



Effects of habitat modification and environmental variables on the diversity of amphibians in western Mexico, along a gradient of environmental disturbance

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Abstract.—The diversity of amphibians that occur in tropical dry forest of western Mexico was evaluated. The study was carried out within an anthropogenic disturbance gradient in which the structure and composition of the habitat in each of the sites analysed was characterised to determine the environmental and structural variables that influence the presence or absence of amphibians in the landscape matrix. Amphibians were recorded in three conserved sites, three rural, and three urban sites from 2015 to 2018. Each site was digitised using Google Earth and ArcGis geographic information systems. Nine sampling sites (buffers), each one km in diameter, were characterised, and within each site, these vertebrates were sampled monthly during the dry season and rainy season to determine the diversity and structure of the amphibian communities. For the entire landscape gradient, 18 species belonging to seven families were recorded. The greatest diversity of species was recorded in the conserved sites, followed by rural sites, and the least diversity in urban sites. The results showed that diversity is determined to a highest extent by the similarity of species among the more conserved sites and the variation in habitat structure determines the biggest diversity of species. The sites with the greatest similarity among species are conserved sites (tropical dry forest) and rural sites, which form a diverse system of crucial habitats for amphibians in this complex landscape. This implies that the participation of different sectors, such as academic, productive, and social is required for the monitoring and maintenance of the physical properties of patches of natural and rural vegetation that enable the permanence of amphibian communities in tropical ecosystems.

Keywords. Anurans, Environmental, Fragmentation, Diversity, Tropical dry forest, Communities

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Introduction

The ecosystems of the Earth are made up of complex matrices of natural elements such as fragments of forests and jungles, as well as disturbed areas, agricultural, and/or urban areas (Haddad et al. 2015). These changes in the landscape over time have caused modifications in the

structure of natural habitats (Baude and Meyer 2023), vegetation, and physical conditions such as humidity and temperature that directly affect the distribution and composition of biological communities (Fahrig 2003). Therefore, such changes have had negative effects on the biological interactions between animal and plant species; for example, the lag in reproductive activity and

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migrations, as well as inbreeding and species extinction, among others. All these factors have had an impact on the functional roles of fauna in ecosystems (Chapin et al. 2000; Berriozabal-Islas et al. 2017; Zhang et al. 2024).

For example, Chapin et al. (2000) described the decline in functional diversity of biological communities due to habitat loss and transformation in important ecosystem services such as seed dispersal, pathogen control, and pollination, to name some of the most important ones. This occurs particularly in tropical environments, which are known to be the most diverse on the planet (Malhi and Grace 2000; Olson and Dinerstein 2002; Alroy 2017). Another important feature of tropical ecosystems is that they contain a great structural complexity that provides environmental conditions such as water, food, appropriate temperatures, and various types of microhabitats which are used by different groups of vertebrates (Brawn 2017). However, they are also the ecosystems most affected by deforestation, the livestock, crops and unsustainable tourism (Brawn 2017; Berriozabal-Islas et al. 2018).

Amphibians, being ectothermic vertebrates, need particular environmental conditions to survive, such as environmental humidity (Vitt and Caldwell 2014), forest cover, optimum temperatures, and the presence of bodies of water such as ponds, rivers, and streams that together provide the ideal conditions for their survival (Barrera-Santos and Urbina-Cardona 2011; Gómez-Hoyos et al. 2016). Therefore, amphibians are considered very sensitive organisms and vulnerable to the slightest changes in the environments they inhabit (Becker et al. 2007). Deforestation of forests and jungles represents a direct threat to biodiversity that could lead to the extinction of amphibians worldwide (Gibbons et al. 2000). For example, deforestation in Mexico has caused the loss of approximately 85% of tropical forest. Of these, dry forests in particular are under severe threat (Rzedowski 2006; López 2012). Trejo and Dirzo (2000) noted that by 2000, 47% of the tropical forest cover of Mexico had disappeared, and the remaining 53% consists of isolated fragments of native vegetation and secondary vegetation, of which only 5% is within protected areas (Arias et al. 2002), indicating a high degree of vegetation loss across temporal and spatial scales.

The demand for space and the change in land use for implementation of agroforestry exert strong selective pressures on amphibian communities at the local and regional level (Ndriantsoa et al. 2017). In this context, little is known about the structural characteristics of amphibian habitat or of the abiotic factors that determine the diversity of amphibians in specific sites, and even less of their diversity along anthropogenic disturbance gradients (Cushman 2006; Hamer and McDonnell 2008).

Subtropical regions have a high diversity of amphibians (Stuart et al. 2004). This is because these types of ecosystems provide optimal biotic and abiotic conditions for their subsistence (Hamer and McDonnell 2008). For example, ambient temperatures play an important role in the physiological and behavioural functions of amphibians (Ruthsatz et al. 2018). Furthermore, local variations in ambient temperatures can determine microhabitat selection and reproduction (Ruthsatz et al. 2018). However, if the thermal environment is modified

by habitat transformation, temperatures increase, particularly at the microclimate scale (González-del-Pliego et al. 2020). Consequently, changes in habitat structure can alter the geographic distribution, temporal activity, physiological and behavioural performance of amphibians (Duarte et al. 2012).

Therefore, in this study, it is hypothesised that the greater the transformation (disturbance) of the natural habitat and of the loss of physical environmental forest properties, the lower the diversity of amphibians will be. The objectives of this study are to determine the changes in amphibian species composition in response to habitat transformation at a regional scale along a disturbance gradient (conserved, rural, and urban sites) of the tropical dry forest (TDF) from central western Mexico. We expect to see the following patterns: i) a different community composition between environments, ii) lower species richness towards disturbed environments, and iii) groupings or conformations among species in conserved and disturbed environments.

Materials and methods

Study area

The study area consists of sites located in the Chamela Biosphere Reserve Natural Protected Area (19°29'17.09" N, 104°59'42.32" W) and adjacent regions (Figure 1). The sampling region is bordered to the southwest by the state of Colima (19°11'05.83" N, 104°36'29.62" W) and to the north by Puerto Vallarta (20°34'41.67" N, 105°13'49.18" W), located between 0 and 100 m.a.s.l. (National Institute of Statistics and Geography [INEGI], 2009). The climate is semi-warm with an average annual temperature of 25 °C, with the highest temperatures in summer (38.5 °C) and the lowest in winter (12 °C). Average annual rainfall ranges from 300 to 800 mm (García, 1973). The dominant vegetation is low deciduous forest with elements of semi-evergreen forest, xeric scrub, induced grassland, and cropland (Rzedowski 2006).

Sampling design

For data collection, we located nine sampling sites; three replicates representing each of the environmental categories (conserved sites, rural sites, and urban sites; Figure 2). Once the limits of each environment were known, each of the sampling sites were selected at least nine km apart whenever possible to avoid pseudoreplication (Figure 1). Each of the sampling sites was configured as a one-kilometre diameter buffer traced around a reference point; the reference points were selected in each environment with the help of a Garmin brand GPS. The buffers were generated from satellite images obtained from the Google Earth Pro version 10.3 program with a spatial resolution of 15 m through 36 control points to georeference them. Once the points (coordinates) had been georeferenced, they were digitised using the Google Earth Pro program and the satellite images were then exported to generate the shapefiles.

Subsequently, each of the categories that characterise the landscape within each buffer was digitised in shapefile format with the geoprocessing tool (ESRI 2002; Figure 2).

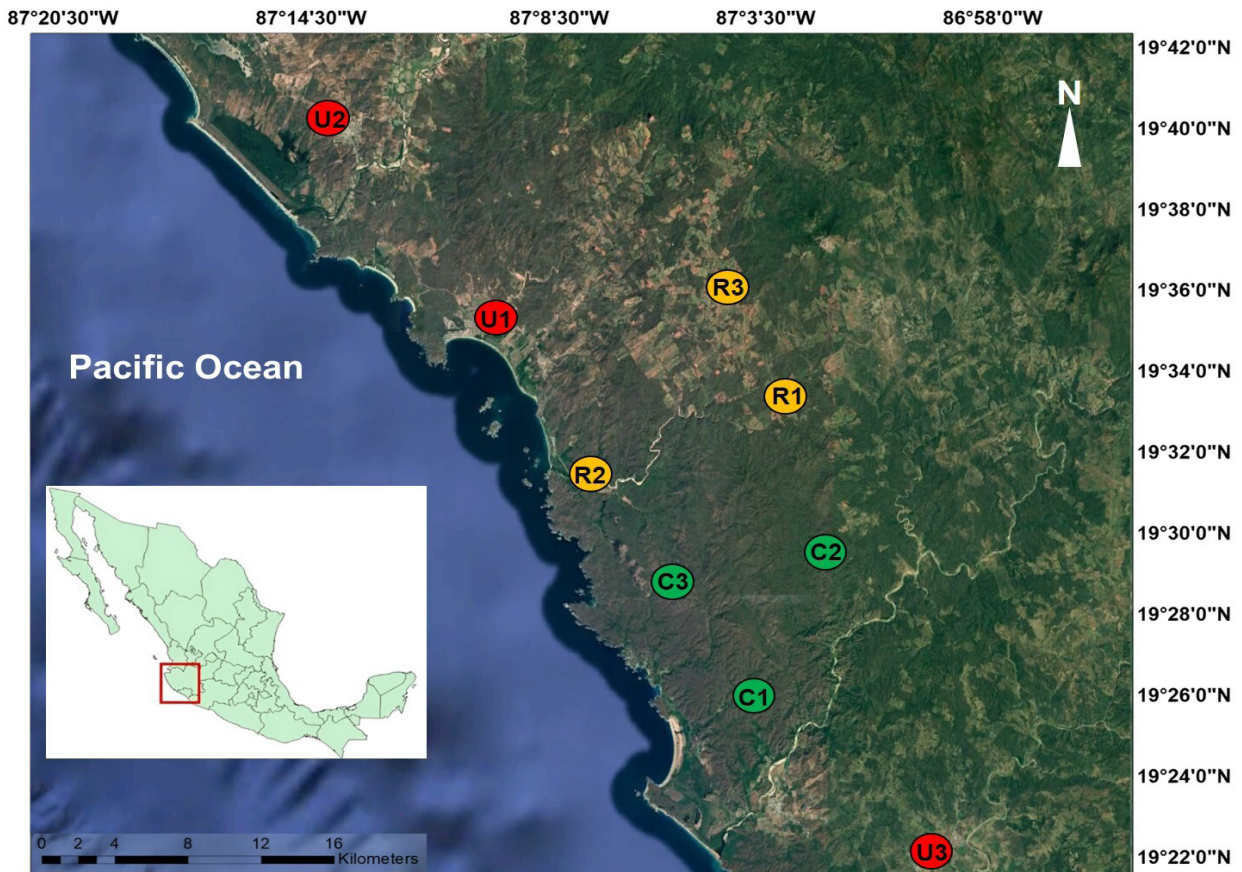


Fig. 1. Map of the study area in the central region of western Mexico. Circles represent 1 km diameter buffers around selected points, which correspond to the amphibian sampling sites. C1 = conserved site 1, C2 = conserved site 2, C3 = conserved site 3, R1 = rural site 1, R2 = rural site 2, R3 = rural site 3. U1 = urban site 1, U2 = urban site 2, U3 = urban site 3. Satellite image from Google Earth Pro© 2019.

The categories were tropical dry forest, semi-evergreen forest, secondary vegetation, urban area, body of water, paved ground, bare soil, dirt road, and cultivated area. This procedure makes it possible to measure the percentage of vegetation cover and land use in each of the buffers (Figure 2).

To establish an association between amphibian diversity and the properties of the habitat, environmental and structural different variables were taken after a selection process. For example, they were identified the variables with the greatest contribution in explaining the spatial-environmental variation for each environmental category, an analysis of bivariate correlation of Pearson was performed among all the environmental variables pairs to check for collinearity among variables in the program STATISTICA ver 10 (StatSoft Inc, 2004), and only variables with correlation values of less than 0.7 ($r < 0.7$) were retained. After this process nine variables were selected: soil depth, number of rocks, number of trees, tree width, ambient temperature, microhabitat temperature, % humidity, % forest cover, and number of water bodies (natural and artificial).

These variables were characterized and counted within each buffer to establish an association between amphibian diversity and the properties of the habitat. These are the variables that are considered important and that can influence the presence or absence of amphibians (Vitt and Caldwell 2014; Nowakowski et al. 2016; Park and Do 2023).

The sites considered to be conserved are described as follows: *Conserved sites*, which are almost entirely made up of tropical dry forest, also have some portions of semi-evergreen forest growing near bodies of water. This type of vegetation is located mainly in the Chamela Biosphere Reserve and surrounding regions (Figure 2). These areas have a dense vegetation cover consisting of trees between 8 and 12 m tall, which give rise to a uniform convex canopy (Rzedowski 2006). The diameter of the trunks does not exceed 60 cm, and the branching of the trees is not deep. It is important to note that the selected sites have a thick layer of soil formed by decomposed organic material (mainly litter, trunks, and branches), as well as rocks.

Rural sites contain a mosaic of different vegetation types and natural water bodies; for example, crops (corn, sugarcane, fruit trees, and vegetables), grazing areas, remnants of low deciduous forest, and thorn scrub (Durán et al. 2002; Rzedowski 2006; Figure 2). Shrubby areas are present, and tree cover can be permanent or temporary throughout the year; tree stratification is vertical, and trees range in height from eight to 12 meters. Crop irrigation provides additional moisture throughout the year in these sites.

The *urban zone* contains native trees and shrubs scattered within the urban perimeter and also includes a variety of ornamental and useful plants, such as fruit trees, that have economic, social, aesthetic, and ecological

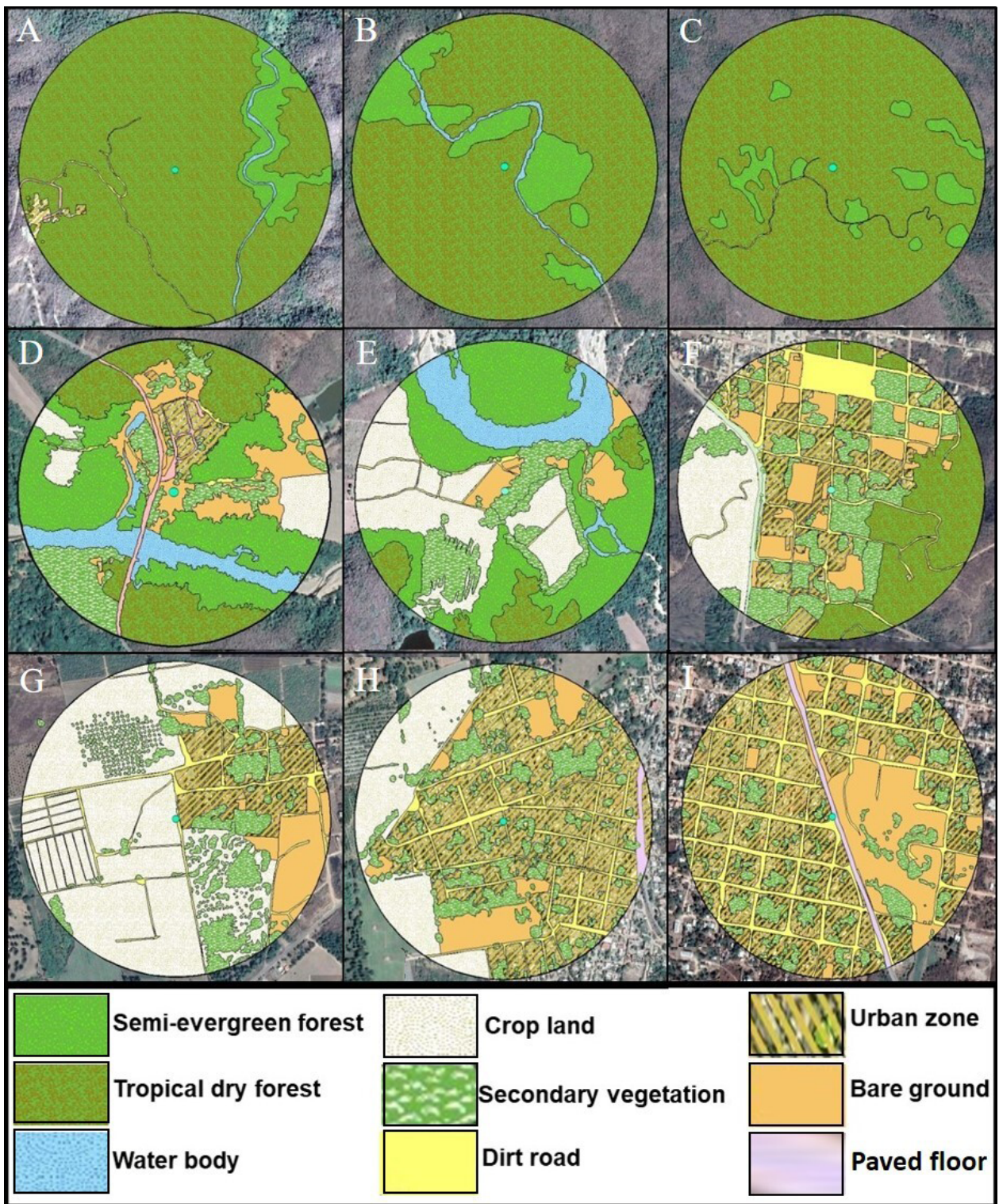


Fig. 2. Characterisation of land use types in 1 km diameter buffer. A, B, and C indicate conserved sites; D, E, and F indicate rural sites, G, H, and I indicate urban sites. The physiography and vegetation in each buffer are shown.

value. The vegetation in these sites is composed mainly of herbaceous plants; species of the Compositae family and induced grasses (Rzedowski 2006; Figure 2). These zones are characterised by strong disturbance caused by the presence of human settlements, structures, dirt roads, livestock, crops, and natural and artificial bodies of water throughout the year.

Data collection

For this study, 32 samplings were carried out, four in the dry season and four in the rainy season of each of the years 2015, 2016, 2017 and 2018. The dry season is from February to May, while the rainy season is from August to November. Each sampling lasted 9 days,

consisting of one day searching for amphibian species per buffer. The search for and collection of amphibians was carried out through direct observation and acoustic sampling. Since the amphibians present in the Chamela region are anurans, males use species-specific calls to announce their position to mates and rivals (Boullhesen et al. 2023). Acoustic identification is a commonly used method for monitoring and identification. Counts were used to estimate relative abundance of calling males and species composition, as well as breeding habitat use (Zamudio-Torres et al. 2020). When we heard an individual's song, we approached it and observed it to record the individual in our database (Köhler et al. 2017). Sampling took place from 09:00 a.m. to 01:00 p.m. and from 08:00 p.m. to 12:00 a.m., consisting of making tours randomly throughout the entire area of each buffer. This was carried out by three people who made notes of the abundance of each species and the characteristics of the habitat where each specimen was recorded under rocks, on leaf litter, riparian vegetation, ponds, streams, or tree cavities (Díaz-García et al. 2017). Therefore, each sampling event consisted of 24 person-hours per day. All possible safety and hygiene measures were taken to prevent the transmission of diseases in the amphibian populations (Lips et al. 2001).

The field work was carried out under scientific collection licenses issued by the Department of Wildlife of the Secretary of Environment and Natural Resources (SEMARNAT, SGPA/DGVS/02726/10, SGPA/DGVS/01902/11, SGPA /DGSV/06622/13, and SGPA/DGVS/02419/13). The specimens were verified *in situ* up to the species level with the guides and dichotomous keys of Smith and Taylor (1966), and Ramírez-Bautista et al. (1994). Once the specimens were identified, they were released at the place where they had been sighted.

Relationship of species richness and habitat

To determine the relationship between amphibian diversity and habitat, a disturbance gradient was determined based on the three types of environments described above. Each of the categorical and structural levels of the habitats was characterised to establish an association between amphibian diversity and the properties of the habitat (Figure 2). In each buffer, quantitative variables were recorded, to determine the characteristics of the habitat; soil depth (SD), number of rocks (NR), number of trees (NT), tree width (TW), ambient temperature (AT), microhabitat temperature (MT), percentage humidity (PH), percentage of forest cover (PFC), and number of water bodies (NWB). The purpose was to determine the most important variables in the structure of communities, diversity, and composition of amphibians (ESRI 2002; Gorresen and Willig 2004; Russildi et al. 2016; Oda et al. 2017).

Analysis of alpha diversity

To assess the completeness of the inventory in each habitat, species accumulation curves were carried out using the bootstrap estimator. The analysis, here based

on 100 iterations, is considered one of the most accurate estimators for evaluating communities made up mostly of rare and/or less dominant species (Magurran 2004). Algorithms were employed to evaluate the species represented by one individual (singletons) and two individuals (doubletons) according to sampling time (Colwell and Coddington 1994). These estimators assume that as the number of samples increases and the curves cross (singletons and doubletons) and the inventories are close to complete (Jiménez-Valverde and Hortal 2003). Species accumulation curves were calculated using ESTIMATES ver. 9 (Colwell and Coddington 1994; Colwell 2013). Rank abundance curves or Whittaker curves were generated to compare the proportional structure of the species among the different types of habitats (conserved, rural and urban sites; Magurran 2010).

Species diversity was determined by obtaining the effective number of species, using the order 1 Hill number (1D) proposed by Jost (2006). This method includes all species, assigning them a weight exactly proportional to their abundance in the community (Jost 2006; Moreno et al. 2011).

Analysis of beta diversity

The degree of similarity in species composition among environments was calculated based on Ward's method, which uses Euclidean distance as a measure to separate species composition among groups (Strauss and von Maltitz 2017). The graphic representation of this similarity is based on a dendrogram. The degree of similarity in species composition among types of habitats was calculated by means of a dendrogram from a cluster analysis by the Ward method, which indicates the correlation coefficient among each type of environment (Magurran 2004).

With the information on species diversity (species richness and abundance) and the habitat characteristics listed above, a canonical correspondence analysis (CCA) was carried out (Braak and Smilauer 2002). This analysis is considered a confirmatory multivariate method that determines which the most important habitat variables are for the presence of amphibian communities. The analysis was carried out using the INFostat ver. 2010 statistical program (García-Cardenete et al. 2014; Becerra-Soria et al. 2022).

Results

Habitat characterisation and landscape composition

The mean land use cover percentages differed significantly between the conserved, rural, and urban site categories (ANOVA, $F_{2,41} = 48.11$, $P = 0.0001$). For the buffers in the conserved sites, a tropical dry forest cover percentage of 80% was found. Original vegetation accounted for 50% cover in rural sites and 5% in urbanised sites, which indicates a very high amount of disappearance of native vegetation in urban sites (Figure 2, Table 1).

Table 1. Percentages of land use coverage for each site analysed (buffers) C conserved, R rural and U urban.

Land use category	Buffer (% coverage/1 km diameter)								
	C1	C2	C3	R1	R2	R3	U1	U2	U3
Tropical dry forest	71	70	80	10	14	18	2	3	0
Semi-evergreen forest	10	20	15	14	20	0	1	0	0
Secondary vegetation	0	0	0	18	18	22	18	14	15
Urban zone	3	0	0	7	2	20	22	34	50
Water body	10	10	5	15	15	0	10	5	5
Paved floor	1	0	0	5	0	5	0	6	9
Bare ground	0	0	0	12	10	11	8	10	8
Dirt road	5	0	0	5	3	8	9	11	13
Crop	0	0	0	14	18	16	30	17	0
Total vegetation/land use	100	100	100	100	100	100	100	100	100

Richness, species diversity and community structure

Eighteen amphibian species were recorded, all belonging to the order Anura, represented by seven families and 14 genera. The Hylidae family was the best represented, with eight species (Figure 3; Table 2). The species accumulation curves show that a completeness percentage of 100% was obtained in all the sites analysed, according to the bootstrap estimator (Figure 4).

The range-abundance curves showed that the conserved and rural sites had similar amphibian communities, in contrast to the urban sites (Figure 5). In the conserved and rural sites, the species *Tlalocohyla smithii*, *Lithobates forreri*, *Exerodonta smaragdina* and *Dendropsophus sartori* were dominant, while in the urbanised sites, the species *Leptodactylus melanonotus*, *Rhinella horribilis*, and *Smilisca baudinii* were well represented.

Uncommon or rare species present in the conserved sites of tropical dry forest and rural sites were *Diaglena spatulata*, *Eleutherodactylus modestus*, *Hypopachus ustus*, and *S. fodiens*. In urbanised sites, *Hypopachus variolosus*, *Trachycephalus vermiculatus*, and *Pachymedusa dacnicolor* were the rarest species.

The species diversity values obtained at the local level (buffer) show that the conserved sites presented higher species diversity compared to sites with some degree of disturbance (Table 3).

Similarity among sites

The similarity analysis showed that the greatest similarity in environment is between the conserved sites (CS) and rural sites (RS) with a correlation coefficient of 0.554 (Figure 6).

Environmental factors associated with species diversity

According to the canonical correspondence analysis, the conserved and rural sites maintain similar environmental and structural conditions, such as environmental temperature, environmental humidity, soil depth, number of water bodies, and width of the trees (Figure 7). The eigenvalues for axis 1 were 0.30486 with an explanation

percentage of 72.72; for axis 2 an eigenvalue of 0.11437 was obtained with a lower explanation percentage of 27.28. This model shows the association among the sets of variables and their linear correlation (Table 4). For axis 2, the linear relationship was high between environmental variables, sites, and species. Thus, most of the species are restricted to the conserved and rural environments, and species such as *Rhinella horribilis*, *Tlalocohyla smithii*, *Leptodactylus melanonotus* and *Lithobates forreri* are closely related to high environmental temperature values, mainly in the urban environment (Figure 7).

Discussion

Ideally, conserved sites should be maintained with native vegetation; however, over time this is unlikely, given the high rates of land use change and deforestation in Mexico (Rosete-Vergés et al. 2014). Therefore, the only alternatives where species can live are agroforestry or agricultural systems (Moreno-Calles et al. 2013; Ndriantsoa et al., 2017; Valdez et al. 2021). According to the results of this study, rural sites present greater structural complexity with respect to the number of land use and vegetation types. The same types of characteristics and properties of the landscape have been reported in other studies, where greater structural complexity is recorded; for example, agroecosystems, such as *acahuales* (fallow fields with shrubs, tall grasses, and productive trees) and shade coffee plantations, contain sites with large portions of native forest cover and secondary vegetation, which together lead to greater physical and structural complexity (Juárez-Ramírez et al. 2016; Oda et al. 2017; Castillo-Peñarredonda et al. 2024). Ndriantsoa et al. (2017) state that a greater number of space–food resources are generated in these sites.

However, this must be taken with caution, since although they are good options for the establishment of various biological groups, the use of pesticides and agrochemicals can impair the establishment of amphibian communities because the skin of these organisms is highly permeable (Aguillón-Gutiérrez et al. 2018). This is reflected when analysing the diversity of amphibian species that show a high sensitivity to transformations in the habitat in which they live; for example, the species *Diaglena spatulata*, *Eleutherodactylus modestus*, and

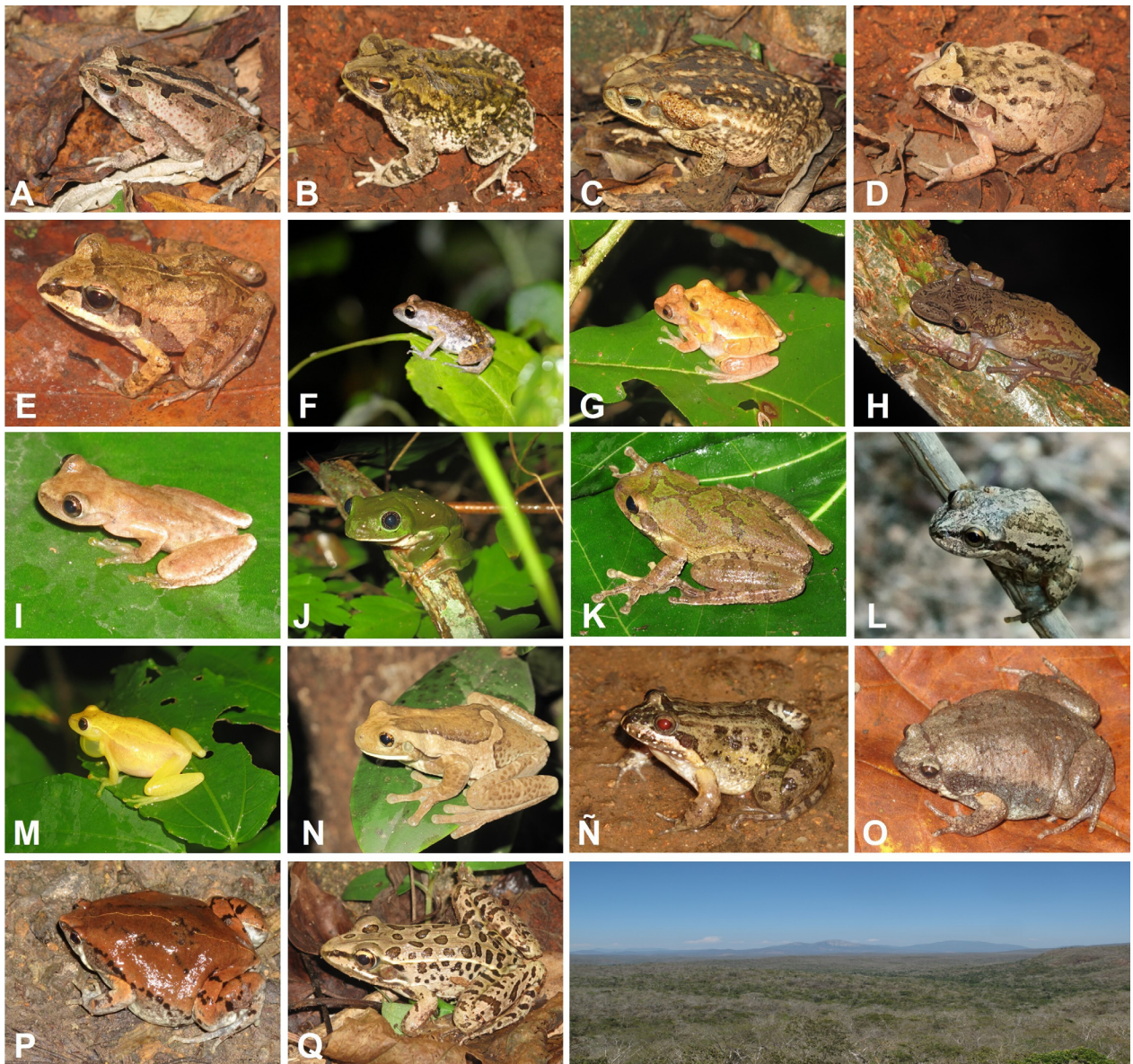


Fig. 3. Species of amphibians that make up the community of the study region. *Incilius marmoratus* = A, *Incilius mazatlanensis* = B, *Rhinella horribilis* = C, *Craugastor hobartsmithi* = D, *Craugastor occidentalis* = E, *Eleutherodactylus modestus* = F, *Dendropsophus sartori* = G, *Diaglena spatulata* = H, *Exerodonta smaragdina* = I, *Pachymedusa dacnicolor* = J, *Smilisca baudinii* = K, *Smilisca fodiens* = L, *Tlalocohyla smithii* = M, *Trachycephalus vermiculatus* = N, *Leptodactylus melanonotus* = Ñ, *Hypopachus ustus* = O, *Hypopachus variolosus* = P, *Lithobates forreri* = Q. Photographs by CBI.

Smilisca fodiens do not tolerate sites with crop and livestock activity, which is why the diversity values analysed at a local scale (buffers) in low deciduous forest show higher values than in modified sites; the same pattern was observed on a regional scale of analysis.

However, these results contrast with what was reported by other studies, which have found a greater diversity of species in agroforestry systems (Macip-Ríos and Casas-Andreu 2008; Suazo-Ortuño et al. 2015). It is worth noting that these sites function as refuges that protect generalist species with the ability to adapt to human presence; for example, *I. marmoratus*, *R. horribilis*, *L. melanonotus*, and *S. baudinii*, which together lead to higher values of species diversity in the analysed sites due to their high abundances (Syamili and Nameer 2018). This is because generalist species that can adapt to modified sites are generally very abundant (Berriozabal-

Islas et al. 2018). For example, some species such as *R. horribilis* and *L. melanonotus* are abundant in rural sites and urban areas. This could be due to the presence of artificial bodies of water, which can influence the establishment and reproduction of generalist species; for example, irrigation canals, livestock watering troughs, and water storage pools are frequently used throughout the year in agroforestry sites (De León and Castillo 2015; Soria-Ortiz et al. 2025). Their presence in urban areas in cities of different regions reflects their tolerance to urbanisation (Lee 1996; Ramírez-Bautista et al. 2014).

Therefore, it is interesting to note that the quality and structure of habitats is very important in determining the richness and diversity of amphibians (Gutiérrez Hernández et al. 2024). For example, the canonical correspondence analysis carried out in this study showed that the most important factors for the presence

Table 2. Richness and abundance of amphibian species recorded at the landscape level and per buffer in the study area. The letters represent the acronyms for the identification of results and graphs for each of the species. ‘Specialist’ refers to a forest specialist species; ‘Generalist’ indicates a species that occupies agroforestry habitats and urban areas.

Families/Species	Species letters	Abundance per-buffer									Species Generalist/Specialist
		C1	C2	C3	R1	R2	R3	U1	U2	U3	
Bufonidae											
<i>Incilius marmoratus</i>	A	5	6	7	3	9	7	1	2	1	Generalist/Specialist (Ramírez-Bautista 1994; Luna-Gómez 2017; Rueda-Hernández 2023)
<i>Incilius mazatlanensis</i>	B				2	1	2				Specialist (García y Ceballos 1994; Ramírez-Bautista 1994)
<i>Rhinella horribilis</i>	C	8	4	5	12	3	8	7	9	35	Generalist (Zug and Zug 1979; Cortés-Suárez 2017)
Craugastoridae											
<i>Craugastor hobartsmithi</i>	D	9	4	3	3	5	2				Specialist (García y Ceballos 1994; Ramírez-Bautista 1994)
<i>Craugastor occidentalis</i>	E	5	4	7	1	1	5				Specialist (González-Hernández et al. 2023)
Eleutherodactylidae											
<i>Eleutherodactylus modestus</i>	F	1	2	1							Specialist (García y Ceballos 1994; Ramírez-Bautista 1994)
Hylidae											
<i>Dendropsophus sartori</i>	G	26	17	8	24	18	30	1	4	1	Generalist/Specialist (García y Ceballos 1994; Ramírez-Bautista 1994)
<i>Diaglena spatulata</i>	H	1	1	2							Generalist/Specialist (García y Ceballos 1994; Ramírez-Bautista 1994; Luna-Gómez et al. 2017)
<i>Exerodonta smaragdina</i>	I	16	24	15	10	13	12				Specialist (Luna-Gómez et al. 2017)
<i>Pachymedusa dacnicolor</i>	J	10	8	9	8	6	7		1	1	Specialist (Luna-Gómez et al. 2017; Soto-Sandoval et al. 2017)
<i>Smilisca baudinii</i>	K	18	15	9	3	16	13	3	9	2	Generalist (García y Ceballos 1994; Ramírez-Bautista 1994; Luna-Gómez et al. 2017)
<i>Smilisca fodiens</i>	L	1	1	1							Generalist/Specialist (Luna-Gómez et al. 2017; Soto-Sandoval et al. 2017)
<i>Tlalocohyla smithii</i>	M	19	16	28	15	12	5	11	4	13	Generalist/Specialist (Luna-Gómez et al. 2017)
<i>Trachycephalus vermiculatus</i>	N	7	3	7	6	4	5	1	2	1	Generalist (Brown 2020)
Leptodactylidae											
<i>Leptodactylus melanonotus</i>	Ñ				17	8	2	27	9	22	Generalist (Jacinto-Maldonado et al. 2013; Ramírez-Bautista et al. 2014)
Microhylidae											
<i>Hypopachus ustus</i>	O	6	7	9	1	1	1				Specialist (Luna-Gómez et al. 2017)
<i>Hypopachus variolosus</i>	P	10	21	15	1	4	3		1		Generalist/Specialist (García y Ceballos 1994; Ramírez-Bautista 1994; Luna-Gómez et al. 2017)
Ranidae											
<i>Lithobates forreri</i>	Q	15	23	10	10	30	4	7	14	4	Generalist (García y Ceballos 1994; Ramírez-Bautista 1994)

Amphibian Diversity Under Habitat Disturbance in Western Mexico

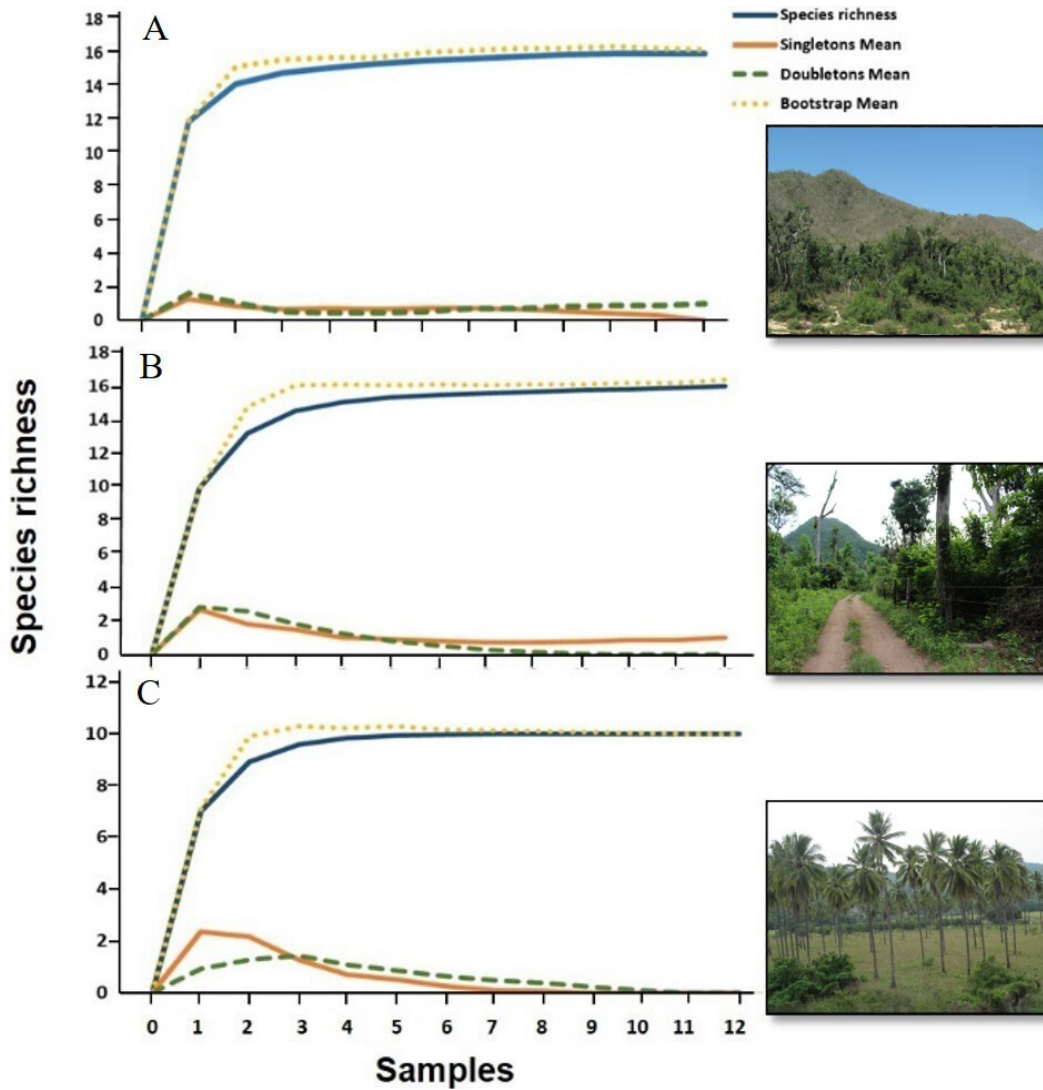


Fig. 4. Species accumulation curves. Inventory completeness is shown for each type of environment. CS=A, RS=B, US=C.

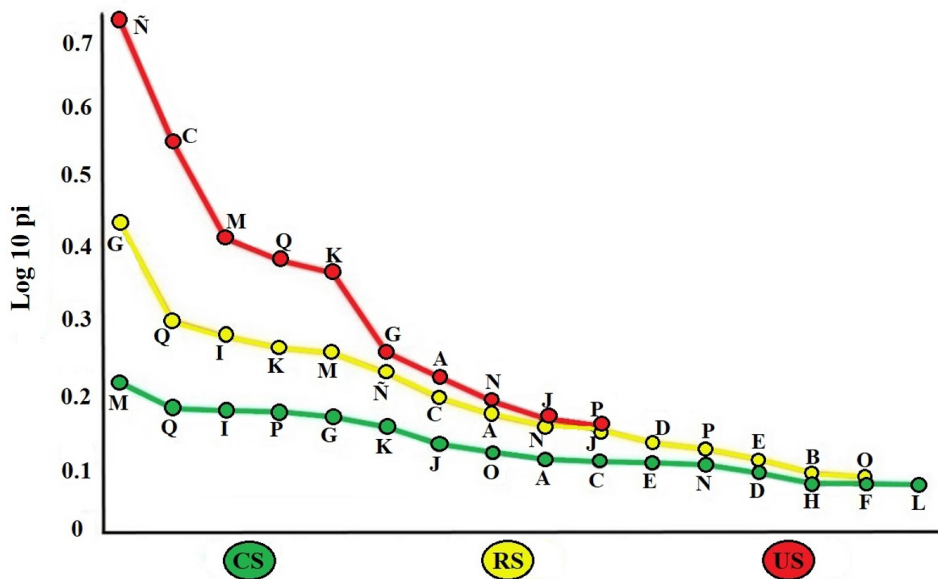


Fig. 5. Range-abundance curves. The structure of the amphibian communities in each analysed site is represented at the landscape level. *I. marmoratus* = A, *I. mazatlanensis* = B, *R. horribilis* = C, *C. hobartsmithi* = D, *C. occidentalis* = E, *E. modestus* = F, *D. sartori* = G, *D. spatulata* = H, *E. smaragdina* = I, *P. dacnicolor* = J, *S. baudinii* = K, *S. fodiens* = L, *T. smithii* = M, *T. vermiculatus* = N, *L. melanonotus* = N̄, *H. ustus* = O, *H. variolosus* = P, *L. forreri* = Q.

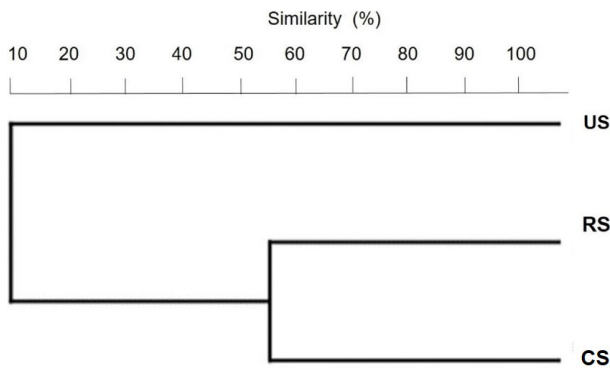


Fig. 6. Cluster analysis shows similarity of species among the different types of analysed habitats.

of amphibians were the presence of water bodies, environmental temperature, and soil depth. These habitat variables turned out to be important in other tropical environments where the diversity of amphibians was also evaluated with respect to the composition and structure of the landscape (Ndriantsoa et al. 2017; González-del-Pliego et al. 2020).

For example, Richter-Boix et al. (2007) found that the matrix of conserved or anthropised habitats that have bodies of water (streams and ponds) largely determines the presence of amphibians regardless of whether they are in conserved sites or rural sites. Pineda and Halffter (2004) note that one of the most important variables for amphibians in many of the evaluated systems, such as the cloud forest, is the availability of lentic or lotic bodies of water. Therefore, streams are important habitats to support species diversity not only in deciduous forest fragments but also in rural sites, according to our results.

However, in this study, it was found that landscape disturbance had a direct negative effect on species diversity and composition. For example, Cordier et al. (2021) note that modification of the habitat by human activities is especially unfavourable for amphibians. This sensitivity to habitat modifications is partly due to the biphasic life history of most amphibians, which require distinct and interconnected habitats for the transition of aquatic offspring into terrestrial adults (Jourdan-Pineau et al. 2022). This is shown in the association among the species composition for each community and the

Table 3. Values of diversity at the local and landscape level of each buffer, conserved sites, rural sites and urban sites are shown.

Site (Buffer)	Diversity value		
	Conserved sites	Rural sites	Urban sites
Gradient/category	12.41	11.28	6.27
C1	9.6	---	---
C2	9.1	---	---
C3	10.4	---	---
R1	---	9.3	---
R2	---	8.9	---
R3	---	9.6	---
U1	---	---	4.4
U2	---	---	3.7
U3	---	---	5.1

Table 4. Correlation percentages between examined variables of each of the environments associated with the presence of amphibians.

Species	Axis 1	Axis 2
<i>Craugastor hobartsmithi</i>	-0.80566	0.60662
<i>Craugastor occidentalis</i>	-1.0434	-0.62479
<i>Dendropsophus sartori</i>	-0.43286	1.3971
<i>Diaglena spatulata</i>	-1.4132	-2.5403
<i>Eleutherodactylus modestus</i>	-1.4132	-2.5403
<i>Exerodonta smaragdina</i>	-0.878	0.23199
<i>Hypopachus ustus</i>	-1.2674	-1.7850
<i>Hypopachus variolosus</i>	-1.1478	-1.6114
<i>Incilius marmoratus</i>	-0.37444	0.44820
<i>Incilius mazatlanensis</i>	-0.198034	3.75359
<i>Leptodactylus melanonotus</i>	2.2996	-0.038618
<i>Lithobates forreri</i>	0.085540	-0.0160422
<i>Pachymedusa dacnicolor</i>	-0.76450	-0.26976
<i>Rhinella horribilis</i>	1.62639	-0.53686
<i>Smilisca baudinii</i>	-0.12235	0.010447
<i>Smilisca fodiens</i>	-1.4132	-2.5403
<i>Tlalocohyla smithii</i>	0.012784	-0.73526
<i>Trachycephalus vermiculatus</i>	-0.297678	0.513617
Conserved sites (CS)	-0.43970	-0.28961
Rural sites (RS)	-0.06496	0.42975
Urban sites (US)	1.08367	-0.20923
Soil depth (SD)	-0.942397	-0.157283
Number of rocks (NR)	-0.851367	-0.360756
Number of trees (NT)	-0.054956	0.428749
Number of water bodies (NWB)	-0.881404	0.99479
Width of the trees (WT)	-0.929538	0.531838
Abundance (Abund)	0.923912	0.207953
Ambient temperature (AT)	0.847965	0.366765
Microhabitat temperature (MT)	-0.281404	0.99479
Environmental humidity (PH)	-0.909035	-0.244206

environmental conditions analysed in this study. For example, *I. marmoratus*, *C. hobartsmithi*, *C. occidentalis*, *D. sartori*, *E. smaragdina*, *P. dacnicolor*, *S. baudinii*, *T. smithii*, *T. vermiculatus*, and *L. forreri* can always be found when forest cover is maintained at a minimum of 50%, as shown in the results.

On the other hand, in rural sites there are species that, due to their morphological and functional traits and reproductive modes, can occur in moderately modified sites (Oda et al. 2017). Therefore, the hypothesis proposed in our work demonstrates that species with generalist traits can be found under certain conditions of habitat disturbance. In contrast, several species did not live in highly modified habitats; this pattern has been found in other studies, in which certain species have been found to be very sensitive to the slightest disturbance of the habitat (Cruz-Elizalde et al. 2016; Oda et al. 2017), particularly the frogs of the family Hylidae, which generally breed in tree holes, bromeliads, or bodies of water such as ponds and slow-flowing streams. For example, Covarrubias et al. (2025) point out that the species *P. dacnicolor*

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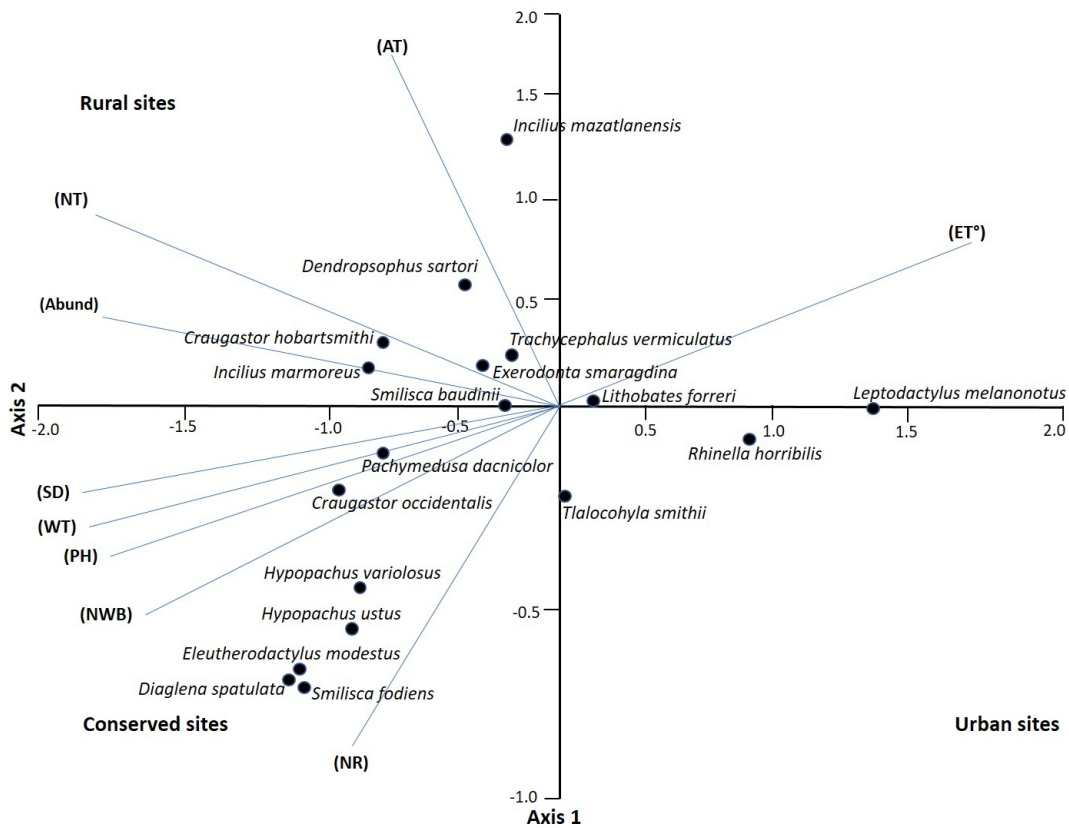


Fig. 7. Canonical correspondence analysis (CCA). Associations of amphibian diversity between sites are shown with respect to their relationship with environmental and microhabitat factors. Sites: Conserved sites, Rural sites, and Urban sites. Environmental variables: soil depth (SD), number of rocks (NR), number of trees (NT), tree width, (WT), ambient temperature (AT), microhabitat temperature (MT), percentage of humidity (PH), abundance (Abund), and number of water bodies (NWB).

is severely affected by highly modified areas such as grasslands and urban areas.

On the other hand, terrestrial species, whose mode of reproduction is based on direct development and whose larval phase does not take place in water, such as the genera *Craugastor* and *Eleutherodactylus*, are the group of species most affected by habitat transformation. This is because these species need soil with organic matter (leaf litter with sufficient moisture) to forage and reproduce (Ramírez-Bautista et al. 2014). Therefore, this group of species can be a good indicator of ecosystem health.

In summary, the amphibian diversity recorded in the study area is relatively high despite the region being a matrix of modified habitats. The results showed that in the sites analysed, there is lower species richness in rural and urban areas, while conserved sites contain the greatest diversity of species. This emphasises the importance of maintaining, as far as possible, sites with forest cover and natural water bodies such as wetlands, ponds, and streams. In addition, preserving the remnants of low deciduous forest contributes to the maintenance of amphibian populations in environmental gradients.

Conclusion

This study reinforces the importance of recording and monitoring variables such as microhabitat temperatures and humidity, as well as other variables which are drastically modified with habitat transformation, such

as soil humidity and the amount of food, for a better estimation of the physiological and behavioural effects on anurans. This may have conservation implications, considering the substantial heating occurring in transformed tropical forest and threatened environments (Bhargava et al. 2017). In a conservation context, the results of this study highlight the importance of considering the differences in the ecological needs and responses of amphibian communities to disturbances caused by humans as well as differences in the characteristics of the habitat. Therefore, when designing conservation actions and management plans in tropical sites, one must consider the ecological properties, functional traits, and physiology of the species that are determinant in the resilience of ecosystems, particularly for productive systems, such as farming systems. The structure of the forest and its composition present an opportunity to combine the conservation of species in sites with productive activities such as livestock and local crop agriculture.

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