

Research Article

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Lightly-harvested rustic cocoa is a valuable land cover for amphibian and reptile conservation in human-modified rainforest landscapes

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Abstract

The conservation of tropical biodiversity depends not only on forest remnants, but also on anthropogenic land covers. Some shade crops are considered wildlife-friendly agroecosystems, but their conservation value is context- and taxon-dependent. Amphibians and reptiles have received less attention despite their high sensitivity to habitat disturbance. We determined the conservation value of lightly-harvested rustic cocoa plantations for herpetofauna in the Lacandona region, Mexico. We compared 12 environmental variables between habitats. Then, we compared the abundance, species number and composition of amphibian and reptile assemblages. Within each habitat, we explored the relationships between environmental variables and abundance and species number. Tree density, litter cover and litter depth were higher in cocoa. Abundance of reptiles and amphibians were higher in cocoa than forest; species number did not differ. Habitat explained some of the variation (8%) in assemblage composition. In cocoa, amphibian abundance was positively related to canopy height and the presence of a humus layer, while reptile abundance was negatively related to relative humidity. We conclude that lightly-used rustic cocoa plantations can be suitable habitat for forest herpetofauna. As long as cocoa plantations do not replace existing forest cover, they can play an important role in the design of wildlife-friendly tropical landscapes.

Introduction

Land-use change and agricultural expansion endanger the integrity of the most diverse terrestrial ecosystems of our planet, the tropical forests (Lewis et al. 2015). Different strategies have been proposed to achieve long-term conservation of biodiversity in human-modified tropical landscapes (Arroyo-Rodríguez et al. 2020, Soley & Perfecto 2021). While some strategies stress the importance of protected forest remnants to conserve biodiversity, others stress the importance of wildlife-friendly agricultural matrices (i.e., land-sharing versus land sparing; Grass et al. 2019). Contrasting strategies have generated much debate, but the emerging view is that they should be complementary (Grass et al. 2019, Arroyo-Rodríguez et al. 2020). Thus, the problem is not deciding which strategy is the best, but how to combine them most effectively for a given context and conservation target. To be able to do this, we need to increase our understanding of the value that agricultural covers in tropical landscapes have as habitat for different groups of organisms.

In the tropics many important cash crops can be grown under a canopy of trees (e.g., coffee, cocoa, cardamom, allspice, etc.), and these shaded agroecosystems have received much attention as potential habitat for biodiversity (Martin et al. 2020). Yet, different groups of organisms are not evenly represented in these studies. Among animals, there is a strong bias towards birds, mammals, and some insect taxa, while other groups, such as amphibians and reptiles, tend to be underrepresented (Palacios et al. 2013). Many species of amphibians and reptiles are highly sensitive to habitat loss and disturbance, which are main drivers of their population declines worldwide (Nori et al. 2015, Doherty et al. 2020). Furthermore, these animal groups are rarely considered in conservation planning and the geographic distributions of many species are not covered by protected areas (Nori et al. 2015). This stresses the importance of assessing the conservation value of agroforests and other anthropogenic vegetation covers to help maintain the herpetofauna in human-modified landscapes (Palacios et al. 2013, Hernández-Ordóñez et al. 2015).

Shaded agroecosystems, even those producing the same crop, can vary tremendously in the ways they are managed, which in turn affects their value as habitat for different groups of

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organisms (Deheuvels et al. 2014, Santos-Heredia et al. 2018, Bennett et al. 2021). Furthermore, habitat requirements differ greatly among taxa and functional groups, with their responses to shaded agroecosystems varying accordingly (e.g., Faria et al. 2007, Borkhataria et al. 2012, Bennett et al. 2021). Thus, it is not surprising that studies of herpetofauna in shaded agroecosystems report variable responses (Palacios et al. 2013). For example, while the decrease in abundance of some arboreal and terrestrial anurans seems to be directly related to loss of canopy cover in shade-coffee plantations (Pineda & Halffter 2004), this same vegetation change may promote the abundance of certain lizard species (Macip-Ríos & Muñoz 2008). Similarly, some studies have found higher species richness in forest compared to shaded cocoa plantations (Lieberman 1986, Heinen 1992), whereas others have found the contrary (Whitfield et al. 2007). Such inconsistencies underscore the need to carry out context-specific studies to guide conservation actions. Knowing which characteristics of an agroecosystem affect amphibian and reptile populations and communities has important management implications, since these variables could be manipulated to favor target taxa (Wanger et al. 2009, Rodríguez Leiva et al. 2014).

Our objective was to determine if rustic cocoa plantations under very low use-intensity could be suitable habitat for amphibians and/or reptiles in the anthropogenic landscapes of a Neotropical biodiversity hotspot, the Lacandona rainforest. To address our objective we asked three questions: (i) How do the cocoa and forest habitats differ in environmental variables that are relevant for herpetofauna?; (ii) How do these habitats differ in the abundance, number of species and assemblage composition of amphibians and reptiles?; (iii) Which environmental variables are more strongly related to the abundance and/or the number of species within each habitat? Land-use change is dramatically threatening the ecological integrity of the Lacandona region in southern Mexico, and it is urgent to design landscapes that can be productive whilst conserving the immense biodiversity of the region (Zermeño-Hernández et al. 2016). We hope that our results can help managers and conservationists design such landscapes for amphibians and reptiles.

Methods

Study site

This study was carried out in the Lacandona rainforest region, in the Mexican state of Chiapas. We worked in the community of Playón de la Gloria, located in the Marqués de Comillas municipality (16°9'20"N, 90°53'50"W; Figure 1). The climate is warm and humid, with mean annual rainfall of 2500–3500 mm (a wetter period occurs between June and November) and mean annual temperature of 24–26°C (INE 2000). The Lacandona rainforest is geomorphologically complex, giving rise to a heterogeneous vegetation, which in turn harbors one of the highest biodiversities in Mesoamerica; in 1978 the Montes Azules Biosphere Reserve (331 200 ha) was established to conserve this biodiversity (INE 2000).

Unfortunately, rates of deforestation and land-use change outside the Reserve have been high for over 50 years, and remaining forest cover in the Marqués de Comillas municipality is ~ 50% (33% old-growth forest and 17% secondary forest; Zermeño-Hernández et al. 2016). The landscape consists of a mosaic of land covers, including some large forest remnants, many smaller forest fragments, human settlements, successional

vegetation, and agricultural covers. The latter are of many types (e.g., cattle pastures, annual crops, oil-palm plantations, shade cocoa, etc.), varying greatly in vegetation structure and management intensity, and thus in their value as potential habitat for animals (Zermeño-Hernández et al. 2016).

Our study was carried out in an area of ca. 100 ha covered by rustic cocoa plantations, and in the abutting large forest remnant (ca. 2000 ha; Figure 1). The forest remnant was a local reserve where hunting and logging were restricted. The cocoa area consisted of approximately 16 plantations, 4–7 ha each, owned by different farmers (see Zárate et al. 2014). During the 1980's, cocoa trees were planted by clearing some understory and midstory vegetation but leaving most of the original forest canopy intact. Plantations were highly active until the 1990's when a fungal disease (*Moniliophthora forreri*) caused yields to drop considerably (Zárate et al. 2014). At the time we carried out this research, the level of cocoa harvest was low, and additional management was limited to some pruning of cocoa trees, removal of a few shade trees (see Santos-Heredia et al. 2018), and occasional harvest of timber and non-timber forest products (MdJ C-L, pers. obs.). Thus, the cocoa plantations that we studied represented the 'friendly' end of the gradient between biodiversity-friendly and intensively managed shaded agroecosystems.

Study design and measurement of environmental variables

We established 24 plots (12 in cocoa and 12 in forest), 25 m x 25 m, separated ≥ 100 m from each other and from the edge between the two vegetation types (Figure 1). In each plot, we measured 12 environmental variables that, based on the literature and our own experience, were considered important for amphibians and/or reptiles: (1) leaf litter depth, (2) percentage of leaf litter cover, (3) shrub density, (4) density of herbaceous plants, (5) maximum canopy height, (6) proportion of humus presence, (7) illuminance, (8) density of trees (including cocoa trees) with DBH (diameter at breast height) ≥ 10 cm, (9) density of fallen trunks and prostrate lianas with diameters ≥ 10 cm, (10) presence of water bodies, (11) air temperature in the understory, and (12) air relative humidity in the understory. See Supplementary Material Appendix S1 for detailed descriptions on how each variable was measured.

Sampling of amphibians and reptiles

We sampled amphibians and reptiles in the 24 plots during the rainy season, in June and July 2015, using visual encounter surveys (VES; Crump & Scott 1994). In each plot we established three parallel strip transects 25 m long and 3 m wide, along two of the plot's borders and in its center. Each strip transect was searched for amphibians and reptiles in the understory (up to 2 m above the ground) by the same team of three people working together (Vonesh et al. 2009). The team leader (MdJ C-L) had several years of experience sampling herpetofauna in different habitat types in the study region, which decreases the probability of introducing sampling bias due to differences in detectability with VES in both habitats. Searching time per plot was 45 min during the day (between 09.00 and 12.00; 15 min per strip transect) and 45 min at night (between 19.00 and 21.00), to cover the periods of maximum activity (Jones 1986). During the study period, each plot was sampled twice, with at least 15 days between samplings, for a total sampling effort of 180 min per plot. Taxonomy follows the Amphibian Species of the World 6.1 database (Frost 2021) and the Reptile Database (Uetz et al. 2021).

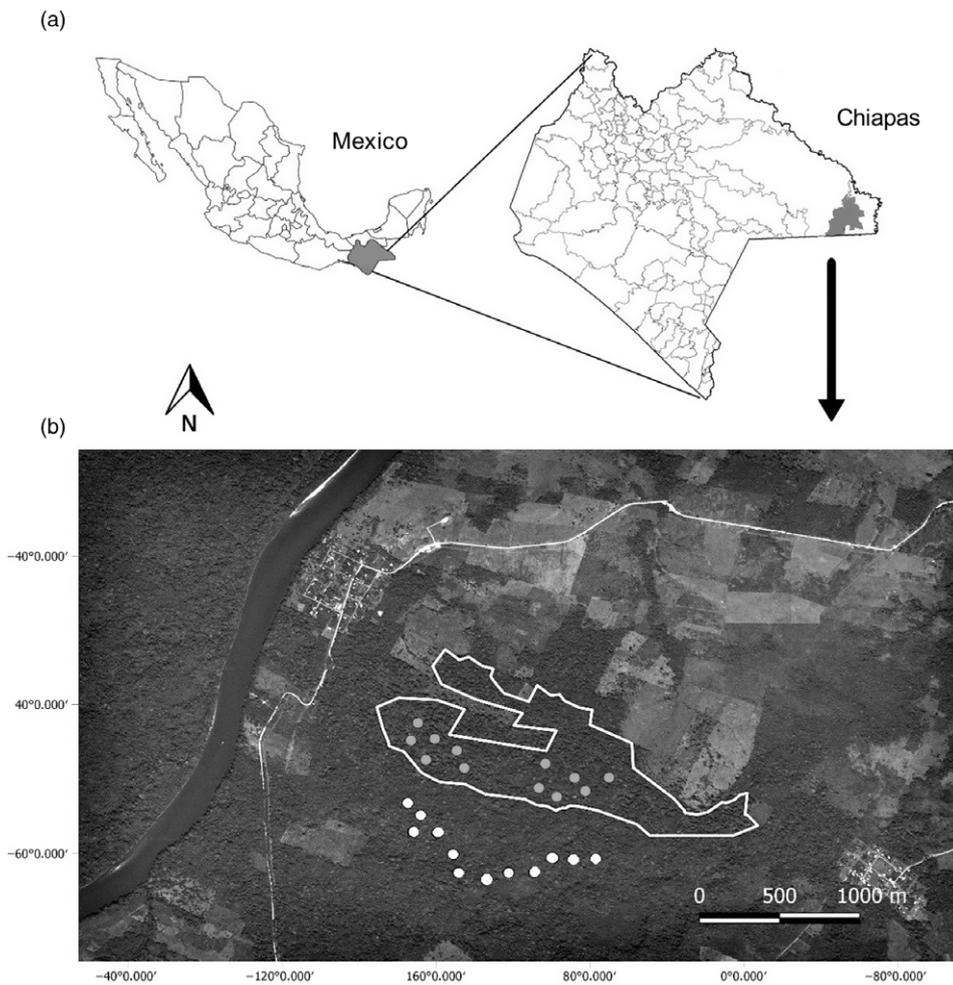


Figure 1. Maps (a) of Mexico showing the location of the state of Chiapas, and of Chiapas showing the location of the Marqués de Comillas municipality. Satellite image (b) showing the area covered by rustic cocoa plantations (white polygon in the center of image) and the forest south of it. Sample plots in cocoa and forest are represented by grey and white circles, respectively. Also shown is the Lacantún river, with the Montes Azules Biosphere Reserve west of it.

Data analyses

Due to the spatial arrangement of our study plots, i.e., all the cocoa plots in one site covered by several cocoa plantations, and all the forest plots in one large forest site, all our statistical inferences are limited to comparing these two sites and cannot be generalized to “all” cocoa plantations versus forest comparisons. It is important that the reader keeps this limitation in mind when considering our results and conclusions.

All analyses were carried out in R 3.6.3 (R Core Team 2020), except where otherwise noted. First, we explored whether environmental variables differed between habitats by fitting linear models with habitat as predictor. Percentage of leaf litter cover, frequency of humus presence, presence of water bodies, and air relative humidity were logit-transformed, while shrub density was log-transformed. Package ‘tidyverse’ (Wickham *et al.* 2019) was used for these analyses. Models were fitted using the ‘lm’ function from base R (R Core Team 2020).

To analyze differences in abundance between habitats, we ran multivariate abundance analyses using the package ‘mvabund’ (Wang *et al.* 2012). This analytical method performs a generalized linear model for the abundance of each species in a community, and then provides both a multivariate test as well as univariate tests for each species. To avoid model-fitting problems, for these analyses we excluded species for which only one (singletons) or two individuals (doubletons) were captured overall.

The number of species was analyzed both at the community (i.e., at the level of habitat) and the assemblage levels (i.e., at the level of plots within habitats), using the complete dataset. At the community level we compared species richness in the cocoa versus forest with rarefaction and extrapolation curves with 95% confidence intervals (bootstrap with 1000 repetitions) using the program iNEXT (Hsieh *et al.* 2016). At the assemblage level we used a generalized linear model to assess the differences between habitats (fixed factor) in mean number of species per plot using a Poisson error distribution with a log-link function.

To analyze assemblage composition (i.e., species composition and the abundance of each species) we first built rank-abundance curves on the full dataset for descriptive purposes. Then, to assess the statistical effect of habitat we performed Canonical Correspondence Analyses (CCA) on abundance matrices (excluding singletons and doubletons) using the ‘vegan’ package (Oksanen *et al.* 2020). CCA uses the chi-square distance, where each term has a weight that is the inverse of its total absolute frequency. Thus, a CCA emphasizes abundance differences occurring in rare species because they have a relatively higher weight than differences occurring in common species. For this analysis we excluded one of the forest sites where no amphibians were recorded.

To analyze the effect of environmental variables on abundance and species number within each habitat, we used the whole dataset to carry out generalized linear models with a multi-model inference approach based on the Akaike (AIC) information criterion

(Anderson 2008). To reduce collinearity, we standardized predictor variables prior to modelling. Both abundance and species number were modelled using a Poisson distribution. Due to the high number of predictor variables (12) relative to our sample size (12 plots), we focused on additive effects only and built all possible models by combining a maximum of two predictors. Then we performed model averaging to obtain best estimates of model parameters and to make inferences on the relevance of predictors (Anderson 2008, Galipaud et al. 2017). Those predictors whose 90% confidence interval did not include zero were included in the final model.

Results

Environmental variables in cocoa versus forest

The cocoa and the forest habitats had similar values for nine of the environmental variables (all p values ≥ 0.1) and differed in the other three (Supplementary Material Figure S1). Rustic cocoa had higher tree density ($F_{1,2} = 56.71$, $p < 0.001$), litter cover ($F_{1,2} = 13.93$, $p = 0.001$) and litter depth ($F_{1,2} = 5.29$, $p = 0.031$) than the forest. The humus layer showed a tendency of occurring more often in cocoa than forest ($F_{1,2} = 3.57$, $p = 0.072$).

Cocoa versus forest: abundance, number of species and assemblage composition

We recorded 1665 individuals belonging to 53 species and 20 families; 438 were amphibians of 18 species and 9 families, and 1217 were reptiles of 35 species and 11 families (Table 1). Only three species of amphibians (17%) were singletons or doubletons, while this was the case for 17 reptile species (49%). The species that we found represent 60% and 55% of all amphibian and reptile species, respectively, reported for the southeastern part of the Lacandona rainforest region (Hernández-Ordóñez et al. 2014, 2015, Russildi et al. 2016). Of all species recorded, 7 amphibian and 10 reptile species are in a threat category according to the Mexican government (NOM-059-SEMARNAT-2010) and/or the IUCN Red List (SEMARNAT 2019, IUCN 2021) (Table 1).

Abundance

A total of 295 amphibians were recorded in cocoa, whereas less than half that number was recorded in forest (143 individuals). The same pattern, but less pronounced, was observed for reptiles, with 652 individuals in cocoa versus 565 in forest. The multivariate abundance analyses showed that the abundance of both amphibians and reptiles was higher in the rustic cocoa habitat than in forest (amphibians: $Dev = 42.3$, $Res.df = 21$, $p = 0.012$; reptiles: $Dev = 38.6$, $Res.df = 22$, $p = 0.034$; Figure 2a,b). These analyses also revealed that, at the level of individual species, three amphibians (*Incilius campbelli*, *Hyalinobatrachium viridissimum*, *Lithobates brownorum*) and two reptiles (*Scincella cherriei*, *Coniophanes bipunctatus*) had higher absolute abundance in cocoa than in forest. Only one species, the reptile *Coleonyx elegans*, was significantly more abundant in forest (Table 1).

Number of species

In the cocoa habitat we found 15 species of amphibians and 26 of reptiles; species numbers were very similar in forest, with 15 amphibian and 27 reptile species. Species richness of amphibians and reptiles at the community level (both rarefied and extrapolated) did not differ between habitats (Supplementary Material Figure S2). At the assemblage level, the analyses also showed that

the mean number of species recorded per plot did not differ between habitats (amphibians: $\chi^2 = 20.4$, $df = 22$, $p = 0.2$; reptiles: $\chi^2 = 16.3$, $df = 22$, $p = 0.7$; Figure 2c,d).

Assemblage composition

The two most abundant species were the same in the two habitats, both for amphibians (*Craugastor laticeps* and *Incilius campbelli*) and reptiles (*Anolis uniformis* and *Scincella cherriei*; Table 1; Supplementary Material Figure S3). The amphibian community showed a more even distribution of species abundances than the reptile community, but distributions for each taxon were similar in the two habitats (Supplementary Material Figure S3). Three amphibian species were only recorded in cocoa, one was a singleton but the other two had abundances of 6 (*Lithobates brownorum*) and 15 individuals (*Hyalinobatrachium viridissimum*). Similarly, three other amphibian species were only found in the forest, but with low abundances (1–3 individuals; Table 1). For reptiles, eight species were only found in cocoa (all singletons except *Coniophanes bipunctatus* with five individuals), while nine species were unique to forest (eight with 1–4 individual, and one with six, *Coleonyx elegans*). The Canonical Correspondence Analyses showed that habitat had a significant power, albeit low, for explaining differences in the structure of the amphibian and reptile assemblages (amphibians: $F_{1,21} = 1.83$, $p = 0.02$, $R^2 = 0.08$; reptiles: $F_{1,22} = 1.84$, $p = 0.009$, $R^2 = 0.077$), emphasizing differences in the abundance of the rare species mentioned above (Figure 3).

Relationships with environmental variables within each habitat

The multi-model inference approach revealed that some environmental variables were associated with the abundance of amphibians and reptiles, but that the identity of these variables varied between groups and habitats (Table 2). On the other hand, none of the environmental variables explained the number of species of amphibians or reptiles in cocoa or forest (Supplementary Material Table S1).

In the cocoa habitat, the abundance of amphibians was positively related to canopy height and the presence of a humus layer (85% of deviance explained by the model), while the abundance of reptiles was negatively related to the relative humidity (42% of deviance explained; Table 2). In the forest habitat, the abundance of amphibians showed a negative association with the presence of water bodies, but the model only explained 24% of the deviance. The abundance of reptiles in forest was also related negatively to the presence of water bodies and positively to illuminance (74% of deviance explained; Table 2).

Discussion

Our findings support the idea that shade cocoa plantations under rustic low-intensity management can be suitable habitat for amphibians and reptiles in human-modified tropical forests. Supporting this idea, we found that most environmental variables we measured were similar in both habitats and that cocoa plantations had the same number of species of reptiles and amphibians as the forest. Interestingly, the abundance of both groups was higher in the cocoa, likely due to more leaf litter in this habitat. Importantly, the cocoa plantations in the Lacandona region not only served as habitat for common generalist species, but also for several species associated with old forest and secondary forest (intermediate successional stage) in the study region (e.g., the

Table 1. Amphibian (Anura and Urodela) and reptile (Squamata) species recorded in two habitats, rustic cocoa and forest, in the Lacandona region, Mexico. For each species, the total absolute (#) and relative (%) abundance recorded per habitat is given; when more than one individual was recorded, the number of plots in which they were found is given in parentheses next to the absolute abundance values. Also shown are the results of the univariate generalized linear model for herpetofauna (only for species with three or more individuals registered) that were part of the multivariate abundance analysis (see text): deviance value (*Dev*) and the associated probability values (*p*) for differences in absolute abundance between habitats. The IUCN/Mexico column indicates the conservation status according to the IUCN Red List, and to the Mexican Government (NOM-059-SEMARNAT-2010), respectively [IUCN categories: NE, Not Evaluated; LC, Least Concern; NT, Near Threatened; VU, vulnerable; Mexican categories (Mex): NoT, Not Threatened; SP, Special protection; Thr, Threatened]. The last column shows the name codes assigned to each species

Order (Suborder) Family	Species	Cocoa (#) (%)		Forest (#) (%)		<i>Dev</i>	<i>p</i>	IUCN/ Mex	Code
ANURA									
Bufonidae	<i>Incilius campbelli</i> (Mendelson, 1994)	57 (12)	19.3	18 (9)	12.6	9.1	0.006	LC/NoT	Ica
	<i>Incilius valliceps</i> (Wiegmann, 1833)	13 (6)	4.4	14 (7)	9.8	0.02	0.90	LC/NoT	Iva
	<i>Rhinella horribilis</i> (Wiegmann, 1833)	2 (1)	0.7	7 (5)	4.9	2.2	0.17	LC/NoT	Rho
Centrolenidae	<i>Hyalinobatrachium viridissimum</i> (Taylor, 1942)	15 (4)	5.1	0	0.0	6.8	0.035	LC/NE	Hvi
Craugastoridae	<i>Craugastor laticeps</i> (Duméril, 1853)	114 (11)	38.6	40 (9)	28.0	5.2	0.095	LC/SP	Cla
	<i>Craugastor loki</i> (Shannon & Werler, 1955)	27 (9)	9.2	17 (7)	11.9	0.8	0.43	LC/NoT	Clo
	<i>Craugastor palenque</i> (Campbell & Savage, 2000)	7 (4)	2.4	4 (2)	2.8	0.4	0.54	NT/NoT	Cpa
	<i>Craugastor psephosypharus</i> (Campbell, Savage, & Meyer, 1994)	0	0.0	1	0.7	–	–	NT/NoT	Cps
Eleutherodactylidae	<i>Eleutherodactylus leprus</i> (Cope, 1879)	6 (5)	2.0	17 (6)	11.9	2.9	0.094	LC/NoT	Ele
Hylidae	<i>Smilisca baudinii</i> (Duméril & Bibron, 1841)	7 (5)	2.4	6 (3)	4.2	0.05	0.83	LC/NoT	Sba
	<i>Tlalocohyla loquax</i> (Gaige & Stuart, 1934)	1	0.3	0	0.0	–	–	LC/NoT	Tlo
	<i>Trachycephalus</i> “ <i>vermiculatus</i> ” (Cope, 1877)	0	0.0	3 (2)	2.1	3.0	0.086	LC/NoT	Tve
Microhylidae	<i>Gastrophryne elegans</i> (Boulenger, 1882)	5 (3)	1.7	1	0.7	2.0	0.21	LC/SP	Gel
Phyllomedusidae	<i>Agalychnis callidryas</i> (Cope, 1862)	0	0.0	1	0.7	–	–	LC/NoT	Acl
Ranidae	<i>Lithobates brownorum</i> (Sanders, 1973)	6 (4)	2.0	0	0.0	6.3	0.022	LC/NoT	Lbo
	<i>Lithobates vaillanti</i> (Brocchi, 1877)	3 (2)	1.0	1	0.7	0.8	0.43	LC/NoT	Lva
URODELA									
Plethodontidae	<i>Bolitoglossa mulleri</i> (Brocchi, 1883)	3 (3)	1.0	2 (2)	1.4	0.2	0.60	VU/NoT	Bmu
	<i>Bolitoglossa rufescens</i> (Cope, 1869)	29 (7)	9.8	11 (6)	7.7	2.6	0.15	LC/SP	Bru
Total amphibians		295		143					
Squamata (Sauria)									
Corytophanidae	<i>Basiliscus vittatus</i> (Wiegmann, 1828)	1	0.2	1	0.2	–	–	LC/NoT	Bvi
	<i>Corytophanes cristatus</i> (Merrem, 1820)	0	0.0	4 (3)	0.7	4.7	0.057	LC/SP	Ccr
Dactyloidae	<i>Anolis biporcatus</i> (Wiegmann, 1834)	0	0.0	1	0.2	–	–	NE/SP	Abi
	<i>Anolis capito</i> (Peters, 1863)	2 (2)	0.3	6 (4)	1.1	1.8	0.21	LC/NoT	Aca
	<i>Anolis lemurinus</i> (Cope, 1861)	3 (2)	0.5	1	0.2	0.8	0.46	LC/NoT	Ale
	<i>Anolis beckeri</i> (Boulenger, 1881)	0	0.0	1	0.2	–	–	LC/SP	Abe
	<i>Anolis rodriguezii</i> (Bocourt, 1873)	8 (4)	1.2	8 (5)	1.4	0	0.98	LC/NoT	Aro
	<i>Anolis uniformis</i> (Cope, 1885)	550 (12)	84.4	474 (12)	83.9	1.8	0.18	LC/NoT	Aun
Eublepharidae	<i>Coleonyx elegans</i> (Gray, 1845)	0	0.0	6 (3)	1.1	4.6	0.034	LC/Thr	Cel
Scincidae	<i>Mesosincus schwartzei</i> (Fischer, 1884)	1	0.2	1	0.2	–	–	LC/NoT	Msc
	<i>Plestiodon sumichrasti</i> (Cope, 1867)	1	0.2	0	0.0	–	–	LC/NoT	Psu
	<i>Scincella cherriei</i> (Cope, 1893)	40 (11)	6.1	18 (7)	3.2	5.9	0.010	LC/NoT	Sch
Sphaerodactylidae	<i>Sphaerodactylus glaucus</i> (Cope, 1866)	2 (2)	0.3	0	0.0	–	–	LC/SP	Sgl
Teiidae	<i>Holcosus festivus</i> (Lichtenstein & Martens, 1856)	2 (2)	0.3	7 (4)	1.2	2.0	0.22	LC/NoT	Hfe
Xantusiidae	<i>Lepidophyma flavimaculatum</i> (Duméril, 1851)	5 (4)	0.8	4 (4)	0.7	0.1	0.74	LC/SP	Lfl
	<i>Lepidophyma</i> sp.	1	0.2	0	0.0	–	–	NE/NoT	Lsp

(Continued)

Table 1. (Continued)

Order (Suborder) Family	Species	Cocoa (#) (%)		Forest (#) (%)		Dev	p	IUCN/ Mex	Code
SQUAMATA (Ophidia)									
Boidae	<i>Boa imperator</i> (Daudin, 1803)	1	0.2	0	0.0	–	–	LC/Thr	Bim
Colubridae	<i>Amastridium sapperi</i> (Werner, 1903)	1	0.2	1	0.2	–	–	LC/NoT	Asa
	<i>Clelia scytalina</i> (Cope, 1867)	0	0.0	1	0.2			NE/NoT	Csl
	<i>Coniophanes bipunctatus</i> (Günther, 1858)	5 (4)	0.8	0	0.0	6.5	0.016	LC/NE	Cbi
	<i>Coniophanes fissidens</i> (Günther, 1858)	5 (3)	0.8	1	0.2	2.9	0.21	LC/NE	Cfi
	<i>Coniophanes imperialis</i> (Baird & Girard, 1859)	0	0.0	4 (2)	0.7	3.1	0.11	LC/NE	Cim
	<i>Imantodes cenchoa</i> (Linnaeus, 1758)	2 (1)	0.3	6 (6)	1.1	2.1	0.17	LC/SP	Ice
	<i>Leptodeira septentrionalis</i> (Kennicott, 1859)	2 (2)	0.3	1	0.2	0.3	0.58	LC/NoT	Lse
	<i>Ninia diademata</i> (Baird & Girard, 1853)	4 (2)	0.6	1	0.2	0.96	0.45	LC/NoT	Ndi
	<i>Ninia sebae</i> (Duméril, Bibron & Duméril, 1854)	0	0.0	2 (2)	0.4	–	–	LC/NoT	Nse
	<i>Oxybelis aeneus</i> (Wagler, 1824)	0	0.0	1	0.2	–	–	LC/NoT	Oae
	<i>Pliocercus elapoides</i> (Cope, 1860)	1	0.2	1	0.2	–	–	LC/NoT	Pel
	<i>Rhadinaea decorata</i> (Günther, 1858)	3 (3)	0.5	1	0.2	1.1	0.30	LC/NoT	Rde
	<i>Scaphiodontophis annulatus</i> (Duméril, Bibron & Duméril, 1854)	0	0.0	2 (2)	0.4	–	–	LC/NoT	San
	<i>Sibon dimidiatus</i> (Günther, 1872)	1	0.2	0	0.0	–	–	LC/NoT	Sdi
	<i>Spilotes pullatus</i> (Linnaeus, 1758)	1	0.2	0	0.0	–	–	LC/NoT	Spu
Elapidae	<i>Micrurus diastema</i> (Duméril, Bibron & Duméril, 1854)	1	0.2	3 (3)	0.5	1.1	0.39	LC/SP	Mdi
Viperidae	<i>Bothriechis schlegelii</i> (Berthold, 1846)	1	0.2	0	0.0	–	–	LC/NT	Bsc
	<i>Porthidium nasutum</i> (Bocourt, 1868)	8 (7)	1.2	8 (6)	1.4	0	0.97	LC/SP	Pna
Total reptiles		652		565					
Total herpetofauna		947		708					

anurans *Craugastor laticeps*, *C. palenque*, and *Incilius campbelli*, the salamanders *Bolitoglossa mulleri* and *B. rufescens*, the lizards *Anolis capito*, *A. uniformis*, *Lepidophyma flavimaculatum*, and the snakes *Bothriechis schlegelii* and *Porthidium nasutum* (Hernández-Ordóñez et al. 2014, 2015; Russildi et al. 2016). Overall, these results have important management implications for designing landscapes that can be productive while conserving these ecologically relevant animal groups.

Our study underscores the fact that agroecosystems whose vegetation is complex and structurally similar to that of the native vegetation are likely to ensure adequate environmental conditions and resources for the local herpetofauna (Macip-Ríos & Muñoz 2008, Orozco-Aguilar 2016, Wanger et al. 2010). In the cocoa habitat, most environmental variables (9 of 12) had similar values to those in forest (Supplementary Material Figure S1). In another study in the same sites, it was also found that tree species richness did not differ between habitats (Zárate et al. 2014). These vegetation similarities were most likely one of the main reasons why both habitats had similar number of amphibian and reptile species and only small differences in assemblage composition (Supplementary Material Figure S3).

Species number is a metric that may be less sensitive to habitat changes (Thompson et al. 2016, Hillebrand et al. 2018), particularly when those changes are more subtle, as between the rustic cocoa and forest we studied. Other studies comparing

herpetofauna in shade cocoa and forest found a similar pattern for one or both groups (Faria et al. 2007; Wanger et al. 2010). More generally, studies comparing biodiversity metrics in conserved forest with those found in disturbed forests (e.g., forest fragments, secondary forests, restoration forests, rustic agroforests, logged forests, etc.) often find that species number is a response variable that maintains, or quickly recovers, its magnitude (e.g., Thompson & Donnelly 2018, Acevedo-Charry & Aide 2019). On the other hand, metrics of species composition may be more sensitive to subtle habitat differences (Díaz-García et al. 2020). In shaded-cocoa, changes in assemblage composition of herpetofauna have been related to an increase in the relative abundance of a few common species (Lieberman 1986, Heinen 1992, Faria et al. 2007). In our study, while we found an increase in the abundance of common species in cocoa, their relative abundances did not change very much between the habitats. Instead, we found a weak effect of habitat on assemblage composition, mostly driven by rare species that were only present (or more frequent) in one of the habitats.

Unlike species number (which did not vary) and assemblage composition (which varied subtly), the abundance of amphibians and reptiles differed strongly between habitats. Abundances were higher in cocoa than in forest, though the pattern was somewhat different between groups: while reptiles increased by 15%, amphibian abundance increased by 106% (Table 1). Also, the increase in

Table 2. Model-averaged coefficients estimates and standard errors (in parentheses) of environmental predictor variables used to model the mean abundance of amphibians and reptiles found per plot in two habitats, cocoa and forest. Those predictors whose 90% confidence interval did not include zero were included in the final model and are shown in bold. Also shown is the amount of deviance explained (% dev. expl.) by each final model. Details on how variables were quantified can be found in Supplementary Material Appendix S1.

Variables	Amphibians Cocoa	Reptiles Cocoa	Amphibians Forest	Reptiles Forest
(Intercept)	3.046 (0.076)	3.89 (0.104)	2.417 (0.172)	3.782 (0.046)
Humus	0.315 (0.055)	0 (0.006)	-0.01 (0.047)	0 (0.001)
Canopy height	0.321 (0.091)	0.001 (0.009)	0.002 (0.033)	0 (0.005)
Herbs	0.01 (0.047)	0.001 (0.007)	0.007 (0.039)	0 (0.005)
Air temperature	0 (0.003)	-0.001 (0.011)	0.001 (0.017)	0 (0.001)
Litter depth	0 (0.003)	0.006 (0.024)	0.008 (0.053)	0 (0.002)
Litter cover	0 (0.003)	0.001 (0.015)	-0.006 (0.033)	0 (0.003)
Trees	0 (0.001)	0.103 (0.117)	0.039 (0.148)	0 (0.001)
Shrubs	0 (0)	0.005 (0.031)	0.001 (0.013)	0 (0.002)
Logs & lianas	0 (0)	0.002 (0.011)	-0.04 (0.119)	0 (0.005)
Illuminance	0 (0)	0.004 (0.021)	0.091 (0.142)	0.243 (0.053)
Water bodies	0 (0)	0.023 (0.058)	-0.366 (0.194)	-0.31 (0.064)
Relative humidity	0 (0)	-0.217 (0.118)	0.032 (0.079)	0 (0.001)
% dev. expl.	85.0	42.1	23.8	74.0

amphibians was more generalized than in reptiles. Five of the seven most abundant species of amphibians had higher abundances in cocoa (*Incilius campbelli*, *Hyalinobatrachium viridissimum*, *Craugastor laticeps*, *Craugastor loki*, and *Bolitoglossa rufescens*). In reptiles, higher abundance was mostly driven by the two most common species (*Anolis uniformis* and *Scincella cherriei*), while most other species were rare in both habitats. In agroforests worldwide, increases in abundance are more frequent than decreases in the case of reptiles, but equally frequent in amphibians (reviewed by Palacios et al. 2013). While most agroforests have edge habitat that can favor the proliferation of a few reptile species, only agroforests that maintain certain structural elements (e.g., understory cover) are able to maintain similar or increased amphibian abundances (Palacios et al. 2013 and references therein).

So, what does the rustic cocoa habitat have that favors herpetofauna in the Lacandona region, in particular amphibians? A few environmental characteristics differed between both habitats, and they were probably responsible for the abundance increases in cocoa. Tree density, leaf litter depth and litter cover had higher values in cocoa (Supplementary Material Figure S1). Higher tree density in the cocoa habitat is caused by the planted cocoa trees (Zárate et al. 2014). In turn, the high density of cocoa trees produces a copious leaf litter. Other studies have also reported more leaf litter in shade-cocoa plantations and have associated this characteristic to increased herpetofaunal abundance (Lieberman 1986, Heinen 1992, Wanger et al. 2010). As suggested by these studies, amphibians and reptiles are likely to find abundant trophic and non-trophic resources in the dense litter and may experience a better and/or less variable microclimate (Whitfield et al. 2007). Contrary to the cocoa habitat, other types of disturbed forests in the region have been found to harbor decreased herpetofaunal abundances (forest fragments, Russildi et al. 2016; secondary forests, Hernández-Ordóñez et al. 2015), further highlighting the high conservation value of this agroforest.

In addition to the environmental variables that differed between habitats, we also found that within each habitat different

environmental variables were related to the abundance of amphibians and reptiles. In cocoa the relationship of environmental variables was relatively weak for reptiles (42% of deviance explained) but strong for amphibians (85% of deviance explained). The abundance of reptiles in cocoa was negatively related to relative humidity, which points to the fact that this group of animals favors less humid microenvironments. On the other hand, the abundance of amphibians was positively related to canopy height and the presence of a humus layer. Similar to leaf litter (see above), the humus layer likely provides abundant resources and microclimatic conditions which are ideal for amphibians (Whitfield et al. 2007). Higher canopies are associated with the presence of large native trees in the cocoa plantations (Zárate et al. 2014). Large trees often have unique morphological characteristics, such as cavities, buttresses, large crowns, and heavy epiphyte loads, all of which provide abundant and diverse resources for many groups of animals (Pinho et al. 2020). The presence of large trees may be of disproportionate importance for the conservation of animals in disturbed habitats. For example, in small rainforest fragments, the presence of forest-dependent arboreal mammals is directly related to the abundance of large trees (Arroyo-Rodríguez et al. 2007). Thus, maintaining a diverse cover of native trees in cocoa agroforests, including large individuals, is a management guideline that would probably not only favor amphibians, but other groups of organisms (e.g., birds; Bennett et al. 2021).

Contrary to the results for the cocoa habitat, in the forest habitat the relationship of environmental variables was strong for reptiles (74% of deviance explained) but weak for amphibians (24% of deviance explained). The abundance of reptiles was positively related to illuminance and negatively to the presence of water bodies. These relationships are not surprising, considering that rainforest reptiles often bask in open areas (Wanger et al. 2010), which might have higher illuminance levels, and prefer drier microhabitats. The abundance of amphibians in forest was also negatively related to the presence of water bodies. This result was unexpected given that other studies have stressed the

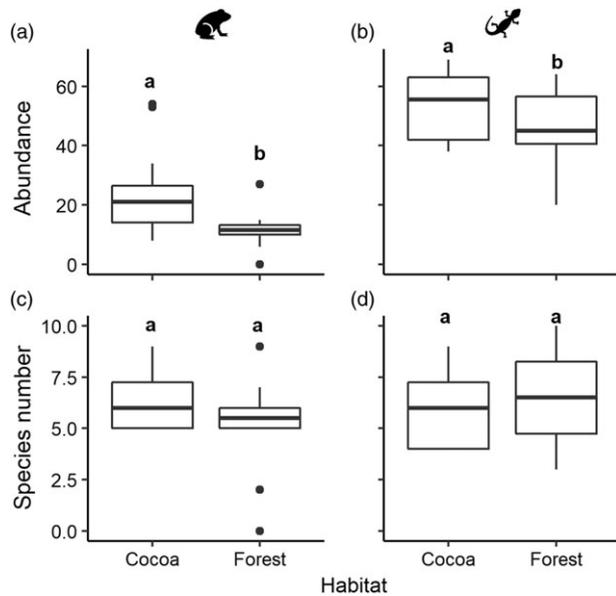


Figure 2. Boxplots of the abundance (a and b) and number of species (c and d) observed per plot in two habitats, cocoa ($n = 12$ plots) and forest ($n = 12$ plots), for amphibians (a and c) and reptiles (b and d). Different letters above box-plots indicate statistical differences determined with multivariate abundance analyses (abundance) and generalized linear modelling (species number). Animal icons used with permission from Microsoft.

importance of the presence of water bodies for the maintenance of amphibians in disturbed habitats (Wanger et al. 2009, Hernández-Ordóñez et al. 2015, Díaz-García et al. 2020). However, given the low explanatory value of the model, we interpret this result as meaning that the presence of water bodies was not very important in determining the abundance of amphibians in forest. This may be because three of the four most abundant species recorded in forest have direct development (*Craugastor laticeps*, *C. loki* and *Eleutherodactylus leprus*), which means that they do not need water bodies to reproduce. Overall, our results on the effect of environmental variables confirm that different variables may be shaping amphibian and reptile communities within versus across habitats. Thus, to maximize our understanding both patterns should be examined, as already pointed out in a previous study (Wanger et al. 2010).

Finally, to properly contextualize our findings, it is important to remember that, for two main reasons, the cocoa habitat we studied probably represents one of the extremes in the “wildlife friendliness” gradient of agroecosystems. First, the cocoa plantations were under very low management intensity (see Methods). Low management intensity, of course, favors biodiversity, but it may not meet the requirements of human sustenance (Bennett et al. 2021). Indeed, many of the shade-cocoa plantations that existed in the region have been replaced by different crops, mostly cattle pasture and annual crops. They are also being replaced by monoculture agroforests, such as oil palm plantations, which are known to have heavily impoverished herpetofaunas (Gallmetzer & Schulze 2015). Intensifying management of the cocoa plantations to make them profitable could decrease the quality of this agroecosystem as habitat for amphibians and reptiles. However, studies have also shown that, if well designed, agroforests or silvopastoral systems can be profitable while providing habitat for animals (e.g., Gordon et al. 2007, Deheuvels et al. 2014, Montoya-Molina et al. 2016, Bennett et al. 2021).

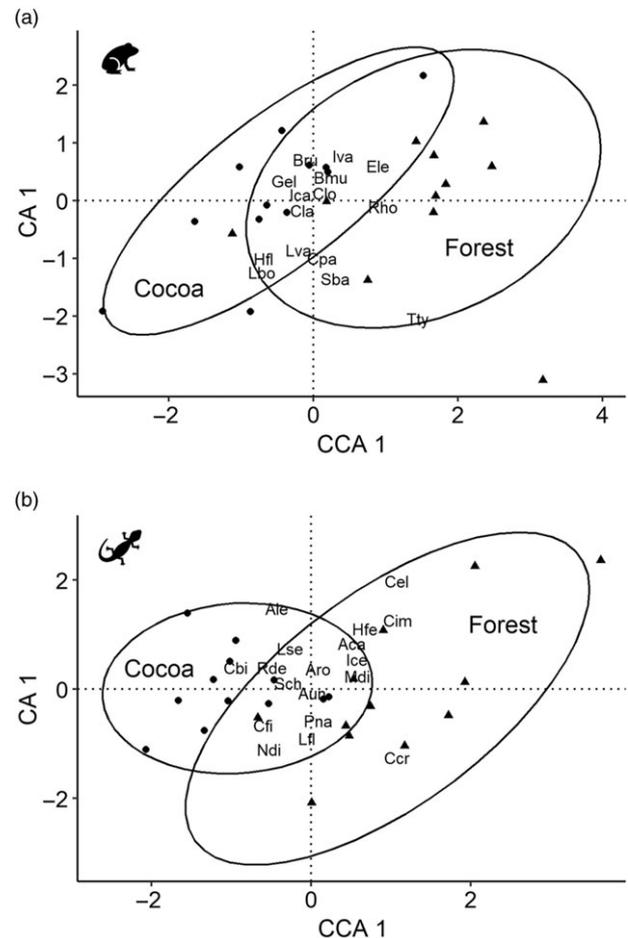


Figure 3. Canonical correspondence analysis for 12 plots of rustic cocoa plantations (circles) and 12 plots of forest (triangles), based on the composition of their amphibian (a) and reptile assemblages (b). Species are shown by a three-letter abbreviation; see Table 1 for full species names. Animal icons used with permission from Microsoft.

Second, landscape composition and configuration most likely played an important role in favoring the maintenance of amphibian and reptile populations in the cocoa habitat. The area of the cocoa plantations was relatively large (100 ha), and, most importantly, it abutted with a large forest area (> 2,000 ha). Both the amount of forest cover in the surrounding landscape and the proximity to forest, are crucial characteristics that are associated positively to the persistence of native biodiversity in anthropogenic tropical landscapes (Acevedo-Charry & Aide 2019, Grass et al. 2019, Arroyo-Rodríguez et al. 2020).

In conclusion, our study indicates that rustic shade cocoa plantations in the Lacandona region can be considered an ecologically-friendly agroecosystem for amphibians and reptiles, including species that are considered forest specialists. Thus, in addition to the high conservation value of forest fragments (Russildi et al. 2016) and secondary forests (Hernández-Ordóñez et al. 2015), an agricultural matrix containing cocoa agroforests could play an important role in the long-term conservation of herpetofauna in the anthropogenic landscapes of this Mesoamerican biodiversity hotspot. However, the potential conservation value of shade cocoa and other types of agroforests for tropical biodiversity will only be maximized, when these agroecosystems replace less suitable agricultural covers, such as cattle pastures and annual crops, rather than replacing forest (Martin et al. 2020).

Supplementary material. To view supplementary material for this article, please visit <https://doi.org/10.1017/S0266467422000219>

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Conflicts of interest. The authors declare none.

Ethical statement. This study complies with ethical standards. Herpetofaunal sampling was approved by the Mexican government secretariat in charge of the environment (Secretaría de Medio Ambiente y Recursos Naturales; permit: Nuim/SGPA/DGVS/02132).

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