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Influence of farm characteristics and surrounding habitat on amphibian communities in Afrotropical cocoa

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Forests are being converted to agriculture throughout the tropics, driving declines in sensitive rainforest taxa. However, low-intensity agricultural systems, such as cocoa agroforestry, may provide refuges for biodiversity. Little is known about the suitability of these systems for vertebrate fauna in the Afrotropics, especially with regards to amphibians. Here, we contribute novel information on amphibian communities in African cocoa farms by investigating the effects of within-farm characteristics and surrounding habitats on the abundance and richness of amphibians. In August–September 2019, we surveyed amphibians in 15 cocoa farms and four primary forest sites in southern Cameroon, capturing 206 individuals of at least 29 species. Overall, responses of amphibians to within-farm characteristics and surrounding habitat varied between species, but at the community level the main responses were a decrease in number of captures with increasing ground vegetation height, and with increasing open agriculture and villages surrounding farms. Species also showed associations with canopy cover in farms (positive for three species), abundance of husk piles in farms (negative for three species), surrounding forest habitat (positive for two species and negative for one) and surrounding plantation or degraded forest habitat (positive for one species). Our results on the effects of surrounding habitat suggest that the composition of amphibian communities in cocoa farms may be largely influenced by the ability of species to disperse through neighbouring habitats. Additionally, we found that the relative abundance of amphibian species differed significantly between forest and cocoa: this effect appeared to be driven largely by tree frog species (genus *Leptopelis*), which were more abundant in forest habitats, suggesting that certain tree frog species may serve as an indicator of primary forest-like conditions. Given the current climate of agricultural intensification in Africa, our results contribute to the initial steps towards identifying amphibian-friendly agricultural practices.

Keywords: agroforestry, leaf litter, microhabitat, open agriculture, tropical forest

INTRODUCTION

The expansion of agriculture is a major driver of deforestation, habitat loss, environmental pollution and land use change worldwide, and thus a primary cause of the current decline in global biodiversity (Foley et al., 2005; Newbold et al., 2015). However, agricultural practices such as agroforestry allow biodiversity conservation whilst maintaining food production (Clough et al., 2011). Agroforestry consists of growing crops that are capable of thriving in shaded or partially shaded conditions, such as coffee, cocoa, and vanilla, under a forest canopy (Tscharntke et al., 2011). Compared with high-intensity monocultures, agroforestry systems support a more diverse community of plants and animals, and can serve as biodiversity refugia in fragmented and deforested landscapes (Bhagwat et al., 2008; Tscharntke et al., 2011).

Cocoa, though originally an understory plant, can be grown in a range of conditions from full-sun monocultures to shaded agroforestry (Tscharntke et al., 2011). Shaded cocoa agroforestry systems maintain a thick canopy of rainforest trees, making them structurally similar to forest (Sonwa et al., 2007; Bisseleua et al., 2013). These systems may support higher levels of biodiversity compared with intensive monocultures; taxa ranging from birds (Clough et al., 2009; Jarrett et al., 2021), to bats (Ferreira et al., 2023), ants (Philpott & Armbrecht, 2006) and epiphytes (Bos & Sporn, 2012) occur at higher abundance and diversity in shaded agroforestry systems. However, most of the research concerning biodiversity in cocoa habitats is from the Americas and Asia, and there is a distinct lack

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of information from the Afrotropics, despite this region producing ~70% of cocoa globally (De Beenhouwer et al., 2013; International Cocoa Organization, 2018).

Amphibians are the most threatened vertebrate group globally, with habitat change being one of the main factors contributing to population declines and extinctions (Stuart et al., 2004; Luedtke et al., 2023). Despite this, amphibians remain one of the lesser studied groups in ecology and conservation (Stuart et al., 2004), with some geographical regions being especially under-represented in the literature. A recent global assessment of amphibian declines identified that there is a high concentration of threatened amphibian species in the Afrotropics, with the major drivers of population declines being disease and habitat loss (Luedtke et al., 2023). Furthermore, data on amphibians in sub-Saharan Africa are still extremely scarce (Luedtke et al., 2023). While identified as a major threat, there is limited research into the effects of habitat change on amphibians in Africa, with a recent bias towards more novel topics such as emerging infectious disease and enigmatic declines (Gardner et al., 2007).

The lack of research on how habitat changes affect amphibians is especially relevant in cocoa agroforestry systems, where different management actions could have varying effects on amphibian communities (Fulgence et al., 2021). The studies that do exist have found encouraging results regarding the conservation value of shaded cocoa agroforestry for amphibian populations. For instance, Brüning et al. (2018) investigated a land-use gradient in Colombia and found that shade-grown coffee and cocoa farms were best for amphibian diversity when compared with non shaded farms and cattle pastures. Several species recorded in their study were only found in one habitat type on their land use gradient, which is unsurprising, given the highly specialised ecology of many amphibians. They concluded that amphibian conservation needs to encompass a mosaic of habitats, and that small-scale agroforestry could have an important role in already modified landscapes (Brüning et al., 2018). Additionally, Wanger et al. (2010) demonstrated the importance of farm management characteristics, such as leaf litter depth and number of log piles, on amphibian species richness in cocoa farms in Indonesia.

Most authors conclude that there is no perfect management of cocoa agroforestry systems that supports all local amphibian fauna, and that this modified habitat cannot replace pristine habitats (Gibson et al., 2011). Nonetheless, there is increasing evidence from the Americas and south-east Asia that low-intensity cocoa farms have conservation value when compared to more degraded habitats. So far, only one published study focused on amphibian communities in African cocoa: Onadeko (2016) found a progressive decline in diversity and number of captures of amphibians from primary forest to cocoa monocultures in Nigeria. An additional study from Ivory Coast investigated tree frog assemblages on a land use gradient that included some cocoa plots; the results indicate a decrease in species richness with increasing habitat modification, with a specific drop off in species with specialised reproductive strategies (Ernst & Rödel, 2008). However, none of these studies consider how farm characteristics (leaf litter, ground-level vegetation, canopy cover) and surrounding habitats may affect the local amphibian communities.

Overall, there is insufficient information on amphibian communities in African cocoa agroecosystems. Here, we take a step to bridge this gap in knowledge by presenting the first focused study on amphibians in Cameroonian cocoa farms. We investigated the effect of within-farm characteristics as well as surrounding habitats on amphibian communities. Considering local characteristics is important when studying amphibians as direct comparisons of categorised habitat types often produce contradictory results due to small-scale habitat characteristics not being considered (Murrieta-Galindo et al., 2013). Specifically, our study was conceived to address the following aims: 1) investigate the effects of within-farm characteristics on the amphibian community; 2) investigate the effect of surrounding habitat on the amphibian community within farms; and 3) compare number of captures of different amphibian genera between cocoa farms and primary forest.

MATERIALS & METHODS

Study area

The study system encompassed 15 smallholder-owned cocoa farms in south-east Cameroon, and four sites in primary forest in the Dja Faunal Reserve in Cameroon. Amphibian surveys were conducted over a 6-week period during the wet season, 5 August–17 September 2019. The cocoa farms were selected based on size (minimum of 1.5 ha) and shade cover (to form a gradient), and were separated by at least 500 m. Farms were located in five different regions: farms in Somalomo (n = 4) were adjacent to the Dja Faunal Reserve, farms in Ayos (n = 7) and Ngoumou (n = 2) were in a semi-degraded landscape with agriculture and small secondary forest patches, and farms in Elat (n = 2) were in heavily degraded agricultural landscape bordering the outskirts of the Cameroonian Capital, Yaoundé (Fig. 1, Appendix I in supplementary material).

Habitat data collection

In each cocoa farm we collected data on ground vegetation height, leaf litter depth, number of water bodies, dead log piles, cocoa husk piles, and canopy cover (Appendix I in supplementary material). These variables are an indication of management intensity; in general, farms managed at low intensity have more ground vegetation and leaf litter, and a denser canopy cover (Tscharntke et al., 2011). At 20 points at least 50 m from the farm edge and at intervals of 12 metres, we measured leaf litter depth and ground vegetation height (in cm) using a simple metre stick, and calculated a mean value for each. We counted the number of husk piles, dead wood piles (trimmed branches, log piles) and water bodies (pools and puddles) visible at each point. Given that we only encountered water bodies in three farms, and that the puddles themselves were small and infrequent, we

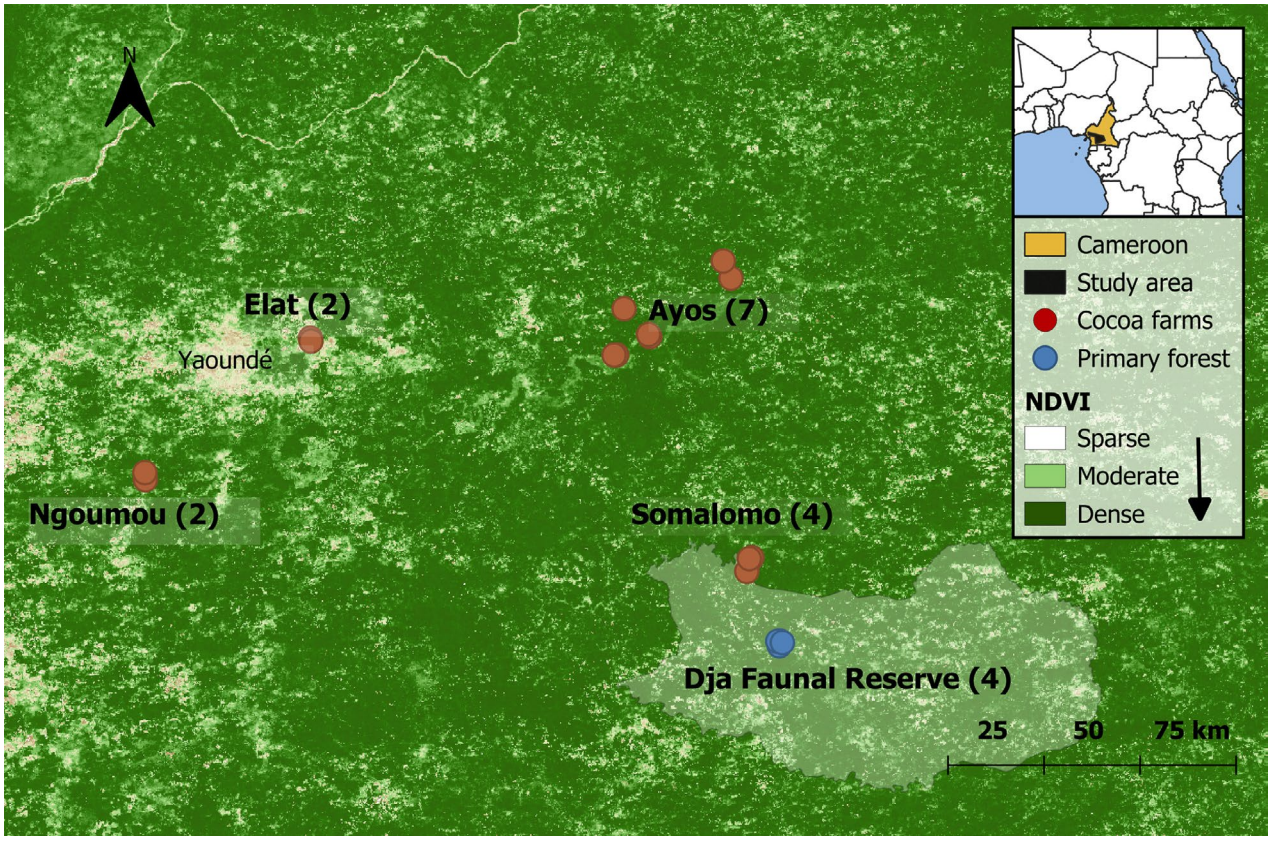

Figure 1. Cocoa farms (n = 15; brown points) and Dja forest sites (n = 4; blue points) sampled in 2019 in Southern Cameroon. The base map shows eMODIS Normalised Difference Vegetation Index (NDVI; January 2020; accessed from www.usgs.gov) where darker green indicates more forested areas and tan indicates urbanised areas and rivers.

did not include this variable in the analyses (Appendix I in supplementary material). We measured shade tree canopy cover by taking ten photographs using a camera with a fish-eye lens on an extendable pole (5 m), at ten locations in each farm, 24 m apart and a minimum of 50 m from farm edge. Using the software ImageJ (Schneider et al., 2012), we converted the photographs to black and white, and then calculated the percentage of black (vegetation) in each photograph. The canopy cover value we use is a mean of the ten pictures (see Jarrett et al., 2021 for details).

We collected surrounding habitat data while walking the boundary of the farms. Using a handheld GPS, we tracked the farm perimeter and marked way-points for changes in habitat bordering the farms. We classified habitats into the following categories: villages, open canopy forest (canopy cover < 50% estimated by eye), closed canopy forest (canopy cover > 50% estimated by eye), open farmland (cultivated cropland with no canopy cover), cocoa agroforestry (cocoa cultivated under > 20% canopy cover), palm plantations and water bodies (we combined pools, swamp, streams and rivers in this parameter). In QGIS (QGIS Development Team, 2018) , we then calculated the percentage of the total boundary length of each farm made up by each of the habitats. For instance, if the perimeter of a farm was 2 km, and 0.5 km of the perimeter was primary forest, this would receive a value of 25%.

Amphibian surveys

We conducted standardised nocturnal surveys once at each site, using a visual search technique aided by frog vocalisations. Surveys were always conducted by the same observer, who was wearing a head torch. Surveying started just after dusk (~18:30 h), with just one farm visited per night. The observer captured amphibians from the ground, leaf litter, ground vegetation, and low branches of cocoa and shade trees up to 3 m high. The farms were divided into three sections, and we conducted one 45-minute search in each section (total search time = 135 minutes). We started a stopwatch at the beginning of a search, and paused the timer whenever a frog was located. We captured individuals in sealable bags containing some added moist vegetation, which we inflated. Once we had captured an individual, we started the timer again and the searching continued, so that the 45 minutes of searching were not affected by how long it took to capture individuals.

Amphibians captured in these surveys were weighed, measured (snout-to-vent length), and identified to species where possible, using the most up to date field guide for the region (Channing & Rödel, 2019). We released all individuals back to the original collection location within 12 hours. We kept photographic records for individuals which we were unable to identify in the field for later identification where possible. However, certain species were indistinguishable morphologically;

for these individuals, identification was left at the genus level. Given limited survey capacity, we faced the trade-off of more comprehensive amphibian surveys at each site (involving multiple visits) versus a larger number of sites surveyed. As the goal of this study was to examine variation in amphibian communities with farm and habitat variables, we prioritised the latter. Thus, we acknowledge that with one visit to each site, our data are unlikely to represent the full amphibian community present, but rather a snapshot of more common species (Veith et al., 2004).

Statistical analyses

Prior to analysis, we checked for collinearity amongst within-farm variables (ground vegetation height, leaf litter depth, husk piles, dead wood piles and canopy cover) and amongst surrounding habitat variables (village, open canopy forest, closed canopy forest, open farmland, cocoa agroforestry, palm plantations and water bodies). The only significant correlation (Spearman's correlation coefficient > 0.7; Dormann et al., 2013) was between husk piles and dead wood piles; we excluded dead wood piles from the analysis as husk piles have been shown to provide valuable habitat for herpetofauna in other tropical agroecosystems (Henderson & Powell, 2001). We then tested all our variables for spatial autocorrelation: the only variable that showed significant spatial autocorrelation (Mantel's test, $p < 0.05$) was village habitat. This was expected given that several farms in close proximity within Elat and Ayos - the most degraded landscapes - were located near urban development. Thus, we kept the variable in the model, but results regarding urban habitat should be interpreted with caution as they may be driven by spatial proximity.

To test the effect of within-farm characteristics (four variables after excluding dead wood piles) on amphibian species abundance, we built a generalised linear model (GLM) for multivariate abundance data using the function 'manyglm' from the package 'mvabund' (Wang et al., 2022). We assumed a Poisson distribution. The 'manyglm' function gives the strong advantage of providing both univariate (species-specific) and multivariate (community-wide) results. Thus, statistical power is maximised in the multivariate analyses by considering data across species, whilst still providing species-specific coefficients to examine which species may be driving relationships (Wang et al., 2022). For rare species with limited data, these multivariate abundance models borrow strength from more common species by assuming there is some shared structure across species, resulting in a shrinkage of the variance and stabilisation of coefficients (Wang et al., 2022). Thus, univariate test statistics from rare species should be interpreted with caution.

To test the effects of surrounding habitat variables on amphibian species abundance, we used the same 'manyglm' approach, after condensing the seven surrounding variables into three principal components using a principal component analysis (PCA). We conducted a PCA because the GLM containing all seven variables was over parametrised and generated nonsensical model predictions. The first three components of the PCA captured 78% of total variance (Appendix II in supplementary material). The first component (PC1) represented more natural surrounding habitats (high closed and open canopy forest, high water bodies, low village). The second component (PC2) represented more degraded surrounding habitat (high open fields and village), and the third component (PC3) represented mostly palm plantation and open canopy forest (for full loadings, see Appendix II in supplementary material). For both multivariate abundance models (within-farm and surrounding habitat), we report overall significance of variables (Wald test statistic and p-value) from multivariate analysis, as well as species-specific estimates and test statistics from univariate tests. We considered a relationship statistically significant when $p < 0.05$ and marginally significant when $p < 0.1$. We then used models to predict species' abundances across a range of within-farm and surrounding habitat scenarios, to visualise the direction and magnitude of effects. We checked models for normality of residuals and over- or under-dispersion.

To assess potential effects on amphibian diversity, we constructed two simple GLMs using species richness as dependent variable, one with the four within-farm variables as predictors, and one with the three PCs of surrounding habitats. We assumed a Poisson distribution. In addition, to assess to what extent our data were representative of the full amphibian community in cocoa farms, we conducted rarefaction and extrapolation of pooled abundance data. These analyses were conducted using package iNEXT (Hsieh et al., 2016). We estimated species richness after extrapolating to double the number of captures and estimated the 95% confidence intervals by a bootstrap method based on 500 replications (Chao et al., 2014).

We used a multivariate GLM to investigate the difference in number of captures of each species between forest and cocoa, by constructing a 'manyglm' object with an explanatory variable for habitat type (forest or cocoa). We report multivariate statistics and univariate tests to assess the species that show the strongest differences between forest and cocoa.

RESULTS

We captured 206 amphibians: 175 in cocoa farms and 31 in the forest sites (Fig. 2). In cocoa, 24 species were identified to species level in the field, and five identified to genus level, and in forest, 11 species were identified to species level, and one to genus level. The most common species were squeaker frogs (*Arthroleptis* sp.; n = 68) and Aubry's tree frog (*Leptopelis aubryi*; n = 21). Total species richness across cocoa sites was estimated at 50 species (95% CIs = 29, 87), implying that further survey effort would be needed to achieve a comprehensive list of species.

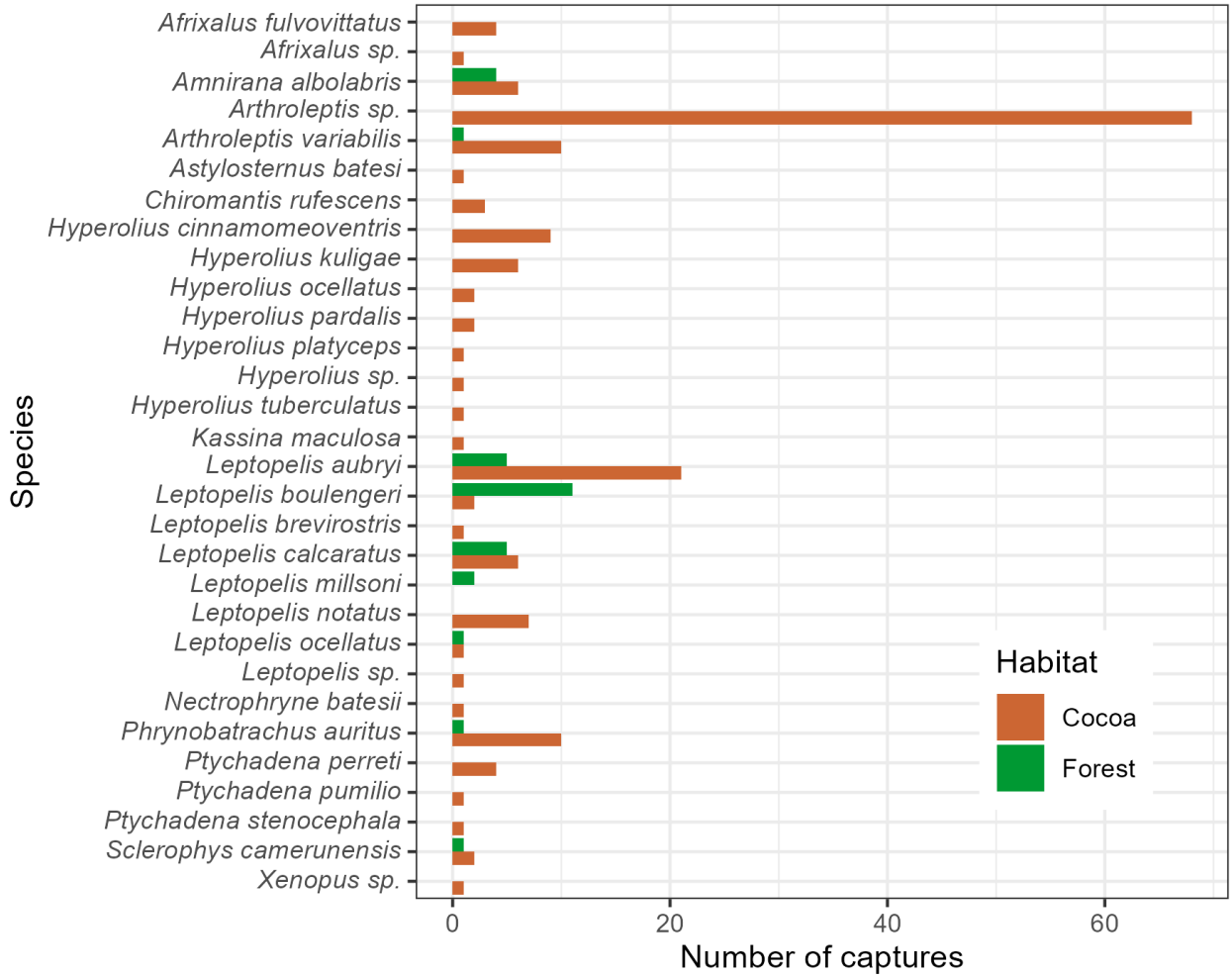

Figure 2. Numbers of captures of amphibians in cocoa (brown) and mature forest (green) plots

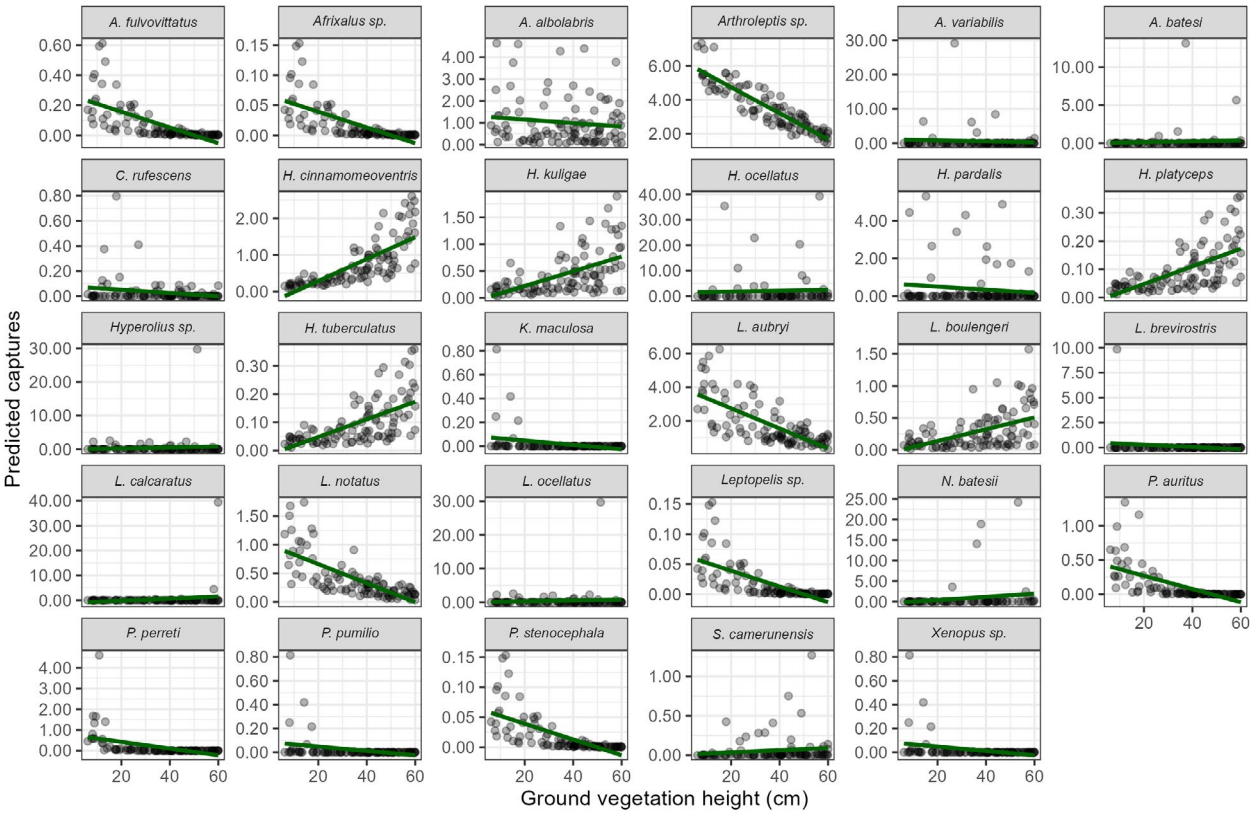

Figure 3. Predicted number of captures of amphibian species with ground vegetation height (cm) in cocoa farms. Predictions were made from multivariate GLMs, with dots representing predicted captures and the green line showing the model coefficient.

Table 1. Effect of boundary and habitat variables on total abundance and abundance of each amphibian species. '+' and '-' indicate direction of significant (p<0.05) or marginally significant (p<0.1) effect, and a blank cell indicates no significant effect.

Species	Boundary			Farm Characteristics			
	PC1 (forest, water)	PC2 (open fields, village)	PC3 (palm, open forest)	Ground vegetation	Leaf litter	Canopy cover	Husk piles
Total abundance		-		-			
Afrixalus aff. *fulvovittatus*							
Afrixalus sp.							
Amnirana cf. *albolabris*		-					
Arthroleptis sp.				-			
Arthroleptis variabilis							-
Astylosternus batesi							
Chiromantis rufescens	-						-
Hyperolius cinnamomeoventris							
Hyperolius kuligae							
Hyperolius ocellatus	+	-					
Hyperolius pardalis							
Hyperolius platyceps							
Hyperolius sp.							
Hyperolius tuberculatus							
Kassina maculosa		-	+				
Leptopelis aubryi							
Leptopelis boulengeri							
Leptopelis brevirostris							
Leptopelis calcaratus				+		+	
Leptopelis cf. *aubryi*				-		-	
Leptopelis notatus		+					
Leptopelis ocellatus							
Leptopelis sp.							
Nectophryne batesii							
Phrynobatrachus auritus				-			
Ptychadena perreti			+	-			+
Ptychadena pumilio		-				+	
Ptychadena stenocephala							+
Sclerophrys camerunensis							-
Xenopus sp.		-					

Effect of within-farm characteristics

Total number of captures of amphibians ranged from five to 20 individuals per farm and decreased significantly with increasing ground vegetation height (Wald value = 5.4, p = 0.04; Table 1; Fig. 3; Appendices III & IV in supplementary material). Univariate tests revealed species-specific responses to within-farm characteristics (Table 1; Fig. 3; Appendices III & IV in supplementary material). The species driving the negative association with ground vegetation height was *Ptychadena perreti* (estimate = -0.25, Wald = 1.5, p = 0.05), and with marginal significance *Arthroleptis* sp. (estimate = -0.02, Wald = 2.3, p = 0.09) and *Phrynobatrachus auritus* (estimate = -0.14, Wald = 2.3, p = 0.09; Fig. 3). In contrast, *Leptopelis calcaratus* was positively associated with ground vegetation height (estimate = 0.7, Wald = 2.1, p = 0.04). *Arthroleptis variabilis*, *Chiromantis rufescens* and *Sclerophrys camerunensis* were negatively associated with husk piles (estimate = -0.76, Wald = 2.0, p = 0.01; estimate = -0.47, Wald = 1.0, p = 0.06 and estimate = -0.5, Wald = 0.8, p = 0.05, respectively). Canopy cover was positively associated with number of captures in three species (*L. calcaratus*, estimate = 0.5, Wald = 1.9, p = 0.08, *Ptychadena pumilio*, estimate = 0.08, Wald = 0.9, p = 0.09 and *Xenopus* sp., estimate = 2.9, Wald = 0.89, p = 0.08). Species richness ranged from two to eight species per farm and was not affected by within-farm characteristics.

Effect of surrounding habitats

For the overall community, abundance was affected by PC2 (open farmland, villages) with marginal significance (Wald = 4.6, p = 0.06; Table 1; Fig. 4; Appendices III & IV in supplementary material). This effect was driven by the following species, all with negative associations to PC2 (Table 1): *Amnirana* cf. *albolabris* (estimate = -1.43, Wald = 2.6, p = 0.007), *Hyperolius ocellatus* (estimate = -3.2, Wald = 1.2, p = 0.02), *Kassina maculosa* (estimate = -7.5, Wald = 1.1, p = 0.07), *P. pumilio* (estimate = -7.5, Wald =

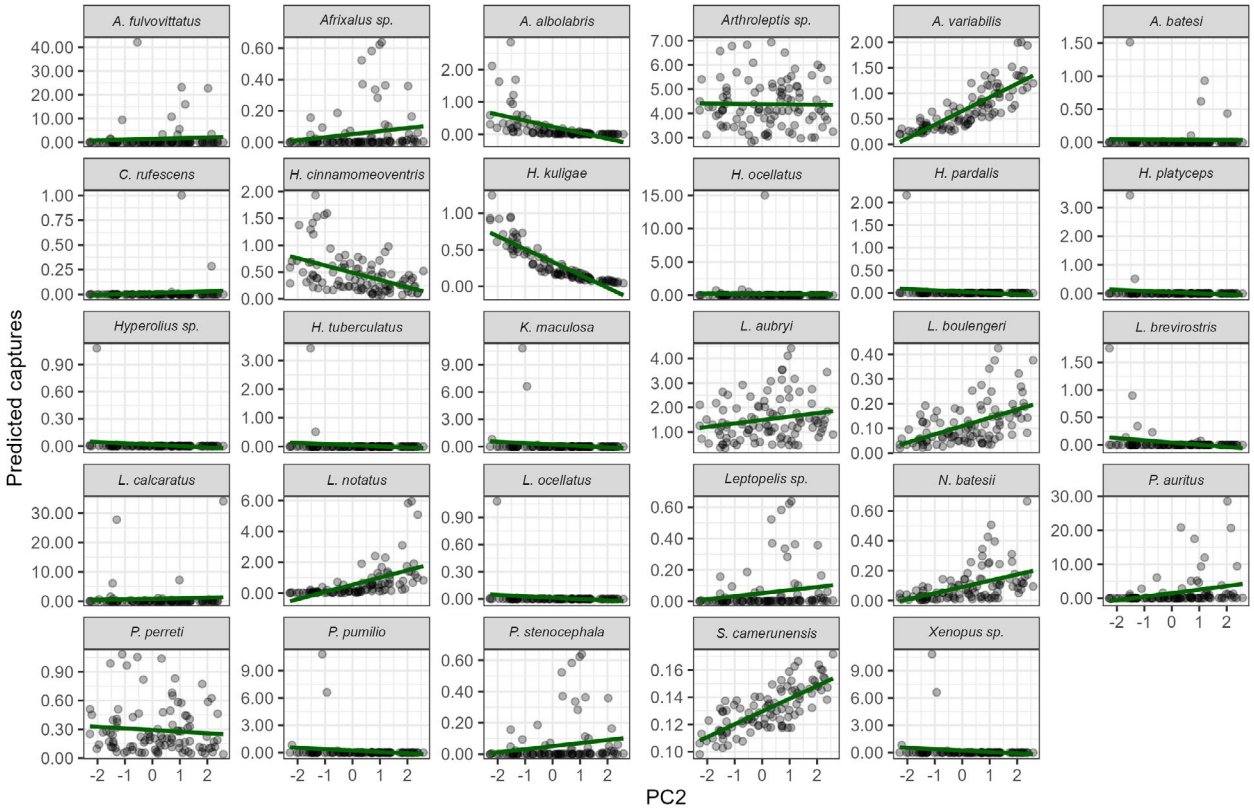

Figure 4. Predicted number of captures of amphibian species with Principal Component 2 in cocoa farms. Predictions were made from multivariate GLMs, with dots representing predicted captures and the green line showing the model coefficient.

Figure 5. A breeding adult female cinnamon-bellied reed frog *Hyperolius cinnamomeoventris*, captured during a nocturnal survey in a cocoa farm near Ayos, Southern Cameroon

1.1, p = 0.08), and *Xenopus* sp. (estimate = -7.5, Wald = 1.1, p = 0.07). The only species positively associated with PC2 was *Leptopelis notatus* (estimate = 0.9, Wald = 2.4, p = 0.04). PC1, which represented surrounding forest and water bodies, had a positive effect on the number of captures of *H. ocellatus* (estimate = 9.34, Wald = 1.5, p = 0.03) and *Hyperolius pardalis* (estimate = 1.5, Wald = 1.21, p = 0.09), and was negatively associated with *C. rufescens* (estimate = -17.2, Wald = 1.5, p = 0.07). PC3, representing palm plantations and open forest, was positively associated with *P. perreti* (estimate = 0.7, Wald = 1.4, p = 0.05). Total species richness was not significantly affected by surrounding habitat explanatory variables.

Comparison of forest and cocoa habitats

Amphibian community abundances varied between cocoa and forest (Wald = 4.5, p = 0.04, Fig. 2; Appendix IV in supplementary material). At a species-level, the strongest effects were for *Leptopelis boulengeri* (estimate = 2.8, Wald = 3.6, p = 0.01) and *L. calcaratus* (estimate = 0.9, Wald = 1.5, p = 0.09), both of which had higher number of captures in forest compared with cocoa.

Natural history observations

We caught 79 squeaker frog individuals (genus *Arthroleptis*), the majority of which (n = 68) were not identified to species level, whilst 11 were identified as *A. variabilis*.

We captured one Bates' tree frog *Nectophryne batesii*, a known forest specialist (Channing & Rödel, 2019), during the nocturnal survey of a cocoa farm adjacent to primary forest in the Somalomo area (this farm had high percentage canopy cover and was largely surrounded by forest; Figs. 1 & 2; Appendix I in supplementary material).

We captured a breeding pair of cinnamon-bellied reed frogs *Hyperolius cinnamomeoventris* in a cocoa farm in the Ayos region, which consists in semi-degraded landscape with forest and agricultural patches (Figs. 1 & 2). We identified them as a breeding pair, as they were captured in amplexus and the female had red thighs, a characteristic feature of breeding adults (Fig. 5) (Channing & Rödel, 2019).

DISCUSSION

Our surveys detected at least 29 species of amphibian in Cameroonian cocoa farms, which is a higher species richness than that reported in other studies in cocoa agroforestry (22 species in Nigeria, four species in Colombia, ten in Indonesia; Wanger et al., 2010; Onadeko, 2016; Brüning et al., 2018). These findings suggest that overall, the low-intensity cocoa farming encountered in Cameroon may be relatively beneficial for amphibian communities. Despite this, our results also indicated that our survey effort did not achieve a comprehensive coverage of the amphibian community. Thus, further survey effort, including multiple visits per site, would be required to establish a comprehensive list of species inhabiting cocoa agroforestry systems in Cameroon.

The habitat surrounding cocoa farms influenced total captures of amphibians, suggesting that a main factor driving amphibian community composition in cocoa farms could be the potential of neighbouring habitats to act as corridors. Amphibians may only be able to disperse through certain habitats (Rothermel & Semlitsch, 2002; Cushman, 2006), and therefore their presence in cocoa farms may depend on the composition of surrounding habitats. Specifically, our findings showed that the number of amphibians captured significantly declined in cocoa farms surrounded by open farmland and villages. The negative effect of open farmland on amphibian occurrence in cocoa farms could be for several reasons: first, agricultural chemicals such as fertilisers and pesticides may be used commonly in open farmland habitats such as cassava or maize fields, and these chemicals pose a significant threat to amphibian survival (Perfecto & Vandermeer, 2008). Chemicals may run off the fields into waterbodies, causing tadpole mortality and other toxic effects (Agostini et al., 2020; Wanger et al., 2023). Additionally, as agriculture intensifies, preferred amphibian habitats including water bodies may be removed, with the absence of canopy cover reducing humidity and drying the leaf litter (Rothermel & Semlitsch, 2002). Several genera encountered in this study such as *Hyperolius*, *Amnirana* and *Ptychadena* have aquatic juvenile stages (Channing & Rödel, 2019); for these groups, population persistence requires water. Indeed, our results indicate significant negative associations between PC2 (open fields, villages) and certain species of each of the genera. Overall, our results suggest that an increasing amount of surrounding open farmland and villages can reduce connectivity of cocoa farms. This is especially important for amphibians due to their limited dispersal ability, compared with more mobile vertebrates such as birds or bats (Cushman, 2006). Our results support the idea that habitat fragmentation is a critical threat to amphibians (Stuart et al., 2004).

The other principal components in our analysis, representing more natural surrounding habitats (closed canopy forest, open canopy forest, water bodies: PC1) and palm plantations and open forest (PC3), appeared less important in determining amphibian captures. *H. ocellatus* and *H. pardalis* responded positively to PC1, largely matching findings from other *Hyperolius* species in Nigeria, which appear to show a preference for low intensity cocoa plantations or forest habitats over cocoa monoculture habitats (Onadeko, 2016). In a study of two *Hyperolius* species in São Tomé, one responded strongly to habitat degradation whilst the other less so, which is attributed to breeding habitat requirements (Strauß et al., 2018). In our system, *H. ocellatus* and *H. pardalis* may find it easier to disperse through forest habitats, where water bodies for breeding are available (Channing & Rödel, 2019). In contrast, *C. rufescens* was negatively associated to PC1: this species is a widespread habitat generalist, which is often associated with human-generated structures such as ditches and ponds, where it builds its foam nests (Coe, 1974). PC3, which mostly represents palm plantations and open canopy forest, was positively associated with *P. peretti*. Whilst palm plantations are usually not favourable habitats for biodiversity, amphibian species adapted to disturbed habitats are found at high abundances in oil palm plantations in south-east Asia forests (Faruk et al., 2013; Paoletti et al., 2018). *Ptychadena peretti* is a habitat generalist, or at least known to thrive outside of rainforest habitats, and therefore may be able to disperse easily through such habitats (Rödel et al., 2002; Onadeko, 2016).

Regarding within-farm characteristics, we found that the main variable that influenced overall captures was ground vegetation height. This relationship was negative for three largely ground-dwelling species, one puddle frog *P. auritus*, one grass frog *P. perreti* and one squeaker frog *Arthroleptis* sp., so that higher ground vegetation resulted in lower number of captures. Given the ground-dwelling lifestyle of these species, this relationship could be associated with reduced detectability, as it may be easier to see frogs when the ground is barer. In contrast, one species of tree frog (*L. calcaratus)*, which would usually perch above ground vegetation height, showed a positive association with ground vegetation height, suggesting that this may be a true response to habitat rather than an effect of detectability.

In addition, we found some species-specific responses to other within-farm characteristics: contrary to expectations, three species responded negatively to husk piles. These negative associations are harder to explain, and may be linked to other unknown variables correlated to the presence of husk piles, for instance if snakes or

other predators are utilising these husk piles (Henderson & Powell, 2001). Canopy cover was positively associated to number of captures in three species, one tree frog (*L. calcaratus*), one squeaker frog (*P. pumilio*) and the clawed frog *Xenopus* sp.. For these three ecologically distinct species, shade trees may provide different opportunities, for instance higher persistence of small water bodies for *Xenopus* sp., and more forest-like structure for *L. calcaratus*.

When we compared cocoa farms to primary forest plots, we found an overall difference in community composition. At a species-level, this was mainly driven by two species of tree frog, that occurred more frequently in forest compared with cocoa. Indeed, these two *Leptopelis* species, Boulenger's tree frog *L. boulengeri* and Spurred tree frog *L. calcaratus*, require dense rainforest habitat (Channing & Rödel, 2019). Though we caught most individuals of these species in the Dja Reserve, we captured two *L. boulengeri* in cocoa farms in semi-degraded landscapes (Ayos & Ngoumou; Fig. 1). We also captured six *L. calcaratus* in cocoa farms; four individuals were from two farms in the Somalomo region (bordering the Dja Reserve), and two individuals were collected from a farm in the Yaoundé region. Thus, these two tree frogs may show a preference for forest habitats, whilst still being able to inhabit low-intensity forest-like cocoa plantations.

This study provides novel evidence on the effect of within-farm characteristics and surrounding habitats on amphibian communities in African cocoa. Our study did not consider certain aspects of agroforestry systems that may influence amphibian communities, for instance, the application of chemicals such as pesticides and herbicides (though information gathered at these study sites previously indicates infrequent and irregular use of chemicals), or the microclimatic conditions found in the understorey. Future studies into amphibians in African cocoa should consider these variables. Additionally, a longer-term study would be useful to understand the seasonal variation in amphibian communities and population dynamics; a longer-term study with repeated surveys at each site would also allow estimation of detection rates, which would provide insights into population density. Finally, the use of molecular methods to improve taxonomic resolution when identifying species could provide valuable input for future studies. Our results contribute to the initial steps towards a deeper understanding of the challenges facing amphibian communities in the Afrotropics and give evidence that expansion of open farmland and urbanisation could be a major threat to these species. Overall, our findings indicate relatively high diversity of amphibian communities in Cameroonian cocoa farms, but with important changes in communities according to the suitability of habitats surrounding these farms. We would therefore conclude that whilst pristine forest is an irreplaceable habitat when it comes to species conservation, low intensity agroforestry may provide a reasonable compromise between wildlife communities and agricultural needs.

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Author contributions

AHM, CJ and LLP conceived the study, AHM collected the data and led the writing, CJ analysed the data and co-led the writing, KC, TTRC and DFF provided field and writing support. All authors read and approved the final version of this manuscript.

Data accessibility

Data used to conduct this study are available at 10.6084/m9.figshare.28227791

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