Original Research Article

Amphibian and reptile communities of upland and riparian sites across Indonesian oil palm, rubber and forest

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A R T I C L E   I N F O

A B S T R A C T

Indonesia is the largest producer of oil palm and the second largest exporter of rubber worldwide; a significant part of the country's rainforests have been converted to agriculture. Conservation measures are needed to assess and 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 reptiles and amphibians. Here we study community composition, species richness and abundance of the herpetofauna of the densely farmed Jambi province, central Sumatra (Indonesia). We compared reptile and amphibian communities of upland and riparian sites of lowland rainforest as well as upland and riparian sites of oil palm and rubber plantations through visual-aural encounter surveys and pitfall trappings. Plantations tended to have lower amphibian abundance when compared to riparian forest, but not compared to upland forest. There is a trend for higher amphibian numbers and species in riparian sites of all habitat types. Rare amphibians were much more abundant in riparian forest and common amphibians were more prevalent in plantations, especially oil palm. Surprisingly, reptile richness and abundance was higher in oil palm plantations than all other habitats. Plantations comprise mostly common reptile and amphibian species of low conservation interest, and communities were markedly different between plantations and forests. Several species were recorded for the first time in the sampled region. We conclude that in our region, riparian sites appear to be important for maintaining amphibian populations, but forest is doubtlessly irreplaceable to conserve rare amphibians. Nevertheless, in our study oil palm monocultures harbored a relatively high reptile density and richness.

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1. Introduction

Plantations are a major landscape component of the once completely forested islands of Indonesia, and oil palm and rubber industries represent an important fraction of the economy: in the period between 2002 and 2011, cash crops, including oil palm and rubber, accounted for 2.2% of the country's GDP (BPS, 2012). Indonesia is the world's biggest producer of palm oil and the second biggest exporter of rubber (Bruinsma & Food and Agriculture Organization of the United Nations, 2003). In parallel, the country has reached a level of primary forest cover loss to cash crops higher than Brazil (Margono et al., 2014), with the island of Sumatra having the highest forest losses. Despite a decline in the annual rate of expansion of oil palm plantations in Sumatra from an average 9%−3.8%, 10% of the area of the island (ca. 8 million ha) is already devoted to oil palm plantations (Gunarso et al., 2013). One of the most recent estimates of the size of rubber plantations indicates that in the Jambi province alone, in central Sumatra, rubber plantations occupy an area of 0.92 million ha in 2013, with an annual net increase of 0.3% since 1990 (Melati, 2018). Given their extent, not only forests but also oil palm and rubber plantations should be considered when assessing biodiversity. Conversion of forest to agriculture is associated with a reduction of species richness and abundance, as well as changes in community composition, in particular a loss of forest species (Fitzherbert et al., 2008). The herpetofauna however is relatively little studied, and with an estimated 82% of the world amphibian species depending on forest environments (Stuart et al., 2004), their vulnerability to agricultural intensification needs to be carefully assessed. From a conservation perspective, reptiles are also the least studied of all terrestrial vertebrates (Tews et al., 2004), and their responses to agricultural conversion are little understood. Teynié et al. (2010) listed 93 species of amphibians and 226 species of reptiles in Sumatra. 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). Herpetofaunal abundance and richness are usually negatively affected by conversion of forest to plantations. Logging, and the monocultures subsequently established, decrease habitat heterogeneity, and therefore offer a smaller variety of niches for species to live in. Amphibian species richness and abundance decrease after an area is logged (Kurz et al., 2016), and the higher the extent of the disturbance, the lower the abundance (Konopik et al., 2015). Oil palm plantations have adverse edge effects on amphibian diversity that stretch for kilometres into adjacent forests (Scriven et al., 2018). Herpetofaunal richness levels in primary forests are consistently found to be significantly higher than both secondary forests and plantations (Gardner et al., 2008; Gibson et al., 2011; Behm et al., 2013; Trimble and Aarde, 2014). Examining patterns of alpha and beta diversity, Gardner et al. (2007) found that eucalyptus plantations where inhabited by significantly less species than primary forests, and Gallmetzer and Schulze (2015) estimated total richness levels of reptile and amphibians species in oil palm plantations that are close to half of those in both forest margins and interiors. However, abundance and richness of amphibians can also on a similar level in oil palm plantations and forests (Faruk et al., 2013).

The changes in herpetofaunal richness after land use conversion are driven by changes in a multitude of environmental variables. Animal communities can change after land use conversion to plantations due to an altered vegetation structure, lower canopy cover, less litter fall, higher average air temperature and lower humidity (Drescher et al., 2016). 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).

Irrespective of land-use, habitats also differ in their topography and proximity to water. Cultivated riparian areas are generally areas of lower agricultural output because of periodical flooding, but they are widely regarded as important wildlife habitats (Maisonneuve and Rioux, 2001; Olson et al., 2007) and of higher conservation value compared to upland areas (Naiman et al., 1993). For herpetofaunal species, riparian areas host a greater abundance (Gomez and Anthony, 1996; Kluber et al., 2008). For amphibians, inconclusive effects of riparian areas on forest and oil palm communities were found (Faruk et al., 2013). So far a comparison between riparian and upland sites in rubber plantations is missing, and in our region, the trends for reptiles are unknown. Taxa differ in their response to forest conversion, and in tropical regions, a variety of responses has been reported. In some cases, total density after clear-cutting can be even higher than before disturbance (Ryan et al., 2002; Todd and Rothermel, 2006). After land-use transformation, disturbance-tolerant amphibians can replace forest species (Wanger et al., 2009; Gallmetzer and Schulze, 2015), and sometimes they coexist with several of them (Gillespie et al., 2012). Amphibian communities after conversion can also be composed of a subset of the species of the original communities, as found by Gardner et al. (2007) in eucalyptus plantations. Reptile communities in plantations are mostly devoid of endemic species in favour of disturbance-tolerant species or species common in open areas (Gardner et al., 2007; Wanger et al., 2009; Gallmetzer and Schulze, 2015). Thus, general trends are hard to detect.

The aim of this study is to describe species abundance, alpha and beta richness, and community composition of amphibians and reptiles in the three most common land-use types of the Jambi province in Sumatra, namely lowland rainforest and plantations of oil palm and rubber, and to assess the environmental drivers of change. We sampled reptiles and amphibians in both upland and riparian sites within each land-use system, and measured the following environmental features: air temperature, relative humidity, precipitation, undergrowth density, leaf litter cover, number of possible hiding spots, and canopy gap fraction. We test the hypothesis that amphibian abundance and richness are unaffected by land use conversion, as demonstrated in a study of the same biogeographic region with a similar herpetofauna in forest and oil palm plantations (Faruk et al., 2013). We did not have any *a priori* hypothesis for reptiles, due to the lack of similar previous studies. Since amphibians might benefit from humidity because of their susceptibility to desiccation and reliance on egg-laying sites, we also hypothesize that riparian areas harbour both a higher species richness and abundance of amphibians compared to drier habitats within the same land-use system. Due to their high heterogeneity, we also hypothesized that beta richness of forests

would be higher than in plantations. We searched for the habitat and climatic variables that are driving richness trends. For both amphibians and reptiles, we expected plantations to be either inhabited by the subset of forest species that have the highest tolerance to disturbance, by species that were not present in the forests that have been converted, or a combination of the two scenarios.

2. Methods

2.1. Study site

We collected data from April 4, 2017 until July 9, 2017 in 24 core plots (Fig. S1) of the Collaborative Research Centre 990 (EFForTS), in the regency of Batang Hari, province of Jambi, Sumatra, Indonesia. The upland core plots design is described in detail by Drescher et al. (2016) but additionally to the upland plots, we also sampled in riparian sites that are not yet described. We sampled the herpetofauna in six habitats: upland and riparian lowland forest, upland and riparian oil palm plantations, and upland and riparian rubber plantations. Our forest sites are primary degraded forest because of past selective logging activities. Plantation plots were not surrounded by forest, and there were no vegetation buffers between riparian plots and the nearest bodies of water. The upland sites were situated on well-drained acrisols. Riparian sites however were next to small rivers or streams and were repeatedly flooded during the rainy season (ca. October until February), so that they displayed the typically stagnic colour pattern within 0.3 m from the surface, indicative of alternating oxidation and reduction caused by temporarily stagnating water. Riparian sites also had lower yields than upland plots. Oil palm plantations were between 9 and 20 years old, and rubber plantations were between 8 and 28 years old at the time of the survey, and all plantations were monoculture smallholdings using less intensive crop management (weeding, fertilizing, harvesting) than company estates (pers. obs.). For each habitat, there were four square, replicate plots of 50×50 m, situated in different plantations. We subdivided each plot in four 25×25 m quadratic sections to assess the variation in environmental features at the plot scale.

2.2. Sampling design

We coupled visual and aural surveys with pitfall traps to use the most effective and cost-efficient sampling method for reptiles and amphibians (Garden et al., 2007). Visual and aural surveys were performed at the same time, and each plot was visited six times for 1 h by two herpetologists (AP and HJ), resulting in 12 person-hours of visual-aural surveys per plot, and 288 person-hours overall. Visual and aural surveys of the herpetofauna were performed twice within each of three time windows, henceforth referred to as midday (11:00−15:00), sunset (18:00−19:00) and night (20:00−24:00) windows. Within the same time window, activity and detection probability of each species were assumed to be constant. Because of logistic reasons, only one plot was sampled per window, resulting in three sampled plots per day. Long travel times between plantation and forest plots, as well as sampling permission restrictions, forced us to sample plantation plots first (April−June 2017), and then forest plots (June−July 2017). However, we randomized our sampling schedule to sample plots of every hydrological status and, during the plantation sampling, of both plantation habitats each day. We also did not sample the same plot twice in the same day.

During visual-aural survey sessions, AP and HJ separately walked randomly and searched animals within all sections, one section at a time for 15 min. All possible hiding spots encountered were inspected, including the tree canopy with binoculars. Whenever the encountered animals were within the reach of the observers, they were temporarily captured, and species-specific morphological characteristics of each individual animal were photographed for identification. Photos were checked to reduce as much as possible the risk of counting animals multiple times during a single session, but checks were not performed between sessions. We did not capture and mark animals due to time and resource constraints as well as the difficulty of capturing amphibians, and especially reptiles. For aural detections, the position of the animals − which were usually not moving − was noted to avoid counting them twice. AP and HJ counted the number of calling individuals and identified the species by the calls if they could not be seen. Aural surveys lessened possible effects of differential detectability among plot types due to undergrowth density or any other environmental features reducing visibility. Calls were recorded using a Sennheiser ME-66 microphone coupled to an Olympus LS-3 recorder and archived online (http://soundefforts.uni-goettingen.de/biosounds/collection/show/18/1). The species, approximate age (juvenile or adult), location in the section, and time of encounter were recorded for all detections. When captured, all animals were released at the point of capture.

We also set up four pitfall traps per plot, one in the centre of each of the four sections. Traps were set up at the end of midday sessions, then left open and checked the following day in the night window, so that they were active for approximately 36 h. Each trap consisted of four perpendicular black plastic fences that were 35 cm high and 5 m long, converging towards a middle point, where a 40 cm wide bucket was dug in the ground. Each trap had a diameter of 10 m, which is the low end of the optimal range suggested by Bury and Corn (1987). Traps were partly filled with litter to provide hiding and shading spots for animals, and the bottom was pierced to avoid rain flooding the traps. When traps were checked, photographic, location and age data were collected for captured animals as during visual-aural surveys.

2.3. Environmental covariates measurement

We measured climatic variables at different scales. In each section and during each sampling session, temperature and relative humidity were measured at waist level using a pocket-sized thermo-hygrometer (Trixie Reptiland, temperature

sensitivity: $\pm 0.1\,^{\circ}$C, relative humidity sensitivity: $\pm 1\%$). Precipitation data were collected with two meteorological stations equipped with a tipping-bucket precipitation transmitter (Thies Clima, Göttingen, Germany). One station measured rainfall for the forest sites and the other for the plantations (Fig. S1). The cumulative precipitation of the 24 h before sampling sessions was extracted. We also measured gap fraction between August 2017 and January 2018 to quantify how much light passes through the canopy. We could not assess all plots at once due to labor and time restrictions, but this period of the year is representative of the canopy conditions during the herpetological survey and the rubber trees were not shedding their leaves then. We took hemispherical canopy photographs at 1.2 m height with a circular fish-eye lens (Sigma 4.5 mm f/2.8 EX DC HSM) from the middle of each plot section. We followed the methodology of Beckschäfer et al. (2013) for the photograph exposure and used the Hemispherical 2.0 plugin in ImageJ 2 (Glatthorn and Beckschäfer, 2014) to extract gap fraction measures for each section. In each section, during one midday session, we also measured habitat variables that were proxies for the niches available to the herpetofauna. Leaf litter cover was measured by averaging the percentages of litter cover within four randomly placed 1×1 m quadrats, while depth was measured by averaging three measurements within each quadrat taken with a ruler held perpendicular to the ground. Undergrowth density was estimated assigning a category from 1 to 5 to each section, with 5 indicating the highest density, whereas average height was measured with measuring tape. Hiding spots were counted by considering any rock, dead tree, dead plant material (such as logs, branch piles, single palm fronds, or frond piles), trash piles and cavities (either in trees or in the ground) judged likely to be used as a den.

We additionally collected data on all the arthropods that fell in the pitfall traps to sample the food items available to the reptiles and amphibians. We identified the arthropods to the order level, and recorded the approximate total length (head to abdomen) of each individual. Our estimates are conservative because some arthropods might have been consumed by the reptiles and amphibians that fell into the traps.

2.4. Data analysis

All analyses were done using R software version 3.3.3 (R Core Team, 2018). We merged the herpetological capture data from our pitfall traps with our visual-aural survey observations and environmental data. We also appended conservation status data from the IUCN Red List for 32 out of the 42 sampled species sampled that were listed (IUCN, 2017). We performed the same analyses separately for reptiles and amphibians. Abundance was analysed overall and also separately for rare and common species, because of their different physiologies and functional traits that might explain diverging responses to different habitats and environmental drivers. Due to the small number of common species, we did not distinguish between common and rare species when analysing species richness. We ranked the identified species by their frequency of occurrence (number of detections) to determine common and rare species. Common species were defined as the smallest subset of the species that occurred most frequently and that made up at least half of the total detections in their respective classes, whereas all other species were classified as rare. It was not possible to calculate other commonness measures: we used this custom definition of rare and common species as most reptiles encountered in our study (8 out of 14) and some amphibians (2 out of 28) were not assessed by the IUCN Red List so that their rarity and distribution ranges were unknown (on Feb 28, 2018).

2.4.1. Abundance and richness differences between habitats

We compared plot-level measures of species richness and abundance (number of detected individuals per session) for amphibians and reptiles to determine which habitats supported higher abundance and richness. We computed abundance per sampling session as we did not mark the animals so that we could not check whether they were the same between sessions, and we treated pitfall trap detections as a separate sampling window. We fitted generalized linear mixed-effects models with Poisson family (GLMER, glmer function, R package lme4 (Bolker et al., 2009), to abundance data, using sampling window nested within plot as random effect and habitat type as a fixed effect. For richness data, we used data over all sessions in each plot. We computed alpha richness as the mean raw species number, and beta richness as the total richness of the corresponding habitat minus the alpha richness (Lande, 1996). We fitted generalized linear models with Poisson family (GLM, glm function, stats package) to both alpha and beta richness, using habitat type as a fixed effect. In case Poisson models were over-dispersed, we used negative binomial models instead. We used these parametric models to test our hypotheses by generating all possible pairwise comparisons among means while testing for significant differences (glht function, R package multcomp, Hothorn et al., 2008). We did not only test comparisons of means that reflected our hypotheses to be able to discover spurious trends that we did not hypothesize. P-values were corrected for the False Discovery Rate (Benjamini and Hochberg, 1995). We used the R package vegan (Oksanen et al., 2015) for generating species accumulation curves (function rarecurve) to assess sampling completeness and for estimating total richness (hereafter extrapolated richness) per habitat and per plot (function estimateR, bias-corrected Chao estimator (Chiu et al., 2014)). We used the extrapolated richness per plot to check the results from our raw alpha richness models and the extrapolated richness per habitat to put our results into perspective.

2.4.2. The environment as determinant of richness

We searched for the environmental drivers of reptile and amphibian raw alpha richness using the environmental covariates that we measured in each plot section as predictors. We computed the standard deviation of climatic variables (temperature, relative humidity, precipitation, gap fraction) across the four plot sections to measure environmental heterogeneity and used the mean of habitat variables to quantify the amount of available niches, except for understory density

where we decided that its standard deviation would better reflect the number of different niches available for species preferring open spaces and those preferring vegetation. We summed the numbers of logs, branch piles, single palm fronds, palm frond piles, and dead trees into a "dead plant material" variable, and cavities in trees and in the ground were summed into a "cavities" variable. Rocks and trash piles were too rare and excluded from further analyses. The mean total length of arthropods (sum of all individuals' lengths) per plot was also used as a predictor and proxy for food availability. We used the full set of predictors to fit generalized linear models to richness data at the plot level with Poisson family. When the resulting model was over-dispersed, we ran negative binomial models instead. We then generated all combinations of predictor variables from the full model to the null model and ranked them by AICc (dredge function, R package MuMIn (Bartoń, 2017)). We finally extracted the best models (within 2 ΔAICc) to average them (model.avg function, R package MuMIn) and assessed each of the predictors' coefficient sign, importance, and significance in the average model.

2.4.3. Variations in community composition between habitats

We visualized the community composition of reptiles and amphibians in different habitats using non-metric multidimensional scaling (NMDS) based on Bray-Curtis distances derived from abundance matrices (R package vegan, Oksanen et al., 2015). We performed permutational multivariate analysis of variance tests (adonis2 function, R package vegan, Oksanen et al., 2015) to assess the overall significance of habitat in structuring the communities.

3. Results

3.1. Sampling

We performed a total of 144 1-h visual and aural encounter surveys, equally distributed between plots and habitats. In addition to the surveys, we also mounted four pitfall 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 1125 animal detections from 44 species, comprising 29 of amphibians (N = 880, all of which were anurans from 6 families) and 15 of reptiles (N = 245, including 11 species of lizards *sensu latu* from 5 families and 3 of Serpentes from 3 families). We had 187 detections (Amphibia = 119, Reptilia = 68) during the midday sessions, 434 at sunset (Amphibia = 318, Reptilia = 116), and 434 at night (Amphibia = 378, Reptilia = 56). Of the 1125 detections, 70 (6.1%) were from pitfall traps, representing 8 species of amphibians (from 4 families) and 2 reptile species (family: Scincidae), all of which were also sampled during the visual encounter surveys, except for an unidentified *Sphenomorphus* individual. All the species detected acoustically were also sampled during the visual surveys. These findings extend the known geographic distribution of 15 species of amphibians and of 8 reptiles previously not recorded in the province of Jambi (Teynié et al., 2010, Table 1). Six detections of *Ansonia* were not identified formally to species level but since only *Ansonia glandulosa* was reported on Sumatra with confidence (Iskandar and Mumpuni, 2004), we assigned these detections to that species. We also assigned the single detected *Sphenomorphus* individual to a morphospecies to count it as a separate — albeit unidentified — species.

3.2. Environmental covariates measurement

Environmental data were collected from all 4 sections of the 24 plots and are summarized in Table 2. Temperature was lower and more constant in forests than in plantations. Relative humidity in forest was slightly higher, but again subject to smaller variations over time. Dead plant material was especially abundant in oil palm, mainly because of frond piles. Cavities in trees or in the ground were mainly present in forest. Leaf-litter cover was much higher in forest and rubber than in oil palm. Undergrowth density was only slightly higher in forest plots. The mean of total arthropod length was much higher in forest plots. Finally, gap fraction was much higher in plantations than forest.

3.3. Abundance and richness differences between habitats

Most animal detections were in oil palm plantations (N = 577 individuals, 24 species), followed by forest sites (N = 327, 27 species) and rubber plantations (N = 221, 28 species). Three species of amphibians (*Fejervarya limnocharis* Gravenhorst, 1829; *Amnirana nicobariensis* Stoliczka, 1870; and *Ingerophrynus parvus* Boulenger, 1887) 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* Duméril and Bibron, 1836) alone represented 73% of all sampled reptiles and was therefore defined as the only common reptile (Fig. 1). When available, the IUCN Red List population status information indicating the size of the population matched our definition of common and rare species.

The mean abundances of reptiles and amphibians are shown in Fig. 2. The alpha and beta raw species richness of reptiles and amphibians are shown in Fig. 3, and the extrapolated alpha richness and total richness per habitat are shown in Fig. S3. For all our response variables we used a P-value level below 0.05 for statistical significance, and between 0.1 and 0.05 for marginally significant trends.

For amphibians, land use conversion from riparian forest to plantations tended to be associated with a decrease in abundance, but not richness. Overall amphibian abundance was highest in riparian forest, but only significantly so when compared to upland rubber sites. Rare amphibians were distinctly more abundant in riparian forest than the other habitats,

Table 1

Summary of the species detected in each land use type, IUCN Red List status, and indication on whether the species had not been previously reported in the province of Jambi (*) or in Sumatra (+), following Teynié et al., (2010).

Class (Order)	Family	Species	Forest	Oil palm	Rubber
Amphibia (Anura)	Bufonidae	Ansonia glandulosa *	1	4	2
		Ingerophrynus biporcatus *	0	4	6
		Ingerophrynus divergens *	31	0	0
		Ingerophrynus parvus	0	73	42
		Ingerophrynus quadriporcatus	1	1	2
	Dicroglossidae	Fejervarya cancrivora	0	3	5
		Fejervarya limnocharis	0	96	53
		Limnonectes blythii *	47	0	7
		Limnonectes macrodon *	6	0	1
		Limnonectes malesianus *	2	0	2
		Limnonectes paramacrodon *	3	0	0
		Occidozyga sumatrana	55	1	0
	Megophryidae	Leptobrachium hasseltii	0	0	1
	Microhylidae	Kalophrynus pleurostigma	5	0	6
		Kaloula baleata	0	0	3
		Microhyla berdmorei *	2	0	0
		Microhyla butleri * +	1	0	0
		Microhyla heymonsi	0	7	1
	Ranidae	Amnirana nicobariensis	4	90	32
		Chalcorana chalconota	19	3	1
		Chalcorana labialis *	2	1	0
		Chalcorana raniceps *	8	1	2
		Hylarana erythraea	0	7	6
		Pulchrana baramica *	1	46	18
		Pulchrana glandulosa *	4	7	1
	Rhacophoridae	Kurixalus appendiculatus *	62	0	5
		Polypedates colletti *	27	0	0
		Polypedates leucomystax	4	11	4
		Rhacophorus bengkuluensis * +	1	0	0
Reptilia (Squamata)	Agamidae	Aphaniotis fusca *	1	0	0
		Draco sumatranus * +	0	0	1
	Colubridae	Dendrelaphis pictus	0	2	1
	Elapidae	Naja sumatrana	0	0	1
	Gekkonidae	Gehyra mutilata *	0	3	0
		Gekko smithii	5	0	0
		Hemidactylus frenatus *	0	166	4
	Lacertidae	Takydromus sexlineatus	0	12	0
	Scincidae	Dasia olivacea	1	0	0
		Eutropis macularia * +	0	2	0
		Eutropis multifasciata	12	5	5
		Eutropis rugifera *	1	6	2
		Sphenomorphus 1	1	0	0
	Typhlopidae	Indotyphlops braminus *	0	1	0
	Varanidae	Varanus rudicollis *	0	0	1

Table 2

Mean values and standard deviations per section for the measured environmental variables in each habitat.

Habitat	Temperature (°C)	Humidity (%)	Cavities	Leaf litter cover (%)	Dead plant material	Undergrowth density (1−5)	Arthropods length (cm)	Gap fraction (%)
Forest riparian	26.57 ± 1.11	86.77 ± 2.72	1.19 ± 1.6	71.12 ± 21.93	1.62 ± 2.92	3.5 ± 0.82	13.22 ± 12.29	3.48 ± 0.84
Forest upland	27.12 ± 1.32	83.65 ± 4.04	1.25 ± 1.88	87.56 ± 10.03	2.81 ± 2.79	3.88 ± 0.81	16.59 ± 14.49	4.81 ± 2.99
Oil palm riparian	29.07 ± 3.38	80.6 ± 10.51	0 ± 0	8.75 ± 6.71	6 ± 2.78	2.38 ± 1.45	7.31 ± 6.01	20.04 ± 9.23
Oil palm upland	28.19 ± 2.46	81.69 ± 9.11	0.62 ± 2.5	12.5 ± 7.53	7.19 ± 1.56	3.19 ± 0.98	9.22 ± 4.88	14.07 ± 3.83
Rubber riparian	28.46 ± 2.92	80.62 ± 10.99	0.31 ± 0.6	73.94 ± 21.15	2.44 ± 2.31	3.19 ± 1.38	4.72 ± 3.53	30.19 ± 12.71
Rubber upland	28.4 ± 2.19	81.97 ± 8.31	0.19 ± 0.4	63.12 ± 28.51	3 ± 3.52	3.69 ± 1.58	3.62 ± 3.9	25.16 ± 12.4

but only marginally significantly (P = 0.06) when compared to oil palm. Common amphibians were distinctly more abundant in plantations that in forests. Amphibian raw (alpha and beta) and extrapolated richness measures were statistically indistinguishable between land use types, but they tended to be low in oil palm.
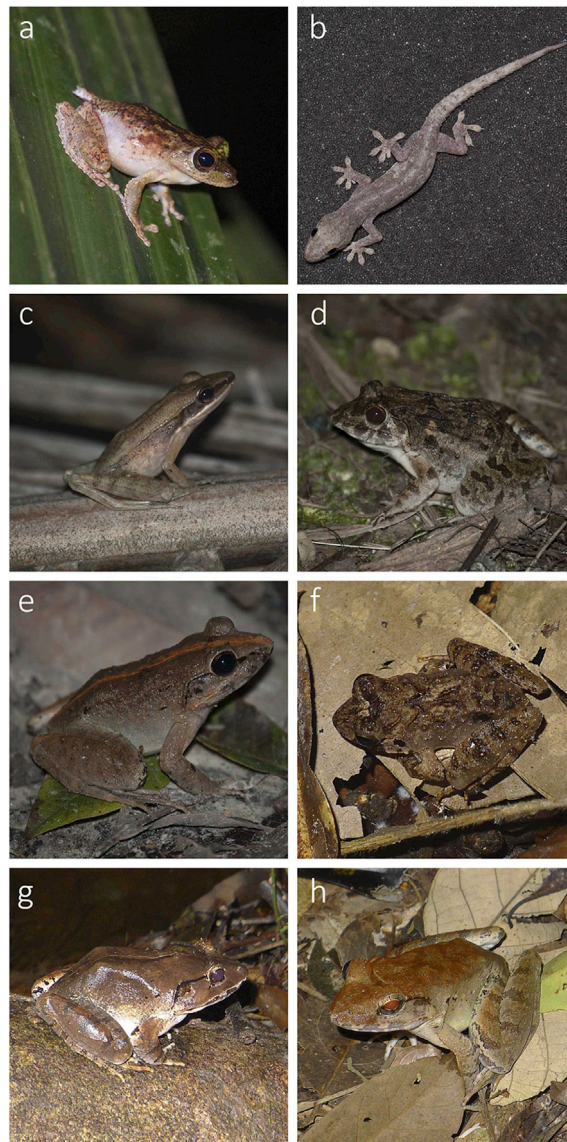
Fig. 1. Photos of common and rare reptile and amphibian species encountered. *Kurixalus appendiculatus* (a), *Hemidactylus frenatus* (b), *Amnirana nicobariensis* (c) and *Fejervarya limnocharis* (d) were the most frequently encountered species. The only sampled species classified not listed in the IUCN Red List or that were not of Least Concern were *Limnonectes blythii*, NT (e), *L. macrodon*, VU (f), *L. malesianus*, NT (g), *L. paramacrodon*, NT (g). Photo credits: Alessio Paoletti. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

For reptiles, land use conversion was associated with a strong increase in abundance in oil palm. Overall and common (*H. frenatus*) reptile numbers were statistically significantly higher in oil palm plantations compared to other habitats, and rare reptiles were also more abundant in upland oil palm compared to the other habitats, except riparian forest. Both raw (alpha and beta) and extrapolated alpha richness measures did not differ between habitats, but extrapolated reptile alpha richness was marginally significantly higher in upland oil palm plantations compared to upland forest and upland rubber ($P = 0.06$).

Amphibian abundance and richness tended to be higher in the riparian habitats of the respective land use types. However, few comparisons were statistically significant: overall and rare amphibians were more abundant in riparian versus upland forest, and common amphibians were more abundant in riparian versus upland rubber sites. Also, only alpha raw richness was higher in riparian versus upland forest, all other comparisons were not significant.

3.4. The environment as determinant of richness

The average model results are presented in Table 3. Amphibian raw alpha richness was significantly positively correlated with undergrowth density standard deviation (importance = 0.66) and with no other continuous variable. Reptile richness
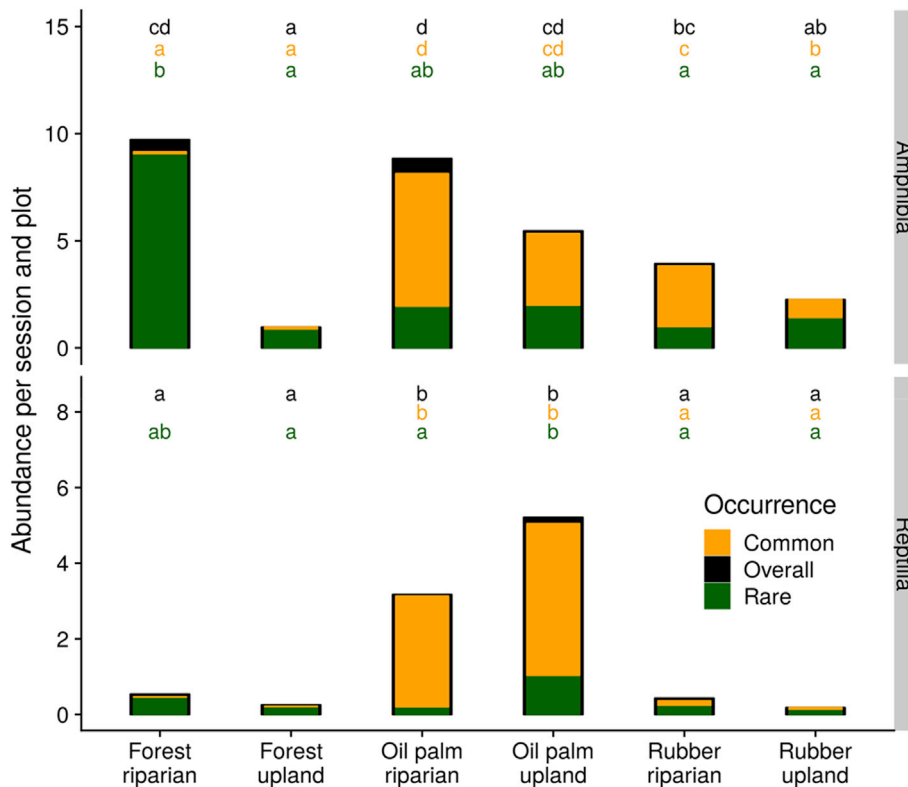
Fig. 2. Mean abundances of amphibians and reptiles per session and plot in each habitat, split between common and rare species. Significant differences between means are indicated by different letter combinations. Black letters indicate differences between overall species richness means (common and rare species confounded). There were no common reptiles in forest, thus no statistical test was conducted. The small discrepancies in some habitats between the sum of the rare and common species and the overall number of species are due to individuals that could not be definitively identified and therefore of unknown occurrence status (i.e mostly *Fejervaya* individuals that could not be reliably assigned to the common *F. limnocharis*, or the rare *F. cancrivora*).

was marginally negatively correlated with the mean of leaf litter cover (P = 0.06, importance = 0.63). Despite appearing often in the best models, the mean of dead plant material was insignificantly, positively correlated with reptile raw alpha richness (P = 0.115, importance = 0.50). The habitat as categorical variable was still present in the average model for amphibians.

3.5. Variations in community composition between habitats

Non-metric multidimensional scaling based on species abundance data showed that the forest amphibian communities were more similar to each other than to plantation communities, which were overlapping each other (Fig. 4). The ADONIS testing whether habitat structured amphibian communities exhibited high statistical significance (51% of total sums of squares explained by the model, P = 0.001, overall test). Reptile communities from the forest were also distinct from plantation communities, but riparian rubber overlapped with riparian forest communities (Fig. 4). The ADONIS testing whether habitat structured reptile communities exhibited high statistical significance (63% of total sums of squares explained by the model, P = 0.001, overall test).

4. Discussion

The amphibian and reptile community compositions differed markedly between forest habitats and plantations, revealing distinct assemblages in plantations. Riparian forest hosted many more rare amphibians than the other habitat types, and plantations had high amphibian counts comprised of common species. Reptiles were considerably more abundant in oil palm habitats, mainly due to the high prevalence of the common house gecko, but many rare reptiles were also found in upland oil palm. Riparian sites tended to harbour more amphibians than their upland counterparts. We found no significant differences between habitats based on our richness measures, except for higher raw alpha richness of reptiles in riparian versus upland forest.
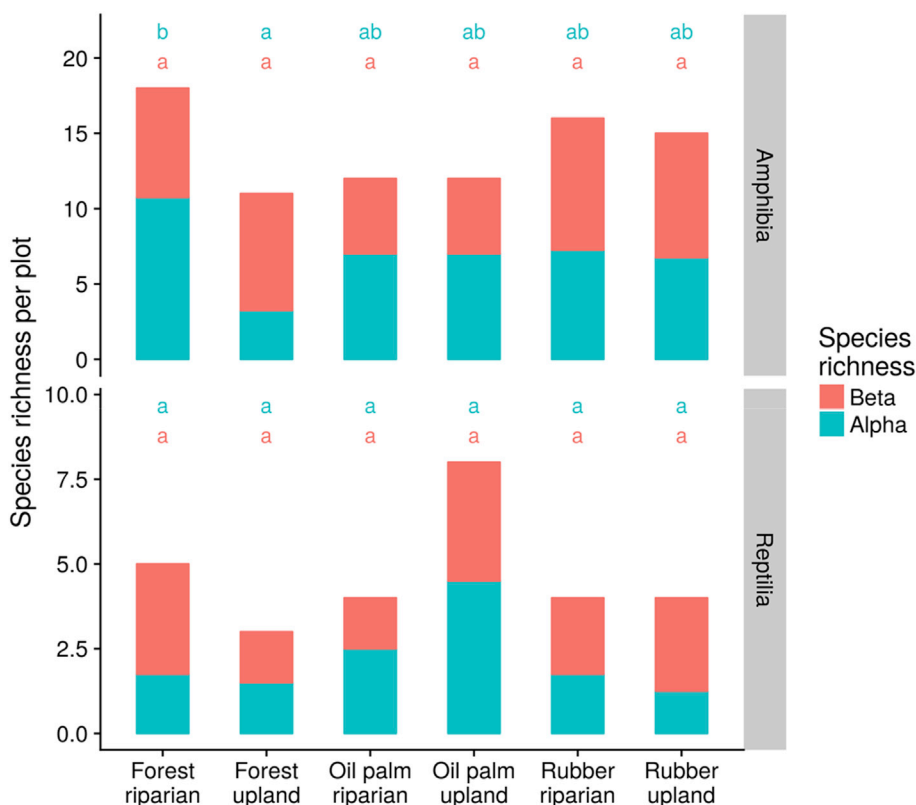
Fig. 3. Raw alpha and beta species richness means per plot for amphibians and reptiles in each habitat. Significant differences between means are indicated by different letter combinations.

Table 3
Summary of the continuous variables included in the average models predicting amphibian and reptile richness.

Class	Predictors	Coefficients	P-values	Importance
Amphibia	Undergrowth density	0.493	0.021	0.657
Reptilia	Dead plant material	0.112	0.115	0.496
	Leaf litter cover (%)	−0.009	0.059	0.63
	Temperature	1.131	0.278	0.296

4.1. Abundance and richness variations

4.1.1. Amphibians

We expected abundance and diversity levels of amphibians to be similar among habitats because of previous studies showing that oil palm plantations have high amphibian abundance and richness (Faruk et al., 2013). In our study, oil palm plantations were the most populated habitat. Oil palm systems are capable of hosting a high abundance of herpetofaunal species, but the communities are composed of few common species. The most common amphibian species in plantations were *Fejervarya limnocharis* and *Amnirana nicobariensis*, which are tolerant to a broad range of habitats (IUCN, 2017). It is possible that the tracks left by trucks that collect the harvest produce bolster amphibians by gathering water where amphibians and amphibian eggs were often observed (pers. obs. AP and HJ). In contrast, rubber plantations were the least populated land use system, but had the highest total species count. Rubber plantations might support high amphibian diversity due to a more heterogeneous and stable tree structure that offers more niches than oil palms whose canopy is constantly disturbed during harvest and whose fronds are continuously removed. Species requiring leaf litter might prefer rubber plantations, as in oil palm plantations all litter fall consists of fronds that are stacked by harvesters. The relatively low number of detections in rubber plots could be due to the low supply of arthropods as food items, and it suggests that large expanses of rubber would be needed to conserve a significant proportion of amphibians. Similarly, forest upland sites had very low numbers of detected amphibians, which might also be due to the dry season during which we sampled. Riparian habitats always harboured more amphibian individuals and species than their respective upland sites, even though the differences were statistically not significant for plantations. This suggests that riparian habitats could be important for amphibians.
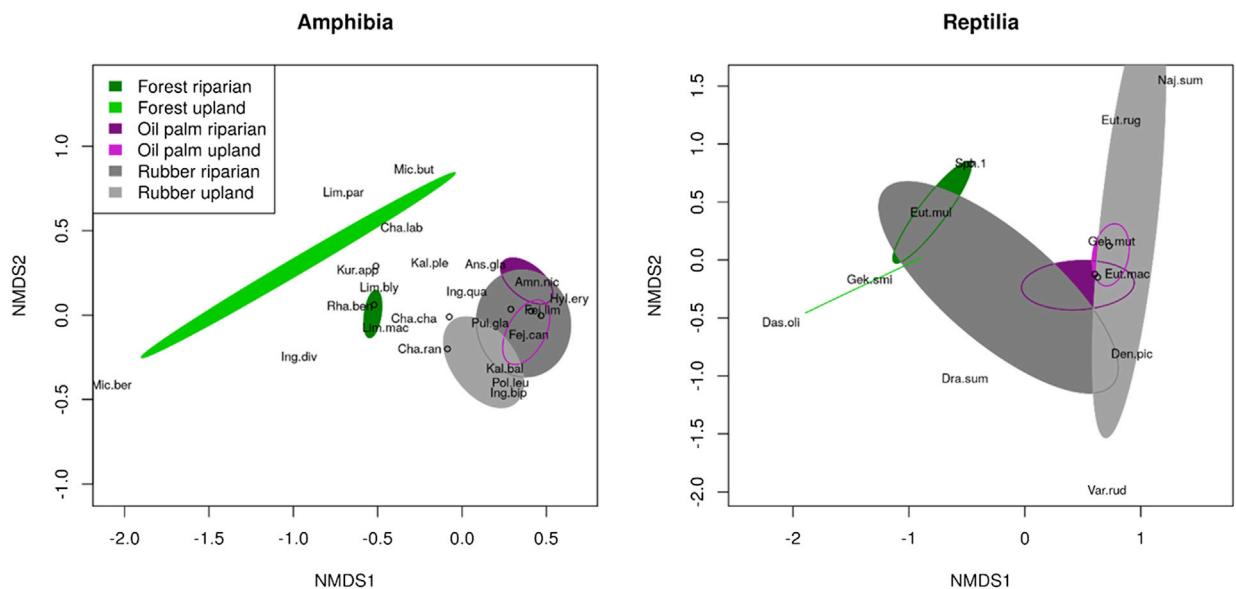
Fig. 4. NMDS (Non-metric Multi-Dimensional Scaling) of amphibians (left) and reptiles (right), obtained from abundance matrices, grouped in ellipses representing 95% confidence intervals for each habitat. Each label represents a species code consisting of the first three letters of the genus and the species name. The line in the right graph represents riparian forest, where one plot was without reptiles.

The weak differences between forest and plantations in our study might be due to the fact that our reference sites were in disturbed, selectively logged forest, which has been shown already to be of inferior value compared to primary forest (Ficetola et al., 2008). Our smallholding plantations were also more heterogeneous than intensively-managed company estates, thus possibly benefiting from the surrounding landscape mosaic, the low input of chemicals, relatively dense understory and low disturbance through harvesting activities.

The detected trends in our amphibian detection data can reasonably be assumed to be an unbiased representation of the communities in the different habitats. The small differences in undergrowth densities suggest that detectability could have been slightly affected by vegetation. However, our pitfall trappings and aural surveys do not require visual contact with the animals, thus countering this detectability issue. 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 (Dodd and Dorazio, 2004; Mackenzie and Royle, 2005; Royle, 2006).

The species accumulation curves for amphibians are close to reaching their respective plateaus, except in upland forest (Fig. S4). Plateaus can be methodological artefacts due to habitat sub-sampling, but sampling each land use across a large geographic region and a wide range of environmental conditions ensured that we sampled most habitats that can be expected in plantations and forests. Although we found few of the usually abundant microhylids (Faruk et al., 2013), we had high counts of individuals of small species, such as *Ingerophrynus* spp., even juveniles. Thus our sampling did not appear to be biased towards larger-sized anurans. Additional sampling in the rain season could help detect additional species, but the large amount of person-hours per plot should ensure a representative sample of the herpetological community. Additionally, the overall success rate of our pitfall traps was 24.0%, which is slightly higher compared to other studies (eg. Garden et al., 2007).

4.1.2. Reptiles

The majority of detected reptile individuals in oil palm were of the species *Hemidactylus frenatus*. It is an invasive species in several tropical and sub-tropical countries (Hoskin, 2010). Other reptile species fared surprisingly well in oil palm plantations, especially in the drier upland habitats, where high extrapolated species richness levels were reached. However the absence of plateaus in reptile species accumulation curves suggest incomplete sampling. Still, extrapolated richness, which is designed to address this, did not differ significantly among the habitats either.

Reptiles, especially arboreal species and snakes, rarely vocalize and are notoriously challenging to observe and indeed, few of them were observed in the plots. We did not use sampling methods for arboreal species like glue traps present because of ethical issues (Ribeiro-Júnior et al., 2008). Also, snakes (mostly *Naja sumatrana*) were detected outside sampling plots more than 20 times (pers. obs. AP and HJ), so their lack in our data set was probably due to their absence rather than missed detections or observer bias. It is likely that reptiles in oil palm were more comprehensively surveyed: in oil palm plantations, the canopy is relatively low and it could be surveyed with binoculars. The higher canopy of rubber and forest sites however was excluded from our sight, thus possibly resulting in under-sampling of arboreal reptiles. However, even in forest, geckos (*Gekko smithii*) and anurans were never heard from high up (there were no detections above 8 m).

4.2. Environmental heterogeneity as determinant of richness

We measured environmental variables covering the most important habitat and climatic features that can affect amphibians and reptiles, independently from the habitat. Our amphibian models align well with previous literature. Ari Janiawati et al. (2016) showed that variation in understory density was positively associated with amphibian richness, suggesting that it provides more niches for amphibians. Additionally, Pilliod et al. (2003) point out that understory variation can protect amphibians against dehydration. However, we could not find conclusive effects of environmental variables on reptile richness, which might be due to the low numbers of detected species.

4.3. Variations in community composition

In spite of similar richness measures among habitats, non-metric multidimensional scaling clearly shows that assemblages are different among habitats for both amphibians and reptiles, especially between forest and plantations. These results contradict studies showing that forest herpetofaunal communities can resist to anthropogenic disturbance (Gillespie et al., 2012) but are in accordance with a larger volume of investigations highlighting the adverse effects of primary forest modifications (Gardner et al., 2008; Gibson et al., 2011; Faruk et al., 2013). 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*, of which we found 170 individuals exclusively in plantations. All of the four species present in our sample that are not considered of Least Concern or not listed in the IUCN Red List (*Limnonectes blythii*, *L. macrodon*, *L. malesianus*, *L. paramacrodon*, see Table 1) were found exclusively in forests, together with roughly half of the animals belonging to the 10 species that have not been evaluated yet. We originally hypothesized that either a subset of the forest communities could take over sympatric species after conversion, or that new species colonize plantations. The latter hypothesis was confirmed: plantations harbour specific reptile and amphibian communities. This is especially true for amphibians, whose assemblages are consistently different among forest and plantations (Fig. 4), whereas in reptiles the trend is slightly less obvious because local communities are replaced mainly by only one species, *Hemidactylus frenatus*, which can reach high population densities.

4.4. 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, of which four species that have not been previously recorded in Sumatra, 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. However, it is possible that some species of reptiles and amphibians were not detected because they were inactive during our sampling period from April to July. The conservation status of 10 out of the 42 species identified during our sampling has not been formally assessed yet (IUCN, 2017). Our sampling area did not even include other areas of high herpetological interest within the Jambi province, such as Kerinci Seblat National Park (Kurniati, 2008), where more species are likely waiting to be recorded, or even described. This lack of knowledge might lead to wrong assessments of conservation needs. This is especially important in areas where agricultural activities have and still are drastically reducing forested areas (Gunarso et al., 2013).

5. Conclusions

Agricultural intensification will likely continue at a high rate in Sumatra and the whole of Indonesia (Margono et al., 2014). Our results are important from a conservation perspective since they highlight the effects of conversion of forests to cash crops by focusing on taxa that have been neglected in conservation studies. Despite the capability of the most common crop in the country, oil palm, to sustain a high number of animals, the amphibians that inhabit plantations are common, disturbance-resistant, and of low conservation value, capable of living in man-made landscapes. Rubber plantations also had low potential for conservation due to the prevalence of common species and the generally low abundances of reptiles and amphibians. Interestingly though, upland oil palm sites sustained high reptile diversity, and plantation habitats generally harboured specific animal communities. The four amphibian species not listed or with a IUCN Red List status different from Least Concern are all forest specialists that rely on streams for breeding and egg-laying (IUCN, 2017). Replacement of forests with plantations will likely induce losses of the local populations of those species, and therefore particular attention should be paid on preserving streambeds and nearby wetlands. We suggest future agricultural intensification to be aimed at sustainable intensification combined with maintaining and restoring the last forest remnants.

Competing interests

The authors declare to have no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2018.e00492.

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