

# **Amphibian and reptile communities of dry and wet sites across Indonesian oil palm, rubber and forests**



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## **Abstract**

Indonesia is the biggest producer of oil palm in the world and among the biggest producers of rubber, and a significant portion of the country's rainforests have been replaced by oil palm and rubber plantations. Conservation measures are therefore needed to assess and possibly reduce the impact of agricultural intensification on the vertebrate fauna, but limited effort has been put so far in understanding the effects of habitat conversion on reptile and amphibian communities. Here we study community composition, species richness and abundance of the herpetofauna of the densely farmed Jambi province, in central Sumatra. We sampled reptiles and amphibians in the lowland forests of the Harapan rainforest and in oil palm and rubber plantations through visual encounter surveys, pitfall trappings and audio recordings. We also measured various environmental features in every habitat to assess what are the best environmental predictors of herpetofaunal abundance and community composition. We found that abundance of reptiles and amphibians in oil palm can be surprisingly high, while none of the richness measures were consistently different between forest and plantations. Additionally, there are often abundance differences among dry and riparian sites of the same land-use system. Only few of the species found in plantations are also found in the nearby forests, and all the most common plantation species are of low conservation interest. We conclude that conversion is detrimental for forest herpetofaunal assemblages. Our study provides new insights on the consequences of habitat conversion on reptile and amphibian communities, often neglected in similar assessments, and proves that communities in plantations have different composition and overall smaller conservation value than those in tropical rainforests.

## **Introduction**

The human population of South-East Asia is rapidly growing, requiring constant agricultural intensification in an area with a very high level of biodiversity (Sodhi et al. 2010). Plantations are nowadays a major component of the landscape of the once completely forested islands of Indonesia, and oil palm and rubber industries represent an important fraction of the economy of several South-East Asian countries. In the period between 2002 and 2011, estate crops, that include oil palm and rubber, accounted for 2.2% of the country's GDP (BPS 2012). They

therefore must not be overlooked when considering the necessity and implementation of conservation measures. Both oil palms (*Elaeis guineensis*) and rubber trees (*Hevea brasiliensis*) are not native to Indonesia, originating from western Africa and South America, respectively, but today the country has become the world's biggest producer of palm oil and one of the biggest producers of rubber (BKPM 2012). Indonesia has recently reached a level of primary forest cover loss to cash crops higher than Brazil (Margono et al. 2014), and despite a recent decline in the annual rate of expansion of oil palm plantations from an average 9% to 3.8%, the island of Sumatra, specifically, is the area in Indonesia with the highest forest losses, with 10% of its total land area devoted to oil palm plantations alone (Gunarso et al. 2013).

Agricultural practices like those used in Indonesia and other human activities are frequently cited as causes of biodiversity loss around the world (Stuart 2004), and conversion of primary and secondary forests to cash crops is often associated with reduction of species richness and abundance, as well as changes in community composition, in a variety of taxa (e.g. Chung et al. 2000, Koh and Wilcove 2008, Brühl and Eltz 2010). With an estimated 82% of the world amphibian species depending on forest environments (Ernst and Rödel 2005), the effects of agricultural intensification on the herpetofauna of tropical rainforests need to be carefully studied to assess its impact on local biodiversity.

Teynié et al. (2010) listed 93 species of amphibians and 226 species of reptiles in Sumatra, with 25.9% (i.e. 83) of the total being endemic to the island. Species surveys are commonly needed to describe communities in a certain area in order to determine where protection is mostly needed (e.g. Welsh and Lind 1988), to provide a starting point for the implementation and effectiveness of conservation measures (Gibbons et al. 1997, Bailey et al. 2005), and to assess spatio-temporal variations in distribution ranges (e.g. Brooks et al. 2011). In general, a detailed a priori knowledge of the ecological consequences of human disturbance on communities of related taxa in specific areas is helpful in order to improve conservation strategies (Bailey et al. 2005). In Sumatra, the uneven distribution of reptile and amphibian species among the different administrative provinces is likely due to insufficient study of the herpetofauna of the island rather than to ecological factors (Teynié et al. 2010). The intense land-use conversion from forest to agriculture that is currently underway urges us to investigate the herpetofaunal communities in the involved land-use systems to understand their response to agricultural intensification.

Different land-use systems have different environmental features (e.g. temperature, humidity,

leaf litter depth, etc.), and the reasons for any observed community changes after conversion may be linked to different vegetation structure, scarcer canopy cover, less litter fall, higher average air temperature, lower humidity, and lower levels of carbon stored in the litter in plantations (Drescher et al. 2016). For example, survival rates in amphibians have been found to decrease when exposed to experimental semi-natural environments with reduced leaf litter height and higher temperatures (deMaynadier and Hunter 1999). Amphibian community richness and abundance are negatively affected after an area is logged (Parris 2004, Kurz et al. 2016), and the higher the extent of the disturbance, the lower the abundance (Konopik et al. 2014). However, different assemblages from different ecosystems do not always respond in the same way to clearance. In some cases, total density after clearcutting was higher than before disturbance (Ryan et al. 2002, Todd and Rothermel 2006), sometimes because of different species-specific responses to disturbance (Clawson et al. 1997), leading to difficulty in deriving general conclusions on how herpetofaunal communities respond to habitat conversion. However, compared to other taxa, limited effort has been so far put into understanding the effects of agricultural intensification on the herpetofauna, and especially on reptiles, which on a conservation perspective are the least studied of all terrestrial vertebrates (Glor 2001, Tews et al. 2004).

The aim of this study is to describe species abundance, richness and composition of amphibians and reptiles in the rainforests and in the other two most common land-use systems, namely palm oil and rubber plantations, of the Jambi province in Sumatra, Indonesia. To make place for these monocultures, forests have been cleared, and the original herpetofaunal communities might have been modified. Riparian areas are generally areas of lower agricultural output but of higher conservation value, so for this study we sampled both dry and riparian sites within each land-use system, to evaluate the extent of any divergences in the assemblages in areas of different hydrological status and the conservation value of each system. Secondly, we measure a set of environmental features of each land-use system in order to find alterations in habitat characteristics that could help explain community structure and any observed shifts.

We expect abundance, richness and assemblage composition modifications to follow the same patterns both in amphibians and reptiles, as shown in previous studies where in several cases the two classes responded in the same way to similar treatments (Wanger et al. 2009). We hypothesize that species abundance is relatively little affected in the plantations, as demonstrated

by earlier studies in comparable environments (Faruk et al. 2013), while richness is higher in forest environments. We also expect to find plantations to be either inhabited mainly by the subset of species that lived in the area before human intervention that have the highest tolerance to disturbance, and possibly of lowest conservation interest, or by species that were rare or entirely absent from the original community. On the other hand, species of higher conservation interest are presumed to be found in forests. Moreover, riparian areas, located close to waterways and therefore potentially more hospitable to herpetofaunal communities, and particularly to amphibians, because of abundance of water and food resources, likely harbour both a higher species richness and abundance compared to drier environments of the same land-use system. Measurements of environmental features were performed not only for the description of the land-use systems *per se*, but also because after habitat conversion the correlations between assemblages and environmental variables could be different than in the previous communities. We hypothesize that environmental features such as air temperature, relative humidity, undergrowth density, leaf litter cover, and number of possible hiding spots provided by piles of palm fronds, dead plant material and cavities in the ground or in the wood can at least partially explain richness, abundance and composition of the assemblages, as summarized in Table 1. We expect average temperature and relative humidity to be respectively higher and lower in plantations than in forests, and, being reptiles and amphibians ectotherms, to be the best predictors. However, because of the different physiology of the two taxa, the extent of the responses might be different, depending on the considered variable. Specifically, in addition to hydrological status, also temperature, humidity and leaf litter cover could have stronger effects on amphibians than on reptiles.

## **Methods**

### **Study site**

We collected data from April 2017 until July 2017 in 24 core plots of the Collaborative Research Centre 990, in the Batang Hari Regency. Sampling and measurements were performed with the same intensity in the three main land-use systems of the province of Jambi, which are lowland forest and oil palm and rubber plantations. We sampled in four plots for each combination of

land-use system and hydrological state, which means 6 habitats: dry and riparian forest, dry and riparian oil palm and dry and riparian rubber. The plots are 50 × 50 m in size and were subdivided in 4 sections for the purpose of the herpetofaunal surveys. This allowed us to detect relationships between herpetofauna and environmental features, which could otherwise remain undetected because of the heterogeneity of the plots and the fine spatial scale at which these relationships occur.

## **Sampling design**

In each plot, we performed a census of the amphibian and reptile species through visual encounter and aural surveys and pitfall trappings. Using only one sampling method might lead to biased abundance and richness estimates as each method is affected by population abundances and detection probabilities of each species (Todd and Rothermel 2006). Coupling visual searches with pitfall traps is the most effective and cost efficient sampling method for reptiles and amphibians (Garden et al. 2007), and in order to maximise the probability of sampling a representative, unbiased portion of each plot's ground-dwelling and arboreal herpetofauna, we also relied on acoustic data for identification. Species identification through calls do not require direct visual contact between the animals and the observers, decreasing the sampling artefact due to vegetation density or other environmental factors that might hinder vision-only searches. The intensity of the sampling was equal in each of the 6 habitats.

Over the 24 hours, sampling was performed within three distinct time windows, henceforth referred to as midday, sunset and night windows, respectively at 11:00-15:00, 18:00-19:00 and 20:00-24:00. Within the same time window, activity and detection probability of each species were assumed to be constant, and therefore the sampling could be started at any time within the window without the need to account for time differences between days. Because of logistic reasons, only one plot was sampled per window, meaning that 3 plots were sampled each day. Long transport times between plantation and forest plots, as well as sampling permission restrictions, forced us to sample plantation plots before forest plots. However, we randomized our sampling schedule to sample plots of every hydrological status and, during the plantation sampling, of every land-use, each day, and avoided sampling the same plot twice in the same day, so as to account for variations between days in sampling favourableness. Finally, once a plot

was visited for the midday sampling, it was automatically scheduled to be visited again the following day in the night window, to allow the pit-fall traps to be left active for roughly 36 hours.

Once encountered, species-specific morphological characteristics of each individual animal were photographed to allow exact species identification. Additionally, vocal calls of amphibians were recorded during surveys using a Sennheiser ME-66 microphone coupled to an Olympus LS-3 recorder at a sampling rate of 44.1 kHz, recording to WAV format. We tried and record as many kinds of calls as possible (e.g. territorial calls before capture or distress calls during handling) for each species. Data on the animal's identification, approximate age (i.e. if juvenile or adult) and location, as well as time of capture, were recorded. Finally, all animals that were temporarily captured to obtain better photographic references were released at the point of capture.

### **Pit-fall trapping**

We set up 4 traps per plot, one in each of the 4  $25 \times 25$ m sections. Each trap consisted of 4 perpendicular black plastic fences 35 cm high, converging towards a middle point, where a 40 cm wide bucket was dug in the ground. Each fence was 5 m long, so that each trap had a diameter of 10 meters, which is the low end of the optimal range suggested by Bury and Corn (1987). The centre of a trap (i.e. the bucket) was placed as close as possible to the centre of the section it was in, provided it did not fall within any of the subplots used for other activities. The orientation of the fences did not need to be the same as that of the plot borders, but could be tilted to fit within the surroundings, and they could cross the subplots if needed. The traps were activated at the end of the midday session and left open until the end of the night session of the following day, when data on the captured animals were collected. Captured animals were identified, photographed, their approximate age determined, and then released.

We collected data on all the arthropods that fell in the traps as well, to have information on the food items available to the reptiles and amphibians. We identified the arthropods to the order level, and assigned to each of them a value describing approximate total length (e.g. 0.5 for length between 0 and 1 cm, 1.5 for length 1-2 cm, ...).

## **Covariates measurement**

In each plot and during each sampling session, temperature and relative humidity were measured using a pocket-sized thermo-hygrometer, and weather conditions (i.e. clear, cloudy or rainy) were also recorded.

During one of the two midday sessions of every plot, estimates of leaf-litter cover and depth, undergrowth vegetation cover and height and number of sites suitable for being used as hiding spots by the target animals were performed in each of the four sections. These covariates are assumed to remain constant over the entire sampling period, so they were measured only once. Leaf litter cover was measured by averaging the percentages of exposed soil within four randomly placed quadrants, while depth was measured by averaging 3 measurements within the quadrants taken with a ruler held perpendicularly to the ground. Undergrowth cover was measured in the same way as leaf litter, but with the help of pictures taken from above the quadrant and looking down, whereas height was measured with measuring tape. Hiding spots were counted by considering any rock, dead tree, dead plant material (such as logs, single palm fronds or branch piles), frond piles, trash piles and cavities (either in trees or in the ground) judged likely to be used as a den.

## **Data analysis**

All analyses were performed using R software version 3.3.3 (R Core Team 2017). For all our response variables we used a p-value level of 0.05 to assess statistical significance. All graphs were created using the ggplot2 package (Wickham 2009).

We merged the arthropod and herpetological capture data from our pitfall traps with our visual survey observation and environmental data. We performed the same analyses separately for reptiles and amphibians and for rare and common species, because of their different physiology that might induce diverging responses to different habitats and environmental drivers. The attribute “common” was assigned to the most frequently occurring species whose cumulative percentage of occurrence was equal to half of the total encounters of their respective classes, whereas all other species were classified as “rare”. We further appended conservation status data from the IUCN Red List (IUCN, 2017).

### **I. Abundance and richness differences between land-use systems and habitat**

We compared alpha and beta richness and abundance of the two classes at the plot scale. We calculated additive beta richness by subtracting the plot's alpha richness from gamma richness, i.e. the total richness of species per habitat (Lande 1996). We fitted generalized linear models to richness and abundance data at the plot scale with Poisson family. In case Poisson models were overdispersed, we used negative binomial models instead. We first ran a full model including land-use type and hydrological status, as well as their interaction. We then generated all comparisons of predictor variables from the full model to the null model and ranked them by AICc (dredge function, R package MuMIn) (Burnham et al. 2004) to check which variables were included in the single best model with the lowest AICc. All other models, including models with  $\Delta\text{AICc} < 2$ , were discarded.

To test our hypotheses, we constructed a model based on habitat (i.e. the six possible combinations between the three land-uses and the two hydrological statuses) as a predictor. We used this parametric model to generate all possible pairwise comparisons among means while testing their significance (glht function, R package multcomp, Hothorn et al. 2008). P-values were FDR (False Discovery Rate)-corrected (Benjamini and Hochberg 2009).

We used the R package vegan (Oksanen et al. 2017) for generating species accumulation curves, rarefied species richness and estimating total richness per habitat to test our hypotheses with different diversity measures. Species accumulation curves (SACs) for all land-use systems were plotted to assess sampling effort as measured by the number of sampled individuals (function rarecurve). We calculated the species richness in each plot type for each class, rarefied to the lowest sampled number of individuals (function rarefy), and used the specpool function to calculate extrapolated richness estimators for each habitat.

### **II. Environmental determinants of richness, abundance and community composition**

We aimed to find the environmental drivers of species richness and abundance of the herpetofauna. As we only had 24 replicates (i.e. the 24 plots), we needed to reduce the number of predictors to a manageable amount to avoid convergence problems with our linear mixed-effects models. All the data concerning environmental predictors coming from variables that we assumed to have similar functions for the herpetofauna and that had been counted in numbers too small to be relevant were collapsed into broader categories. Specifically, the numbers of logs, branch piles, single palm fronds and dead trees were subsequently collectively referred to as

dead plant material, and cavities in trees and in the ground were analysed as cavities. Predictors that could not be grouped with other variables and that did not represent a recurring feature in any of the land-uses analysed, i.e. rocks and trash piles, were excluded from further analyses. Furthermore, leaf-litter depth and undergrowth height were discarded, given that we measured presence of leaf-litter cover and undergrowth density variables, which were more accurate as they were measured over larger areas. This revision allowed us to reduce the number of predictors by five while still accounting for a comprehensive set of eight environmental features. All the considered predictors and their expected effects on reptile and amphibian richness and abundance are presented in Tab. 1. We scaled all environmental predictors to prevent convergence problems with the mixed effects models. We used this full set of predictors to fit generalised linear mixed-effects models to abundance and richness data at the survey scale (GLMER, glmer function, R package lme4) (Bates et al. 2015) using section nested within plot as a random effect and Poisson family. When the resulting model was over-dispersed, we ran negative binomial mixed-effects models instead. We then generated all comparisons of predictor variables from the full model to the null model and ranked them by AICc (dredge function, R package MuMIn) (Barton et al. 2016). We finally evaluated the best model and assessed each of the variables' coefficient sign, strength, and significance.

### **III. Variations in composition between forest- and plantation communities**

We visualized the community compositions of reptiles and amphibians in different plot types using non-metric multidimensional scaling (NMDS) based on Bray-Curtis distances derived from abundance matrices (R package vegan (Oksanen et al. 2015)). To detect any possible influences on the output due to highly different abundance values between species we performed NMDS using presence/absence community matrices as well. We performed ADONIS tests to assess the significance of habitat in structuring the communities.

## **Results**

## Sampling

We performed a total of 144 one-hour visual and aural encounter surveys, equally distributed between 24 plots of 3 land-use systems (oil palm plantations, rubber plantations and lowland forest) and 2 hydrological statuses (riparian and dry). In addition to the surveys, we also mounted 2 sets of 4 pit-fall traps in each plot, for a total of 192 trap installations, of which 46 (24.0%) were successful in capturing at least one reptile or amphibian.

We identified a total of 1147 animals from 42 species, comprising 28 amphibians (N=897, all of which were anurans from 6 families) and 14 reptiles (N=250, including 11 species of lizards *sensu latu* from 5 families and 3 of Serpentes from 3 families). 197 animals (Amphibia=124, Reptilia=73) were found during the midday sessions, 446 at sunset (Amphibia=330, Reptilia=116), and 434 at night (Amphibia=378, Reptilia=56). 70 of the 1147 animals identified (6.1%) were captured with traps, representing 7 species of amphibians (from 4 families) and 1 of reptiles (family: Scincidae), all of which have also been sampled during the visual encounter surveys. This result extends the geographic distribution of 15 species of amphibians and 8 of reptiles previously not recorded in the province of Jambi (Teynié et al. 2010) (Table 2). In addition to vertebrates, pitfall traps collected a total of 466 arthropods from 11 orders.

## Covariates measurement

Environmental data were collected from all 4 sections of the 24 plots and are summarized in Table 3. Temperature was found to be lower and more constant in forests than in plantations. Relative humidity in forest, instead, was slightly higher, but again subject to smaller variations over time. Piles of palm fronds were never found outside oil palm plantations, whereas other forms of dead plant material were especially abundant in forest. Cavities in trees or in the ground were mainly present in forest plots as well. The estimates of leaf-litter cover were much higher in riparian plantations compared to dry ones, while cover estimates in forest were always high. Undergrowth density was only slightly higher in forest plots. Finally, the mean sum of arthropod sizes was much higher in forest plots.

## Abundance and richness variations

The highest abundance of animals was found in oil palm plantations (N= 548 individuals), followed by lowland forest (N=305) and rubber plantations (N=213). Three species of amphibians (*Fejervarya limnocharis*, *Amnirana nicobariensis* and *Kurixalus appendiculatus*) were defined as common species in the subsequent analyses as they made up at least 50% of the total amount of amphibian encounters. Among reptiles, the house gecko *Hemidactylus frenatus* alone represented 73% of all sampled reptiles and was therefore the only common reptile (Table 4). Therefore, no distinction between common and rare species was made for reptiles when analysing richness.

Abundance of all amphibian species combined was higher in riparian areas. For the three most common anurans, the same was true only in oil palm and rubber plots, while riparian forests were the only habitat with significantly more rare species. Reptiles were more abundant in oil palm, and especially in dry oil palm plots. *Hemidactylus frenatus* encounters followed the same pattern, with also a slight increase in number in rubber plots compared to forests. Rare reptiles, too, were mainly found in dry oil palm, and in intermediate amounts in riparian forests (Fig. 1). The naïve richness counts followed the opposite pattern than that observed for abundance, with rubber plantations being the richest system (N=27 species), followed by forest (N= 25) and finally oil palm plantations (N= 23). Both alpha and beta richness were always higher for amphibians than for reptiles, independently of hydrological status and land-use (Fig. 2).

Differences in beta richness estimates between habitats were negligible for amphibians, whereas alpha richness among forest habitats was significantly different, with higher species counts in riparian plots, and intermediate levels in all other habitats. Both alpha and beta richness in reptiles were comparable in all habitats, but a trend towards gamma diversity being higher in dry oil palm is visible (Fig. 2).

Rarefying the observed amphibians communities to the lowest sample, which was found in dry forest (N=27), we estimated dry forest to be the richest system (11.0 species) (Fig. 3), while the Bootstrap estimator pointed at riparian forest to be the richest (18.6 species). Rarefying reptile communities (smallest sample: dry rubber, N = 5), we estimated the highest species count to be 4.0, in dry rubber (Fig. 4), whereas the Bootstrap estimator was highest in dry oil palm (10.1 species) (Table 5).

## Environmental determinants of abundance

The best generalized linear mixed-effect models showed that arthropod size always have a strong positive effect on abundance of amphibians, while temperature and undergrowth density always had negative effects. In addition to that, abundance of amphibians was positively driven by the presence of cavities and dead plant material, but the coefficients were only marginally significant. For common amphibians, frond piles have negative effects. Cavities had a positive, marginally significant effect on the abundance of rare amphibians (Table 6).

For reptiles too, arthropod size always had a positive effect. In the model including all reptile species, humidity and temperature also had positive effects, while the effect of frond piles was negative. For the common *Hemidactylus frenatus*, too, temperature and humidity had positive effects, while those of frond piles were negative. For rare species, humidity and leaf litter cover had negative effects (Table 6).

The categorical habitat variable was contained in all best models.

## Variations in composition between forest- and plantation communities

Visualization of amphibian communities through non-metric multidimensional scaling based on species abundance data showed that the forest communities were more similar to each other than they were to plantation communities, which in turn overlapped to various degrees (Fig. 5). The ADONIS test testing for the significance of the habitat variable in structuring the communities was highly significant ( $R^2=0.51$ , p-value=0.001).

Reptile communities from all habitats were more distinct than amphibian communities, with little overlap (Fig. 6). The ADONIS test for the significance of habitat was highly significant ( $R^2=0.63$ , p-value=0.001).

Simpler presence/absence matrices were generated for amphibians and reptiles. The NMDS could not reliably be generated for the 14 species of reptiles, but for amphibians, the outcome confirmed the result of the abundance NMDS, and the ADONIS test was highly significant ( $R^2=0.56$ , p-value=0.001) (Fig. 7).

## Discussion

In this study we sampled reptile and amphibian species in the three most widespread land-use systems of Sumatra, lowland rainforests and oil palm and rubber plantations, through visual encounter surveys, pitfall trappings and audio recordings, and we measured environmental predictors to assess what factors are mainly responsible for shaping reptile and amphibians communities. We found that overall abundance and naïve richness counts follow opposite patterns in the three land-use systems and that both alpha and beta richness between replicates of the same land-use system are always higher for amphibians than for reptiles. Amphibian alpha richness was the only richness measure that was not constant in all habitats. Environmental predictors were analysed with generalised mixed effect models. Different predictors had different relevance on abundance depending on the class and on the rarity of the species considered, but food availability had positive effects in all cases, and the categorical habitat variable was contained in all best models. Hydrological status of the sites was important for amphibians. Our use of non-metric multidimensional scaling to visualize the composition of the herpetofaunal communities showed that community compositions were not the same in all habitats.

### Knowledge of the Sumatran herpetofauna

The herpetofauna of the island of Sumatra has been unevenly studied, with great differences in the number of recorded species among the different administrative provinces (Teynié et al. 2010). Our sample included 23 species never before recorded in the Jambi province, according to the most complete and recent checklist, which the authors themselves describe as tentative (Teynié et al. 2010). The high number of newly recorded species revealed that under-sampling might explain most of the inter-province discrepancies, rather than ecological factors. The conservation status of 10 out of the 42 species identified during our sampling has not been formally assessed by the IUCN yet (IUCN 2017). Furthermore, our sampling area was relatively small and did not include other areas of high herpetological interest within the Jambi province, such as Kerinci Seblat National Park (Kurniati 2006), where more species are likely waiting to be recorded, or even described. This lack of knowledge might lead to wrong assessments of conservation needs according to the principle that what is not known cannot be protected. This is especially important in areas where agricultural activities have and still are drastically reducing forested areas (Gunarso et al. 2013).

## **Abundance and richness variations**

We expected abundance levels to be similar among habitats, because of previous studies on plantations (e.g. Faruk et al. 2013) where oil palm hosted relatively high number of amphibians. However, in our study, animal counts in oil palm plantations were even higher than in all other habitats, with almost twice as many encounters as in forest. Total richness was not directly proportional to the amount of animals found in a land-use system, since the most populated system was also the poorest, and the least populated, rubber, was found to be the richest. Oil palm systems are therefore capable of hosting a high abundance of herpetofauna, but only few species are in fact capable of taking advantage of the niches that the habitat offers. The most common species in plantations were *Fejervarya limnocharis* and *Amnirana nicobariensis*, which are tolerant to a broad range of habitats (IUCN, 2017), and *Hemidactylus frenatus*, which is an invasive species in several countries (Hoskin 2011). Beta diversity was constant in all habitats for both classes, and no difference was found even between forest and plantations. However, there seemed to be a trend towards lower beta richness values in oil palm and, in reptiles, a trend towards higher gamma richness in dry oil palm. Sample rarefaction and the Bootstrap estimator confirmed that the lowest amphibian richness values were in oil palm plantations, with highest, similar values, in rubber and forest plots. This confirmed, at least for amphibians, our hypothesis that forests host the highest richness, but the difference in richness between forest and rubber was not as strong as expected. We assumed that environmental variables do not affect richness *per se*, and that it is rather the heterogeneity of the environment that determines the richness of a habitat, in turn driving the niche availability that allows for numerous species to coexist. Rubber plantations can be structurally similar to forests, with similar degrees of heterogeneity that offer a variety of niches for many species to coexist (Table 3), while in oil palm plantations, where a more drastic manipulation of the landscape takes place with the use of herbicides and the accumulation of frond piles, the plots are generally more homogeneous. Indeed, for reptiles the extrapolated richness levels were slightly higher in rubber than in forest. However, despite reptile richness estimates deriving from sample rarefaction having similar patterns to amphibians, the Bootstrap estimator predicted a higher richness in dry oil palm.

## **Environmental determinants of abundance**

Reptiles and amphibians being ectotherms, temperature was found to be a relevant factor in predicting abundance of the herpetofauna in almost all cases. Arthropod food availability had

clear positive effects in all cases, but despite the much higher amounts of it in the forest, patterns were not as clearly different from the plantations, meaning that other environmental drivers possibly cancel out its positive influence. When significant, availability of dead plant material and leaf litter cover, which could be used as hiding spots, and undergrowth density, that offered more spatial resources for the animals, always had negative effects. These counterintuitive patterns could point at sampling artefacts due to decreased animal detectability in environments rich in hiding spots and vegetation. However, the extensive visual encounter surveys performed by experienced observers at different times of the day and the use of multiple sampling methods ensured maximum detectability (Kenneth Dodd and Dorazio 2004, Mackenzie and Royle 2005, Royle 2006). Pit fall trappings and identification by audio cues are indirect methods that do not require visual contact with the animals, thus avoiding the detectability issue altogether. Additionally, the overall success rate of our pitfall traps was 24.0%, which is slightly higher than the rate of previous studies which involved the use of pitfall traps (e.g. Garden et al. 2007). Our sample can confidently be assumed to be an unbiased representation of the herpetofauna communities in the different visited habitats. The species accumulation curves in several habitats, especially for amphibians, are close to reaching their respective plateau (Fig. 3, 4), confirming that our sampling has been efficient. The unexpected negative effect of hiding spots and vegetation density could be due to other drivers that were not taken into account in our study. For example, the features we measured might be favourable for other animals who use the same resources as the herpetofauna or that rely on the herpetofauna as prey, like birds, whose richness is enhanced by undergrowth height in plantations (Azhar et al. 2014), or rodents, that can be present in plantations in large numbers (Wood and Fee 2003). Positive effects on multiple taxa might therefore eventually decrease abundance and richness of amphibians and reptiles. Moreover, the fact that our categorical habitat variable was always included in our best environmental models suggests that other unmeasured predictors play a role for the herpetofauna. Predator communities, in addition to possibly explaining the negative effects of certain environmental predictors, might also help explain differences in community composition among habitats. Consequences of habitat conversion on the composition of the communities of several taxa have already been assessed (e.g. Chung et al. 2000, Koh and Wilcove 2008, Brühl and Eltz 2010). Among the taxa affected might also be predators of reptiles and amphibians, and different predator communities among habitats would in turn shape herpetofaunal communities.

Another factor that future studies could consider is disturbance caused by routine land-use-specific practices, such as rubber tapping, palm frond cutting and oil palm harvesting, which introduce different amounts of disturbance to the local animals. We suggest that future studies should account for these factors to achieve a more comprehensive understanding of the drivers of the herpetofaunal communities. Rainfall and canopy cover measurements are environmental predictors we could not include in our data analysis, but they are expected to influence the herpetofauna.

Hydrological status is of relevance for amphibians, that have a higher abundance in riparian sites of all land-use systems. This confirms our hypothesis that riparian habitats are of higher importance for amphibians, even in plantations, as they rely on water in their early life stages. However, in terms of alpha and beta richness, the hydrological status made no difference, except in forest. Efforts made to maintain riparian sites within plantation landscapes would therefore likely only increase the number of animals, without any gains in richness. The importance of hydrological status is not as clear for reptiles, but there seems to be an overall trend towards dry sites to be more favourable for their abundance and richness. This is a more surprising result than its importance for amphibians, as despite their lower dependence on waterways for reproduction, we assumed riparian areas to be richer in resources that would allow all herpetofauna to profit. An explanation for this negative trend might be similar to that for the counterintuitive effects of vegetation density, in which other animals might outcompete reptiles when resources are plentiful.

### **Variations in community composition**

In spite of similar richness measures among habitats, non-metric multidimensional scaling clearly shows that assemblages are different, especially between forest and plantations. Species found in plantations were species of low conservation concern, often found in inhabited areas (Sheridan 2009, Gillespie et al. 2012, IUCN 2017), like the house gecko *Hemidactylus frenatus*, invasive in many parts of the world (Hoskin 2011), of which we found 170 individuals, exclusively in plantations. All of the 4 species present in our sample in the IUCN Red List that are not considered of least concern were found exclusively in forests, together with roughly half of the animals belonging to the 10 species that have not been evaluated yet. Non-metric multidimensional scaling of herpetofaunal communities from abundance matrices showed marked differences in community composition, and the same result came from the amphibian

presence/absence matrix as well. These are strong indications that species are very different in forest and plantations. Our results confirm what other authors have found analysing assemblage composition of other taxa (Fitzherbert et al. 2008). We originally hypothesized that either a subset of the forest communities could take over sympatric species after conversion, or that new species colonize plantations, and the latter was confirmed. These new species might reach the new plots simply by pouring in from already existing plantations, which are widespread in many parts of the island, and possibly with help from the frequent human presence necessary to establish and maintain the crops. The fact that several of the plantation species are human commensals might support the hypothesis that species found in plantations might be accidentally introduced during human activities. The similar results obtained from abundance and presence/absence matrices indicated that the modification of the assemblages does not depend on species abundance, but it is so drastic to involve even the most common species.

### **Future perspectives**

Since there were relatively few species which occur frequently in the different habitats, an interesting next step could be to predict the presence or absence of common species singularly in response to environmental predictors like the ones we included here. This would improve our understanding of the links between herpetofauna and environments, helping to pinpoint the environmental components that are most important to address in conservation measures to hinder the replacement of the original communities by high numbers of animals of low conservation concern. Enrichment experiments in plantations are currently underway in the Harapan landscape, close to our study area, to increase biodiversity diversity in plantations without reducing crop yield (e.g. Teuscher et al. 2016). This approach could be implemented in the future with information from accurate analyses of the herpetofauna-environment relationships, to provide in plantations those environmental factors that forest species depend mostly on.

### **Conclusion**

Agricultural intensification will likely continue at a high rate in the future in Sumatra and the entire Indonesia. Our results are important from a conservation perspective since they further highlight the effects of conversion of forests to cash crops by focusing on taxa that have been often neglected in conservation studies. We showed that conversion induces losses of forest-specific species in herpetofaunal communities, and we therefore suggest herpetofauna be taken

into higher consideration when planning land-use conversion or any other agricultural activities. Despite the capability of the most common crop in the country, oil palm, to sustain a high number of animals, diversity estimates are nonetheless lower than in forests, and the species that inhabit plantations are not the same as in the previous communities, but are instead species that are disturbance-resistant, capable of living in man-made landscapes, and of low conservation interest. In the light of this study, further tropical rainforest clearance should be discouraged to avoid additional diversity losses. So far, in Indonesia, the land sharing philosophy has dominated in agricultural activities, with much of the available land having been converted to relatively low-yield crops that are inhabited by relatively high numbers of vertebrates. We demonstrated that plantation assemblages are of little conservation interest, and to prevent additional forest communities from being replaced, we suggest future agricultural intensification to be aimed at shifting towards a land sparing approach, focused more on increasing yield of the already existing crops rather than on land expansion.

## Tables

Environmental predictor	Richness and abundance	
	Amphibians	Reptiles
Air temperature	-	-
Relative humidity	+	+
Dead plant material	+	+
Fronid piles	+	+
Cavities	+	+
Leaf-litter cover	+	+
Undergrowth density	+	+
Arthropod size	+	+
Habitat	+/-	+/-

**Table 1:** Environmental predictors and expected effects on richness and abundance of the herpetofauna. Count data regarding logs, single palm fronds and branch piles were collapsed into the broader dead plant material category, number cavities in trees and holes in the ground were regarded as cavities, and leaf litter depth and undergrowth height were left out of the analyses because of their redundancy and their lower accuracy compared to leaf-litter cover and undergrowth density.

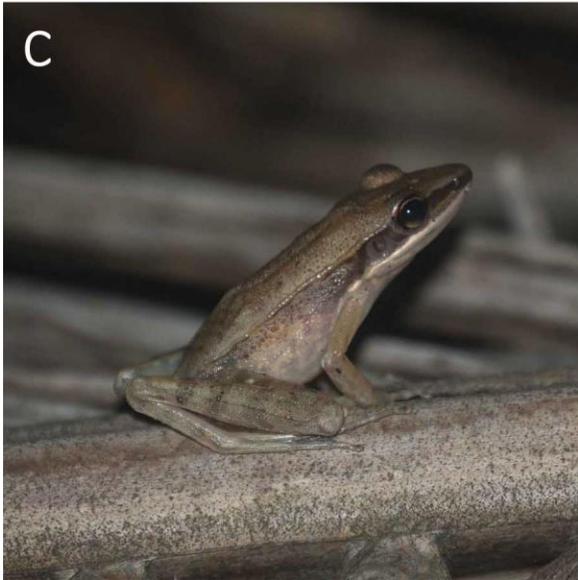
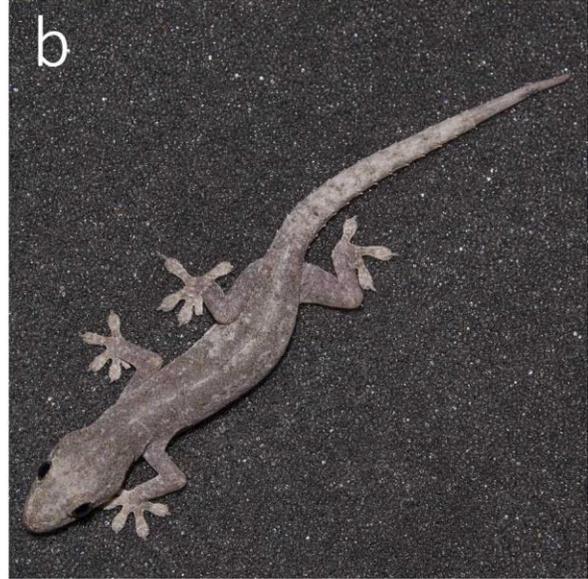
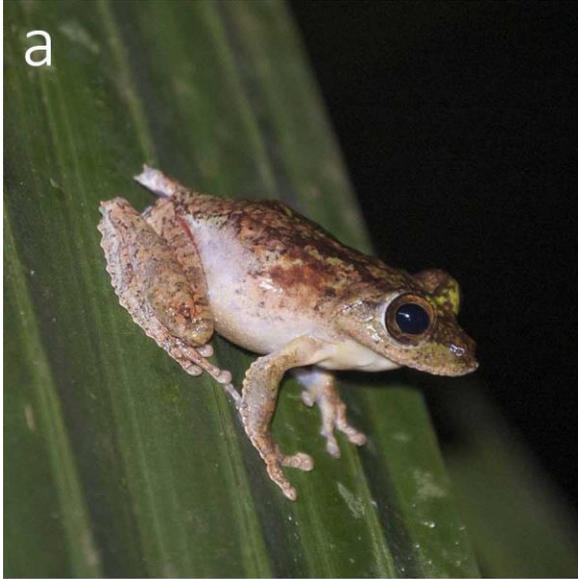
Species	Family	Order	Class	Total count	Forest	Oil palm	Rubber	IUCN	Range extension
<i>Aphaniotis fusca</i>	Agamidae	Squamata	Reptilia	1	1	0	0	LC	1
<i>Draco sumatranus</i>	Agamidae	Squamata	Reptilia	2	1	0	1	NE	1
<i>Dendrelaphis pictus</i>	Colubridae	Squamata	Reptilia	3	0	2	1	NE	0
<i>Naja sumatrana</i>	Elapidae	Squamata	Reptilia	1	0	0	1	LC	0
<i>Gehyra mutilata</i>	Gekkonidae	Squamata	Reptilia	3	0	3	0	NE	1
<i>Gekko smithii</i>	Gekkonidae	Squamata	Reptilia	5	5	0	0	LC	0
<i>Hemidactylus frenatus</i>	Gekkonidae	Squamata	Reptilia	170	0	166	4	LC	1
<i>Takydromus sexlineatus</i>	Lacertidae	Squamata	Reptilia	13	0	12	1	LC	0
<i>Dasia olivacea</i>	Scincidae	Squamata	Reptilia	1	1	0	0	LC	0
<i>Eutropis multifasciata</i>	Scincidae	Squamata	Reptilia	20	11	4	5	NE	0
<i>Eutropis rugifera</i>	Scincidae	Squamata	Reptilia	10	1	6	3	NE	1
<i>Eutropis macularia</i>	Scincidae	Squamata	Reptilia	2	0	2	0	NE	1
<i>Indotyphlops braminus</i>	Typhlopidae	Squamata	Reptilia	1	0	1	0	NE	1
<i>Varanus rudicollis</i>	Varanidae	Squamata	Reptilia	1	0	0	1	NE	1
<i>Ingerophrynus parvus</i>	Bufo	Anura	Amphibia	64	0	44	20	LC	0
<i>Ingerophrynus divergens</i>	Bufo	Anura	Amphibia	31	31	0	0	LC	1
<i>Ingerophrynus biporcatus</i>	Bufo	Anura	Amphibia	8	0	3	5	LC	1
<i>Ingerophrynus quadriporcatus</i>	Bufo	Anura	Amphibia	4	1	1	2	LC	0
<i>Fejervarya limnocharis</i>	Dicroglossidae	Anura	Amphibia	154	0	94	60	LC	0
<i>Fejervarya cancrivora</i>	Dicroglossidae	Anura	Amphibia	8	0	3	5	LC	0
<i>Limnonectes blythii</i>	Dicroglossidae	Anura	Amphibia	58	50	0	8	NT	1
<i>Limnonectes macrodon</i>	Dicroglossidae	Anura	Amphibia	7	6	0	1	VU	1
<i>Limnonectes malesianus</i>	Dicroglossidae	Anura	Amphibia	4	2	0	2	NT	1
<i>Limnonectes paramacrodon</i>	Dicroglossidae	Anura	Amphibia	3	3	0	0	NT	1
<i>Occidozyga sumatrana</i>	Dicroglossidae	Anura	Amphibia	55	54	1	0	LC	0
<i>Leptobrachium hasseltii</i>	Megophryidae	Anura	Amphibia	1	0	0	1	LC	0
<i>Kalophrynus pleurostigma</i>	Microhylidae	Anura	Amphibia	8	5	0	3	LC	0

<i>Kaloula baleata</i>	Microhylidae	Anura	Amphibia	3	0	0	3	LC	0
<i>Microhyla heymonsi</i>	Microhylidae	Anura	Amphibia	8	0	7	1	LC	0
<i>Microhyla berdmorei</i>	Microhylidae	Anura	Amphibia	2	2	0	0	LC	1
<i>Microhyla butleri</i>	Microhylidae	Anura	Amphibia	1	1	0	0	LC	1
<i>Amnirana nicobariensis</i>	Ranidae	Anura	Amphibia	126	4	90	32	LC	0
<i>Chalcorana chalconota</i>	Ranidae	Anura	Amphibia	25	21	3	1	LC	0
<i>Chalcorana raniceps</i>	Ranidae	Anura	Amphibia	11	8	1	2	LC	1
<i>Chalcorana labialis</i>	Ranidae	Anura	Amphibia	3	2	1	0	NE	1
<i>Hylarana erythraea</i>	Ranidae	Anura	Amphibia	13	0	7	6	LC	0
<i>Pulchrana baramica</i>	Ranidae	Anura	Amphibia	64	1	46	17	LC	1
<i>Pulchrana glandulosa</i>	Ranidae	Anura	Amphibia	12	4	7	1	LC	1
<i>Kurixalus appendiculatus</i>	Rhacophoridae	Anura	Amphibia	67	62	0	5	LC	1
<i>Polypedates colletti</i>	Rhacophoridae	Anura	Amphibia	27	27	0	0	LC	1
<i>Polypedates leucomystax</i>	Rhacophoridae	Anura	Amphibia	19	4	11	4	LC	0
<i>Rhacophorus bengkuluensis</i>	Rhacophoridae	Anura	Amphibia	1	1	0	0	NE	1

**Table 2:** Summary of the species encountered during the sampling, including number of individuals per land-use, IUCN Red List status, and indication on whether the species had been previously reported in the province of Jambi (1 = new record, 0 = previously recorded), according to Teynié et al. 2010.

Environmental predictor	Land use Habitat	Forest		Oil palm		Rubber	
		Dry	Riparian	Dry	Riparian	Dry	Riparian
Temperature	Mean	27.1	26.6	28.2	29.1	28.4	28.5
	Range	6.7	4.6	9.4	14.4	9.4	14.3
Humidity	Mean	83.6	86.8	81.7	80.6	82.0	80.6
	Range	19	11	36	47	39	38
Frond piles	Mean	0.0	0.0	6.9	5.9	0.0	0.0
	Range	0.0	0.0	5.0	9.0	0.0	0.0
Cavities	Mean	1.3	1.2	0.6	0.0	0.2	0.3
	Range	7.0	6.0	10.0	0.0	1.0	2.0
Dead plant material	Mean	2.8	1.6	0.5	0.4	3.0	2.4
	Range	7.0	8.0	3.0	2.0	11.0	7.0
Leaf litter cover	Mean	87.6	71.1	12.5	8.8	63.1	73.9
	Range	33.0	78.0	25.0	20.0	80.0	68.0
Undergrowth density	Mean	3.9	3.5	3.2	2.4	3.9	3.2
	Range	2.0	3.0	3.0	4.0	4.0	4.0
Arthropod length	Mean	16.6	14.1	9.8	8.4	5.3	5.4
	Range	63.5	44.0	14.5	19.5	12.0	12.5

**Table 3:** Mean values and ranges of all the measured environmental variables in each habitat.



**Table 4:** The most common species in our samples: *Kurixalus appendiculatus* (a), *Hemidactylus frenatus* (b), *Amnirana nicobariensis* (c) and *Fejervarya limnocharis* (d).

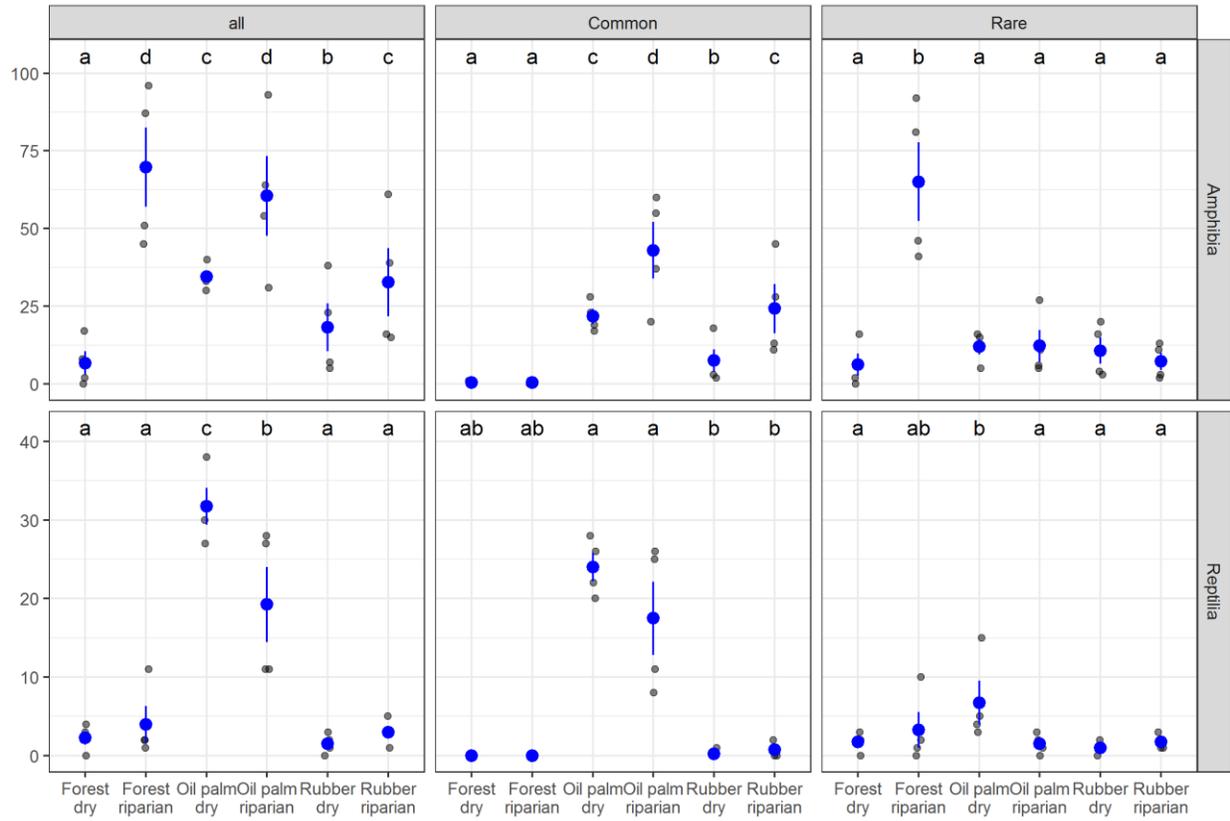
Class	Richness measure	Land-use		Forest		Oil palm		Rubber	
		Habitat	Dry	Riparian	Dry	Riparian	Dry	Riparian	
Amphibia	Rarefaction richness		11	8.9	7.4	6	10.6	7.9	
	Bootstrap estimator		13.7	18.6	11.9	12.8	17.5	17.5	
Reptilia	Rarefaction richness		2.7	2.2	2	1.4	4	2.9	
	Bootstrap estimator		3.3	4.9	10.1	0.4	4.9	4.7	

**Table 5:** Richness estimates obtained from rarefaction to the smallest sample sizes (for amphibians N = 27, in dry forest; for reptiles: N = 5, in riparian forest) and Bootstrap estimators.

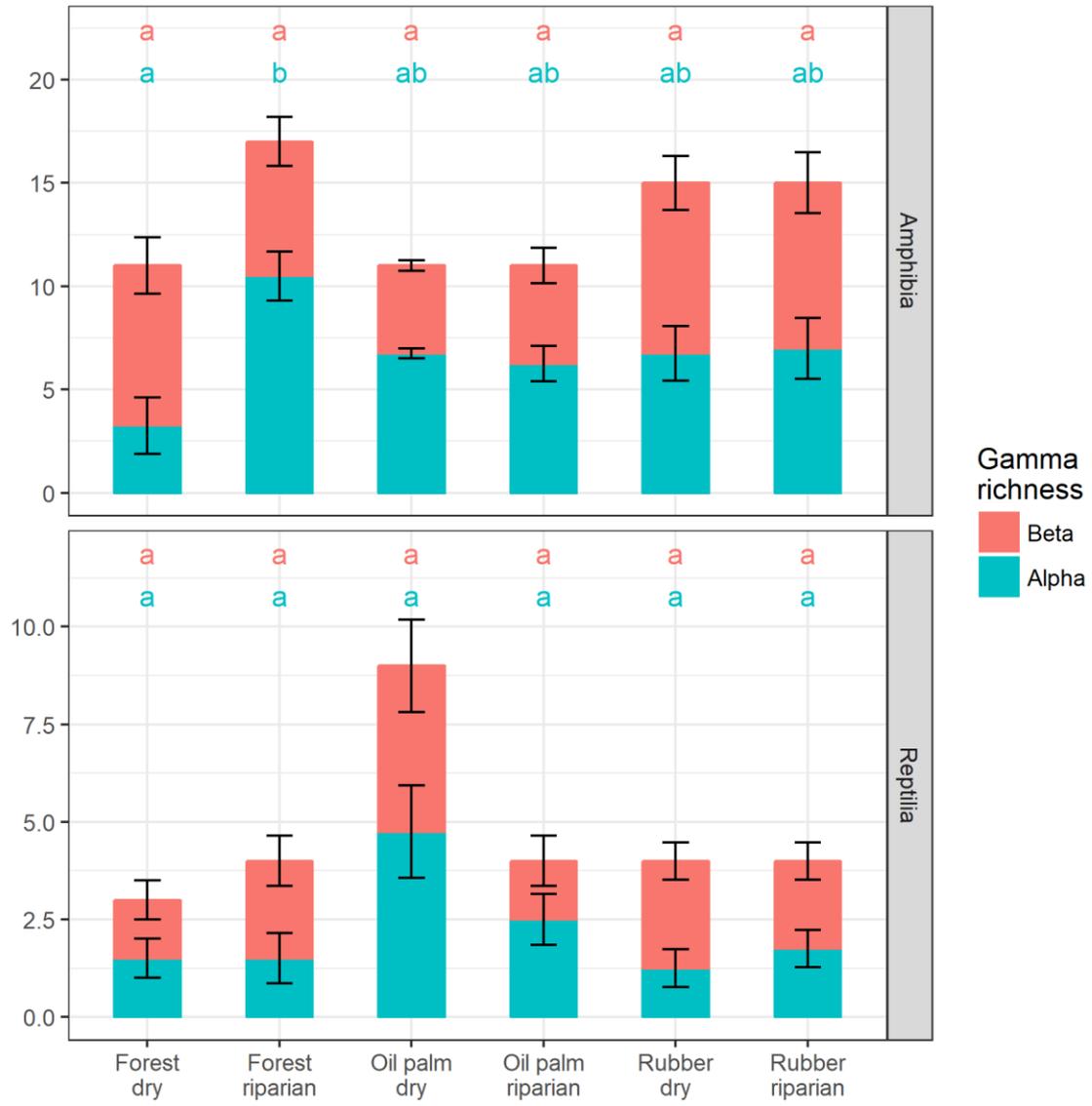
Class	Response	Scaled predictor	Coefficient	Significance
Amphibia	Abundance all species	Arthropod length	1.42149	***
		Cavities	0.30361	.
		Dead plant material	-0.34876	.
		Temperature	-0.2662	***
		Undergrowth density	-0.50143	**
	Abundance common species	Arthropod length	1.2058	***
		Cavities	0.2861	
		Dead plant material	-0.3503	.
		Frond piles	-0.8739	*
		Temperature	-0.1656	**
	Abundance rare species	Arthropod length	1.65248	***
		Cavities	0.39943	.
		Dead plant material	-0.38667	
		Temperature	-0.48974	***
		Undergrowth density	-0.62539	*
Abundance all species	Arthropod length	1.1796	***	
	Frond piles	-0.9414	**	
	Humidity	0.4066	*	
	Temperature	0.4208	*	
Reptilia	Abundance common species	Arthropod length	9.24E+01	***
		Cavities	2.95E-01	
		Frond piles	-1.20E+00	***
		Humidity	8.90E-01	***
		Temperature	6.69E-01	**
	Abundance rare species	Leaf litter cover	-0.5691	*
		Arthropod length	1.0542	***
		Humidity	-0.4428	***

**Table 6:** Summary of the effects of all the environmental predictors fitted in the generalized mixed-effect best models on abundance of amphibians and reptiles. “\*\*\*” indicates  $p\text{-value} \leq 0.001$ , “\*\*” indicates  $p\text{-value} \leq 0.01$ , “\*” indicates  $p\text{-value} \leq 0.05$ , and “.” indicates  $0.1 \leq p\text{-value} < 0.5$ .

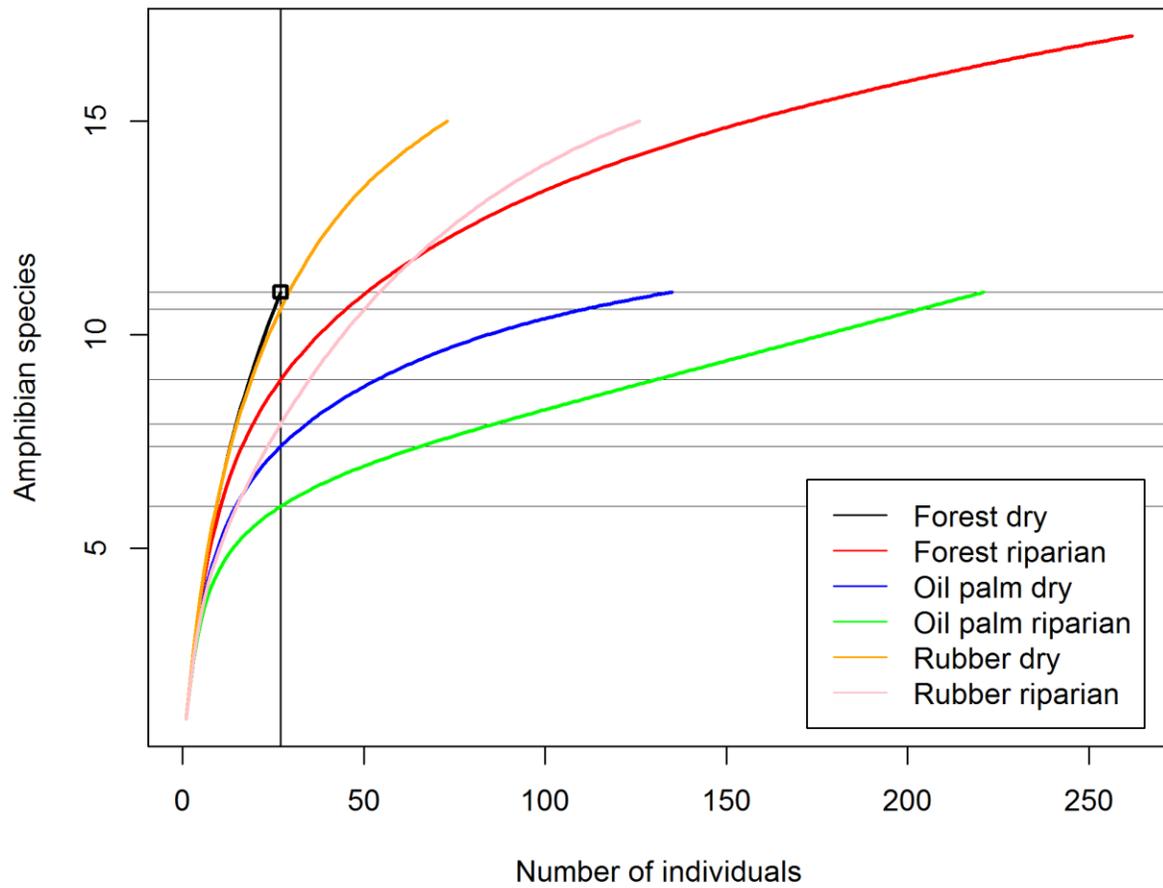
# Figures



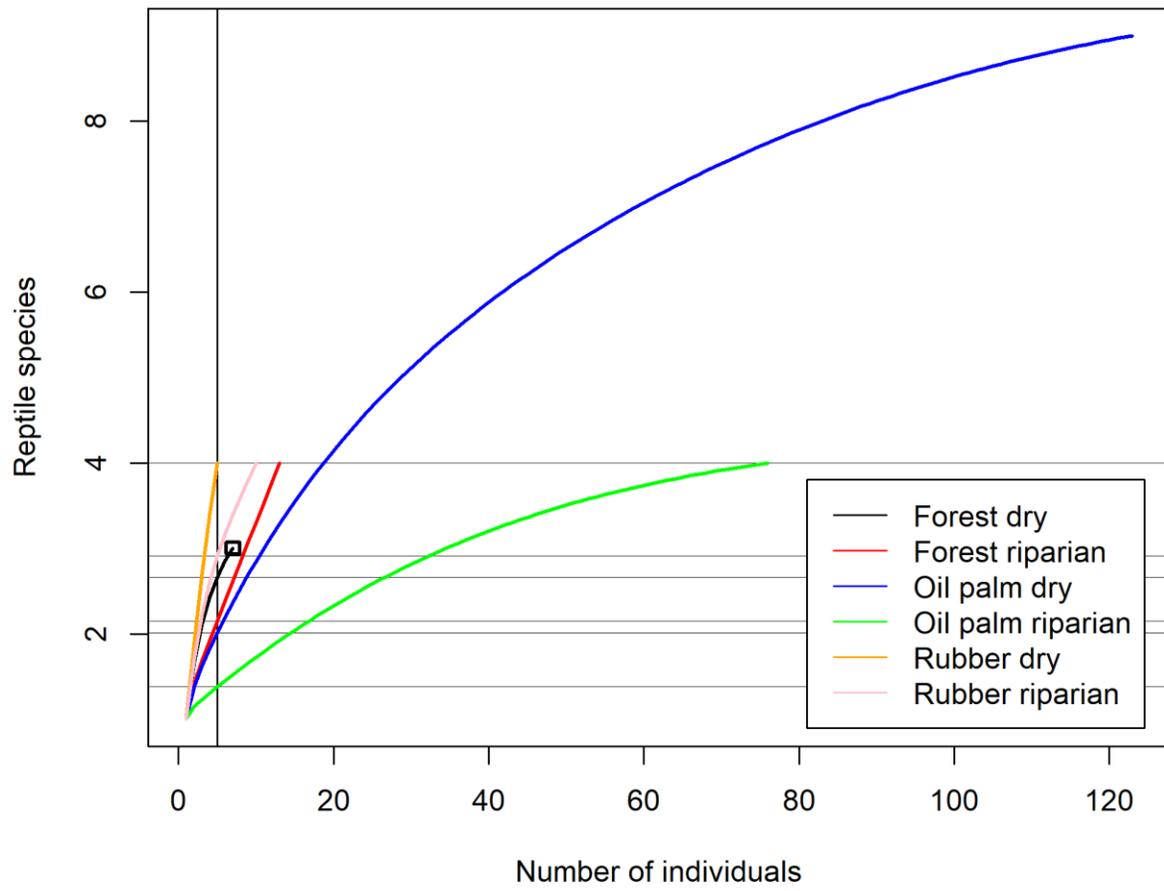
**Fig. 1:** Richness and abundance of amphibians and reptiles per habitat, with and without distinction between common and rare species.



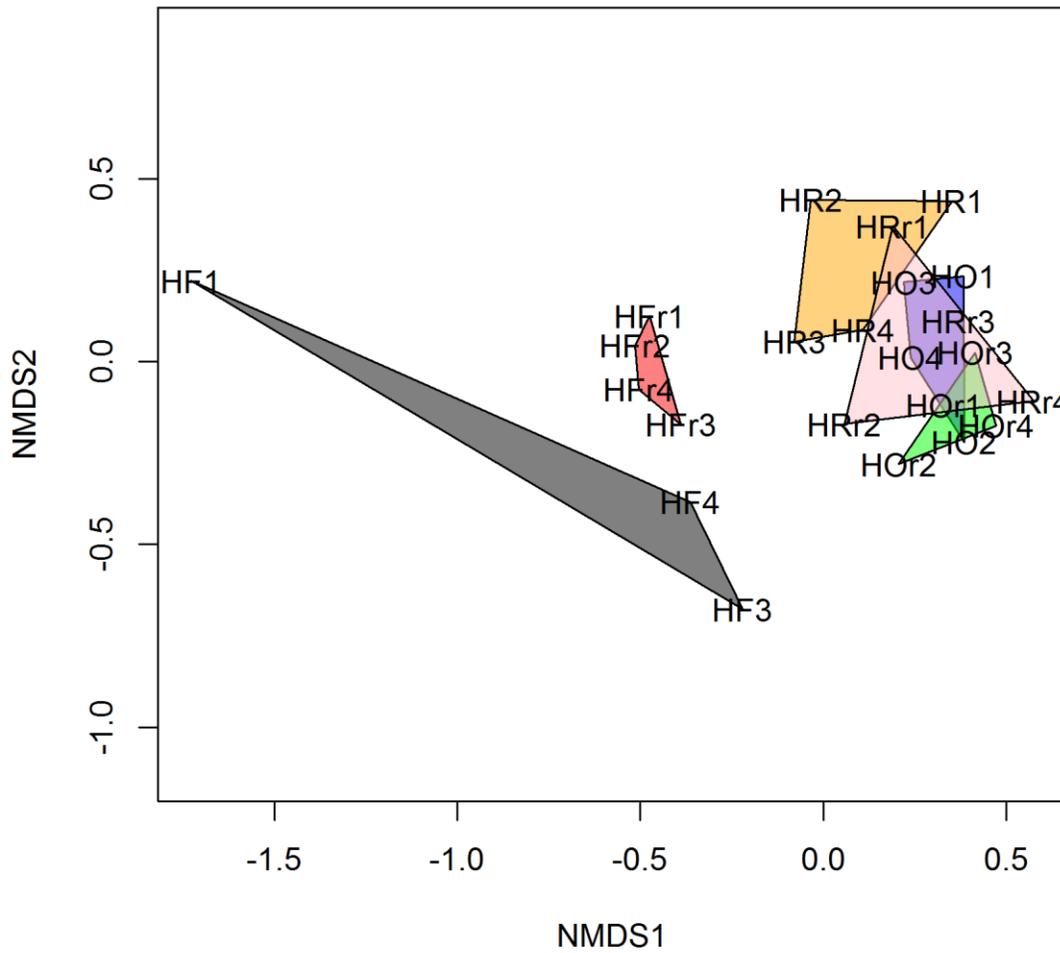
**Fig. 2:** Alpha and beta richness of all amphibian and reptile per habitat.



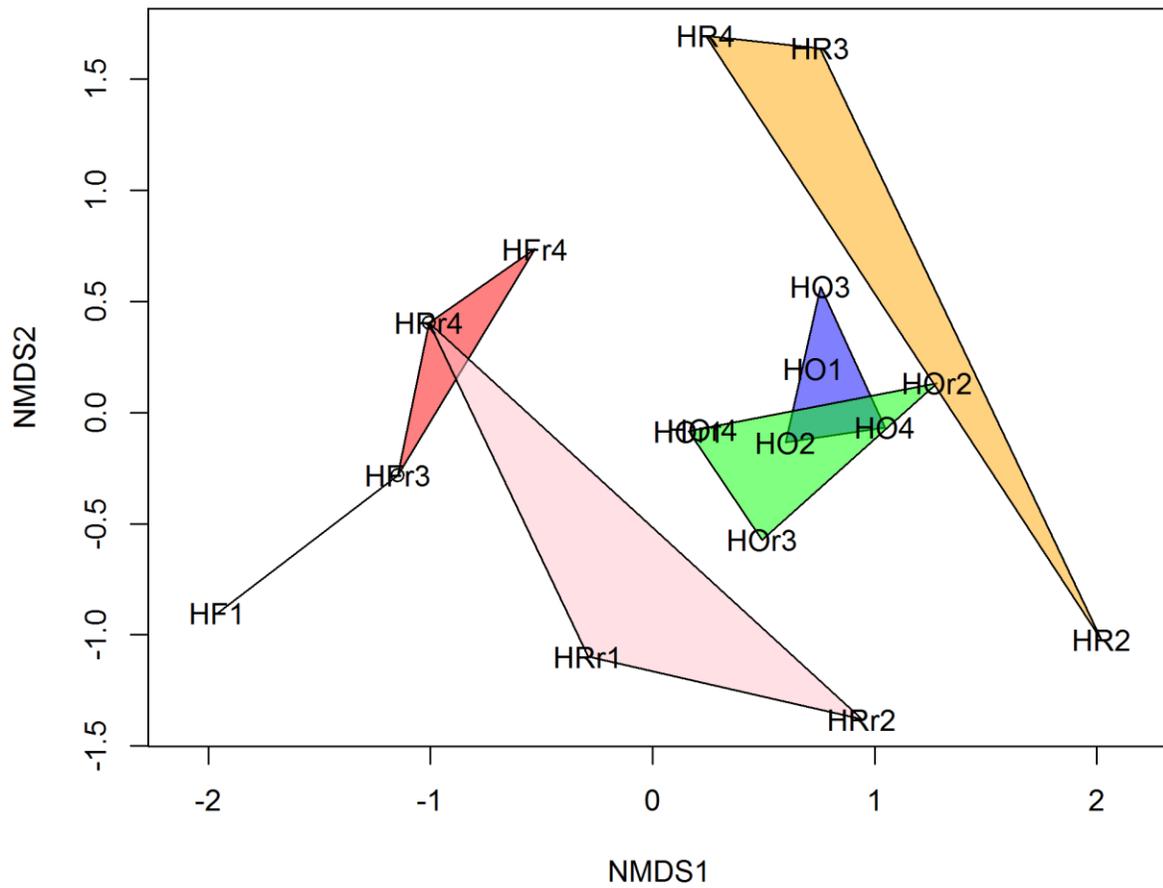
**Fig. 3:** Species accumulation curve (SAC) of amphibians in the different habitats.



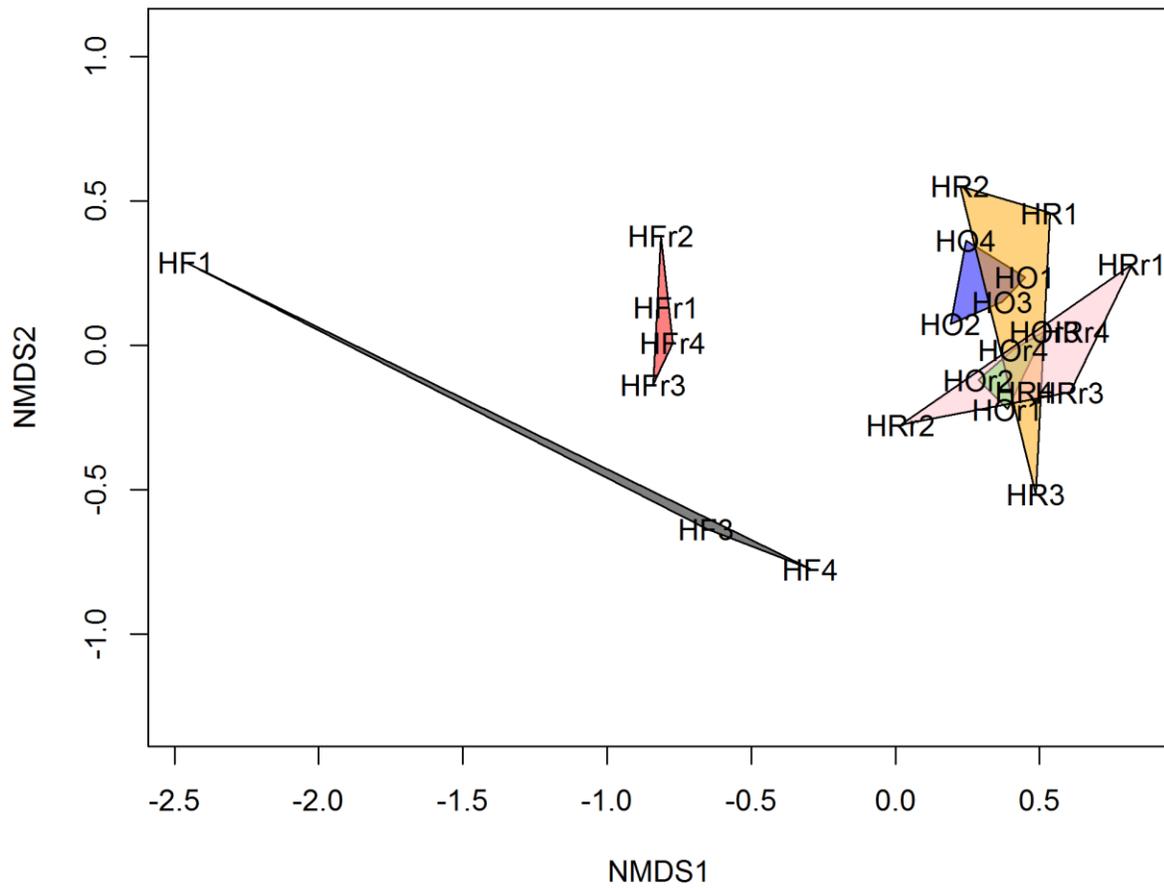
**Fig. 4:** Species accumulation curve (SAC) of reptiles in the different habitats.



**Fig. 5:** NMDS (Non-metric Multi-Dimensional Scaling) of amphibians, obtained from an abundance matrix.



**Fig. 6:** NMDS (Non-metric Multi-Dimensional Scaling) of reptiles, obtained from an abundance matrix.



**Fig. 7:** NMDS (Non-metric Multi-Dimensional Scaling) of amphibians, obtained from a presence/absence matrix.

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