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Research Article

Applying niche-based models to predict endangered-hylid potential distributions: are neotropical protected areas effective enough?

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Abstract
Tropical amphibians face a severe decline crisis with ca. 35% of species being currently threatened in the Neotropics. We selected 16 endangered-hylid species and used species records to model their potential geographical distribution for the continental Neotropics. We found that there is a strong influence of slope in hylid geographical distribution that interacts synergistically with maximum rainfall and temperature changes over the year. We identified some intersecting areas of species overprediction along southern Neotropics, which could be important for future biological surveys searching for undescribed microendemic hylid species. Nine of the 16 studied hylids have small geographic ranges with only 25% of its potential distribution being currently protected in the Neotropics. The remaining seven species are still in need of additional conservation areas to ensure the protection of at least 25% of its original distribution range in Mesoamerica. Most Neotropical endangered hylids have only the periphery of their distribution protected with its core distribution outside protected areas. These species may be especially threatened because they now occur in small, isolated subpopulations due to habitat fragmentation and loss. We suggest that conservation efforts for Neotropical hylids should be focused on restricted-range species and in the establishment of additional conservation area networks in Mesoamerica. Remaining habitats for threatened hylids need to be managed as a coordinate network including site-scale and landscape-scale actions to buffer the extinction-driven process caused by inbreeding, genetic drift, and demographic stochasticity.

Keywords: Endangered species, conservation biogeography, tree frogs, MaxEnt, protected areas, habitat fragmentation.

Resumen
En la actualidad, los anfibios tropicales enfrentan una crisis muy severa con un 35% de especies en peligro de extinción en el Neotrópico. Se seleccionaron 16 hílidos en peligro de extinción y se usaron registros de especies para modelar su distribución geográfica potencial a lo largo del neotrópico continental. Se encontró que hay una fuerte influencia de la pendiente topográfica en la distribución potencial de los hílidos que interactúa sinérgicamente con la precipitación máxima y los cambios de temperatura a lo largo del año. Se identificaron algunas áreas de sobrepredicción de especies a lo largo del sur del neotrópico con gran potencial para direccionar futuras expediciones biológicas en busca de nuevas especies microendémicas de hílidos. Nueve de las 16 especies de hílidos estudiadas presentaron rangos geográficos muy restringidos presentando solo el 25% de su distribución geográfica potencial dentro de áreas naturales protegidas en el Neotrópico. Las otras siete especies requieren la implementación de nuevas áreas de conservación que aseguren la protección de por lo menos el 25% de su rango de distribución original en Mesoamérica. Algunos de los hílidos amenazados presentan solo su periferia conservada con su núcleo de distribución fuera de las áreas protegidas. Estas especies podrían estar especialmente amenazadas dado que se distribuyen actualmente en pequeñas subpoblaciones aisladas debido a la fragmentación y pérdida del hábitat. Es recomendable que los esfuerzos de conservación para los hílidos neotropicales se enfoquen en especies de distribución restringida y en el establecimiento de redes de áreas de conservación en Mesoamérica. Los hábitats remanentes para la conservación de los hílidos amenazados debe ser manejado como una red coordinada que incluya acciones a escalas finas y de paisaje que amortigüen los procesos causante s de extinción por endogamia, deriva genética, y estocasticidad demográfica.

Palabras clave: Especies amenazadas, biogeografía de la conservación, ranas arborícolas, MaxEnt, áreas protegidas, fragmentación de hábitat.

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Introduction

Neotropical anurans are a key component of biodiversity because they are an integral part of terrestrial and aquatic ecosystems linking these environments and playing important roles in species interaction networks, as they feed upon plants and algae, prey upon small animals, and serve as food for larger predators [1]. The Neotropics harbor *ca.* 3046 amphibian species (2065 in South America and 685 in Mesoamerica; [2]) and 35% of anuran species are current threatened with extinction, being classified by The World Conservation Union (IUCN) as “critically endangered”, “endangered” or “vulnerable”. This percentage increases up to 41% if we add species considered to be “near threatened” [3] without taking into account rare species classified as “data deficient”. Furthermore, relative to other animal groups, an outstandingly high proportion of amphibians are in higher threat categories [4, 5]. Amphibian populations are also declining worldwide and such high threats at the population and species level is causing growing concern [6-9].

The leading factors that threaten amphibians and determine their population declines are habitat fragmentation and loss, which affect amphibians through population isolation, inbreeding, edge effects, and the disconnection between aquatic and terrestrial environment (also known as habitat split) which are key systems for amphibian reproduction [2, 6, 8, 10]. Amphibians are also threatened by climate shifts and increasing ultraviolet-B radiation [7, 11], introduction of alien species [12], and fungal diseases [13]. The later is particularly important in the Neotropics given that Chytridiomycosis infection, caused by the fungus *Batrachochytrium dendrobatidis*, has been responsible for decline of many populations even in undisturbed environments in this particular region [7, 13].

In the face of such a drastic scenario of population decline and species extinctions, the necessity of high-quality accurate data on amphibian geographic distribution from which to derive reliable science-based studies is quite obvious. However, our knowledge about biodiversity remains inadequate and plagued by the so-called Wallacean shortfall [14, 15]. This refers to the fact that for the majority of taxonomic groups geographical distributions are poorly understood and contain many gaps. This is especially problematic in the Neotropical region, in which species records are fairly sparse and highly uneven [16, 17]. For Neotropical frog species, in particular, few data on geographical distribution is linked to their huge diversity, associated to the existing of highly specialized species that occur in very specific microhabitats. The low number of taxonomists relative to the number of species to be studied strengthens even further the lack of availability on frog distribution across this realm. To a certain extent, the lack of field records may be overcome by summing expected distributions of species obtained through ecological niche modeling [18]. Species distribution models attempt to provide detailed predictions of distributions by relating presence of species to environmental predictors, providing researchers with novel tools to explore questions in ecology, evolution, and conservation [18]. Ecological niche modeling while relating species locality records and environmental coverage data also provides informative biogeographical data for poorly known tropical landscapes [19]

A wide range of methods has been used for predicting species potential geographic distributions [20], but despite their frequent use, the number of occurrence records available for individual species from which to generate predictions is often limited. Records are even scarcer for rare species that are difficult to sample and limit the availability of locality records. This, in turn, affects the performance of species distribution models, given that they seem to depend on sample size [20]. Due to the difficulty to obtain rigorous records of species absences, presence-only data are effective for modeling species distributions. This kind of data is the raw material of maximum entropy machine-learning methods, which were designed to predict species distributions under current environmental conditions, and have demonstrated to be one of the highest performing methods when ranked against other approaches [18].

Methods for predicting species potential distribution across different geographical scales have been applied also in conservation planning exercises (e.g. [21-23]) and invasive species ecology (e.g. [24-25]). The results of these studies, coupled with high threat levels imposed to amphibians, clearly highlight the need for creating effective strategies to maximize conservation efforts for these vertebrates and call for an urgent evaluation of existing ones [26]. To date, natural protected areas seem still to be the best option for safeguarding species across multiple spatial scales as the *in situ* conservation of viable populations in natural ecosystems is widely recognized as a fundamental requirement for the maintenance of biodiversity [27-28]. However, to attain such a thing we need to know how much biodiversity is currently protected and where new protected areas should be established to move toward complete coverage [29]. We call this approach a Gap Analysis, defined as a planning approach based on assessment of the comprehensiveness of existing protected-area networks and identification of gaps in their coverage (see [27]). Several gap analyses at regional and continental scales revealed that coverage of biodiversity by existing networks of protected areas is actually inadequate (e.g. [23, 30]. Nevertheless, no study so far has addressed the effectiveness of the Neotropical network of protected areas in representing threatened amphibians (*but see* [31]), although a comprehensive set of areas for the conservation of threatened anurans has been recently proposed for the entire region (*see* [3]).

In this study we focused our efforts in Neotropical threatened hylids (Amphibia: Hylidae) because they are the largest anuran family in this realm having 587 threatened species in continental Neotropics [5], and they also hold the best individual species records for this region. Our objective was, therefore, twofold: (1) we aimed, by modeling species ecological niches, to predict endangered-hylid potential geographic distributions across the continental Neotropical region and their relation with topographic and climatic variables; (2) we evaluated the effectives of the network of protected areas in representing these threatened species along the continental Neotropics (an optimistic estimate), and along Mesoamerica (a conservative approach).

Methods

Scope of study

We centered our analyses in the continental Neotropics (Mesoamerica and South America) which are composed by 17 countries (Belize, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, El Salvador, French Guiana, Guatemala, Guyana, Honduras, Mexico, Nicaragua, Panama, Peru, Suriname and Venezuela) spanning a total area of 16.133.914 Km^2 (Fig. 1). On the one hand, the Neotropics encompass six megadiversity countries and more than 10,000 vertebrate species [32], harboring more than a half of the World’s amphibians [2]. It holds the largest remaining wilderness areas in the World [33], and includes most of the tropical ecosystems still offering significant options for successful broad-scale conservation action. On the other hand, it also supports about 462.409.877 people with a mean rate of population growth reaching 1.48% [34]. This entails a huge human footprint on natural resources altering patterns of biodiversity and ecosystem services within this region [35].

Fig. 1. Study area (gray color) along Neotropical continental region.

Species occurrence data

In order to derive species distribution models we selected *a priori* endangered-hylid species (*sensu* [5]) given that species with restricted ecological niches have smaller geographic ranges (such as endemics) providing more robust and precise niche distribution models [36-40]. We started our study with a dataset of species geographical records obtained from HerpNet (http://www.herpnet.org/), CONABIO (http://www.conabio.gob.mx/remib/doctos/remib_esp.html), WWF (http://www.worldwildlife.org/wildfinder), the Global Amphibian Assessment (http://www.globalamphibians.org), and Species Link (http://splink.cria.org.br). We choose 16 endangered-hylid species (*sensu* [5]), being six of genus *Plectrohyla* (which have 41 endangered species in the Neotropics), one of genus *Hylomantis* (which have 8 endangered species in the Neotropics), two of genus *Isthmohyla* (which have 14 endangered species in the Neotropics), one of genus *Ptychohyla* (which have 13 endangered species in the Neotropics), two of genus *Duellmanohyla* (which have 8 endangered species in the Neotropics), one of genus *Charadrahyla* (which have 5 endangered species in the neotropics), one of genus *Bromeliohyla* (which have 2 endangered species in the Neotropics), and two of genus *Agalychnis* (which have 6 endangered species in the Neotropics). All these species had at least 19 independent locality records. This produced a dataset of 551 individual records with a mean number of records per species equal to 32.4, ranging from 19 to 58 (Appendix 1).

A typical problem in potential distribution modeling is that species geographical data are often presence only, rather than presence-absence, resulting in a lack of information about species that have been searched in the field, but not found. One way to mitigate this limitation is to use species records to model expected geographical distribution in the study region [41]. The geographical distribution of species are most accurately predicted in multi-dimensional environmental space using ecological niche modeling on the basis of climatic and topographic variables [42]. These variables, in turn, have a potential influence on the distribution of amphibians across the Neotropics [43]. We assumed that each species has a unique distribution within an environmental space determined by its genetic constitution and its physiological requirements [44]. Species ecological niche distribution is also constrained by ecological interactions (*sensu* realized niche [45]). Hence, the challenge of identifying distributional areas for species requires two conditions to be met: favorable abiotic conditions and favorable biotic factors. As highlighted by Papes and Gaubert [46], a third condition – the geographical accessibility (i.e. landscape configuration, dispersal abilities of species), both historical and actual, are also determinants of the actual presence of species (*see also* [47]).

Ecological niche distribution modeling

We predicted the geographical distribution for the 16 endangered-hylid species based on ecological niche models generated by MaxEnt software version 3.2.1 [42, 48]. MaxEnt estimates species distributions based on presence-only occurrence data by finding the distribution of maximum entropy, subject to the constraint that the expected value of each environmental variable under this estimated distribution should match its empirical average [48]. The obtained model reveals the relative probability of a species distribution over all grid cells in the defined geographical space, in which a high probability-value associated to a particular grid cell indicates the likehood of this cell having suitable environmental conditions for the modeled species [18].

We obtained 19 environmental variables from the WorldClim database (http://www.worldclim.org/), which were interpolated from global climate datasets at a resolution of 0.01° or 1 km^2 approximately [49]. We also used additional spatial layers of topography, slope and topoindex from 0.01° U.S. Geological Survey's Hydro-1K (http://edc.usgs.gov/products/elevation/gtopo30/gtopo30.html).

All this totaled 22 layers of topographical and environmental variables (Table 1). All these layers were clipped to an area circumscribed between 32.72 N to -33.74 S and 118.40 E to -34.79 W, which included the countries of Belize, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, El Salvador, French Guiana, Guatemala, Guyana, Honduras, Mexico, Suriname, Nicaragua, Peru, Panama and Venezuela.

Table 1. Codes for 22 environmental and topographic variables layers used to model amphibian's distribution.

Variable Code	Variable Type	Source
BIO1	Annual Mean Temperature	WorldClim
BIO2	Mean Diurnal Range: Mean of monthly (max temp - min temp)	WorldClim
BIO3	Isothermality: (P2/P7)* 100	WorldClim
BIO4	Temperature Seasonality (standard deviation *100)	WorldClim
BIO5	Max Temperature of Warmest Month	WorldClim
BIO6	Min Temperature of Coldest Month	WorldClim
BIO7	Temperature Annual Range (P5-P6)	WorldClim
BIO8	Mean Temperature of Wettest Quarter	WorldClim
BIO9	Mean Temperature of Driest Quarter	WorldClim
BIO10	Mean Temperature of Warmest Quarter	WorldClim
BIO11	Mean Temperature of Coldest Quarter	WorldClim
BIO12	Annual Precipitation	WorldClim
BIO13	Precipitation of Wettest Month	WorldClim
BIO14	Precipitation of Driest Month	WorldClim
BIO15	Precipitation Seasonality (Coefficient of Variation)	WorldClim
BIO16	Precipitation of Wettest Quarter	WorldClim
BIO17	Precipitation of Driest Quarter	WorldClim
BIO18	Precipitation of Warmest Quarter	WorldClim
BIO19	Precipitation of Coldest Quarter	WorldClim
h_dem	Elevation (m asl)	USGS
h_slope	Slope (degrees) based on local differences in DEM	USGS
h_topoindex	Index of the topographic maps	USGS

We run MaxEnt under the "auto-features" mode as suggested by Phillips and Dudik [42]. The use of default settings is reasonable given that its use has been validated in studies over a wide range of species, environmental conditions, individual species records, and in cases in which sample selection bias occurred (*see* [42]). We configured the machine-learning algorithm to use 75% of species records for training data set and 25% for testing the model. We also selected the logistic output format because it is robust to unknown prevalence, being also easier to interpret as the estimated species probability of presence given the constraints imposed by environmental variables [42]. In this case, grid cells with a small logistic value are predicted to be unsuitable or only marginal suitable for the studied species given their assumed ecological niche [42]. We reclassify each species map using the 10 percentile training presence of the logistic threshold of the distribution model. MaxEnt determined the heuristic estimate of relative contributions of each climatic and topographic variable in each species distribution model and we performed a Principal Component Analysis (PCA) to reduce dimensionality and obtain a smaller number of species groups based on the percentage of contribution delivered by each variable, using Statistica 6.0 software [50].

Ecological niche modeling cannot include aspects such as biogeography or species natural history, ignoring if some species may have failed to disperse due to geographical barriers or were excluded from an area due to resource competition, for instance [42]. We selected, therefore, only those models with AUC values above 0.75 in the training data (as suggested by Elith [18]) and those in which the test data curve (in the ROC sensitivity–specificity plot – *see* [48]) overcame the random-prediction curve. Based on this, we assumed that those models were robust enough to predict species presences included in our sampling data. As an example, an AUC=0.75 means that in places where a species is present, in 75% of cases the predicted value will be higher than where the species has not been recorded. Moreover, when evaluating AUC as the correct ranking of random suitable sites versus random unsuitable sites, a model with AUC = 0.75 ranks the suitability of the site correctly in 75% of the cases (*see* [20]).

Table 2. Number of registers, AUC values of ecological niche geographic distribution models and the heuristic estimate of relative contributions for most important variables for 16 endangered hylids in the Neotropics. See methods for further details.

			PCA		Relative contributions of variables to MaxEnt model										
Species name	**n**	Training AUC	**Factor 1**	**Factor 2**	**bio_1**	**bio_2**	**bio_3**	**bio_4**	**bio_5**	**bio_6**	**bio_7**	**bio_8**	**bio_9**	**bio_10**	**bio_11**
Agalychnis annae	19	0.99	0.443814	-0.156837	8.8	0.5	3.2	13.1	0	0	3.6	0	0	0	0
Agalychnis moreletii	55	0.96	0.639559	0.671141	0.2	1.1	0.2	8.4	0	2.9	1.5	0	0.3	0	0.7
Bromeliohyla dendroscarta	31	1	0.496048	0.278266	0	0.2	0.1	24.5	0	0	0	0	0	0	0.1
Charadrahyla chaneque	31	0.999	0.165998	**0.943509**	0	0	0	18.4	0	0	0.6	0	0	0	0
Duellmanohyla ignicolor	20	1	0.117177	**0.931961**	0	0	0.5	13.4	0	0	0.1	0	0	0	0
Duellmanohyla uranochroa	38	0.998	**0.884368**	0.279314	4.8	0.2	0.8	13	0.1	0.6	0.5	0.3	0	0	0
Isthmohyla rivularis	34	0.998	**0.886048**	0.333874	3.2	0.6	0	13.6	0.6	0.5	0	0.6	0	0	0
Isthmohyla tica	25	0.998	**0.83327**	0.192583	6.5	2	0	14.3	0.2	0	0	0	0.3	0	0
Hylomantis lemur	22	0.972	**0.802224**	0.233919	3	1.4	0	10.5	0	0	3.6	0	0.8	0	0
Plectrohyla arborescandens	27	1	0.411753	-0.164562	0	0	0.3	16.3	0	0.2	4.3	0	0.2	0	0
Plectrohyla cyclada	38	0.999	0.588646	**0.74086**	0	0	0.1	17.2	0	2.1	0.8	0	0.6	0	0.8
Plectrohyla glandulosa	20	0.998	**0.747525**	0.414038	0	0.8	0	0.4	0	0	0.6	0	0.3	0	0
Plectrohyla guatemalensis	27	0.973	-0.045198	**0.772113**	0.1	0	0	1.7	0.2	0.2	2.9	0	0	1.5	0
Plectrohyla pentheter	24	0.999	**0.759612**	0.32932	0	0.4	4.5	2.3	0	0.8	0.3	0	0.3	0	0.4
Plectrohyla sagorum	49	0.872	0.273098	**0.936158**	0	0.1	0	2.5	0	0	0	0	0	0	0
Ptychohyla leonhardschultzei	58	0.998	**0.720736**	0.35036	0	0	5.5	1.4	0	0.4	0	0	0	0	0
Mean	32.38	0.984625	—	—	1.78824	0.93529	1.08235	10.5765	0.06471	0.45294	1.18235	0.05882	0.16471	0.08824	0.11765
Standard deviation	12.36	0.032494	—	—	2.76245	2.05789	1.80459	6.99603	0.15387	0.82243	1.47277	0.15835	0.24223	0.3638	0.25796

Table 2 continued.

			PCA		Relative contributions of variables to MaxEnt model										
Species name	**n**	Training AUC	**Factor 1**	**Factor 2**	**bio_12**	**bio_13**	**bio_14**	**bio_15**	**bio_16**	**bio_17**	**bio_18**	**bio_19**	**h_dem**	**h_slope**	**h_topoind**
Agalychnis annae	19	0.99	0.443814	-0.156837	0	1.3	4.3	0	13.3	0	1.3	18.6	28.5	3.4	0.1
Agalychnis moreletii	55	0.96	0.639559	0.671141	0	15.2	1.3	6.6	15.6	0.5	2.6	2.5	1.2	38.8	0.3
Bromeliohyla dendroscarta	31	1	0.496048	0.278266	0	7.5	25.1	20.6	0	0	0.1	0	4.3	17.3	0.1
Charadrahyla chaneque	31	0.999	0.165998	**0.943509**	0	45.8	0.2	0.1	0.2	0	2	0.7	0	31.6	0.4
Duellmanohyla ignicolor	20	1	0.117177	**0.931961**	0	32.6	0.5	6.9	0	5.3	0	6.9	0.1	20.3	13.3
Duellmanohyla uranochroa	38	0.998	**0.884368**	0.279314	7.2	0.2	7.2	0	4.4	0	2.6	22.9	2.6	32.5	0
Isthmohyla rivularis	34	0.998	**0.886048**	0.333874	0.5	0	4.9	0.5	13.6	0	1.1	19.4	1.2	39.7	0
Isthmohyla tica	25	0.998	**0.83327**	0.192583	12.6	0	0.5	0.1	2.1	0	0.6	22.5	11.8	26.5	0
Hylomantis lemur	22	0.972	**0.802224**	0.233919	11.7	0	16.5	0	0	1	0.6	11.8	0.5	29.5	9.1
Plectrohyla arborescandens	27	1	0.411753	-0.164562	0	0	19.1	5.4	0	0	4.7	0.9	40.5	7.2	0.9
Plectrohyla cyclada	38	0.999	0.588646	**0.74086**	0	19.3	3.8	8.3	8	0	0.1	0.2	2	36.5	0.1
Plectrohyla glandulosa	20	0.998	**0.747525**	0.414038	0	1.5	0.5	0.5	0	0	16.7	3.3	0.4	74.5	0.5
Plectrohyla guatemalensis	27	0.973	-0.045198	**0.772113**	6.3	34	1.4	7.5	0	5.9	0.1	15.9	13.5	8.3	0.3
Plectrohyla pentheter	24	0.999	**0.759612**	0.32932	0	0.2	2.3	22.7	12.6	0	2.4	2.7	8.8	38.1	1.2
Plectrohyla sagorum	49	0.872	0.273098	**0.936158**	0.3	36.4	0.6	8.6	8.8	0.7	0	10.5	0.8	30.6	0
Ptychohyla leonhardschultzei	58	0.998	**0.720736**	0.35036	0	0.2	4	27.1	10.9	0.3	4	4.5	1.8	39.6	0.2
Mean	32.38	0.984625	—	—	2.34706	12.3353	5.42353	6.75882	5.26471	0.83529	2.58824	9.61765	7.30588	29.3941	1.56471
Standard deviation	12.36	0.032494	—	—	4.29798	15.7296	7.50787	8.72289	6.00437	1.82207	4.00029	8.60401	11.2331	16.4753	3.71651

Current protected areas and their effectiveness in species conservation

As a final goal, we assessed the conservation status of potential distributions for the 16 studied species. We calculated the proportion of species potential distribution currently covered by the Neotropical protected-area network for all studied species using data available from the World Database of Protected Areas [51] at a resolution of 0.5º or 3025 km^2 approximately. Although the IUCN recognizes six categories of protected areas, we focused our analyses to categories I to IV, i.e. those which are managed primarily for biodiversity conservation [52]. We performed calculations in ArcGIS 3.2a [53] in which we masked out the areas outside of designated reserves, which allowed for evaluation of the extent of species potential geographic range which is under protection, and that in which no protection exists. Here, we considered as protected only those grid cells having ≥ 25% of their surface filled by natural reserves (*see* [54]). In conservation studies, analysis of range-map data at inappropriate resolutions may lead to optimistic estimates of species representation in reserves [55]. Given that only *Hylomantis lemur* is reported to be marginally distributed outside Mesoamerica (in the Darién region, just across the border to Colombia), we also assessed the conservation status of species potential distributions under more conservative models, in which we used only predictions made within the limits of Mesoamerica, and in which species probability of occurrence was between 90-100%.

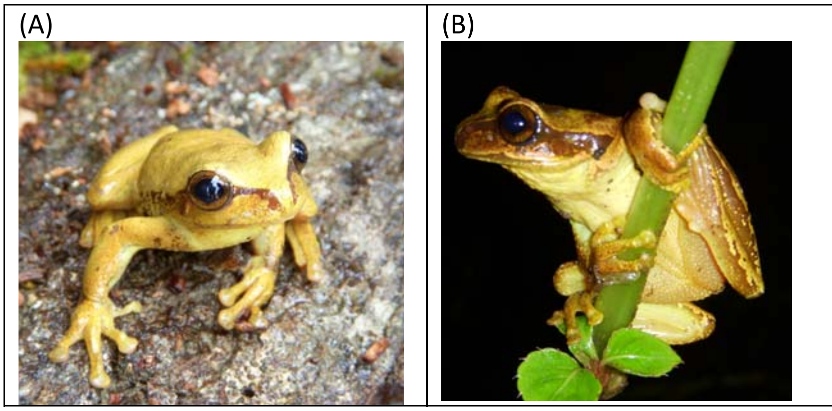

Fig. 2. Two threatened amphibians in Guerrero State, Mexico, which were included in this study. (A) *Plectrohyla pentheter*, (B) *Ptychohyla leonhardschultzei* (Photographs by J.N. Urbina-Cardona).

Results

Relative contribution of variables to species distribution models

The most important variables contributing to 52% of species distribution models were slope (Mean=29.4%, SD=16.4), precipitation of wettest month (bio13; Mean=12.3%, SD=15.7) and temperature seasonality (bio4; Mean=10.6%, SD=7) (Table 2). Based on the percent contribution of each of the 22 variables to each species distribution models we identified two species groups according to the two first factors of the PCA, which explained 69.5% of variance (Table 2). The first group is composed by *Duellmanohyla uranochroa*, *Isthmohyla rivularis*, *Isthmohyla tica*, *H. lemur*, *Plectrohyla glandulosa*, *Plectrohyla pentheter* (Fig. 2A) and *Ptychohyla leonhardschultzei* (Fig. 2B); whereas the second harbors the species *Charadrahyla chaneque*, *Duellmanohyla ignicolor*, *Plectrohyla cyclada*, *Plectrohyla guatemalensis* and *Plectrohyla sagorum* (Table 2).

Table 3. Predicted geographic range distribution attained by the application of niche-based models to endangered hylid species in the Neotropics and only in Mesoamerica. Protected range and percentage of protection were calculated by overlapping spatial locations of Neotropical protected areas (IUCN I-IV). Predicted range distributions and their percentage of protection, in Mesoamerica, are more conservative given that only grid cells having 90-100% probability of species occurrence were considered. See methods for further details.

		Predicted distribution (km2)			**Predicted distribution in Mesoamerica (km2)**		
Species	**IUCN threat category**	**Geographic range**	**Protected range**	**% protection**	**Geographic Range**	**Protected range**	**% protection**
Agalychnis annae	EN	199045	79255	39.82	19086.599	8981.929	47.06
Agalychnis moreletii	CR	602139.615	135516.344	22.51	42040.416	7983.936	18.99
Bromeliohyla dendroscarta	CR	170300	43550	25.57	45533.389	2869.227	6.3
Charadrahyla chaneque	EN	423821.967	79616.273	18.79	32185.246	3492.972	10.85
Duellmanohyla ignicolor	EN	375266.407	77381.581	20.62	24825.053	3492.972	14.07
Duellmanohyla uranochroa	CR	243888.373	103252.012	42.34	21082.584	14096.639	66.86
Isthmohyla rivularis	CR	221835.635	83399.392	37.6	9106.678	0	0
Isthmohyla tica	CR	151152.749	59117.519	39.11	12849.149	7734.439	60.19
Hylomantis lemur	EN	267601.268	99764.609	37.28	14096.638	8108.686	57.52
Plectrohyla arborescandens	EN	488026.602	123794.798	25.37	33183.238	4490.964	13.53
Plectrohyla cyclada	EN	335222.91	84066.806	25.08	23078.567	1247.49	5.41
Plectrohyla glandulosa	EN	305828.803	114607.937	37.47	23203.316	2120.733	9.14
Plectrohyla guatemalensis	CR	1140806.716	384488.255	33.7	52768.831	13722.391	26
Plectrohyla pentheter	EN	102625.005	13659.984	13.31	7983.937	374.247	4.69
Plectrohyla sagorum	EN	353520.449	62104.942	17.57	31436.752	7110.694	22.62
Ptychohyla leonhardschultzei	EN	261314.424	59160.78	22.64	19460.845	374.247	1.92
Mean	—	352649.745	100171.015	28.67	25745.077	5387.598	22.823
Standard deviation	—	246889.066	81767.178	9.33	12989.391	4489.167	22.374

Species potential distribution models

Among evaluated hylids, 62.5% of species had small potential geographic distributions with range values being under the mean predicted range (Fig. 3A, Table 3): *P. pentheter*, *I. tica*, *B. dendroscarta*, *Agalychnis annae*, *I. rivularis*, *D. uranochroa*, *P. leonhardschultzei*, *H. lemur*, *P. glandulosa* and *P. cyclada*. Most endangered hylids have relatively small geographic ranges based on their potential distribution (mean 352,650 km^2; minimum: 102,625 km^2, maximum: 1,140,806 km^2), encompassing 3% or less of the Neotropics (Table 3, Appendix 2). When potential distributions were restricted to grid cells in Mesoamerica, the results were similar, although predicted ranges were even smaller, as expected (Fig. 3B, Fig. 4).

Effectiveness of the Neotropical network of protected areas

Most cells with similar environmental conditions have *ca.* 35% of its total area covered by protected areas in the Neotropics (Fig. 3C). This means about 4235 km^2 of area covered in each of these cells, ranging from 0 to 12,100 km^2. When potential distributions were restricted to

Mesoamerica, most cells presented only 10% (about 1210 km^2) of their area protected by natural reserves (Fig. 3D).

Within the 557 cells having ≥25% of its surface protected, all studied species had at least 13% of their potential niche distribution represented. We found that ten species have more than 25% of their potential range current protected, but six are still in need of additional area to be protected in at least a quarter of its potential distribution range (Table 3). Mean proportion of geographic range protection was *ca.* 29% (ranging from 13 to 42%) and nine species were under this value. The most protected species was *D. uranochroa*, with 42.34% of its range included in protected areas, whereas less protected were *P. sagorum* and *P. pentheter*, having 17.57% and 13.31%, respectively, of their potential distribution located inside reserves (Table 3). Most species had only the edge of their geographic range included in protected areas, but only few species had the core of its distribution protected by natural reserves (*see* Fig. 5).

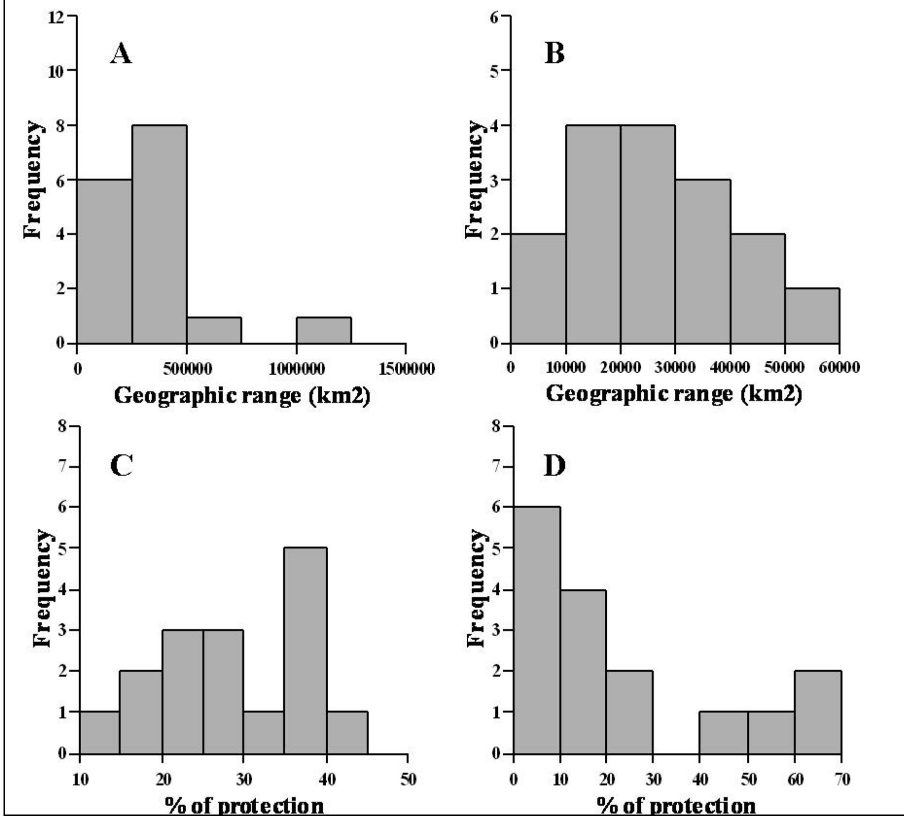

Fig. 3. (A) Number of grids per area protected in the Neotropical region, (B) number of grids per area protected in Mesoamerica region, (C) number of species per geographic range class (measured in Km^2) in the Neotropical region, and (D) number of species per geographic range class in Mesoamerica region.

When conservative models were evaluated (i.e. those in which only grid cells having a 90-100% probability of species occurrence in Mesoamerica), results were somewhat different. We find that eleven species are in need of additional cells to be protected in at least 25% of its potential distribution in Mesoamerica. Moreover, the species *I. rivularis* had no part of its range included in protected areas. Other species, such as *P. leonhardschultzei*, *P. pentheter*, *P. cyclada*, *B. dendroscarta* and *P. glandulosa* had less than 10% of its potential geographic distribution protected in this region. Conversely, four species (*D. uranochroa*, *I. tica*, *H. lemur* and *A. annae*) were more protected under this conservative scenario.

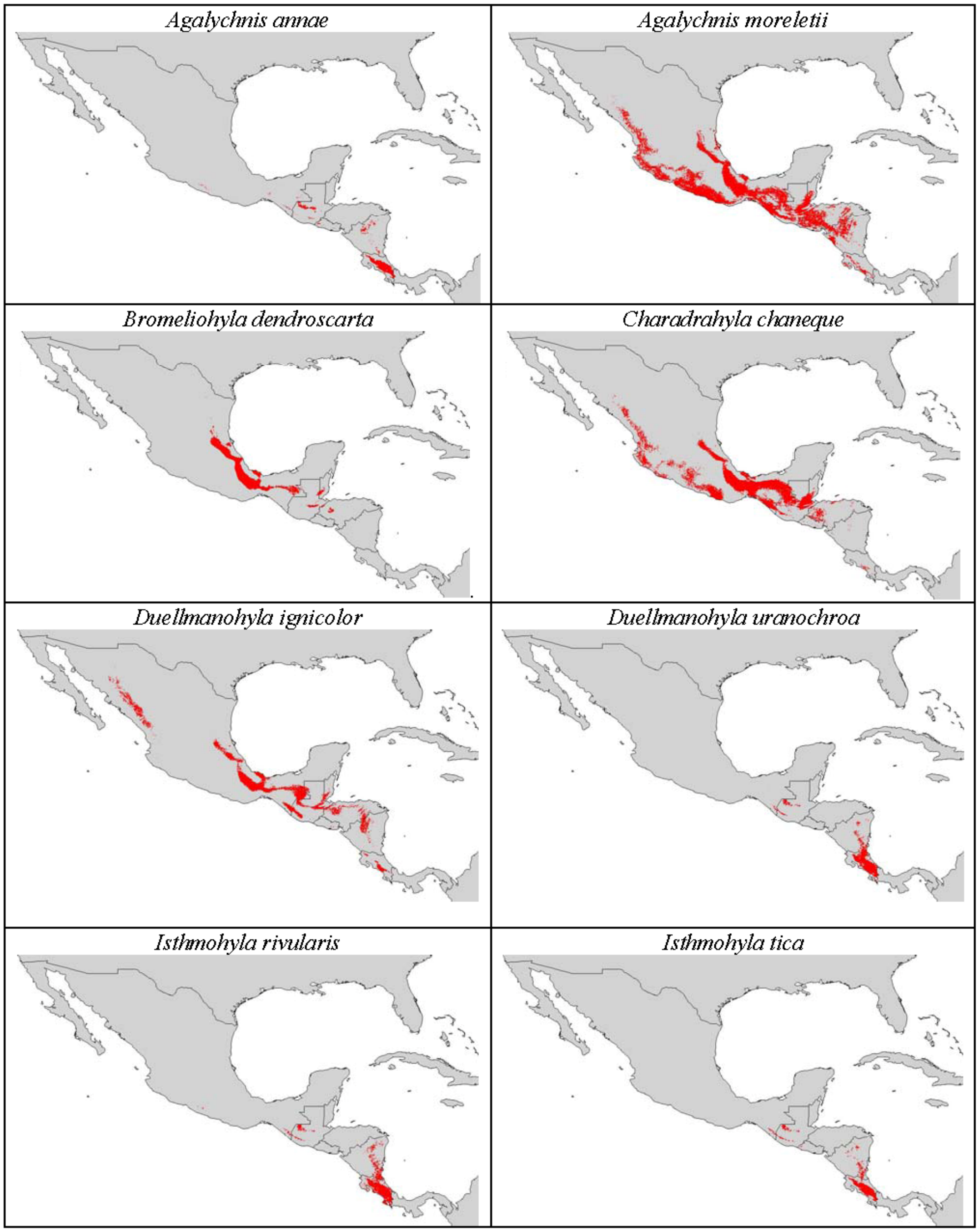

Fig. 4. Potential geographic distribution of each of the 16 endangered-hylid species in Mesoamerica.

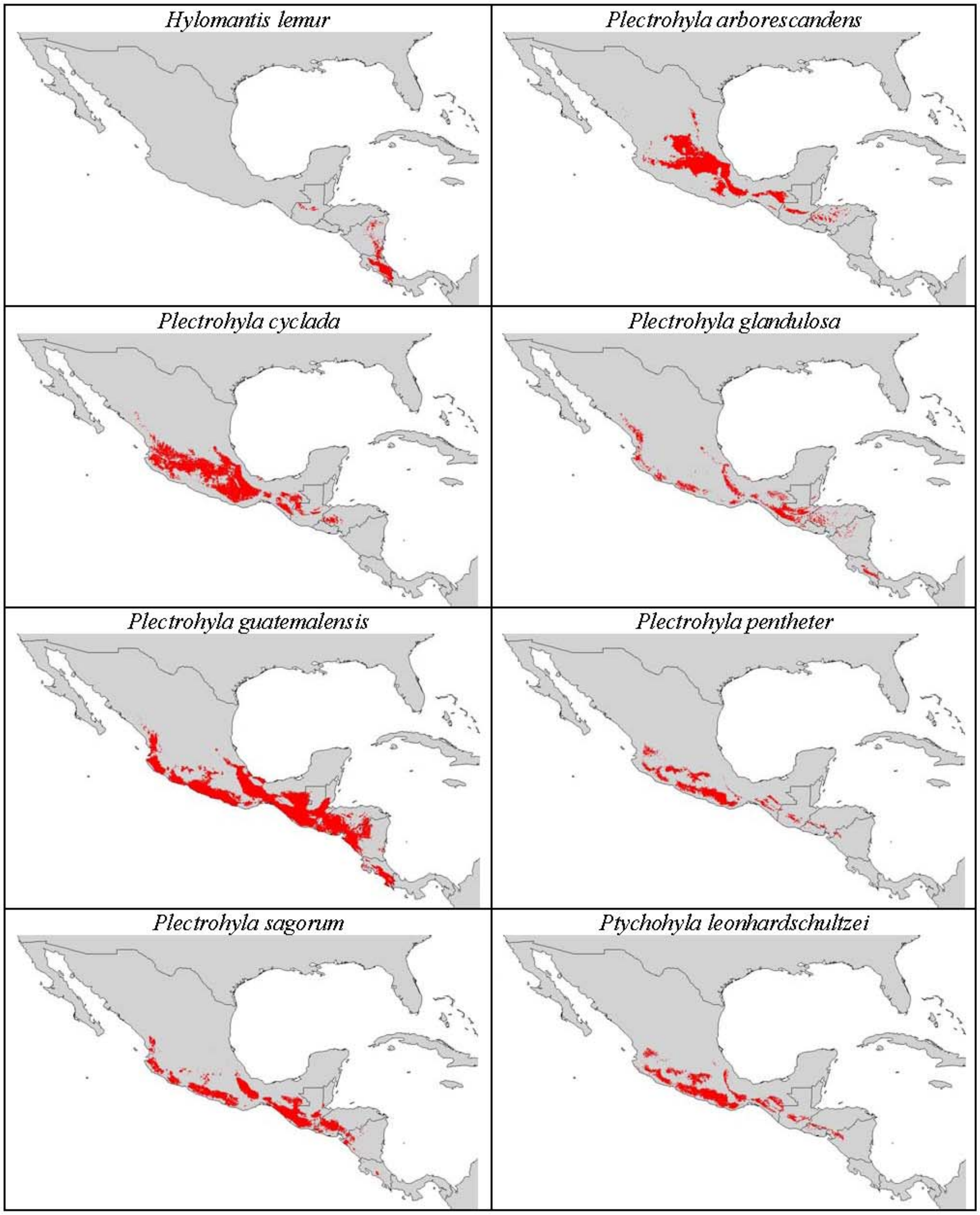

Fig. 4 continued. Potential geographic distribution of each of the 16 endangered-hylid species in Mesoamerica.

Discussion

This is one of the few studies applying niche-based models to predict potential geographic distributions of endangered hylids in the continental Neotropics. It is also the first attempt to evaluate the effectiveness of the Neotropical network of protected areas in representing and safeguarding hylids. Our results demonstrate that the extent of occurrence of ecological niche of some Neotropical endangered hylids may be much larger than the current species distribution reported by international conservation agencies [56], albeit the proportion of their geographic range currently under protection is still low for most species, especially if their potential distributions are restricted to Mesoamerica.

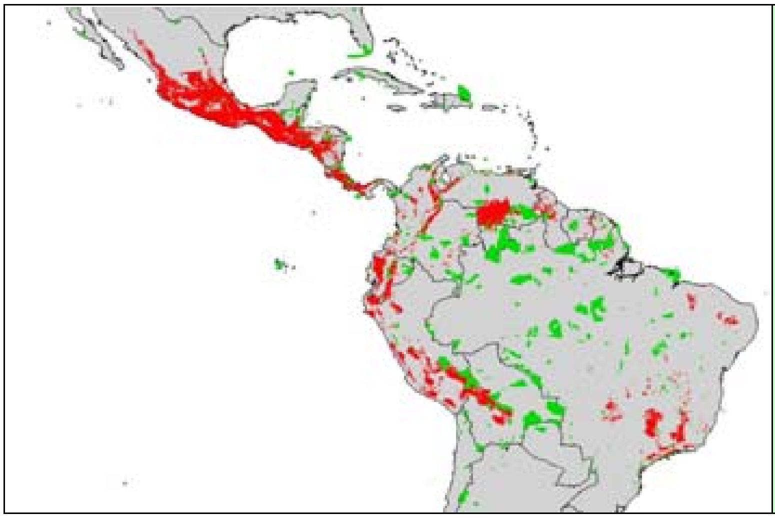

Fig. 5. Total (summed) potential geographic distribution of the 16 endangered-hylid species evaluated (shown in red) and the network of Neotropical protected areas (shown in green).

For lack of better alternatives, range maps and estimates of species geographic ranges based on niche-modeling techniques have become the baseline data for many broad-scale analyses in ecology and conservation biogeography [15, 57]. In this study we found that climate and topography exert a great deal of influence on threatened hylids´ distribution. Such influence is not as simple as reported by literature (*see* [43]). It seems that there is a strong influence of slope (more than elevation) that interacts synergistically with rainfall and temperature to determine species geographic distribution. Hence, the relation between hylid species occurrence with climatic variables is not as simple given that the utmost variables determining species potential distributions in this study were maximum precipitation and temperature change over a year. Taking that into consideration at a microenvironment scale, some important variables influencing amphibian ensembles are canopy cover, understory density, leaf litter cover and temperature [10, 58]. This gives us an insight about how drastic could be climate change effecting threatened Neotropical hylids distribution at different spatial scales.

It is also known that extent of occurrence maps obtained by niche-based models can overestimate species current distribution and geographic range sizes, biasing broad-scale ecological patterns and their correlates [57]. Following current distribution maps of the Global Amphibian Assessment [56], all 16 studied species have geographic distributions historically restricted to Mesoamerica. Nevertheless, all potential distribution models seem to present a certain degree of over prediction in South America (Appendix 2). This does not mean that not all studied species necessarily occur at overpredicted areas. The environmental conditions of a predicted ecological niche could be represented in multiple areas along a geographical space [45]. However, species do not use all suitable ecological niches available along the geographical space, since it is constrained by species behavior, dispersal ability, and inter and intra-specific interactions that take place at local and landscape scales [18, 59]. This is the main reason why we have built more conservative species distribution models, restricted to Mesoamerica. In that case, the probability of occurrence of a given hylid species is indeed high and, therefore, the degree of geographic range overestimation may be low – reflecting actual species distributions and some particular areas needing more detailed surveys in order to confirm the occurrence of species. In fact, when modeling species actual distributions (which are based on real species occurrence data [47]) over-predicted areas could indicate the occurrence of some phylogenetically close-related hylids which are expected to have similar ecological niches. Overlapping areas of overprediction in South America could be themselves extremely important for the discovery of unknown distributional areas and undescribed species (*see* [19]), which, in turn, could be as threatened as the modeled ones due to their microendemicity patterns.

We suggest the use of MaxEnt (instead of other presence-only methods [18, 48, 60]) to assess the effectiveness of protected areas in representing endangered species because: (1) this software constrains predicted species ranges reducing and avoiding commission errors (*i.e.* when a model predicts the presence of a given species in particular areas, although it is known that this species is not present there [48, 61]). Commission errors (or false positive rate) could lead to erroneous conservation decisions focusing financial investments and management efforts in non-priority areas; (2) Although MaxEnt generates high omission errors or false negative rate (*i.e.* when a model predicts the absence of a species in particular areas, though it is known that this species is indeed present there [48, 61]), such errors are preferable when models are conceived for conservation purposes [62]. Loiselle *et al.* [62], for instance, demonstrated that using distribution models that minimize false positives (such as MaxEnt's models) for well known taxa, priority areas highlighted for conservation matched up those previously selected by experts in biogeography, ecology and taxonomy.

Implications for conservation

When predicting species distributions for the entire Neotropics, we found that six hylids (*P. pentheter*, *P. sagorum*, *C. chaneque*, *D. ignicolor*, *Agalychnis moreletii* and *P. leonhardschultzei*) are still in need of additional conservation areas to ensure the protection of 25% of its potential distribution range. Most important however, was the finding that *P. pentheter* while holding the smallest potential distribution range (102,625 Km^2), also have the smaller percentage of its range (13.3%) included in protected areas. Restricted-range species, such as *P. pentheter*, are worthwhile given that they usually tend to be endemic. Several global conservation assessments highlight endemic species as a worthwhile conservation goal, e.g. the Global 200 ecoregions [63], and the Biodiversity Hotspots [32]. Some studies also pointed out that endemic species also provide a useful guideline for identifying conservation priorities at a global or regional scale [9, 64]. We suggest, therefore, that Neotropical hylids with restricted ranges should receive marked attention of conservationists and policy makers, especially if they are threatened of extinction, like *P. pentheter*.

Under more conservative models that predicted species geographic range within Mesoamerica, the number of species needing additional areas for the protection of at least a quarter of its potential geographic range increased up to ten. We found that most Neotropical endangered hylids have only the periphery of their distribution protected, and this aspect is critical given that human population growth is much higher around protected area edges than in other rural areas [65]. When predicted distributions of species were restricted to Mesoamerica, mean percent range protected decreased from *ca.* 29% to *ca.* 23%. For the species *I. rivularis*, in particular, range protection fell from 37.6% to 0%. Species like that have most of their protected range located in South America, but as mentioned before, to date we have no data on the occurrence of these species at sites predicted by our models. Many species may be actually threatened because they now occur in small and isolated subpopulations due to habitat fragmentation. Whereas the sites where they survive need to be managed as a coordinated network, the lack of protection of species core distribution usually implies in protecting populations threatened by several ecological and genetic processes like inbreeding, genetic drift, and demographic stochasticity. In the longer term, site-scale actions for effective protection of these species will likely need to be supported by broad-scale approaches, such as the restoration of connectivity. Recently, Loyola *et al.* [3] proposed priority sets of Neotropical regions that should be sufficiently covered in a reserve system to protected threatened anurans with distinct reproductive modes. Most of their proposed areas for the conservation of species requiring aquatic habitats for their reproduction are found in Mesoamerica. The results of our study, while being attained at a finer spatial scale, corroborate and push even further the need of effective natural protected areas in this region if endangered anurans that require aquatic habitats – which are the majority of species with reported population declines (*see* [26, 66]) – are meant to be protected.

Niche-based distribution modeling is an innovative analytical approach to evaluate the effectiveness of protected areas, especially in regions lacking comprehensive databases of species distribution. Combination of niche-based distribution modeling and reserve selection algorithms is also a promising approach [67-68]. It works as an effective tool that should be applied in systematic conservation planning to identify and interconnect priority regions, particularly those already covered by natural protected areas [69]. Moreover, it is an efficient tool for identifying gaps in actual reserve systems, especially when it highlights regions that surround protected areas and, therefore, complement proposed conservation plans [69-71]. Although amphibians and reptiles are not commonly used as biodiversity surrogates in systematic conservation planning [22], recently, niche-based distribution models combined with reserve selection techniques were used to pinpoint conservation priorities in India [22] and Mexico [72]. These authors generated models to different taxa to find overall congruences among different taxonomic groups. Such congruence is obviously attractive given that it indicates that priorities identified for a particular species subset would be effective for non-target ones. In a recent essay, Bode *et al*. [73] found that funding allocations were less sensitive to choice of taxon assessed than to variation in economic costs of land acquisition and species threat. These results strengthen confidence in decisions guided by single taxonomic groups [73].

Finally, among the leading factors that threaten amphibians, habitat loss, habitat fragmentation, and habitat split are the most important and, perhaps, the major causes of species extinction in general [2, 6-8]. All these factors are thought to be minimized within a network of natural protected areas, which remains as the cornerstone of conservation strategies. Loucks *et al.* [28] have demonstrated that, globally, species endemism, species richness, and to a lesser extent threatened species explained better the global pattern of protected area coverage. Our results, by mapping threatened species potential geographic distribution, revealed that we need more protected areas in Mesoamerica contributing to other studies that have highlighted this for other taxonomic groups such as amphibians and reptiles [3, 8, 23, 74], and carnivores [54, 75]. Given the rapid ongoing transformation of habitats worldwide, proactive attitudes are imperative and uncertainty cannot be used as a pretext for not performing researches or not implementing conservation actions [44]. Besides the inherent uncertainties associated with field data, geographical databases and niche-modeling algorithms; niche-based distribution models have a major potential use in ecology, biogeography, conservation biology and policy that should be better explored. Gaps in geographic range protection presented here helps to pinpoint were conservation assessments should be focused to ensure the persistence of endangered hylids in the Neotropical region.

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Appendix 1. Historical geographic records of each of the 16 endangered-hylid species in the Neotropical region.

Species name	Latitude	Longitude	Species name	Latitude	Longitude
Agalychnis annae	8.760970	-82.966700	*Hylomantis lemur*	9.766670	-83.766670
Agalychnis annae	9.110000	-82.770000	*Hylomantis lemur*	9.767500	-83.803670
Agalychnis annae	9.733300	-82.966700	*Hylomantis lemur*	9.795280	-84.398000
Agalychnis annae	9.740030	-83.865480	*Hylomantis lemur*	9.878620	-83.618580
Agalychnis annae	9.754840	-83.803670	*Hylomantis lemur*	9.922320	-83.596470
Agalychnis annae	9.766670	-83.766670	*Hylomantis lemur*	10.000000	-83.550000
Agalychnis annae	9.767500	-83.803670	*Hylomantis lemur*	10.027190	-83.988170
Agalychnis annae	9.767500	-83.803670	*Hylomantis lemur*	10.039850	-83.988170
Agalychnis annae	9.767670	-83.801630	*Hylomantis lemur*	10.068830	-83.972820
Agalychnis annae	9.850000	-83.433300	*Hylomantis lemur*	10.076980	-83.892230
Agalychnis annae	9.933300	-84.050000	*Hylomantis lemur*	10.077330	-83.967800
Agalychnis annae	9.933300	-84.083298	*Hylomantis lemur*	10.079700	-83.971000
Agalychnis annae	9.933300	-84.183300	*Hylomantis lemur*	10.220000	-83.650000
Agalychnis annae	9.938620	-84.052620	*Hylomantis lemur*	10.283330	-84.800000
Agalychnis annae	9.983330	-84.083330	*Hylomantis lemur*	10.286680	-84.433150
Agalychnis annae	10.027170	-83.942370	*Hylomantis lemur*	10.333330	-84.750000
Agalychnis annae	10.220000	-83.650000	*Plectrohyla arborescandens*	18.610000	-97.600000
Agalychnis annae	10.300000	-84.816667	*Plectrohyla arborescandens*	18.628330	-97.325000
Agalychnis annae	10.482330	-84.903900	*Plectrohyla arborescandens*	18.683330	-97.333330
Agalychnis moreletii	12.040000	-86.480000	*Plectrohyla arborescandens*	18.690000	-97.340000
Agalychnis moreletii	13.869000	-89.621000	*Plectrohyla arborescandens*	18.699720	-97.315560
Agalychnis moreletii	14.384170	-90.759440	*Plectrohyla arborescandens*	18.703610	-97.360560
Agalychnis moreletii	14.960000	-89.170000	*Plectrohyla arborescandens*	18.715000	-97.308330
Agalychnis moreletii	15.030000	-92.150000	*Plectrohyla arborescandens*	18.716670	-97.300000
Agalychnis moreletii	15.036390	-92.145278	*Plectrohyla arborescandens*	18.716670	-97.350000
Agalychnis moreletii	15.150000	-92.280000	*Plectrohyla arborescandens*	18.730000	-97.290000
Agalychnis moreletii	15.180000	-89.610000	*Plectrohyla arborescandens*	18.883330	-96.866670
Agalychnis moreletii	15.305560	-92.393060	*Plectrohyla arborescandens*	18.920000	-97.130000
Agalychnis moreletii	15.340000	-92.610000	*Plectrohyla arborescandens*	19.033330	-97.250000
Agalychnis moreletii	15.362500	-92.654170	*Plectrohyla arborescandens*	19.066670	-97.033330
Agalychnis moreletii	15.376670	-92.632220	*Plectrohyla arborescandens*	19.150000	-96.965000
Agalychnis moreletii	15.376940	-92.490000	*Plectrohyla arborescandens*	19.366670	-97.066670
Agalychnis moreletii	15.483330	-89.866670	*Plectrohyla arborescandens*	19.385000	-96.971670
Agalychnis moreletii	15.803610	-91.315830	*Plectrohyla arborescandens*	19.515560	-96.984720
Agalychnis moreletii	15.883330	-91.258060	*Plectrohyla arborescandens*	19.521670	-96.997220
Agalychnis moreletii	15.940000	-96.480000	*Plectrohyla arborescandens*	19.595280	-97.044170
Agalychnis moreletii	15.950000	-96.470000	*Plectrohyla arborescandens*	19.609440	-96.896390
Agalychnis moreletii	16.016670	-97.066670	*Plectrohyla arborescandens*	19.616670	-97.033330
Agalychnis moreletii	16.140000	-97.050000	*Plectrohyla arborescandens*	19.788000	-97.292670

Appendix 1 …. continued

Species name	Latitude	Longitude	Species name	Latitude	Longitude
Agalychnis moreletii	16.150000	-97.080000	*Plectrohyla arborescandens*	19.790000	-97.350000
Agalychnis moreletii	16.340000	-98.050000	*Plectrohyla arborescandens*	19.830000	-97.340000
Agalychnis moreletii	16.583330	-89.033333	*Plectrohyla arborescandens*	19.870000	-97.310000
Agalychnis moreletii	16.723610	-93.090280	*Plectrohyla arborescandens*	20.120000	-98.120000
Agalychnis moreletii	16.750000	-99.750000	*Plectrohyla cyclada*	16.550000	-96.980000
Agalychnis moreletii	16.854170	-93.411110	*Plectrohyla cyclada*	17.010000	-96.720000
Agalychnis moreletii	16.868060	-93.375000	*Plectrohyla cyclada*	17.126670	-96.695000
Agalychnis moreletii	16.870000	-93.450000	*Plectrohyla cyclada*	17.180000	-97.180000
Agalychnis moreletii	16.890000	-93.290000	*Plectrohyla cyclada*	17.190000	-96.980000
Agalychnis moreletii	17.090000	-92.800000	*Plectrohyla cyclada*	17.240000	-96.060000
Agalychnis moreletii	17.100000	-90.330000	*Plectrohyla cyclada*	17.280000	-96.000000
Agalychnis moreletii	17.308330	-93.100000	*Plectrohyla cyclada*	17.320000	-96.500000
Agalychnis moreletii	17.556940	-93.106940	*Plectrohyla cyclada*	17.340000	-97.050000
Agalychnis moreletii	17.566670	-96.550000	*Plectrohyla cyclada*	17.470000	-96.670000
Agalychnis moreletii	17.690000	-96.330000	*Plectrohyla cyclada*	17.580000	-96.510000
Agalychnis moreletii	17.716670	-96.366670	*Plectrohyla cyclada*	17.583330	-96.350000
Agalychnis moreletii	17.750000	-96.316670	*Plectrohyla cyclada*	17.590000	-96.490000
Agalychnis moreletii	18.050000	-96.470000	*Plectrohyla cyclada*	17.620000	-96.350000
Agalychnis moreletii	18.150000	-95.300000	*Plectrohyla cyclada*	17.620000	-96.380000
Agalychnis moreletii	18.233330	-95.133330	*Plectrohyla cyclada*	17.630000	-96.340000
Agalychnis moreletii	18.333330	-94.933330	*Plectrohyla cyclada*	17.635500	-96.360000
Agalychnis moreletii	18.376670	-95.013060	*Plectrohyla cyclada*	17.650000	-96.340000
Agalychnis moreletii	18.490000	-95.050000	*Plectrohyla cyclada*	17.650000	-96.360000
Agalychnis moreletii	18.496390	-95.061940	*Plectrohyla cyclada*	17.666670	-96.350000
Agalychnis moreletii	18.550000	-95.200000	*Plectrohyla cyclada*	17.670000	-96.320000
Agalychnis moreletii	18.566670	-95.200000	*Plectrohyla cyclada*	17.670000	-96.330000
Agalychnis moreletii	18.860000	-97.030000	*Plectrohyla cyclada*	17.670000	-96.370000
Agalychnis moreletii	18.860000	-97.070000	*Plectrohyla cyclada*	17.675000	-96.330000
Agalychnis moreletii	18.870000	-97.021670	*Plectrohyla cyclada*	17.680000	-96.330000
Agalychnis moreletii	18.870000	-97.030000	*Plectrohyla cyclada*	17.681000	-96.330000
Agalychnis moreletii	18.882780	-96.955830	*Plectrohyla cyclada*	17.682000	-96.330000
Agalychnis moreletii	18.888330	-96.930000	*Plectrohyla cyclada*	17.683330	-96.350000
Agalychnis moreletii	20.050000	-97.500000	*Plectrohyla cyclada*	17.684000	-96.330000
Agalychnis moreletii	20.051390	-97.652220	*Plectrohyla cyclada*	17.685500	-96.330000
Agalychnis moreletii	20.206670	-96.776670	*Plectrohyla cyclada*	17.690000	-96.370000
Bromeliohyla dendroscarta	17.100000	-90.330000	*Plectrohyla cyclada*	17.709000	-96.310000
Bromeliohyla dendroscarta	17.590000	-96.500000	*Plectrohyla cyclada*	17.710000	-96.310000
Bromeliohyla dendroscarta	17.621940	-96.343889	*Plectrohyla cyclada*	17.720000	-96.320000
Bromeliohyla dendroscarta	17.650000	-96.340000	*Plectrohyla cyclada*	17.750000	-96.730000
Bromeliohyla dendroscarta	17.650000	-96.360000	*Plectrohyla cyclada*	18.158320	-96.999780
Bromeliohyla dendroscarta	17.683330	-96.350000	*Plectrohyla cyclada*	18.170000	-96.920000

Appendix 1 …. continued

Species name	**Latitude**	**Longitude**	**Species name**	**Latitude**	**Longitude**
Bromeliohyla dendroscarta	17.716670	-96.366670	*Plectrohyla cyclada*	18.173700	-97.008600
Bromeliohyla dendroscarta	17.820000	-96.740000	*Plectrohyla glandulosa*	14.383330	-89.133330
Bromeliohyla dendroscarta	18.340000	-94.940000	*Plectrohyla glandulosa*	14.787220	-91.653530
Bromeliohyla dendroscarta	18.607190	-95.143708	*Plectrohyla glandulosa*	14.800000	-91.666670
Bromeliohyla dendroscarta	18.750000	-97.000000	*Plectrohyla glandulosa*	14.900000	-91.300000
Bromeliohyla dendroscarta	18.850000	-97.040000	*Plectrohyla glandulosa*	14.929870	-91.825260
Bromeliohyla dendroscarta	18.866670	-97.033330	*Plectrohyla glandulosa*	14.940000	-91.870000
Bromeliohyla dendroscarta	18.870000	-97.021670	*Plectrohyla glandulosa*	14.944080	-91.855780
Bromeliohyla dendroscarta	18.870000	-97.022500	*Plectrohyla glandulosa*	14.953110	-91.851130
Bromeliohyla dendroscarta	18.870000	-97.030000	*Plectrohyla glandulosa*	14.959750	-91.850510
Bromeliohyla dendroscarta	18.875000	-96.841670	*Plectrohyla glandulosa*	14.960000	-89.170000
Bromeliohyla dendroscarta	18.880000	-97.000000	*Plectrohyla glandulosa*	14.966670	-91.851130
Bromeliohyla dendroscarta	18.888330	-96.930000	*Plectrohyla glandulosa*	14.966670	-91.851920
Bromeliohyla dendroscarta	18.900000	-97.016670	*Plectrohyla glandulosa*	14.966670	-91.860430
Bromeliohyla dendroscarta	18.933330	-97.000000	*Plectrohyla glandulosa*	14.966670	-91.870520
Bromeliohyla dendroscarta	19.126390	-96.985833	*Plectrohyla glandulosa*	14.970000	-91.870000
Bromeliohyla dendroscarta	19.132170	-96.999330	*Plectrohyla glandulosa*	14.977970	-91.847270
Bromeliohyla dendroscarta	19.150000	-96.980000	*Plectrohyla glandulosa*	14.980000	-91.790000
Bromeliohyla dendroscarta	19.200000	-96.766670	*Plectrohyla glandulosa*	15.180000	-89.610000
Bromeliohyla dendroscarta	19.207170	-96.808330	*Plectrohyla glandulosa*	15.419480	-90.749500
Bromeliohyla dendroscarta	19.410000	-97.000000	*Plectrohyla glandulosa*	17.090000	-92.800000
Bromeliohyla dendroscarta	19.620000	-96.920000	*Plectrohyla guatemalensis*	9.940000	-74.170000
Bromeliohyla dendroscarta	20.000000	-97.520000	*Plectrohyla guatemalensis*	12.040000	-86.480000
Bromeliohyla dendroscarta	20.640000	-98.390000	*Plectrohyla guatemalensis*	14.794080	-91.677870
Bromeliohyla dendroscarta	21.790000	-98.210000	*Plectrohyla guatemalensis*	14.929870	-91.825260
Charadrahyla chaneque	16.530000	-94.400000	*Plectrohyla guatemalensis*	14.960000	-89.170000
Charadrahyla chaneque	16.654720	-94.468610	*Plectrohyla guatemalensis*	15.060000	-92.090000
Charadrahyla chaneque	16.940000	-99.600000	*Plectrohyla guatemalensis*	15.080000	-92.090000
Charadrahyla chaneque	17.030000	-97.560000	*Plectrohyla guatemalensis*	15.083330	-92.083330
Charadrahyla chaneque	17.100000	-90.330000	*Plectrohyla guatemalensis*	15.088070	-91.089710
Charadrahyla chaneque	17.148610	-93.006940	*Plectrohyla guatemalensis*	15.110000	-92.100000
Charadrahyla chaneque	17.155560	-93.013890	*Plectrohyla guatemalensis*	15.110000	-92.110000
Charadrahyla chaneque	17.170000	-93.040000	*Plectrohyla guatemalensis*	15.129440	-92.114167
Charadrahyla chaneque	17.190000	-93.000000	*Plectrohyla guatemalensis*	15.130000	-92.120000
Charadrahyla chaneque	17.190000	-93.050000	*Plectrohyla guatemalensis*	15.130000	-92.130000
Charadrahyla chaneque	17.481940	-93.102780	*Plectrohyla guatemalensis*	15.150000	-92.280000
Charadrahyla chaneque	17.583330	-96.350000	*Plectrohyla guatemalensis*	15.180000	-89.610000
Charadrahyla chaneque	17.620000	-96.370000	*Plectrohyla guatemalensis*	15.316670	-92.733330
Charadrahyla chaneque	17.635500	-96.360000	*Plectrohyla guatemalensis*	15.401400	-90.856620
Charadrahyla chaneque	17.650000	-96.355000	*Plectrohyla guatemalensis*	15.425000	-92.341670
Charadrahyla chaneque	17.650000	-96.360000	*Plectrohyla guatemalensis*	15.440000	-92.890000

Appendix 1 …. continued

Species name	Latitude	Longitude	Species name	Latitude	Longitude
Charadrahyla chaneque	17.670000	-96.330000	*Plectrohyla guatemalensis*	15.690000	-92.930000
Charadrahyla chaneque	17.670000	-96.370000	*Plectrohyla guatemalensis*	15.750000	-92.283330
Charadrahyla chaneque	17.675000	-96.330000	*Plectrohyla guatemalensis*	16.280000	-92.880000
Charadrahyla chaneque	17.680000	-96.330000	*Plectrohyla guatemalensis*	16.650000	-94.190000
Charadrahyla chaneque	17.681000	-96.330000	*Plectrohyla guatemalensis*	17.090000	-92.800000
Charadrahyla chaneque	17.683330	-96.350000	*Plectrohyla guatemalensis*	17.100000	-90.330000
Charadrahyla chaneque	17.684000	-96.330000	*Plectrohyla pentheter*	15.916670	-96.416670
Charadrahyla chaneque	17.685000	-96.330000	*Plectrohyla pentheter*	15.994830	-96.534500
Charadrahyla chaneque	17.685500	-96.330000	*Plectrohyla pentheter*	16.020000	-96.530000
Charadrahyla chaneque	17.691000	-96.360000	*Plectrohyla pentheter*	16.030000	-96.510000
Charadrahyla chaneque	17.700000	-96.320000	*Plectrohyla pentheter*	16.030000	-96.520000
Charadrahyla chaneque	17.709000	-96.310000	*Plectrohyla pentheter*	16.150000	-97.080000
Charadrahyla chaneque	17.710000	-96.310000	*Plectrohyla pentheter*	16.216670	-97.150000
Charadrahyla chaneque	17.820000	-96.740000	*Plectrohyla pentheter*	16.220000	-96.950000
Duellmanohyla ignicolor	9.940000	-74.170000	*Plectrohyla pentheter*	16.220000	-97.140000
Duellmanohyla ignicolor	15.150000	-92.280000	*Plectrohyla pentheter*	16.220000	-97.150000
Duellmanohyla ignicolor	17.100000	-90.330000	*Plectrohyla pentheter*	16.248020	-97.147380
Duellmanohyla ignicolor	17.620000	-96.370000	*Plectrohyla pentheter*	16.250000	-97.150000
Duellmanohyla ignicolor	17.620000	-96.380000	*Plectrohyla pentheter*	16.270000	-97.150000
Duellmanohyla ignicolor	17.630000	-96.340000	*Plectrohyla pentheter*	16.280000	-97.140000
Duellmanohyla ignicolor	17.630000	-96.370000	*Plectrohyla pentheter*	16.283330	-97.133330
Duellmanohyla ignicolor	17.633330	-96.366670	*Plectrohyla pentheter*	16.283330	-97.150000
Duellmanohyla ignicolor	17.670000	-96.370000	*Plectrohyla pentheter*	16.470000	-96.980000
Duellmanohyla ignicolor	17.683330	-96.350000	*Plectrohyla pentheter*	16.930000	-95.920000
Duellmanohyla ignicolor	17.690000	-96.360000	*Plectrohyla pentheter*	16.940000	-95.710000
Duellmanohyla ignicolor	17.690000	-96.390000	*Plectrohyla pentheter*	17.060000	-97.860000
Duellmanohyla ignicolor	17.695000	-96.370000	*Plectrohyla pentheter*	17.150000	-97.900000
Duellmanohyla ignicolor	17.716670	-96.366670	*Plectrohyla pentheter*	17.166670	-97.883330
Duellmanohyla ignicolor	17.720000	-96.310000	*Plectrohyla pentheter*	17.230000	-98.880000
Duellmanohyla ignicolor	17.720000	-96.320000	*Plectrohyla pentheter*	17.433330	-99.583330
Duellmanohyla ignicolor	17.730000	-96.320000	*Plectrohyla sagorum*	9.940000	-74.170000
Duellmanohyla ignicolor	17.810000	-96.240000	*Plectrohyla sagorum*	14.383330	-89.133330
Duellmanohyla ignicolor	17.820000	-96.740000	*Plectrohyla sagorum*	14.766670	-91.666670
Duellmanohyla ignicolor	18.240000	-96.780000	*Plectrohyla sagorum*	14.876290	-91.772110
Duellmanohyla uranochroa	9.110000	-82.770000	*Plectrohyla sagorum*	14.920000	-91.920000
Duellmanohyla uranochroa	9.300000	-83.800000	*Plectrohyla sagorum*	14.930000	-91.910000
Duellmanohyla uranochroa	9.519930	-83.757250	*Plectrohyla sagorum*	14.935040	-91.883670
Duellmanohyla uranochroa	9.614000	-83.786160	*Plectrohyla sagorum*	14.937300	-91.879020
Duellmanohyla uranochroa	9.687030	-83.803670	*Plectrohyla sagorum*	14.939560	-91.869720
Duellmanohyla uranochroa	9.711840	-83.746550	*Plectrohyla sagorum*	14.939560	-91.874370
Duellmanohyla uranochroa	9.775710	-83.766670	*Plectrohyla sagorum*	14.953110	-91.869720

Appendix 1 …. continued

Species name	**Latitude**	**Longitude**	**Species name**	**Latitude**	**Longitude**
Duellmanohyla uranochroa	9.842330	-83.907500	*Plectrohyla sagorum*	15.080000	-92.090000
Duellmanohyla uranochroa	9.902170	-83.627720	*Plectrohyla sagorum*	15.080560	-92.091670
Duellmanohyla uranochroa	10.000000	-83.550000	*Plectrohyla sagorum*	15.083330	-92.083330
Duellmanohyla uranochroa	10.000000	-84.000000	*Plectrohyla sagorum*	15.110000	-92.100000
Duellmanohyla uranochroa	10.027190	-83.988170	*Plectrohyla sagorum*	15.129440	-92.114167
Duellmanohyla uranochroa	10.050000	-84.074210	*Plectrohyla sagorum*	15.150000	-92.280000
Duellmanohyla uranochroa	10.061580	-83.991920	*Plectrohyla sagorum*	15.180000	-89.610000
Duellmanohyla uranochroa	10.063360	-84.077750	*Plectrohyla sagorum*	15.200000	-92.420000
Duellmanohyla uranochroa	10.200000	-84.000000	*Plectrohyla sagorum*	15.316670	-92.733330
Duellmanohyla uranochroa	10.200000	-84.200000	*Plectrohyla sagorum*	15.320000	-92.305000
Duellmanohyla uranochroa	10.216700	-84.183300	*Plectrohyla sagorum*	15.330000	-92.290000
Duellmanohyla uranochroa	10.217390	-84.172620	*Plectrohyla sagorum*	15.341940	-92.257222
Duellmanohyla uranochroa	10.220000	-83.650000	*Plectrohyla sagorum*	15.347780	-92.252500
Duellmanohyla uranochroa	10.226760	-84.180160	*Plectrohyla sagorum*	15.360000	-92.480000
Duellmanohyla uranochroa	10.227810	-84.492670	*Plectrohyla sagorum*	15.362220	-92.654170
Duellmanohyla uranochroa	10.244030	-84.170280	*Plectrohyla sagorum*	15.370830	-92.601390
Duellmanohyla uranochroa	10.283330	-84.800000	*Plectrohyla sagorum*	15.381390	-92.625000
Duellmanohyla uranochroa	10.286680	-84.796670	*Plectrohyla sagorum*	15.390000	-92.410000
Duellmanohyla uranochroa	10.291670	-84.810900	*Plectrohyla sagorum*	15.410000	-92.630000
Duellmanohyla uranochroa	10.293930	-84.802670	*Plectrohyla sagorum*	15.410000	-92.640000
Duellmanohyla uranochroa	10.300000	-84.800000	*Plectrohyla sagorum*	15.420830	-92.566670
Duellmanohyla uranochroa	10.300000	-84.816667	*Plectrohyla sagorum*	15.430000	-92.630000
Duellmanohyla uranochroa	10.303000	-84.808830	*Plectrohyla sagorum*	15.440000	-92.340000
Duellmanohyla uranochroa	10.306150	-84.819600	*Plectrohyla sagorum*	15.445560	-92.108333
Duellmanohyla uranochroa	10.331520	-84.433600	*Plectrohyla sagorum*	15.660000	-92.740000
Duellmanohyla uranochroa	10.333330	-84.750000	*Plectrohyla sagorum*	15.662220	-92.816390
Duellmanohyla uranochroa	10.424400	-84.020000	*Plectrohyla sagorum*	15.700000	-92.640000
Duellmanohyla uranochroa	10.482330	-84.903900	*Plectrohyla sagorum*	15.750000	-92.283330
Duellmanohyla uranochroa	10.500000	-84.900000	*Plectrohyla sagorum*	15.799720	-93.088060
Duellmanohyla uranochroa	10.933330	-85.450000	*Plectrohyla sagorum*	15.801110	-93.074440
Isthmohyla rivularis	8.520000	-82.280000	*Plectrohyla sagorum*	15.802220	-93.068890
Isthmohyla rivularis	8.603270	-83.103270	*Plectrohyla sagorum*	15.815830	-93.070560
Isthmohyla rivularis	8.650000	-83.150000	*Plectrohyla sagorum*	15.816670	-93.064440
Isthmohyla rivularis	8.934830	-82.800270	*Plectrohyla sagorum*	16.152780	-93.643330
Isthmohyla rivularis	9.110000	-82.770000	*Plectrohyla sagorum*	16.201390	-93.582500
Isthmohyla rivularis	9.492750	-83.690220	*Plectrohyla sagorum*	16.280000	-92.880000
Isthmohyla rivularis	9.711840	-83.746550	*Ptychohyla leonhardschultzei*	15.850000	-96.460000
Isthmohyla rivularis	9.727810	-83.794630	*Ptychohyla leonhardschultzei*	15.910000	-96.490000
Isthmohyla rivularis	9.792240	-83.740890	*Ptychohyla leonhardschultzei*	15.933330	-96.233330
Isthmohyla rivularis	9.793560	-83.973020	*Ptychohyla leonhardschultzei*	15.936940	-96.470000
Isthmohyla rivularis	9.800000	-83.800000	*Ptychohyla leonhardschultzei*	15.949500	-96.471000

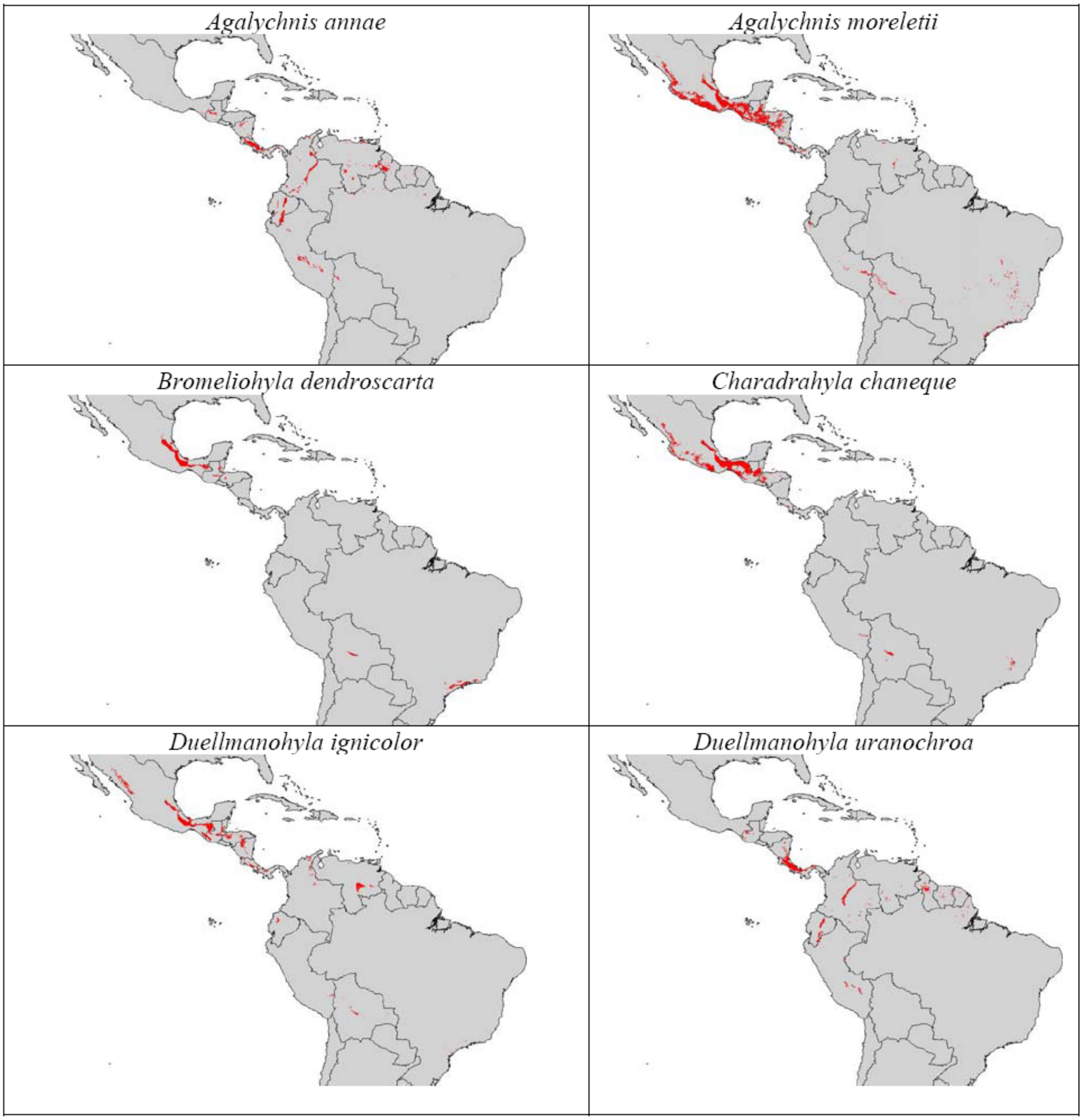
Appendix 1 …. continued

Species name	Latitude	Longitude	Species name	Latitude	Longitude
Isthmohyla rivularis	9.908000	-83.959670	*Ptychohyla leonhardschultzei*	15.994830	-96.534500
Isthmohyla rivularis	10.063360	-84.077750	*Ptychohyla leonhardschultzei*	16.020000	-96.530000
Isthmohyla rivularis	10.074410	-84.116700	*Ptychohyla leonhardschultzei*	16.030000	-96.510000
Isthmohyla rivularis	10.083300	-84.083300	*Ptychohyla leonhardschultzei*	16.030000	-96.520000
Isthmohyla rivularis	10.083330	-84.066670	*Ptychohyla leonhardschultzei*	16.080000	-97.080000
Isthmohyla rivularis	10.089900	-84.066930	*Ptychohyla leonhardschultzei*	16.110000	-97.070000
Isthmohyla rivularis	10.200000	-84.000000	*Ptychohyla leonhardschultzei*	16.140000	-97.060000
Isthmohyla rivularis	10.205600	-84.166670	*Ptychohyla leonhardschultzei*	16.150000	-95.916670
Isthmohyla rivularis	10.216700	-84.183300	*Ptychohyla leonhardschultzei*	16.150000	-97.080000
Isthmohyla rivularis	10.226760	-84.180160	*Ptychohyla leonhardschultzei*	16.180000	-96.090000
Isthmohyla rivularis	10.227810	-84.492670	*Ptychohyla leonhardschultzei*	16.216670	-97.150000
Isthmohyla rivularis	10.244030	-84.170280	*Ptychohyla leonhardschultzei*	16.220000	-97.140000
Isthmohyla rivularis	10.277510	-84.761840	*Ptychohyla leonhardschultzei*	16.220000	-97.150000
Isthmohyla rivularis	10.297550	-84.805870	*Ptychohyla leonhardschultzei*	16.225000	-97.491670
Isthmohyla rivularis	10.300000	-84.700000	*Ptychohyla leonhardschultzei*	16.233330	-97.100000
Isthmohyla rivularis	10.300000	-84.800000	*Ptychohyla leonhardschultzei*	16.250000	-97.150000
Isthmohyla rivularis	10.300000	-84.816667	*Ptychohyla leonhardschultzei*	16.260000	-95.940000
Isthmohyla rivularis	10.306150	-84.819600	*Ptychohyla leonhardschultzei*	16.260000	-97.150000
Isthmohyla rivularis	10.333330	-84.750000	*Ptychohyla leonhardschultzei*	16.280000	-97.140000
Isthmohyla rivularis	10.424400	-84.020000	*Ptychohyla leonhardschultzei*	16.280000	-97.150000
Isthmohyla rivularis	10.533300	-85.250000	*Ptychohyla leonhardschultzei*	16.281390	-95.901110
Isthmohyla rivularis	10.731130	-85.233330	*Ptychohyla leonhardschultzei*	16.283330	-97.133330
Isthmohyla tica	8.520000	-82.280000	*Ptychohyla leonhardschultzei*	16.330000	-98.050000
Isthmohyla tica	8.857670	-82.848550	*Ptychohyla leonhardschultzei*	16.433330	-96.983330
Isthmohyla tica	8.933330	-82.833333	*Ptychohyla leonhardschultzei*	16.465000	-96.999300
Isthmohyla tica	8.934830	-82.800270	*Ptychohyla leonhardschultzei*	16.470000	-96.980000
Isthmohyla tica	8.943830	-82.845600	*Ptychohyla leonhardschultzei*	16.478320	-96.997000
Isthmohyla tica	8.950000	-82.840830	*Ptychohyla leonhardschultzei*	16.585000	-95.801390
Isthmohyla tica	9.110000	-82.770000	*Ptychohyla leonhardschultzei*	16.630560	-96.957778
Isthmohyla tica	9.727810	-83.794630	*Ptychohyla leonhardschultzei*	16.650000	-98.070000
Isthmohyla tica	9.740030	-84.023550	*Ptychohyla leonhardschultzei*	16.650000	-98.090000
Isthmohyla tica	9.773080	-83.798270	*Ptychohyla leonhardschultzei*	16.759450	-95.460690
Isthmohyla tica	9.773420	-83.783680	*Ptychohyla leonhardschultzei*	16.790000	-95.120000
Isthmohyla tica	9.775710	-83.766670	*Ptychohyla leonhardschultzei*	16.820000	-95.120000
Isthmohyla tica	9.800000	-83.800000	*Ptychohyla leonhardschultzei*	16.930000	-95.920000
Isthmohyla tica	9.955170	-83.773320	*Ptychohyla leonhardschultzei*	16.940000	-95.710000
Isthmohyla tica	10.076980	-83.892230	*Ptychohyla leonhardschultzei*	16.950000	-95.733330
Isthmohyla tica	10.116840	-83.958330	*Ptychohyla leonhardschultzei*	16.988330	-97.893889
Isthmohyla tica	10.200000	-84.000000	*Ptychohyla leonhardschultzei*	16.990000	-97.890000
Isthmohyla tica	10.216700	-84.183300	*Ptychohyla leonhardschultzei*	17.030000	-97.560000
Isthmohyla tica	10.227810	-84.492670	*Ptychohyla leonhardschultzei*	17.080000	-96.050000

Appendix 1 …. continued

Species name	**Latitude**	**Longitude**	**Species name**	**Latitude**	**Longitude**
Isthmohyla tica	10.286680	-84.433150	*Ptychohyla leonhardschultzei*	17.100000	-97.880000
Isthmohyla tica	10.300000	-84.816667	*Ptychohyla leonhardschultzei*	17.111670	-97.876111
Isthmohyla tica	10.303000	-84.808830	*Ptychohyla leonhardschultzei*	17.250000	-100.350000
Isthmohyla tica	10.424400	-84.020000	*Ptychohyla leonhardschultzei*	17.329000	-99.473000
Isthmohyla tica	10.933330	-85.450000	*Ptychohyla leonhardschultzei*	17.333330	-99.483330
Hylomantis lemur	5.510000	-76.970000	*Ptychohyla leonhardschultzei*	17.420000	-100.190000
Hylomantis lemur	8.520000	-82.280000	*Ptychohyla leonhardschultzei*	17.421110	-100.195278
Hylomantis lemur	8.700000	-82.283330	*Ptychohyla leonhardschultzei*	17.583330	-96.447500
Hylomantis lemur	8.716670	-79.900000	*Ptychohyla leonhardschultzei*	17.670000	-96.690000
Hylomantis lemur	9.110000	-82.770000	*Ptychohyla leonhardschultzei*	21.790000	-98.210000

Appendix 2. Potential geographic distribution of each of the 16 endangered-hylid species in the Neotropical region.



Agalychnis annae

Agalychnis moreletii

Bromeliohyla dendroscarta

Charadrahyla chaneque

Duellmanohyla ignicolor

Duellmanohyla uranochroa

Appendix 2, continued


Isthmohyla rivularis


Isthmohyla tica

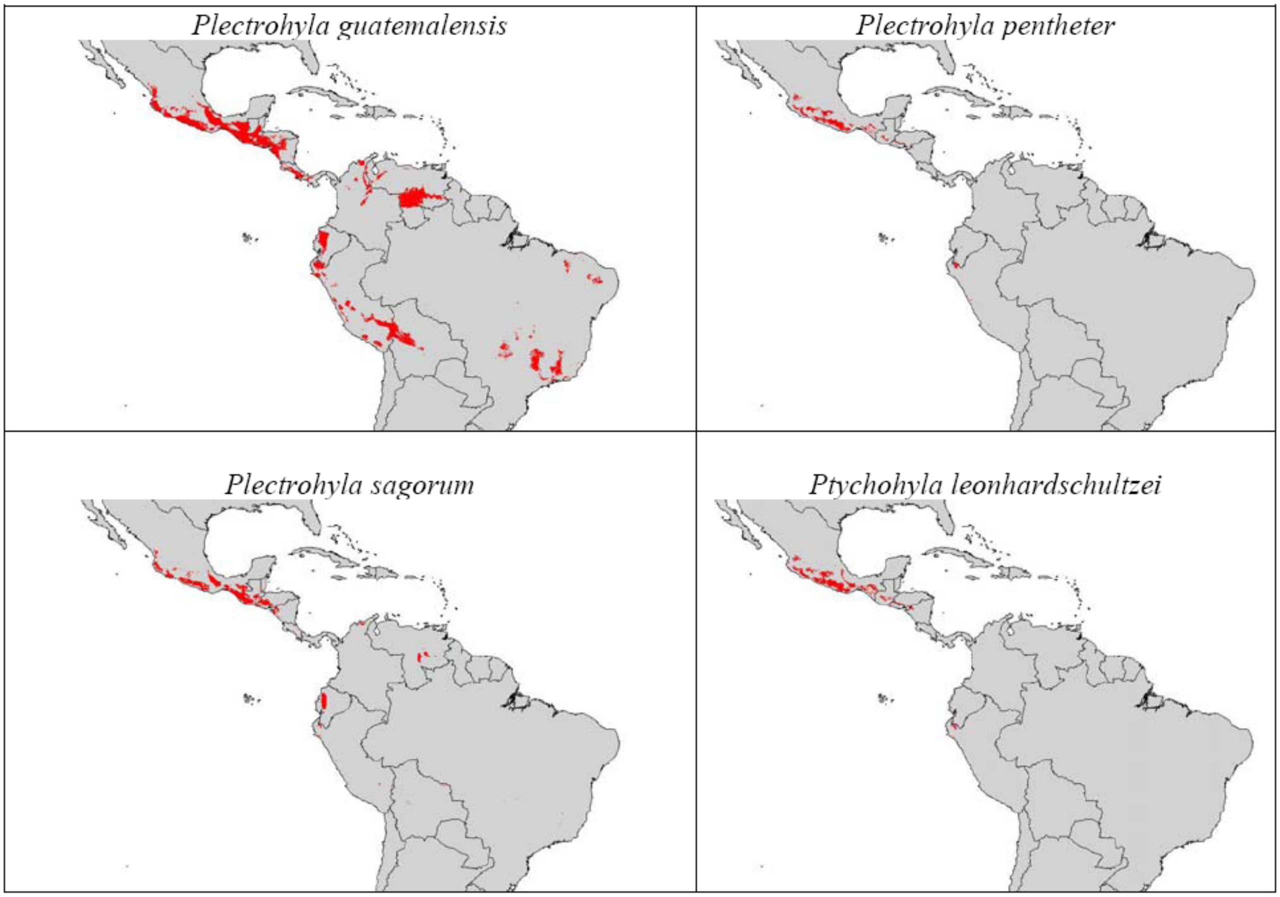

Hylomantis lemur


Plectrohyla arborescandens


Plectrohyla cyclada


Plectrohyla glandulosa

Appendix 2, continued



Plectrohyla guatemalensis

Plectrohyla pentheter

Plectrohyla sagorum

Ptychohyla leonhardschultzei