f5 = La Purísima, f6 = Cordón Pico El Loro-Paxtal, f7 = El Cielo, f8 = Sierra de Vallejo, f9 = Ciénega del Fuerte, and f10 = Parque Otomí-Mexica.

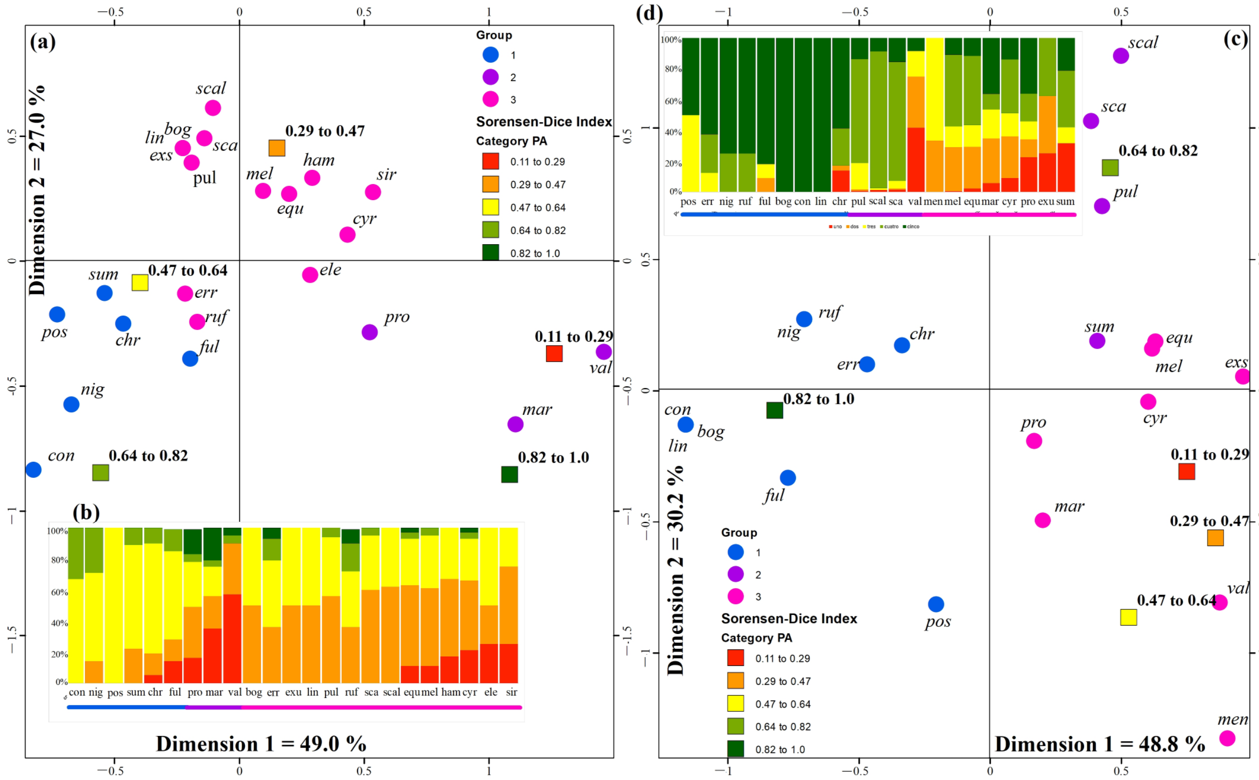

Figure 4. Canonical position of species of the genus *Thamnophis* (circles) and five categories of Sorensen-Dice index weighted for federal (squares, (**a**)) and state (**c**) PAs. The canonical position of species and categories of the Sorensen-Dice index weighted were obtained from correspondence analyses. The percentage of federal and state PAs occupied by each species ((**b**) and (**d**), respectively), where the colors correspond to the category of the Sorensen-Dice index (squares).

The association of the frequency of the occurrence of the 21 *Thamnophis* species with five categories of the Sorensen-Dice index weighted state PAs was significant ($X^2_{\text{d.f.}=80} = 604.0$, $p < 0.001$), where the first two dimensions extract 79.0% of the variation in data. The median of the Sorensen-Dice index weighted on PAs was 0.44, which is lower than state PAs. The 21 *Thamnophis* species predicted to occur in state PAs were clustered in three groups. The first group includes *T. bogerti*, *T. conanti*, *T. chrysocephalus*, *T. errans*, *T. lineri*, *T. nigridicaudus*, *T. postremus*, and *T. rufipunctatus*, which tend to occur in PAs with high representativity (0.82 to 1.0). The second group cluster was *T. scalaris*, *T. scaliger*, *T. pulcrilatus*, and *T. sumichasti*, which were more frequent in PAs with high representativity (Figure 3d,e, 0.64 to 0.82 index). The rest of the species occurred more frequently in PAs with very low to medium representativity (from 0.11 to 0.64).

3.2. Complementarity

Eight federal PAs contain 24 species that potentially can be distributed in at least one of 152 federal PAs (Figure 3a,c), where C.A.D.N.R. 043 Estado de Nayarit (Figure 3c is the PA with the highest richness). Ten state PAs contain 21 species that can potentially be distributed in at least one of 388 state PAs that contain at least one species (Figure 3d,f), where PAs Cerro Colorado contain eight species (Figure 3f), contained all species (Figure 3a,f).

3.3. Risk of Local Extirpation

The association of the distribution of the 25 *Thamnophis* species in Mexico with the five human footprint categories was statistically significant ($X^2_{\text{d.f.}=100} = 709.9$, $p < 0.001$), where the first two dimensions explain the 97.1% of variations in data. The generalized k-means analysis generated three groups of species in the function of the percent distribution in five categories of the human footprint. *Thamnophis elegans*, *T. mendax*, *T. hammondii*, *T. nigrocaudus*, *T. errans*, *T. exsul*, and *T. rufipunctatus* occur in areas with the highest percentage of untransformed environments (Figure 5a). *Thamnophis lineri*, *T. godmani*, *T. bogerti*, *T. cyrtopsis*, *T. marcianus*, *T. chrysocephalus*, *T. fulvus*, and *T. eques* occur in the average conditions of Mexico and tend to be more frequent in areas with a low human footprint. *Thamnophis melanogaster*, *T. validus*, *T. pulchrilatus*, *T. postremus*, *T. proximus*, *T. sumichrasti*, *T. conanti*, *T. scalaris*, and *T. sirtalis* occur more frequently in areas with a medium to very high human footprint (Figure 5a,b and Table S3).

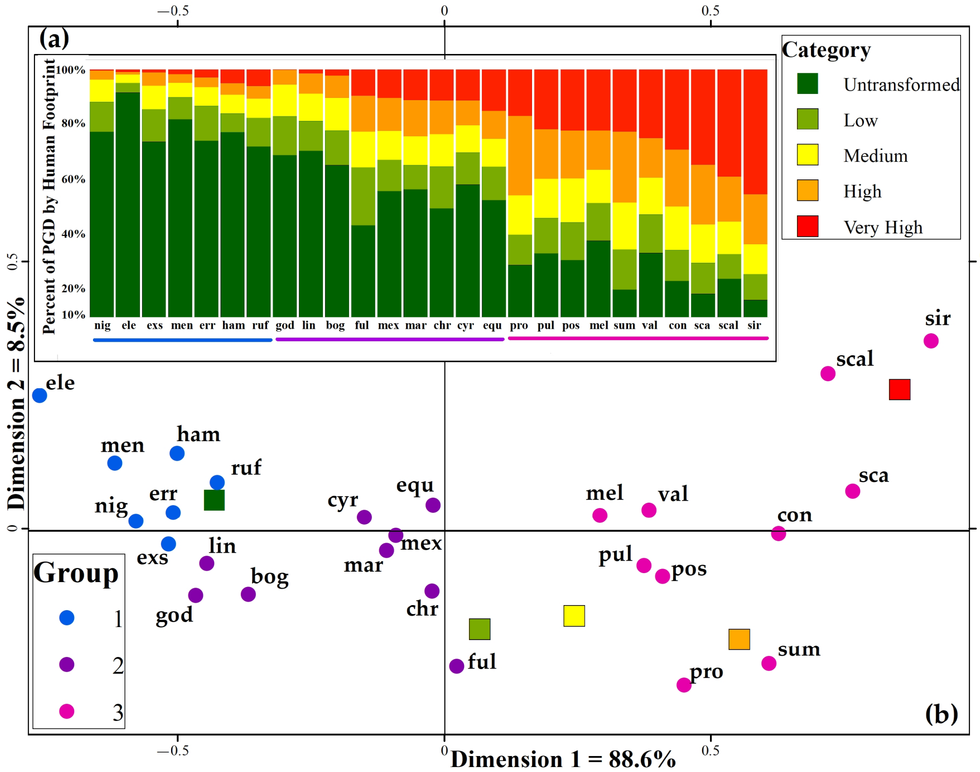

Figure 5. (**a**) Percentage of PGD of three groups of the *Thamnophis* species (bars) by category of human footprint (colors), which was ordered from those untransformed (dark green) to a very high human footprint (red). The color of squares corresponds to human footprint categories. (**b**) Canonical position of association of the *Thamnophis* species with categories of human footprint in Mexico obtained from simple correspondence analysis (abbreviations of species are listed in Table 2).

The association of species with the human footprint inside federal PAs shows that PAs with more than four species tend to occur in PAs with a medium to very high human footprint; while PAs with less than three species were more frequent with a high percentage of untransformed federal PAs (Figure 6a and Table S4). The species *T. scalaris*, *T. scaliger*, *T. sumichasti*, and *T. pulcrilatus* tend to occur in PAs with very high to low human footprint and with a richness from four to ten species; therefore, these species are at local extirpation risk in federal PAs. The species *T. sirtalis*, *T. elegans*, *T. exul*, and *T. hammondii* tend to occur in PAs with an untransformed area and with one to four species (Figure 6a and Table S5). The rest of the species and PAs do not present an association with human footprint categories (Figure 5).

State PAs with less than three species were associated with the highest untransformed areas and *T. fulvus*, *T. conanti*, *T. proximus*, *T. marcianus*, *T. errans*, *T. mendax*, *T. exsul*, and *T. rufipunctatus* were more frequent (Figure 7a and Table S6). The species *T. scalaris*, *T. scaliger*, *T. sumichasti*, *T. melanogaster*, *T. eques*, and *T. cyrtopsis* tend to occur in PAs with very high to low human footprint and with a richness of four to ten species; therefore, these species are in local extirpation risk in state PAs. *Thamnophis nigricaudus* and *T. postremus* tend to occur in PAs from a low to medium human footprint (Figure 7b and Table S7).

Thamnophis conanti presents a different response between the federal and state PAs; in the state PAs it occurs in areas with a very high human footprint, while in federal PAs it occurs in areas with a high percentage of untransformed environments.

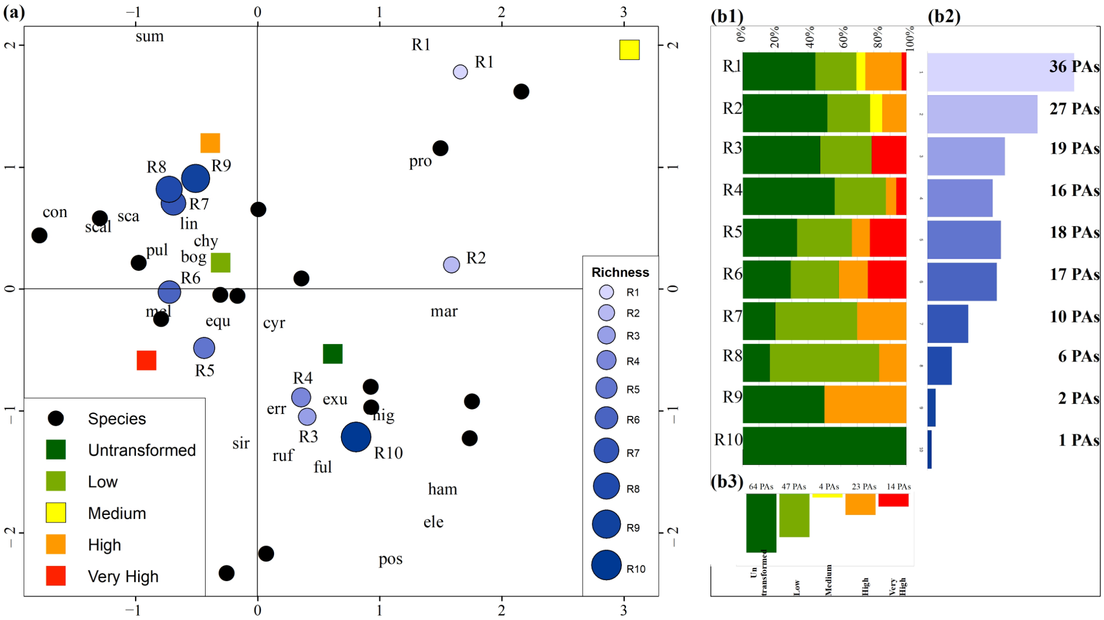

Figure 6. Canonical position of the *Thamnophis* species ((**a**), black circles) in federal PAs (blue marine circles), and the five categories of human footprint (squares) obtained from multiple correspondence analysis (abbreviations are listed in Table 2). The size of circles corresponds to the number of species that occur in this PA. (**b1**) Percentage of federal PAs of each category of human footprint by number of species. (**b2**) Number of federal PAs by number of species (richness). (**b3**) Number of federal PAS by human footprint category.

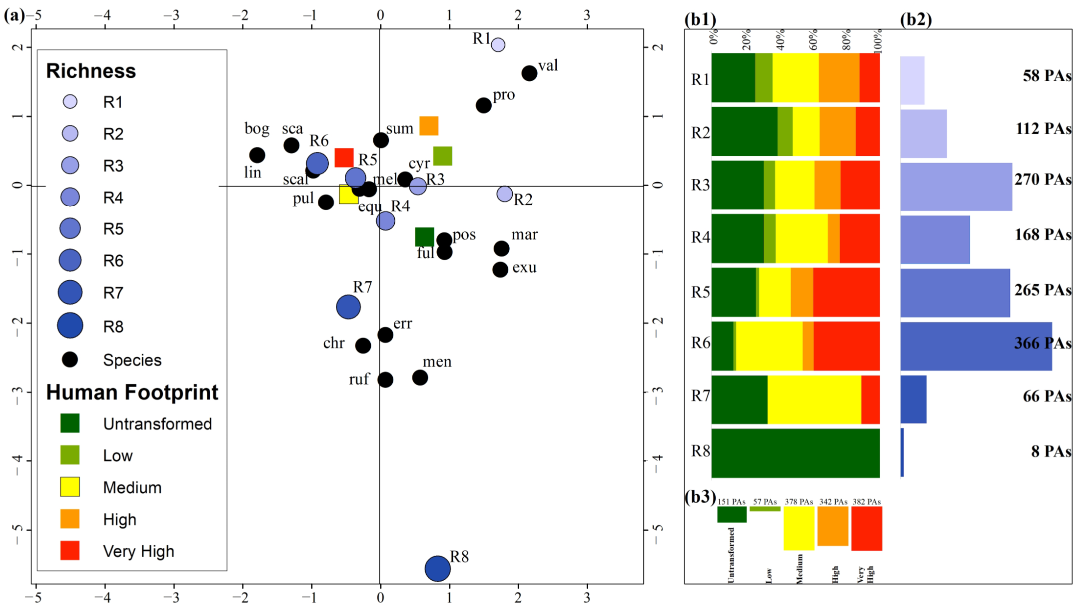

Figure 7. Canonical position of the *Thamnophis* species ((**a**), black circles) in state PAs (blue marine circles), and the five categories of human footprint (squares) obtained from multiple correspondence analysis (abbreviations are listed in Table 2). The size of circles corresponds to the number of species that occur in this PA. (**b1**) Percentage of state PAs of each category of human footprint by number of species. (**b2**) Number of state PAs by number of species (richness). (**b3**) Number of state PAs by human footprint category.

4. Discussion

In this study, the presence of the species of the genus *Thamnophis* in Mexico can be considered adequate, since 92.6% of the species are found in at least one PA and eight national and ten state PAs are necessary to contain these species, in contrast to other regions or groups where there is low representativeness on PA [8,64–67]. However, only the presence of a species in a PA is not sufficient to maintain viable populations [1]. For example, in Japan, a high representativeness of vascular plants in their PAs was found, but there is an underrepresentation of theareas at lower elevations [68]. In the case of the present study, it was found that in 17 species their PGD is conserved inside PAs (federal and state). The best protected species are those with the highest PGD, while the least protected species are the ones with lowest PGD. In addition, there is environmental degradation within the areas that may affect the persistence of these species [5,11,12]. For example, the threatened species *T. melanogaster*, *T. sumichrasti*, *T. conanti*, *T. scalaris*, and *T. sirtalis* are subject to special protection. *T. pulcrilatus* are distributed in areas with a medium to very high human footprint at country scale, which also occurs inside both federal and state PAs. A similar scenario occurs at global scales, due to nearly 32.8% of protected land being under intense human modification [5].

On the other hand, the *Thamnophis* species demonstrated a pattern contrary to expectations, since within PAs with a medium to very high human footprint, more species were present, while in PAs with a high percentage of untransformed environments, less species were present. In the state PAs, a lower richness occurred; their area was smaller and their surface was more affected by the human footprint than federal PAS; however, they show a more regional representativity than federal PAs. Therefore, it is necessary to expand this study with other vertebrates, invertebrates, and vascular plants species to corroborate this tendency. If this tendence is replicated in other taxa, then the Mexican government must reevaluate their conservation politics due to PAs with higher biological representativity being smaller and more affected by human activities (roads, agriculture, and urban settlements).

Species richness is commonly mediated by the effects of ecological, geographical, and evolutionary processes, including humans [14,69], but some studies reveal that highly modified and seminatural ecosystems are characterized by a dominance of positive and negative relationships between environmental heterogeneity and species richness, e.g., ref. [70]. It has been suggested that human effects on species richness are not easily detected on a large geographic scale due to the large proportion of shared variance with the environment, and under this principle the contribution of human impact is almost as important as current environmental conditions in explaining richness patterns [71]. Two meta-analyses suggested that the relationships between environmental heterogeneity and species richness are predominantly negative when studied at smaller spatial scales [72], or when considering animal taxa within landscapes of low- to mid-urbanization level [73].

The present study may be useful to update or generate management plans for the PAS focused on the conservation of *Thamnophis* and other reptile species with similar distribution, since this study highlights areas with a medium to very high human footprint (Figure 3a,b, Tables S6 and S8). In this way, all the species that inhabit PAs with a medium to very high human footprint are at local extirpation risk. A prospective study predicts the reduction in the future distribution of the *Thamnophis* species in central Mexico, where human activity is very intense [36]. A reductions in suitable area available for *Thamnophis* and other species will cause the reduction and isolation of their populations, with possible stochastic demographic effects [74,75] that can convert normal population fluctuations into local extinctions [74]. Therefore, the implementation of conservation and restoration strategies is necessary in PAs with a medium to high human footprint.

Most studies that analyze the representativeness of species in PAs use presence–absence data [68]. However, this indicator assigns the same weight to a species that is distributed in a small fraction of the PAs as to a species that is found in the entire area. Thus, the present study analyzed the percentage of distribution within the PAs as an indicator of its presence, which can more accurately reflect the degree of conservation of the species in the PAs. For example, the 81.5% of species that were present in state PAs or the percentage inside of PAs with more than two species were higher than expected in Mexico, but only 7.4% of the species coincide with their PDG inside estate PAs at 17%.

The main source of variation in this study is the generation of potential distribution models. A study [76] reports the main sources of errors in the generation of PGD. The methods used in this study are not free of these biases, but attempts were made to eliminate information redundancy and spatial autocorrelation, but this cannot solve the problem of low field records, especially for species with restricted distribution, such as the *T. godmani* complex. Additionally, although MaxEnt is considered an algorithm with a reasonable predictive ability, it is also a source of error [77–79] as it can make biases, but no algorithm is error-free [80]. Presence-only algorithms, such as Maxent, represent regional factors that affect both the presence and absence of species and could be used as an indicator of the regional PGD of species [46]. Finally, the study used a mixture of climatic, topographic, regionalization, and land cover variables that together can better explain the distribution of a species than climatic variables alone.

The current network of PAs must be expanded, first to fulfill Aichi Target 11 and second to conserve Mexico's environmental capital. The challenge is great since approximately half of Mexico has undergone environmental alterations [15], there is high environmental variability [16], the reduction in native vegetation varies among regions [81], and the taxa have different niche requirements, so they occur in different places [16]. The present study proposes that a better picture of the representativeness of species within PAs should consider the area that species occupy within PAs and the degree of the human footprint. In addition, it is necessary to carry out this exercise with other taxa to have more elements to modify, and create new PAs that maximize the richness and minimize the area to be protected.

Predictive scenarios that evaluate the preservation of Mexican snake habitats consider that limiting or stopping economic activities is not a sufficient measure for the conservation of snake species [82,83]. Given the conditions of the increasing anthropogenic impact, according to the evaluation of the human footprint, it is necessary to implement measures that consider reptiles as highly dependent on climatic conditions and therefore more vulnerable than other groups of vertebrates to changes due to agriculture, urban development, invasive species, logging, and climate change [84,85].

Considering that many *Thamnophis* species occupy biodiversity hotspots in various ecoregions and biogeographic boundaries [26], it is suspected that such landscape characteristics, together with historical events, have generated the patterns of differentiation of these snake species [27,35,86]. However, a deeper understanding of the role that geography and history have played in the diversification of the phylogeny of *Thamnophis* [35] is necessary to understand the evolution of trait plasticity in these snakes.

5. Conclusions

This study proposes that at least 17% of species PGD will be found inside PAs and in areas with a smaller human footprint. This proposed percentage was greatly exceeded because national PAs contain 85.2% of the species, while the state PAs contain 77.7% of the species. An average of 13.4% of the PGD of these species is found inside PAs, and two species are found outside. Eight national PAs and 12 state PAs contained all species that can potentially be distributed within PAs. In 13 national PAs and 10 state PAs, the *Thamnophis* species presented a greater risk from human activities. Nine species (33%) were identified with a high risk of anthropogenic pressure; therefore, their persistence could be at risk (*T. conanti*, *T. hammondii*, *T. postremus*, *T. proximus*, *T. pulcrilatus*, *T. scalaris*, *T. scaliger*, *T. sirtalis*, *T. sumichasti*, and *T. valida*). Declaring PAs is insufficient to conserve species, since the impact that humans have on the environment occurs inside them. Therefore, restoration strategies should be implemented to ensure the sustainability of ecosystems.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/ecologies5040041/s1, Table S1: Summary of the collection records used to predict the geographic distribution of the species and validation values of the models generated; Table S2: Presence–absence of *Thamnophis* species in federal PA; Table S3: Presence–absence of *Thamnophis* species in state PA; Table S4: Percent of PDG of each species by human footprint category; Table S5: Canonical scores and richness of federal PA obtained from multiple canonical analyses; Table S6: Percent of federal PA by human footprint category; Table S7: Canonical scores and richness of state PA obtained from multiple canonical analyses; Table S8: Percent of state PA by human footprint category.

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