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„Temporal species turnover in amphibian and reptile species assemblages: a comparison between forest and oil palm plantations"

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Acknowledgments

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Abstract

It is well documented that oil palm plantations are characterized by significantly lower species richness and show a markedly different species composition than tropical rainforests. However, very little is known about the temporal dynamics or stability of species communities in oil palm plantations compared to forests. Therefore, amphibians and reptiles were surveyed in 2013 and again in 2018/2019 at forest interior, forest margin and oil palm plantation sites in a lowland area in southwestern Costa Rica. In 2018, one third more individuals of amphibians and more than twice as many individuals of reptiles were found than in 2013, but no significant differences were found in species richness. Habitat-specific differences in changing species composition between the two survey years was only detected for reptiles, which showed a more pronounced change in oil palm plantations and forest margin when compared to forest interior. This could indicate that these disturbed habitats may be less well buffered against seasonally changing climatic conditions. Even though changes in functional diversity did not show any habitat-specific pattern, leading to the conclusion that trait-specific requirements did not change in a habitat-specific manner, functional richness and functional dispersion did change significantly over the years for reptiles. It remains to be studied to what extent these higher temporal dynamics of reptile populations in oil palm plantations actually reflect species-specific changes in abundance, driven by greater changes in environmental conditions in oil palm plantations, compared to forest habitats. Alternatively, seasonal changes in weather conditions could have species-specific effect on reptile activity.

Keywords

Introduction

During the last decades, new cropland became one of the biggest threats to remaining tropical rainforests (Gibbs et al. 2010). Habitat loss and fragmentation are major threats for biodiversity, not only in natural ecosystems but also in human-dominated areas (Fahrig et al. 2011). Although habitat fragmentation has a weaker effect on biodiversity than habitat loss, it causes substantial changes in habitat quality (Sala et al. 2000; Höbinger et al. 2011). However, it is not only important to protect pristine or largely undisturbed ecosystems by establishing protected areas. Human-dominated landscapes can also provide important habitats for many indigenous species (Bennett et al. 2006). Agricultural areas often represent mosaics of different land-use systems, e.g., pastures, plantations and annual cultures, with an interspersion of human settlements, roads and streams (Bennett et al. 1990; Daily et al. 2003). Nowadays, oil palm (*Elaeis guineensis*) plantations are a big part of tropical agricultural landscapes (Koh 2007). While many studies already documented that these monocultures have impoverished species assemblages, now dominated by widespread and disturbance tolerant species (Fayle et al. 2010; Fitzherbert et al., 2008; Freudmann et al. 2015; Foster et al., 2011), our knowledge on temporal species turnover in this land-use system is very limited.

Strong negative effects of oil palm cultivation on species richness and particularly the fraction of forest-dependent species is reported for the herpetofauna (Gallmetzer & Schulze 2015). Amphibians and reptiles are among the most threatened animal groups with significant declines on a global scale. With 32.5% of amphibian species threatened, it is the highest percentage of all vertebrate taxa (listed as "vulnerable", "endangered", "critically endangered" in the IUCN Red List). In total 43% of the populations of these species are in decline (Heatwole, 2013; Li et al. 2013; Wake & Vredenburg, 2008; IUCN 2020). While Central America in specific hosts 6.8% of existing amphibian species worldwide, it had to face a tremendous decline of amphibian populations and mass-mortality occurrences (Whitfield et al., 2016). Whereas factors such as diseases, climate change and environmental pollution all contribute to the reduction of biodiversity, habitat loss and degradation still represent one of the major threats to amphibians and reptiles (Gibbons et al. 2000; Beebee & Griffiths 2005; Venvces & Köhler 2008). Abiotic and biotic factors may prove to have additive effects and their impacts may be species- or even population-specific, as argued for amphibians. Hence, causes of declines can differ spatially and temporally (Blaustein & Kiesecker 2002).

In this study, we re-sampled forest and oil palm plantation sites at a lowland area in Costa Rica, which were already surveyed five years ago, to quantify habitat-specific differences in species turnover as

well as temporal changes in assemblage structure and functional diversity. In particular, we want to test the following hypotheses:

Hypothesis 1: On the level of study sites, we expect a more stable species composition in oil palm plantations as the majority of species consist of widespread and abundant generalists, often rather tolerant against disturbance (Gallmetzer & Schulze 2015). These species often have a high reproductive output and a high capacity to disperse. Hence such species should be more resilient against local extinctions (Isaac et al. 2009). In contrast, the highly diverse rainforest species assemblages containing many specialists with low reproductive output are shaped by more stochastic processes. This may result in a higher species turnover on a small scale (study site level).

Hypothesis 2: On the habitat level, we expect fewer temporal changes in forest habitats than in the human-modified land-use system, which may suffer an ongoing loss of rarer species, hence resulting in an ongoing biotic homogenization of species assemblages (Baiser et al. 2012, Olden et al. 2004).

Hypothesis 3: Functional diversity of amphibians already proved to decline dramatically from forest sites to oil palm plantations (Gallmetzer & Schulze 2015). We assume that an ongoing loss of habitat specialists in oil palm plantations may result in a further decline in functional diversity of species assemblages. In contrast, functional diversity at rainforest sites may have remained similar over the period of five years.

Hypothesis 4: Amphibians and reptiles may respond differentially to ongoing disturbances with amphibian populations suffering more substantially than reptiles, as documented by a study on the effects of natural and human disturbances on herpetofaunal species assemblages of a tropical dry forest area in Mexico (Suazo-Ortuño et al. 2018). Although our study area is located in a lowland rainforest region with a more humid climate, also here amphibians may be more severely affected by a changing microclimate than reptiles.

Methods

Study area and study sites

This study took place in the proximity of the Tropical Research Station La Gamba (N 08.701028° W 083.201720°) situated at the edge of the Piedras Blancas National Park on the Pacific slope of southern Costa Rica (Golfo Dulce Region) (Höbinger et al. 2012). The Golfo Dulce region holds the last remaining moist and wet evergreen forests on the Pacific slope of Costa Rica, with annual precipitation of about 6.000 mm (Huber & Weissenhofer 2019). Additionally, it is characterized by mosaics of settlements, fallows, pastures, water bodies and various land-use systems, primarily oil palm plantations (Freudmann et al. 2015).

We assessed amphibian and reptile species assemblages at 15 study sites where a herpetofaunal survey was already conducted in 2013 (Gallmetzer & Schulze 2015). Sites were relocated using GPS (Appendix Table A1). The study sites represent forest interior, forest margin, and oil palm plantation sites (N = 5 spatial replicates of each habitat type). Forest interior (FI) is characterized as pristine or old-growth secondary forest (at least 80 years old), which is at least 200 m away from the nearest forest edge. Forest margin (FM) sites are located parallel to a defined forest edge, adjacent to human-dominated areas (e.g., plantations, gardens, pastures). Oil palm plantations (OP) with study sites had a size of 10-50 ha and were situated near forest margins and open cultivated lands (Gallmetzer & Schulze 2015). The locations of all study sites are indicated in Fig. 1.
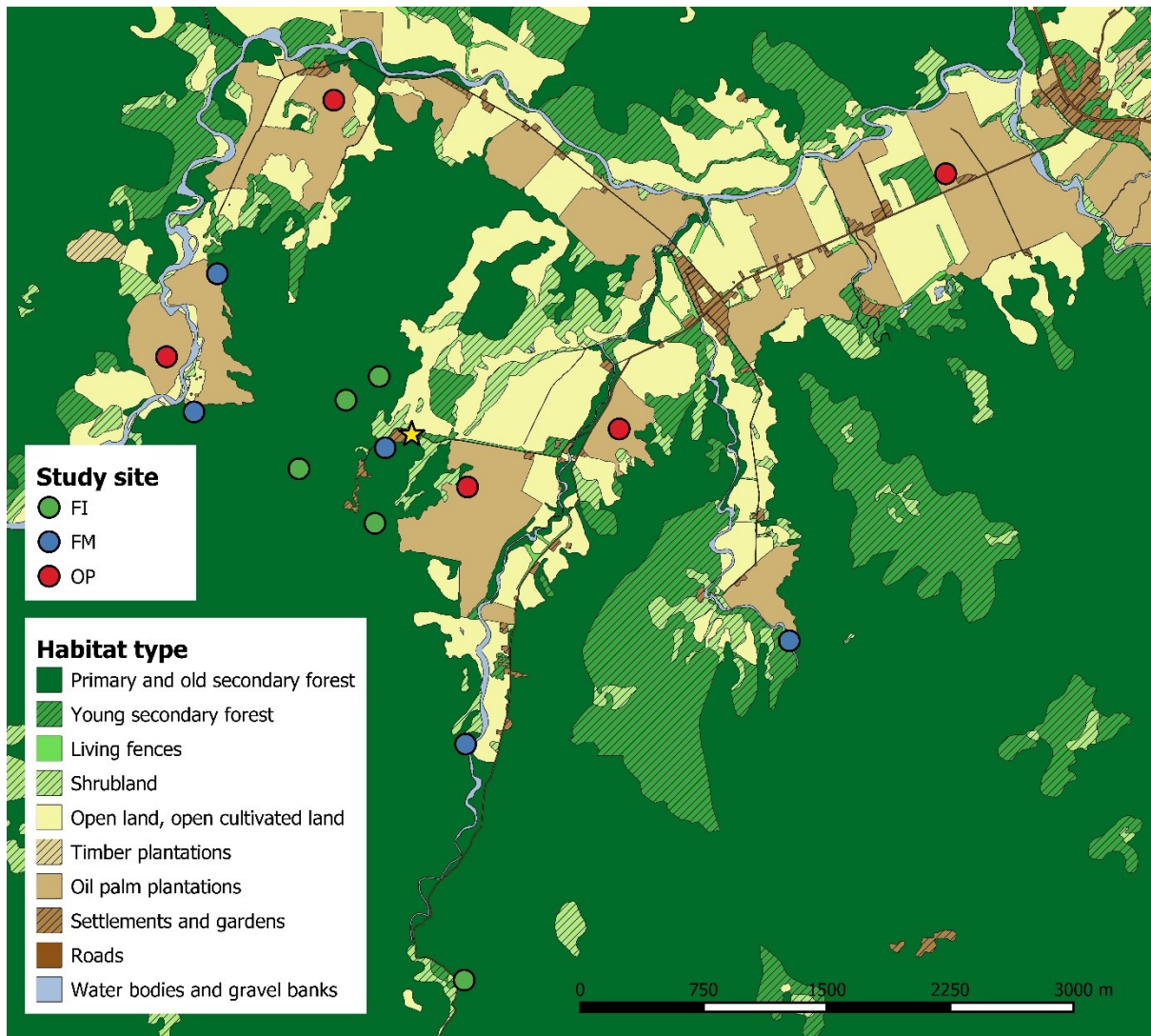
Figure 1. Map of the study area indicating the 15 study sites (FI - forest interior, FM - forest margins, OP - oil palm plantations) and the location of the tropical research station La Gamba (⭐).

Survey of reptiles and amphibians

Fieldwork was conducted between 12 November 2018 and 22 January 2019 (Appendix Table A2). We used distance- and time-constrained visual encounter surveys to assess the herpetofauna of our study sites (Kurz et al. 2014). Therefore, at each sampling site, all visually detected amphibians and reptiles were recorded along a 100 m transect, which was surveyed for two-man hours during each visit (Gallmetzer and Schulze 2015). All surveys were conducted by Jennifer Insupp, usually accompanied by at least one trained field assistant. Each transect was sampled 10 times, five times during the day (between 06:30 and 16:30) and five times during night (between 21:30 and 05:00). At night, a head torch was used for searching amphibians and reptiles. Sampling sites were surveyed in random order and during all weather conditions, except heavy rain. All individuals which were visually detected within a band of 2 m at both sites of each transect were counted. We determined the species identity of each specimen using available field guides (Franzen & Kollarits 2018, Leenders 2016, Leenders

2019). Photographs were taken for documentation and particularly of those specimens, which couldn't be identified in the field to allow for later identification using additional references (e.g., Köhler 2011, Savage 2002, AmphibiaWeb, 2020). Nomenclature follows that of Franzen & Kollarits (2018).

Data analysis

Specimens that could not be identified to species level, either because they escaped or were too young for reliable species identification, were excluded from all analyses. Since individuals of the species *Craugastor crassidigitus* and *Craugastor fitzingeri* often could not be caught, but the only significant identification feature differentiating them is located on the posterior thighs, we combined these species for all analyses as *Craugastor crassidigitus/fitzingeri*. Due to their very similar appearance, the individuals of *Smilisca sordida* and *Smilisca sila* were also combined and furthermore referenced as *Smilisca sordida/sila*.

Unless we stated otherwise, all statistics were calculated with R 3.6.1 (R CoreTeam 2019) and R Studio Version 1.2.5001 (2009-2019 R Studio, Inc.). We assessed habitat-specific changes in species richness, species composition, species turnover, and functional diversity, separately for amphibians and reptiles.

To evaluate temporal changes in species richness, species accumulation curves were calculated for all three habitats and between years. The R package "iNEXT" was used to compute individual-based rarefaction curves and extrapolate them to twice the sample size (Chao et al., 2014; Hsieh, Ma & Chao 2016). However, for comparing predicted species numbers between habitats and years only the numbers of species predicted for twice the sample size of the smaller sample were considered. Graphics were made with the R package ggplot2 (tidyverse; Wickham & Chang, 2015).

Differences in species composition between sites x sampling years were quantified using Bray-Curtis dissimilarities. In advance, abundances were square-root transformed to increase the relative contribution of rarer species to the Bray-Curtis values. Subsequently, a nonmetric multidimensional scaling (NMDS) ordination was used to investigate patterns of variation in anuran and reptile community composition across forest and plantation habitats and the two sampling years 2013 and 2018. The NMDS was calculated with function ''metaMDS'' from R package vegan with the final arrangement that had the lowest residual stress out of twenty random beginning configurations (Oksanen et al., 2016). NMDS ordinations with a stress value of < 0.20 were treated as being reliably visualizing the differences in the composition of sampled species assemblages. To test for habitat-

specific differences of changes in species composition over the period of 5 years, a Kruskal-Wallis test was calculated testing for differences between species assemblages sampled in 2013 and 2018 at individual sites.

To analyse if changes in relative abundances between 2013 and 2018 are related to species' distribution range size, species were divided into three categories: (1) Endemics that are only found on the Pacific slope of southwestern Costa Rica and western Panama; (2) Range-restricted species that are located on both slopes along Central America; (3) Widespread species, which can be found beyond the borders of Central America (information on species distributions extracted from Leenders 2016, 2019). Paired Wilcoxon tests were used to test for changes in relative abundances.

To examine functional diversity (FD) measures, a species-trait matrix between all habitats was created for amphibians and reptiles (Appendix A5 and A6). For amphibians, we used the ecological traits resource quantity, daily activity, microhabitat use, oviposition site and reproduction mode (Table 1). Reptiles were categorized by resource quantity, daily activity and diet (Table 2). Classifications were done based on various sources (Leenders 2016 & 2019, AmphibiaWeb 2019, Franzen & Kollarits 2018).

Table 1 Trait matrix used for calculating functional diversity indices for amphibians.

Trait	Trait category	Type
Resource quantity	Body size (BS): Mean of maximum body length of male and female [mm]	continuous (range: 17-181.5)
Activity	diurnal (D) nocturnal (N)	binary (yes, no)
Vertical stratification	ground-dwelling (GD) arboreal (VE)	binary (yes, no)
Oviposition site	Lotic systems (LO) Lentic systems (LE) Ground (GR) Leaf litter (LL) Phytotelmata (PH) Leaf surface (LS)	binary (yes, no)
Reproduction	Clutches (CS) Indirect Development (DV)	binary (yes, no)

Table 2 Trait matrix used for calculating functional diversity indices for reptiles.

Trait	Trait category	Type
Resource quantity	Body size (BS): Mean of maximum body length of male and female [mm]	continuous (range: 100-2500)
Activity	diurnal (D) nocturnal (N)	binary (yes, no)
Diet	Herbivorous (HE) Eggs (EG)	binary (yes, no)

Invertebrates (IN)
Small vertebrates (SV)

These matrices were then computed to form species-site matrices to calculate four FD indices, functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) and functional dispersion (FDis) (Mouchet et al. 2010; Villéger et al. 2008). All FD indices were calculated in R 3.6.1 (R CoreTeam 2019) with the package "FD" (Laliberté & Legendre 2010) to quantify habitat-specific temporal changes in ecological functions of the herpetofauna. FRic quantifies the volume of space of a functional convex hull occupied by the community; FDiv describes the divergence in the distribution of species characteristics within the volume occupied by each functional trait; FEve the regularity of the distribution in abundance on this volume (Villéger et al. 2008). FDis is an index that accounts for the abundance of species in multidimensional trait space by moving their centroids toward more abundant ones and weighting distances between individuals based on relative population sizes. It can also be used as a proxy measure to understand how closely related different taxonomic groups might actually appear (Laliberté & Legendre 2010). Paired *t*-tests were applied on all four functional diversity indices to measure differences between years. Kruskal-Wallis rank-sum test was assessed to evaluate between-habitat differences in the temporal change of the FD measures, using the site-specific differences of the FD values.

Results

Abundance and species richness

In total, we recorded 1404 individuals, 874 amphibians and 530 reptiles in 2018 (Table 3, for details see Appendix Table A3). Though we almost found a similar number of amphibian species than in 2013, we recorded 300 more individuals in 2018. In comparison to 2013, six more reptile species were recorded and more than double the number of individuals (Table 3). While each transect was surveyed equally (in total 150 transect walks) in 2018, during the study of Gallmetzer & Schulze (2015) only 143 transect walks were done.

Table 3. Numbers of individuals and species (in brackets) recorded for the three habitats (FI – forest interior, FM – forest margin, OP – oil palm plantation) in 2013 and 2018.

Habitat type	Amphibians		Reptiles	
	2013	2018	2013	2018
FI	133 (21)	277 (20)	123 (13)	208 (17)
FM	146 (19)	252 (19)	102 (12)	246 (16)
OP	289 (11)	345 (15)	36 (7)	76 (10)
Total	**568 (27)**	**874 (28)**	**261 (19)**	**530 (25)**

The estimated completeness of the recorded species inventory for amphibians across all five habitats was 88.69% for the year 2013 and 97.18% for the year 2018 (compare species accumulation curves in Fig. 2), we got closer to the estimated total amphibian species (Tab. 4). Furthermore, the performance of species accumulation curves for forest margin and oil palm plantation indicates a close reach point to the estimated species richness (Fig. 2).

Table 4. Diversity estimated for rarefied and extrapolated samples up to the double of the smaller reference sample size with Hill number *Species richness (q=0)* observed and predicted (in brackets). Species numbers are shown for amphibians and reptiles, each separated into habitats and in total for the years 2013 and 2018.

Habitat type	Species richness recorded (predicted)			
	Amphibians		Reptiles	
	2013	2018	2013	2018
FI	21 (28.07)	20 (19.72)	13 (16.42)	17 (17.85)
FM	19 (25.08)	19 (19.56)	12 (13.45)	16 (15.27)
OP	11 (13.19)	15 (16.33)	7 (7.84)	10 (9.78)
Total	27 (30.44)	28 (28.81)	19 (24.10)	25 (24.89)

Since we observed twice the number of reptile individuals in 2018, the recorded number of species was closer to the predicted number of species when compared to 2013 (Tab. 4). However, neither total species richness nor species richness analysed separately for the three habitat types did differ between both years in amphibians as well as in reptiles (compare overlapping 95% confidence intervals in Fig. 4).
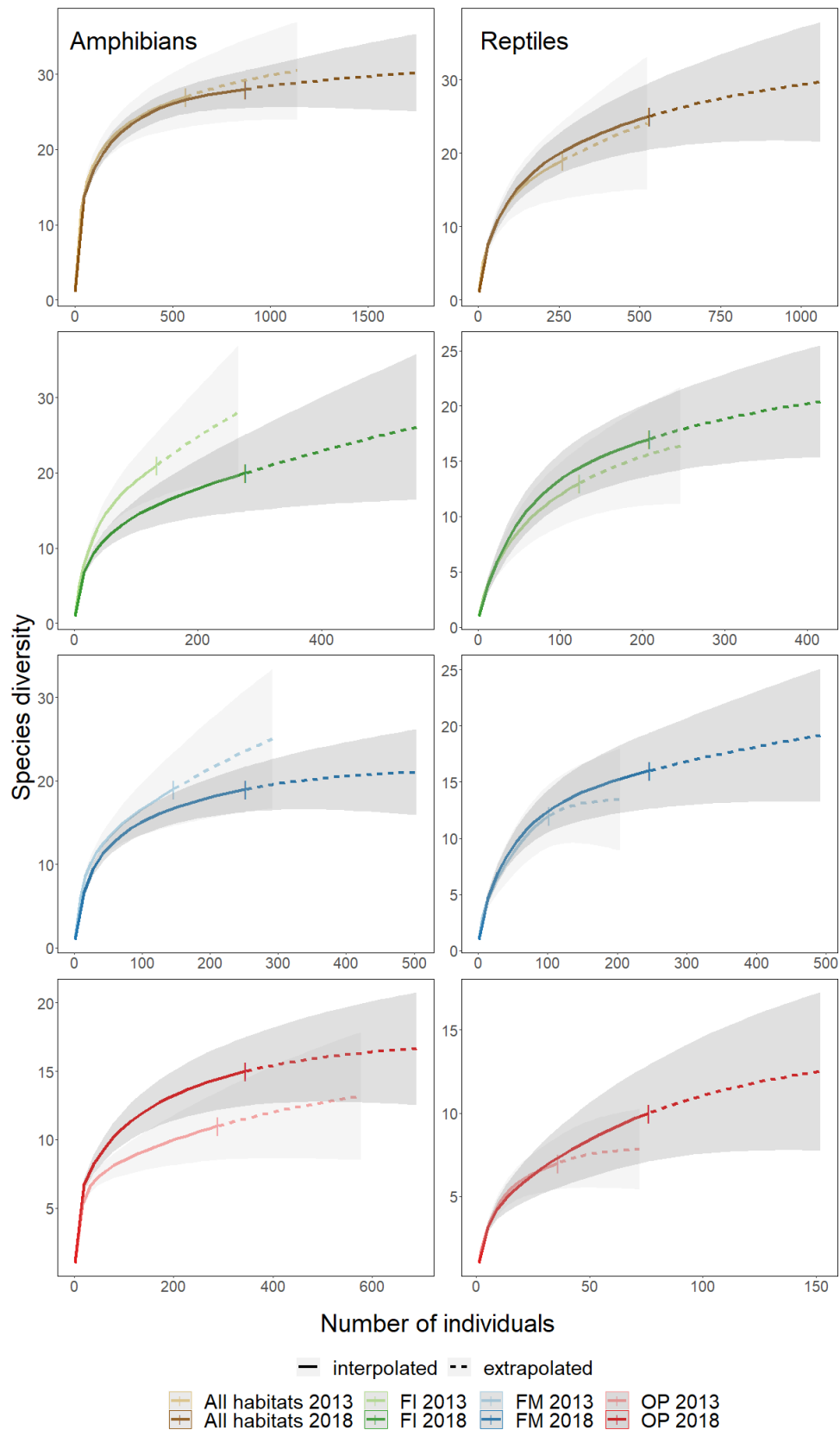
Figure 2. Species accumulation curves (±95% CI) for all habitats pooled (brown), forest interior (FI, green), forest margin (FM, blue) and oil palm plantations (OP, red), separately calculated for both years 2013 and 2014. Continuous lines show interpolated, dashed lines extrapolated parts of the curves.

Species composition

To visually analyse similarity relationships of sampled amphibian and reptile assemblages sampled between sites and years NMDS plots were calculated. Both taxa show a clear difference when comparing oil palm plantations to forest interior and forest margin, respectively. For both amphibians and reptiles, we see a clearer dissimilarity between the two forest habitats and oil palm plantations in both sampling years (Fig. 3).
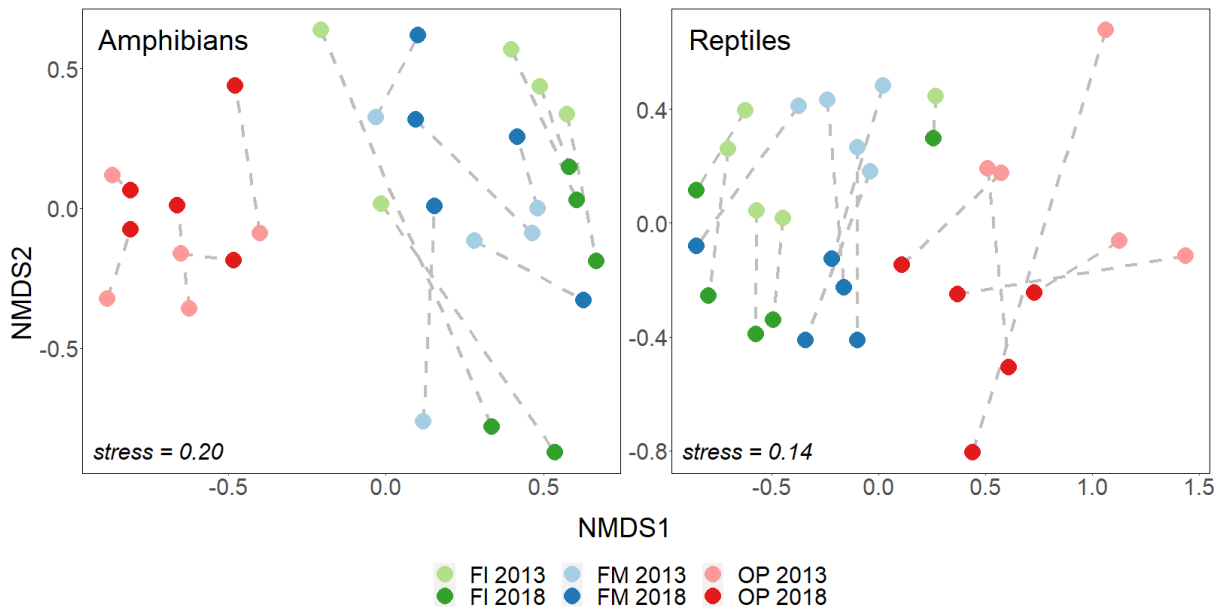
Figure 3. NMDS ordinations based on Bray-Curtis indices (with √x transformed abundances) visualising dissimilarity relationships in species composition in amphibians and reptiles between forest interior (FI), forest margin (FM) and oil palm plantation (OP) sites. Comparison between 2013 (lighter colours) and 2018 (darker colours). Grey broken lines connect samples taken in both years at the same sites.

The extent of changes in species composition at individual sites between both years (quantified as Bray-Curtis dissimilarities) differed significantly between habitats in reptiles (Kruskal-Wallis test: chi=8.96, df=2, p=0.0113), but not in amphibians (chi=4.46, df=2, p=0.1075). For amphibians, graphs show a wide range between the different FI sites. For habitat FM, in contrast, a very similar composition can be seen within the sites, although there is one outlier (FM5) (Fig. 4).
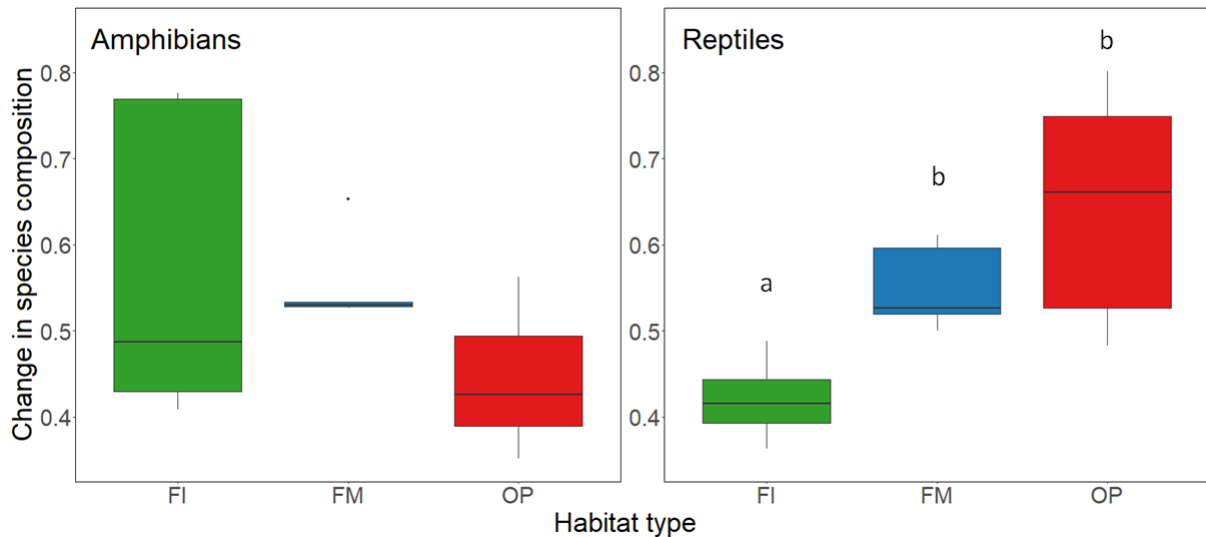
Figure 4. Change in species composition (Bray-Curtis dissimilarities) of amphibians and reptiles. Boxplots show median (bars) ± 25% quartiles (boxes) and min.-max. (whiskers) between 2013 and 2018 at forest interior (FI), forest margin (FM) and oil palm plantation (OP) sites. Different letters indicate significant differences between habitat types (results of pairwise Wilcox tests using FDR-adjusted p values).

Changes in relative abundance

Though no significance was found in amphibians, either in changes between habitat types nor range size, reptile species with the most abundant species (N ≥ 5 individuals per species) showed a significant change in relative abundance for all habitats combined between the years (V=13, p=0.0252) and between the habitats forest interior in 2013 and 2018 (V=15, p=0.0348) and forest margin in comparison to the previous year (V=20, p=0.0442).

Changes in relative abundances were calculated for the most abundant species (N ≥ 5 individuals per species) between 2013 (individuals: amphibians: 561, reptiles: 254) and 2018 (individuals: amphibians: 862, reptiles: 516). While for amphibians the highest increase in changes in relative abundances was measured for range-restricted species *Smilisca sordida/sila* (+11.85%) and *Craugastor crassidigitus/fitzingeri* (+10.76%), the highest decrease was found for the widespread species *Engystomops pustulosus* (-12.01%) (Fig. 5). For reptiles, however, the greatest increase and decrease was found for the two range-restricted species *Anolis limifrons* (+6.76%) and *Holcosus leptophrys* (-9.78%), respectively (Fig. 5).
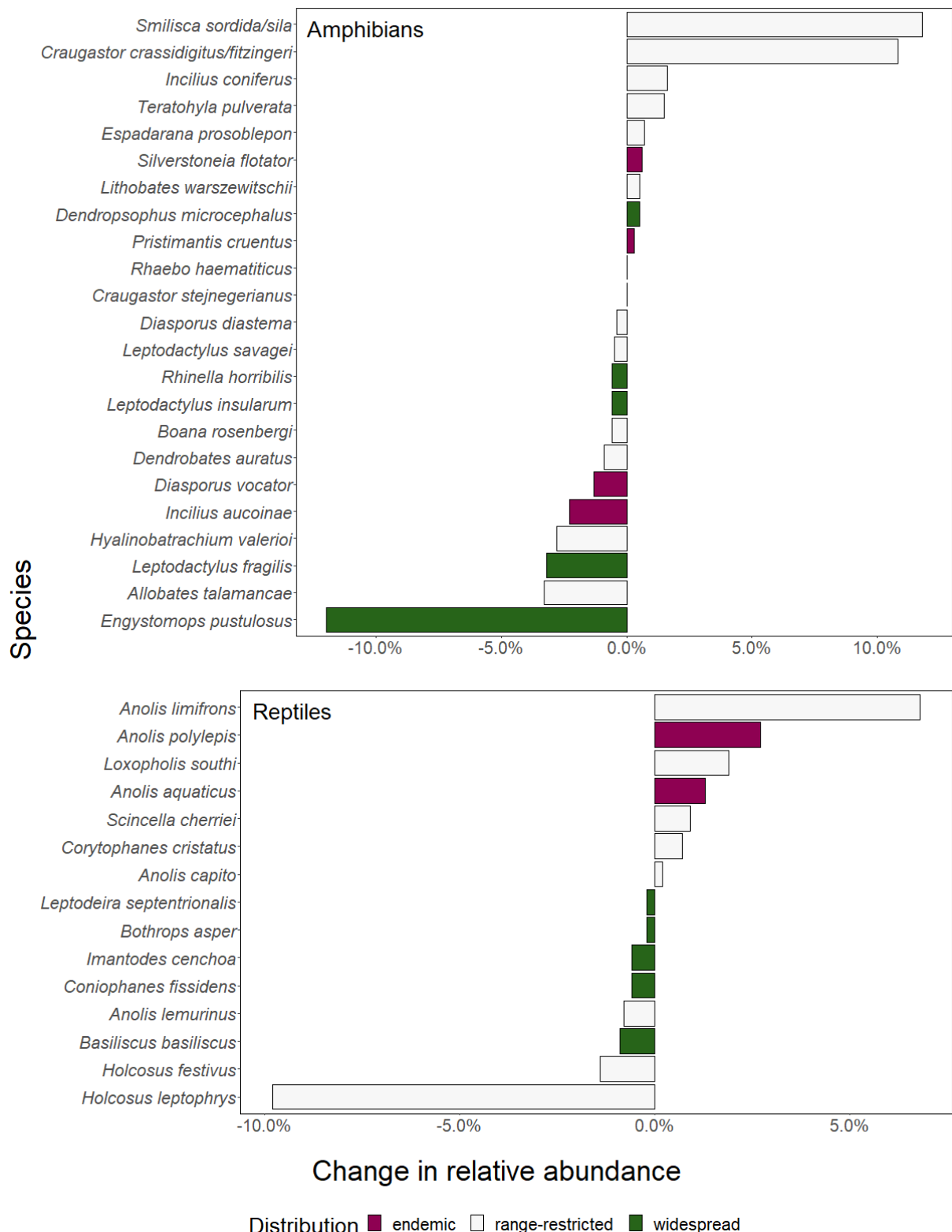
Figure 4. Change in relative abundance of abundant species (N ≥ 5 individuals) between 2013 and 2018. Bar colours indicate different range size (endemic, range-restricted, widespread) of amphibians and reptiles. Species are ordered according to their relative abundance change from highest increase (top) to the highest decrease (bottom).

Functional diversity

While FD measures did not differ between the years in amphibians, the output of the paired *t*-tests showed significant differences for functional richness (*t*= -2.38, df= 12, p= 0.034) and functional dispersion (*t*=2.21, df=14, p=0.044) in reptiles (Tab. 5). The positive number of the *t*-value of functional richness signifies that the first condition (year 2018) had higher mean than the second (year 2013), whereas the negative number of the *t*-value of functional dispersion describes a smaller mean for 2018.

Table 5 Results of paired *t*-tests testing for changes in functional diversity measurements between the years 2013 and 2018 (N=15). FD indices: Functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) and functional dispersion (FDis). Tests were calculated separately for amphibians and reptiles. (* indicate significant p-values)

Paired *t*-test	Amphibians			Reptiles		
	t	*df*	*p*	*t*	*df*	*p*
FRic	0.24742	14	0.8082	2.3829	12	0.03458*
FEve	-1.9383	14	0.07302	-1.9061	12	0.08087
FDiv	1.0254	14	0.3226	0.18485	12	0.8564
FDis	0.98491	14	0.3414	-2.208	14	0.04443*

None of the four functional diversity measurements proved to change differentially between habitats over the 5 years (Fig. 6, Tab. 6).
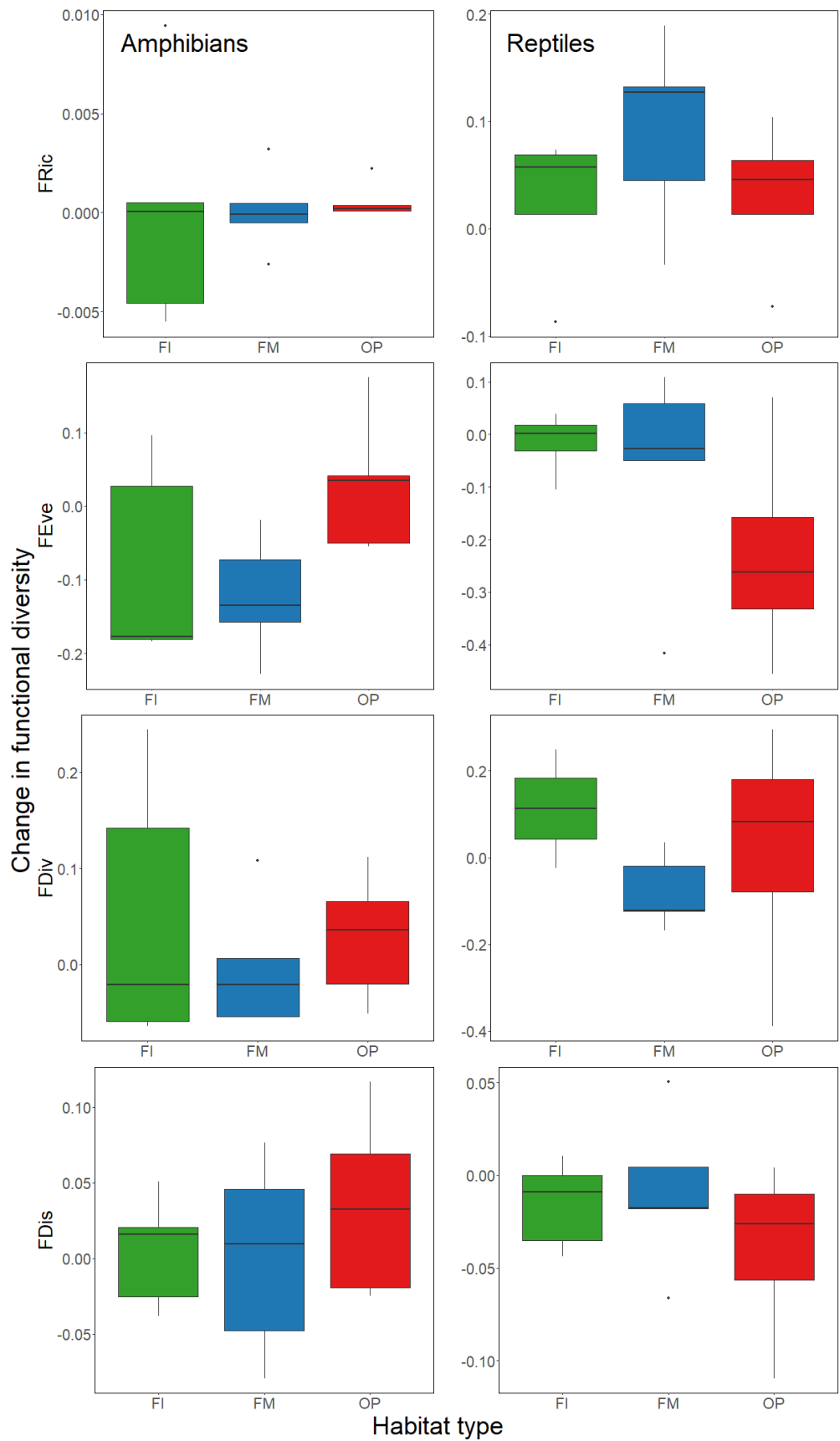
Figure 5. Changes in four different functional diversity measurements. Boxplots show median (bars) ± 25% quartiles (boxes) and min.-max. (whiskers) between 2013 and 2018 for amphibians and reptiles of forest interior (FI), forest margin (FM) and oil palm plantation (OP) sites. FD indices: FRic – functional richness, FEve – functional evenness, FDiv – functional divergence, FDis – functional dispersion.

Table 6. Results of Kruskal-Wallis rank-sum tests testing for changes in functional diversity measurements (quantified as differences between the values calculated for 2018 and 2013) between the three sampled habitat types. FD indices: Functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) and functional dispersion (FDis). Tests were calculated separately for amphibians and reptiles.

| Kruskal-Wallis rank-sum test	Amphibians		Reptiles	
	Chi	*P*	*Chi*	*p*
FRic	0.54	0.7634	1.74	0.4181
FEve	4.46	0.1075	1.53	0.4654
FDiv	0.78	0.6771	3.38	0.1843
FDis	1.22	0.5434	1.22	0.5434

Discussion

Abundance and species richness

Surprisingly, a higher number of both amphibians and reptiles were recorded in 2018. Due to the resulting larger sample size in 2018, the numbers of found species were closer to the predicted total numbers than in the previous year. However, when corrected for differences in sample size, no significant difference in species richness between years for any of the three habitats was detected for either amphibians or reptiles. Suazo-Ortuño et al. (2008) mentioned increased abundance in various amphibian species in disturbed habitats compared to forest sites, even though species richness declined. In the study of Paoletti et al. (2018) oil palm plantations had a higher abundance in amphibians compared to upland forest and the highest species richness and abundance in reptiles than all other habitats. However, species assemblages in oil palm plantations were only composed of a few common species of low conservation interest, as also seen in this study. In our study, the most abundant amphibian species in plantations in 2018 were 5 frog species, which represented 89.0% of the total abundance in OP, in 2013 these species made up 86.5% of the total abundance in OP. Most amphibian species observed in oil palm plantations are ground-dwelling and use puddles for their reproduction (Leenders 2019). Heavy vehicles which are used to carry the palm fruits, create tracks which fill up with water and get occupied by amphibians (Paoletti et al., 2018). Additionally, due to a decreased structural diversity of the understorey layer in OP, amphibians lack hiding places and therefore can be more visible and easier to detect during surveys.

In 2018, the most common reptile species in oil palm plantations were *Anolis limifrons*, *Anolis polylepis* and *Basiliscus basiliscus* (82.9% of total abundance in OP), in 2013 it was only *Anolis polylepis* and *Basiliscus basiliscus* (61.1% of total abundance). This might be an indicator that colonization of human-

modified areas still occurs, as generalist species easier take over and dynamically change disturbed areas over time (Cordier et al., 2021). Some studies indicate that agricultural areas don't significantly alter species richness of reptile assemblages, and such development may be connected to the increase in the abundance of prey (Suazo-Ortuño et al., 2008, Cordier et al., 2021). Researchers noticed an increase in insect diversity and abundance in human-modified areas (Heliölä et al., 2001) and a greater species turnover due to different disturbance intensities due to mosaics of different land-use systems (Hill & Hamer, 2004).

A crucial bias between the herpetofaunal surveys compared in this study is that the data were collected in two different seasons. In 2013, surveys were conducted during rainy season and due to difficult weather conditions and heavy rain only 143 walks could be conducted; the seven missing transect visits refer to night walks, mostly in plantations (Gallmetzer et al., 2015). In 2018/19 the study was carried out during the drier months, with higher temperature und less precipitation. More open, uncovered areas, e.g., in plantations, can increase soil temperature and the availability of basking sites and creates new thermoregulation microsites (Suazo-Ortuño et al., 2008), which could be a reason for the higher abundance of reptiles. On the contrary, amphibians don't tolerate change in moisture and temperature easily, as they have permeable skin and are dependent on terrestrial and aquatic habitats (Li et al., 2013). Oil palm plantations aren't well buffered against climate conditions, e.g., radiation and air temperature (Hardwick et al., 2014), which is reflected by the decline of the relative abundance of *E. pustulosus* and the species of the genus *Leptodactylus*, which usually thrive in these human-modified areas (Tab. A7).

Species composition

For both amphibians and reptiles, our results show a stronger difference in species composition for both years between forest habitats and oil palm plantations. This confirms earlier findings that oil palm plantations and other human-modified areas are characterized by strongly modified species assemblages, when compared to forest habitats (Faruk et al., 2013; Gallmetzer & Schulze, 2015; Scriven et al., 2018). However, the extent of species turnover in amphibians between the two survey years did not differ between the three sampled habitats. In both survey years, the majority of species found in oil palm plantations were generalists. Specialists are rarely able to adapt to human disturbances due to their need of special habitat requisites, whereas generalists may be even thriving from these developments (Cordier et al. 2021). Further, no species of the families *Dendrobatidae* and *Ranidae* were recorded in oil palm plantations in both survey years and only two individuals (*Espadarana prosoblepon*) of the family *Centrolenidae* were found in one of the plantations in 2018. Their necessity of dense vegetation and streams or other permanent water bodies due to their

reproduction cycle and semi-aquatic lifestyle (Leenders, 2019) only allows them to breed and live in undisturbed areas. Hence, entire taxonomic groups do not find suitable conditions for reproduction in oil palm plantations.

The temporal changes in reptile species composition between both survey years was highest at oil palm plantations but even differed significantly between forest interior and forest margin. Even though many studies were conducted on the effects on amphibians and/or herpetofauna (Almeida-Gomes et al., 2016; Cushman, 2006; Whitfield et al., 2016), rather few studies exist with a particular focus on reptiles (Cordier et al., 2021). Among reptiles, 11 out of the 29 species found in 2018 were not recorded in 2013, while only 3 species could be exclusively found in 2013 (Table A3). The reason for this could be the different seasons in which the surveys were conducted.

The 2013 period was between July and September, whereas in 2018/2019 the transects were resampled between November and January. Climate tables show that the average temperature during the conducted months in 2013 was between 26.5°C and 27.1°C, and in 2018 between 27.6°C and 28.2°C. In 2013, monthly precipitation ranged from 542 mm to 769.5 mm in the months of July to September, while in 2018/2019, the values were lowest in the months of December and January with 249 mm and 124 mm respectively, and 790 mm in November (Universität Wien, 2022). While temperatures remain fairly consistent throughout the year, precipitation has a distinct seasonal pattern (Weissenhofer et al., 2008). Changes of weather conditions between seasons can impact the behaviour of amphibians and reptiles (Acevedo-Charry & Aide, 2019).

In addition, microclimates strongly differ between forest and human-modified areas with distinct effects on vegetation. Canopy cover has an extreme effect on climate conditions in habitats, e.g., dense canopies can shield air and soil underneath the canopy from over 95% of light, which keeps the forest cool during the day and maintains high relative humidity (Hardwick et al., 2015). On the contrary, oil palm plantations have lower canopy cover (Kurz et al., 2014) and therefore is found to be up to 6.5°C warmer than primary forest, as plant cover regulates incoming solar radiation by absorbing, scattering and reflecting it (Hardwick et al., 2014). Hence, temperature may induce more thermal stress for amphibians and reptiles (Kurz et al., 2014). As amphibians are sensitive to solar radiation and shifts in temperature and moisture (Suazo-Ortuño et al., 2008), only few species can tolerate those conditions. Reptiles can't generate body heat internally, so they are dependent on external factors that maintain their body temperature (Leenders, 2019) and may benefit from it. Due to a warmer period and less precipitation, it appears to be a valid explanation for the change in species composition.

Relative abundance change

For amphibians, the greatest changes occurred in range-restricted and widespread species. Changes of resource availability through time may lead to movement between habitats. Some amphibians, such as species of *Leptdodactylidae* and in general treefrogs (*Hylidae*) can strongly increase their abundance in specific habitats during the reproductive season (Urbina-Cardona et al., 2006).

Biggest relative abundance changes in amphibians were found in *Smilisca sila/sordida* (+11.85%). Both species are reproducing during the dry season, when water levels are lower. Hence, it may be easier to detect them during their breeding season between January and May, when males try to attract females with sometimes large choruses near streams and rivers (Leenders, 2019). This behaviour correlates with the high abundance during our survey in 2018/19. *Craugastor crassidigitus/fitzingeri* (+10.76%) showed the second highest increase in relative abundance which can be explained by the ability to survive well in forest and disturbed areas. It is an abundant and very adaptable species in areas with tree cover and available leaf litter (Leenders, 2019), hence it is not surprising that individuals increased especially in forest sites. The greatest decrease was found in the explosive breeder *Engystomops pustulosus* (-12.01%), which occurred primarily in oil palm plantations (Tab. A8). Since its reproduction activity peaks in the wet season, when temporary ponds for oviposition are available, the relative abundance decline documented for the dry season in 2018/19 is not surprising. The species with the highest increase (*Smilisca sordida/sila*) and decrease (*Engystomops pustulosus*) in relative abundance, both occur in oil palm plantations (Leenders, 2019), indicating that seasonally changing environmental conditions are particularly evident in this habitat.

In reptiles, the relative abundance changes are much more difficult to interpret. It is possible, however, that adaptations to seasonal changes in weather conditions play a role here, which are already manifested at a higher taxonomic level. Thus, four of the five *Anolis* species show an increase and both *Holcosus* species a decrease in their relative abundance. That differences in habitat selection are not responsible for this is demonstrated by the *Anolis* species. The two species with the greatest increase in relative abundance, *Anolis polylepis* and *A. limifrons*, exhibit very different habitat preferences. Whereas *A. polylepis* is most abundant in forest interiors and at forest edges, *A. limifrons* is more a character species of highly disturbed habitats and could be found most frequently in oil palm plantations.

Functional diversity

Only the FD indices FRic and FDis differed weakly between 2013 and 2018, but exclusively in reptiles. In amphibians no change of any of the FD measures could be found. FRic measures functional richness but is not a useful tool to estimate dispersion, because its sensitive to outliers. FDis integrates information on relative abundance in addition to functional richness (Laliberté & Legendre 2010). Therefore, it is reasonable that these two measurements are both significant, the mean FRic showed an increase towards 2018, whereas the mean FDis had declined in 2018. Due to the inclusion of species abundance, the centroid of the calculated trait space shifted to the more abundant species (Laliberté & Legendre 2010). This may be illustrated by the uneven ratio species richness/abundance. From the 530 reptile individuals found in 2018, 325 (61.3%) individuals were from the species *Anolis polylepis* and 46 (8.6%) individuals from the same genus, the species *Anolis limifrons* (Tab. A4). Even though *A. polylepis* is limited in range, it is very adaptable and is found in various habitats, even in agricultural areas. *A. limifrons* was not recorded in 2013, which is surprising, because of its wide habitat range and toleration of different environmental condition.

The extent of temporal changes in all four FD measurements did not differ between habitats in both amphibians and reptiles, indicating that changes in none of the different aspects of FD was habitat specific. Hence, our third hypothesis that an ongoing loss of functional diversity may be visible in oil palm plantations could not be verified. An explanation could be the already species-poor vegetation and the low structural heterogeneity in this land-use system, which remained very similar. Therefore, this strong environmental filter did not facilitate any changes in the species assemblages between years, only allowing generalists or certain species adapted to strongly human-modified habitats to occur in oil palm plantations.

Studies indicate that even though species richness declines in some human-modified areas, functional diversity may still remain the same due to a high redundancy in species assemblages (Riemann et al. 2017).
Specific trait combinations and a turnover in species composition imply that, although being similarly clustered, assemblages pass through distinct environmental filters depending on resources, that occur in different environments (Riemann et al., 2017). We suspected a stronger impact on amphibians than reptiles due to their stronger response to human disturbances. However, this could not be confirmed in this study. Amphibians and reptiles have very different distinct trait combinations (Table A5) and therefore respond differentially to disturbance and land-use change (Cordier et al., 2021)

Conclusion & conservation implications

The study confirmed the low conservation value of oil palm plantations for the herpetofauna. Although the comparison of two survey periods did show only a significant species turnover in reptiles, it is evident that only certain amphibian and reptile species can settle and survive in oil palm plantations. Mainly generalists and explosive breeders use the plantations as breeding sites, resulting in a higher number of individuals during the reproductive season, as seen by temporal changes in relative abundance for the species *Smilisca sila/sordida* and *E. pustulosus*. Although there seems to be no significant difference between habitats, it is rather the microclimatic conditions that seem important. Species that depend on diverse vegetation and dense canopy cover do not appear to find suitable conditions in oil palm plantations. Due to the rapid development of climate change caused by humans compared to geological scale, most amphibians cannot adapt their evolutionary and biological factors (Heatwole, 2013).

Reptiles, in contrast, had a significant change in species composition, forest interior was significant different to forest margin and oil palm plantations. Species-specific changes occurred in disturbed areas, possible reasons could be that they are more adaptable to heat and high temperature, because of their external dependency of heat regulation and so can move easier between habitats.

A long-term monitoring is highly recommended to evaluate habitat specific dynamics and changes in the structure and composition of species assemblages. The period of five years is a first initial indication of mid-term impacts of oil palm plantations, but these areas need to be scientifically monitored and controlled for years to obtain accurate data on temporal species turnover in amphibian and reptile species assemblages.

Changes of species assemblages due to habitat alteration is only the beginning of a chain of further threats to amphibians and reptiles. It leads to a decrease of faunal and floral distinction among regions and biomes, so called biotic homogenization, which has been seen in many human-modified landscapes, where only a few widespread species benefit from it (McKinney, 2006; Olden et al., 2004). Implementing microhabitats with heterogenous vegetation and canopy structure in oil palm plantations may determine the future of herpetofauna biodiversity in human-modified areas (Anamulai et al., 2019, Suazo-Ortuño et al., 2008).

References

Anamulai, S., Sanusi, R., Zubaid, A., Lechner, A. M., Ashton-Butt, A., & Azhar, B. (2019) Land use conversion from peat swamp forest to oil palm agriculture greatly modifies microclimate and soil conditions. PeerJ, 7:e7656. https://doi.org/10.7717/peerj.7656

Acevedo-Charry, O., & Aide, T. M. (2019). Recovery of amphibian, reptile, bird and mammal diversity during secondary forest succession in the tropics. *Oikos, 128*(8), 1065–1078. https://doi.org/10.1111/oik.06252

Almeida-Gomes, M., & Rocha, C. F. D. (2014). Diversity and distribution of lizards in fragmented Atlantic forest landscape in Southeastern Brazil. *Journal of Herpetology*, *48*(3), 423–429. https://doi.org/10.1670/12-187

Almeida-Gomes, M., Vieira, M. V., Rocha, C. F. D., Metzger, J. P., & de Coster, G. (2016). Patch size matters for amphibians in tropical fragmented landscapes. *Biological Conservation*, *195*, 89–96. https://doi.org/10.1016/j.biocon.2015.12.025

AmphibiaWeb (2019). Information on amphibian biology and conservation [WWW Document]. University of California, Berkeley. URL: https://amphibiaweb.org/

Baiser, B., Olden, J. D., Record, S., Lockwood, J. L., & McKinney, M. L. (2012). Pattern and process of biotic homogenization in the New Pangaea. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1748), 4772–4777. https://doi.org/10.1098/rspb.2012.1651

Banks-Leite, C., Ewers, R. M., & Metzger, J. P. (2012). Unraveling the drivers of community dissimilarity and species extinction in fragmented landscapes. *Ecology, 93*(12), 2560-2569.

Beebee, T. J. C., & Griffiths, R. A. (2005). The amphibian decline crisis: A watershed for conservation biology? *Biological Conservation, 125*(3), 271–285. https://doi.org/10.1016/j.biocon.2005.04.009

Blaustein, A. R., & Kiesecker, J. M. (2002). Complexity in conservation: lessons from the global decline of amphibian populations. *Ecology*, 5, 597-608.

Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., & Ellison, A. M. (2014). Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs, 84*(1), 45–67 http://purl.oclc.org/estimates

Cordier, J. M., Aguilar, R., Lescano, J. N., Leynaud, G. C., Bonino, A., Miloch, D., Loyola, R., & Nori, J. (2021). A global assessment of amphibian and reptile responses to land-use changes. *Biological Conservation, 253*, 108863. https://doi.org/10.1016/j.biocon.2020.108863

Cushman, S. A. (2006). Effects of habitat loss and fragmentation on amphibians: A review and prospectus. *Biological Conservation*, *128*(2), 231–240. https://doi.org/10.1016/j.biocon.2005.09.031

Daily, G.C., Ceballos, G., Pacheco, J., Suzan, G., & Sanchez-Azofeifa, A. (2003). Countryside biogeography of Neotropical mammals: conservation opportunities in agricultural landscapes of Costa Rica. *Conservation Biology* 17(6), 1814–1826.

Fahrig, L., Baudry, J., Brotons, L., Burel, F. G., Crist, T. O., Fuller, R. J., Sirami, C., Siriwardena, G. M., & Martin, J. L. (2011). Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters*, *14*(2), 101–112. https://doi.org/10.1111/j.1461-0248.2010.01559.x

Faruk, A., Belabut, D., Ahmad, N., Knell, R. J., & Garner, T. W. J. (2013). Effects of oil-palm plantations on diversity of tropical anurans. *Conservation Biology*, *27*(3), 615–624. https://doi.org/10.1111/cobi.12062

Fayle, T. M., Turner, E. C., Snaddon, J. L., Chey, V. K., Chung, A. Y. C., Eggleton, P., & Foster, W. A. (2010). Oil palm expansion into rain forest greatly reduces ant biodiversity in canopy, epiphytes and leaf-litter. *Basic and Applied Ecology*, *11*(4), 337–345. https://doi.org/10.1016/j.baae.2009.12.009

Fitzherbert, E. B., Struebig, M. J., Morel, A., Danielsen, F., Brühl, C. A., Donald, P. F., & Phalan, B. (2008). How will oil palm expansion affect biodiversity? *Trends in Ecology and Evolution,* 23(10): 538–545. https://doi.org/10.1016/j.tree.2008.06.012

Foster, W.A., Snaddon, J.L., Turner, E.C., Fayle, T.M., Cockerill, T.D., Ellwood, M.F., et al. (2011). Establishing the evidence base for maintaining biodiversity and ecosystem function in the oil palm landscapes of South East Asia. Philosophical *Transactions of the Royal Society B,* 366 (1582), 3277-3291.

Franzen, M., & Kollarits, D. (2018). Pocket Guide to the Amphibians and Reptiles of La Gamba, Costa Rica. *Laurenti-Verlag*.

Freudmann, A., Mollik, P., Tschapka, M., & Schulze, C. H. (2015). Impacts of oil palm agriculture on phyllostomid bat assemblages. *Biodiversity and Conservation*, *24*(14), 3583–3599. https://doi.org/10.1007/s10531-015-1021-6

Gallmetzer, N., & Schulze, C. H. (2015). Impact of oil palm agriculture on understory amphibians and reptiles: A Mesoamerican perspective. *Global Ecology and Conservation*, *4*, 95–109. https://doi.org/10.1016/j.gecco.2015.05.008

Gardner, T. A., Barlow, J., & Peres, C. A. (2007). Paradox, presumption and pitfalls in conservation biology: The importance of habitat change for amphibians and reptiles. *Biological Conservation*, *138*(1–2), 166–179. https://doi.org/10.1016/j.biocon.2007.04.017

Gibbons J.W., Scott D.E., Ryan T.J., Buhlmann K.A., Tuberville T.D., Metts B.S., Greene J.L., Mills T., Leiden Y., Poppy S., & Winne C.T. (2000). The global decline of reptiles, Déjà Vu amphibians. *BioScience* 50(8), 653–666. https://academic.oup.com/bioscience/article/50/8/653/243214

Gibbs, H. K., Ruesch, A. S., Achard, F., Clayton, M. K., Holmgren, P., Ramankutty, N., & Foley, J. A. (2010). Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(38), 16732–16737. https://doi.org/10.1073/pnas.0910275107

Hardwick, S. R., Toumi, R., Pfeifer, M., Turner, E. C., Nilus, R., Ewers, R. M. (2015) The relationship between leaf area index and microclimate in tropical forest and oil palm plantation: Forest disturbance drives changes in microclimate. *Agricultural and Forest Meteorology,* 201, 187-195. http://dx.doi.org/10.1016/j.agrformet.2014.11.010

Heatwole, H. (2013). Worldwide decline and extinction of amphibians. In K. Rohde (Ed.), The balance of nature and human impact, 259–278. Cambridge: Cambridge University Press.

Heliölä, J., Koivula, M. & Niemelä, J. (2001). Distribution of carabid beetles (Coleoptera, Carabidae) across a boreal forest–clearcut ecotone. *Conservation Biology*, 15(2), 370–377.

Hill, J. K. & Hamer, K., C. (2004). Determining impacts of habitatmodification on diversity of tropical forest fauna: the importance of spatial scale. *Journal of Applied Ecology*, 41(4), 744–754.

Höbinger, T., Schindler, S., Seaman, B. S., Wrbka, T., & Weissenhofer, A. (2012). Impact of oil palm plantations on the structure of the agroforestry mosaic of La Gamba, southern Costa Rica: Potential implications for biodiversity. *Agroforestry Systems*, *85*(3), 367–381. https://doi.org/10.1007/s10457-011-9425-0

Hsieh, T. C., Ma, K. H., & Chao, A. (2016). iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, *7*(12), 1451–1456. https://doi.org/10.1111/2041-210X.12613

Huber, W., & Weissenhofer, A. (2019). The La Gamba Research Station in Costa Rica - History, Nature and Research. *Acta ZooBot Austria,* 156, 3–11.

Isaac, J. L., Vanderwal, J., Johnson, C. N., & Williams, S. E. (2009). Resistance and resilience: Quantifying relative extinction risk in a diverse assemblage of Australian tropical rainforest vertebrates. *Diversity and Distributions*, *15*(2), 280–288. https://doi.org/10.1111/j.1472-4642.2008.00531.x

IUCN (2020). The IUCN Red List of Threatened Species. Version 2020-3. https://www.iucnredlist.org

Kurz, D. J., Nowakowski, A. J., Tingley, M. W., Donnelly, M. A., & Wilcove, D. S. (2014). Forest-land use complementarity modifies community structure of a tropical herpetofauna. *Biological Conservation*, *170*, 246–255. https://doi.org/10.1016/j.biocon.2013.12.027

Köhler G. (2011). Amphibians of Central America. Herpeton Verlag, Offenbach.

Leenders, T. (2016). Amphibians of Costa Rica: a field guide. *Cornell University Press*.

Leenders, T. (2019). Reptiles of Costa Rica: a field guide. *Cornell University Press*.

Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology,* 91(1), 299–305. http://www.ecolag.univ-montp2.fr/softwarei

Li, Y., Cohen, J. M., & Rohr, J. R. (2013). Review and synthesis of the effects of climate change on amphibians. *Integrative Zoology,* 8(2), 145–161. https://doi.org/10.1111/1749-4877.12001

MacArthur, R.H., & Wilson, E.O. (1967). The Theory of Island Biogeography. *Princeton University Press*, Princeton.

Matthews, T. J., Cottee-Jones, H. E., & Whittaker, R. J. (2014). Habitat fragmentation and the species-area relationship: A focus on total species richness obscures the impact of habitat loss on habitat specialists. *Diversity and Distributions*, *20*(10), 1136–1146. https://doi.org/10.1111/ddi.12227

McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation*, 127(3), 247–260. https://doi.org/10.1016/j.biocon.2005.09.005

Mouchet, M. A., Villéger, S., Mason, N. W. H., & Mouillot, D. (2010). Functional diversity measures: An overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, *24*(4), 867–876. https://doi.org/10.1111/j.1365-2435.2010.01695.x

Nekola, J. C., & Mcgill, B. J. (2014). Scale dependency in the functional form of the distance decay relationship. *Ecography*, *37*(4), 309–320. https://doi.org/10.1111/j.1600-0587.2013.00407.x

Nopper, J., Lauströer, B., Rödel, M. O., & Ganzhorn, J. U. (2017). A structurally enriched agricultural landscape maintains high reptile diversity in sub-arid south-western Madagascar. *Journal of Applied Ecology*, *54*(2), 480–488. https://doi.org/10.1111/1365-2664.12752

Norfolk, O., Eichhorn, M. P., & Gilbert, F. S. (2015). Contrasting patterns of turnover between plants, pollinators and their interactions. *Diversity and Distributions*, *21*(4), 405–415. https://doi.org/10.1111/ddi.12295

Olden, J. D., Poff, N. L. R., Douglas, M. R., Douglas, M. E., & Fausch, K. D. (2004). Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology and Evolution*, *19*(1), 18–24. https://doi.org/10.1016/j.tree.2003.09.010

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H. (2016). Vegan: Community ecology package. R package version 2.3-3. URL: http://CRAN.R-project.org/package=vegan

Paoletti, A., Darras, K., Jayanto, H., Grass, I., Kusrini, M., & Tscharntke, T. (2018). Amphibian and reptile communities of upland and riparian sites across Indonesian oil palm, rubber and forest. *Global Ecology and Conservation*, *16*, e00492. https://doi.org/10.1016/J.GECCO.2018.E00492

Riemann, J. C., Ndriantsoa, S. H., Raminosoa, N. R., Rödel, M. O., & Glos, J. (2015). The value of forest fragments for maintaining amphibian diversity in Madagascar. *Biological Conservation*, *191*, 707–715. https://doi.org/10.1016/j.biocon.2015.08.020

Riemann, J. C., Ndriantsoa, S. H., Rödel, M. O., & Glos, J. (2017). Functional diversity in a fragmented landscape — Habitat alterations affect functional trait composition of frog assemblages in Madagascar. *Global Ecology and Conservation*, *10*, 173–183. https://doi.org/10.1016/J.GECCO.2017.03.005

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., Poff, N. L. R., Sykes, M. T., Walker, B. H., Walker, M., & Wall, D. H. (2000). Global biodiversity scenarios for the year 2100. *Science,* 287(5459), 1770–1774. https://doi.org/10.1126/science.287.5459.1770

Savage, J.M. (2002). The Amphibians and Reptiles of Costa Rica: A Herpetofauna Between Two Continents, Between Two Seas. Univ. of Chicago Press, Chicago.

Scriven, S. A., Gillespie, G. R., Laimun, S., & Goossens, B. (2018). Edge effects of oil palm plantations on tropical anuran communities in Borneo. *Biological Conservation*, *220*, 37–49. https://doi.org/10.1016/j.biocon.2018.02.006

Suazo-Ortuño, I., Alvarado-Díaz, J., & Martínez-Ramos, M. (2008). Effects of conversion of dry tropical forest to agricultural mosaic on herpetofaunal assemblages. *Conservation Biology*, *22*(2), 362–374. https://doi.org/10.1111/j.1523-1739.2008.00883.x

Suazo-Ortuño, I., Benítez-Malvido, J., Marroquín-Páramo, J., Soto Y., Siliceo, H., & Alvarado-Díaz, J. (2018). Resilience and vulnerability of herpetofaunal functional groups to natural and human disturbances in a tropical dry forest. *Forest Ecology and Management*, 426, 145-157.

Universität Wien (2022). Scientific information on the Golfo Dulce region. Klimadaten 1998–2020 [Excel Document]. https://www.lagamba.at/forschung/wissenschaftliche-informationen

Urbina-Cardona, J. N., Olivares-Pérez, M., & Reynoso, V. H. (2006). Herpetofauna diversity and microenvironment correlates across a pasture-edge-interior ecotone in tropical rainforest fragments in the Los Tuxtlas Biosphere Reserve of Veracruz, Mexico. *Biological Conservation*, *132*(1), 61–75. https://doi.org/10.1016/j.biocon.2006.03.014

Vences, M., & Köhler, J. (2008). Global diversity of amphibians (Amphibia) in freshwater. *Hydrobiologia*, 595, 569-580.

Vieira, M. v., Olifiers, N., Delciellos, A. C., Antunes, V. Z., Bernardo, L. R., Grelle, C. E. V., & Cerqueira, R. (2009). Land use vs. fragment size and isolation as determinants of small mammal composition and richness in Atlantic Forest remnants. *Biological Conservation*, *142*(6), 1191–1200. https://doi.org/10.1016/j.biocon.2009.02.006

Villéger, S., Mason, N.W.H., & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology,* 89, 2290-2301.

Wake, D. B., & Vredenburg, V. T. (2008). Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *Proceeding of the National Academy of Sciences of the United States of America*, 105, 11466–11473. https://www.pnas.org/doi/pdf/10.1073/pnas.0801921105

Watling, J. I., Nowakowski, A. J., Donnelly, M. A., & Orrock, J. L. (2011). Meta-analysis reveals the importance of matrix composition for animals in fragmented habitat. *Global Ecology and Biogeography*, *20*(2), 209–217. https://doi.org/10.1111/j.1466-8238.2010.00586.x

Weissenhofer, A., & Huber, W., Mayer, V., Pamperl, S., Weber, A. & Aubrecht, G. (2008). *Natural and Cultural History of the Golfo Dulce region, Costa Rica*. Land Oberösterreich, Oberösterreichische Landesmuseen.

Whitfield, S. M., Lips, K. R., & Donnelly, M. A. (2016). Amphibian decline and conservation in Central America. *Copeia*, 104(2), 351–379. https://doi.org/10.1643/CH-15-300

Appendix

Zusammenfassung

Es ist gut dokumentiert, dass Ölpalmplantagen durch einen deutlich geringeren Artenreichtum gekennzeichnet sind und eine deutlich differenzierte Artenzusammensetzung aufweisen als tropische Regenwälder. Über die zeitliche Dynamik oder Stabilität von Artengemeinschaften in Ölpalmplantagen, im Vergleich zu Wäldern, ist jedoch sehr wenig bekannt. Deshalb wurden 2013 und 2018/2019 Amphibien und Reptilien im Waldinneren, am Waldrand und in Ölpalmplantagen in einem Tieflandgebiet im Südwesten Costa Ricas untersucht. Im Jahr 2018 wurden ein Drittel mehr Individuen von Amphibien und mehr als doppelt so viele Individuen von Reptilien gefunden als im Jahr 2013, jedoch wurden keine signifikanten Unterschiede im Artenreichtum festgestellt. Lebensraumspezifische Unterschiede in der sich verändernden Artenzusammensetzung zwischen den beiden Erhebungsjahren wurden nur bei Reptilien festgestellt, die sich in Ölpalmplantagen und am Waldrand, im Vergleich zum Waldinneren, deutlicher veränderten. Dies könnte darauf hindeuten, dass diese gestörten Lebensräume weniger gut gegen saisonal wechselnde klimatische Bedingungen gewappnet sind. Obwohl die Veränderungen in der funktionellen Vielfalt kein Habitat spezifisches Muster aufwiesen, was darauf schließen lässt, dass sich die Merkmalsanforderungen nicht Habitat spezifisch verändert haben, haben sich die Indizes „functional richness" und „functional dispersion" bei den Reptilien im Laufe der Jahre signifikant verändert. Es muss noch untersucht werden, inwieweit diese höhere zeitliche Dynamik der Reptilienpopulationen in Ölpalmplantagen tatsächlich artspezifische Veränderungen der Abundanz widerspiegelt, die durch stärkere Veränderungen der Umweltbedingungen in Ölpalmplantagen, im Vergleich zu Waldhabitaten, angetrieben werden. Alternativ könnten auch saisonale Veränderungen der Wetterbedingungen artspezifische Auswirkungen auf die Reptilienaktivität haben.

Tables

Table A1. Study sites

Habitat	Site	Coordinates	
		Latitude	Longitude
Forest interior	FI1	N 8.696130°	W 83.203659°
	FI2	N 8.670956°	W 83.198562°
	FI3	N 8.702917°	W 83.205308°
	FI4	N 8.699113°	W 83.207890°
	FI5	N 8.704233°	W 83.203474°
Forest margin	FM1	N 8.700300°	W 83.203112°
	FM2	N 8.683977°	W 83.198558°
	FM3	N 8.689779°	W 83.180629°
	FM4	N 8.702217°	W 83.213737°
	FM5	N 8.709846°	W 83.212481°
Oil palm plantation	OP1	N 8.698166°	W 83.198537°
	OP2	N 8.705249°	W 83.215272°
	OP3	N 8.701415°	W 83.190139°
	OP4	N 8.719463°	W 83.206079°
	OP5	N 8.715599°	W 83.172103°

Table A2. Dates of surveys

Site	Day					Night				
	1	2	3	4	5	1	2	3	4	5
FI1	13/11/2018	24/11/2018	08/12/2018	27/12/2018	15/01/2019	14/11/2018	02/12/2018	14/12/2018	27/12/2018	14/01/2019
FI2	17/11/2018	27/11/2018	14/12/2018	03/01/2019	17/01/2019	19/11/2018	09/12/2018	20/12/2018	02/01/2019	17/01/2019
FI3	12/11/2018	21/11/2018	05/12/2018	26/12/2018	07/01/2018	12/11/2018	21/11/2018	11/12/2018	25/12/2018	11/01/2019
FI4	18/11/2018	26/11/2018	06/12/2018	21/12/2018	08/01/2019	18/11/2018	26/11/2018	12/12/2018	26/12/2018	19/01/2019
FI5	15/11/2018	26/11/2018	09/12/2018	18/12/2018	12/01/2019	15/11/2018	26/11/2018	13/12/2018	28/12/2018	13/01/2019
FM1	14/11/2018	21/11/2018	07/12/2018	26/12/2018	11/01/2019	15/11/2018	21/11/2018	14/12/2018	27/12/2018	14/01/2019
FM2	17/11/2018	27/11/2018	14/12/2018	03/01/2019	17/01/2019	19/11/2018	09/12/2018	20/12/2018	02/01/2019	17/01/2019
FM3	16/11/2018	23/11/2018	09/12/2018	25/12/2018	14/01/2019	16/11/2018	03/12/2018	17/12/2018	03/01/2018	15/01/2019
FM4	22/11/2018	02/12/2018	11/12/2018	22/12/2018	12/01/2019	23/11/2018	04/12/2018	13/12/2018	28/12/2018	13/01/2019
FM5	20/11/2018	04/12/2018	15/12/2018	02/01/2019	16/01/2019	23/11/2018	07/12/2018	21/12/2018	07/01/2019	21/01/2019
OP1	14/11/2018	22/11/2018	05/12/2018	23/12/2018	21/01/2019	14/11/2018	22/11/2018	12/12/2018	08/01/2019	19/01/2019
OP2	20/11/2018	04/12/2018	15/12/2018	02/01/2019	16/01/2019	28/11/2018	07/12/2018	21/12/2018	07/01/2019	21/01/2019
OP3	15/11/2018	23/11/2018	09/12/2019	25/12/2018	14/01/2019	16/11/2018	03/12/2018	17/12/2018	03/01/2018	15/01/2019
OP4	19/11/2018	04/12/2018	15/12/2018	02/01/2019	16/01/2019	23/11/2018	10/12/2018	23/12/2018	08/01/2019	22/01/2019
OP5	19/11/2018	03/12/2018	17/12/2018	28/12/2018	18/01/2019	22/11/2018	10/12/2018	25/12/2018	09/01/2019	22/01/2019

Table A3. Presence/absence of species, indicated by + (presence) and - (absence)

Species	FI		FM		OP	
	2013	2018	2013	2018	2013	2018
Amphibians						
Plethodontidae						
Bolitoglossa lignicolor	+	-	-	+	-	+
Oedipina alleni	+	+	-	-	-	-
Bufonidae						
Incilius aucoinae	+	+	+	+	+	+
Incilius coniferus	-	+	+	+	-	+
Rhaebo haematiticus	-	-	+	+	+	-
Rhinella horribilis	-	+	+	-	+	+
Centrolenidae						
Espadarana prosoblepon	+	+	+	+	-	+
Hyalinobatrachium colymbiphyllum	+	-	+	+	-	-
Hyalinobatrachium valerioi	+	+	+	+	-	-
Sachatamia albomaculata	+	+	-	+	-	-
Teratohyla pulverata	-	-	-	+	-	-
Craugastoridae						
Craugastor crassidigitus/fitzingeri	+	+	+	+	+	+
Craugastor stejnegerianus	+	+	+	+	+	-
Dendrobatidae						
Allobates talamancae	+	+	+	+	-	-
Dendrobates auratus	-	-	+	-	-	-
Phyllobates vittatus	+	-	-	-	-	-
Silverstoneia flotator	+	+	+	+	-	-
Eleutherodactylidae						
Diasporus diastema	+	+	-	+	-	+
Diasporus vocator	+	+	+	-	-	-
Hylidae						
Agalychnis callidryas	-	-	-	-	-	+
Boana rosenbergi	+	+	+	-	+	+
Dendropsophus microcephalus	+	-	-	-	-	+
Scinax boulengeri	-	+	-	+	-	-
Smilisca sordida/sila	+	+	+	+	+	+
Leptodactylidae						
Engystomops pustulosus	+	+	-	+	+	+
Leptodactylus fragilis	-	-	-	-	+	+
Leptodactylus insularum	-	-	+	-	+	+
Leptodactylus savagei	+	+	+	+	+	+
Ranidae						
Lithobates warszewitschii	+	+	+	+	-	-
Strabomantidae						
Pristimantis cruentus	+	+	+	-	-	-
Reptiles						
Alligatoridae						
Caiman crocodilus	-	-	+	-	-	-

Phyllodactylidae						
Thecadactylus rapicauda	-	+	-	-	-	-
Corytophanidae						
Basiliscus basiliscus	+	+	+	+	+	+
Corytophanes cristatus	+	+	-	+	-	-
Dactyloidae						
Anolis aquaticus	-	+	-	+	-	-
Anolis capito	+	+	+	-	-	-
Anolis lemurinus	-	-	-	-	+	+
Anolis limifrons	+	+	+	+	-	+
Anolis polylepis	+	+	+	+	+	+
Iguanidae						
Iguana iguana	+	-	-	-	-	-
Scincidae						
Marisora unimarginata	-	-	+	-	-	+
Scincella cherriei	+	+	-	+	-	-
Gymnophthalmidae						
Loxopholis southi	-	+	-	+	-	-
Teiidae						
Holcosus festivus	+	+	+	+	+	-
Holcosus leptophrys	+	+	+	+	-	-
Holcosus quadrilineatus	-	-	-	+	-	-
Colubridae						
Chironius flavopictus	-	-	-	-	-	+
Leptodeira septentrionalis	-	+	-	+	+	+
Mastigodryas melanolomus	-	-	+	-	-	-
Oxybelis aeneus	-	-	-	+	-	-
Tantilla supracincta	-	-	-	+	-	-
Dipsadidae						
Coniophanes fissidens	+	+	+	-	-	+
Imantodes cenchoa	+	+	+	-	-	-
Sibon nebulatus	-	-	-	+	-	+
Siphlophis compressus	-	+	-	-	-	-
Elapidae						
Micrurus alleni	-	-	-	-	+	-
Viperidae						
Bothrops asper	+	+	+	+	+	+
Bothriechis schlegelii	-	-	-	+	-	-
Porthidium porrasi	+	+	-	-	-	-

Table A4. Number of all species found in 2013 and 2018

Species	individuals		no. of sites	
	2013	**2018**	**2013**	**2018**
Amphibians				
Plethodontidae				
Bolitoglossa lignicolor	1	2	1	2
Oedipina alleni	1	1	1	1
Bufonidae				

Species	individuals		no. of sites	
	2013	**2018**	**2013**	**2018**
Incilius aucoinae	32	29	10	9
Incilius coniferus	3	19	2	6
Rhaebo haematiticus	2	3	2	2
Rhinella horribilis	6	4	3	3
Centrolenidae				
Espadarana prosoblepon	7	17	6	5
Hyalinobatrachium colymbiphyllum	3	1	2	1
Hyalinobatrachium valerioi	18	3	4	3
Sachatamia albomaculata	1	3	1	2
Teratohyla pulverata	0	13	0	2
Craugastoridae				
Craugastor crassidigitus/fitzingeri	102	251	14	15
Craugastor stejnegerianus	33	51	9	9
Dendrobatidae				
Allobates talamancae	26	11	4	3
Dendrobates auratus	5	0	1	0
Phyllobates vittatus	1	0	1	0
Silverstoneia flotator	28	48	5	6
Eleutherodactylidae				
Diasporus diastema	4	3	3	3
Diasporus vocator	10	4	6	2
Hylidae				
Agalychnis callidryas	0	1	0	1
Boana rosenbergi	6	4	5	3
Dendropsophus microcephalus	1	6	1	2
Scinax boulengeri	0	4	0	3
Smilisca sordida/sila	12	122	4	7
Leptodactylidae				
Engystomops pustulosus	141	112	7	8
Leptodactylus fragilis	47	44	5	4
Leptodactylus insularum	43	61	6	4
Leptodactylus savagei	26	36	13	12
Ranidae				
Lithobates warszewitschii	7	15	4	3
Strabomantidae				
Pristimantis cruentus	2	6	2	2
Reptiles				
Alligatoridae				
Caiman crocodilus	1	0	1	0
Phyllodactylidae				
Thecadactylus rapicauda	0	1	0	1
Corytophanidae				
Basiliscus basiliscus	32	60	10	8
Corytophanes cristatus	5	14	3	8
Dactyloidae				
Anolis aquaticus	0	7	0	3

Species	individuals		no. of sites	
	2013	2018	2013	2018
Anolis capito	3	7	3	4
Anolis lemurinus	3	2	2	2
Anolis limifrons	5	46	5	11
Anolis polylepis	153	325	12	15
Iguanidae				
Iguana iguana	1	0	1	0
Scincidae				
Marisora unimarginata	2	1	1	1
Scincella cherriei	1	7	1	5
Gymnophthalmidae				
Loxopholis southi	0	10	0	6
Teiidae				
Holcosus festivus	6	5	4	4
Holcosus leptophrys	28	5	8	3
Holcosus quadrilineatus	0	2	0	2
Colubridae				
Chironius flavopictus	0	1	0	1
Leptodeira septentrionalis	5	9	2	6
Mastigodryas melanolomus	1	0	1	0
Oxybelis aeneus	0	1	0	1
Tantilla supracincta	0	1	0	1
Dipsadidae				
Coniophanes fissidens	3	3	3	3
Imantodes cenchoa	3	3	3	2
Sibon nebulatus	0	2	0	2
Siphlophis compressus	0	1	0	1
Elapidae				
Micrurus alleni	1	0	1	0
Viperidae				
Bothrops asper	7	13	6	8
Bothriechis schlegelii	0	1	0	1
Porthidium porrasi	1	3	1	3

Table A5. Traits matrix amphibians: Resource quantity: Mean of maximum body length of male and female: Body size (BS); activity: day (D), night (N); vertical stratification: ground active (GD), vegetation (VE); oviposition site: lotic systems (LO), lentic systems (LE), ground (GR), leaf litter (LL), phytotelmata (PH), leaf surface (LS); Reproduction: clutches (CS), Indirect development (DV)

Species	Resource quantity	Activity		Vertical stratification		Oviposition site						Reproduction	
	BS	D	N	GD	VE	LO	LE	GR	LL	PH	LS	CS	DV
Agalychnis callidryas	79	0	1	0	1	0	0	0	0	0	1	0	1
Allobates talamancae	23	1	0	1	0	0	0	0	1	0	0	0	1
Boana rosenbergi	87	0	1	1	1	0	1	0	0	0	0	1	1
Bolitoglossa lignicolor	160	0	1	1	1	0	0	0	0	0	0	0	0
Craugastor crassidigitus/fitzingeri	43	1	1	1	1	0	0	1	1	0	0	0	0
Craugastor stejnegerianus	20	1	1	1	0	0	0	1	1	0	0	0	0
Dendrobates auratus	41	1	0	1	0	0	0	0	1	0	0	0	1
Dendropsophus microcephalus	29	0	1	1	1	0	0	0	0	0	1	0	1
Diasporus diastema	22.5	0	1	1	1	0	0	0	0	1	1	0	0
Diasporus vocator	17	0	1	1	1	0	0	0	1	0	1	0	0
Engystomops pustulosus	34.5	0	1	1	0	0	1	0	0	0	0	1	1
Espadarana prosoblepon	29.5	0	1	0	1	0	0	0	0	0	1	0	1
Hyalinobatrachium colymbiphyllum	29	0	1	0	1	0	0	0	0	0	1	0	1
Hyalinobatrachium valerioi	25	0	1	0	1	0	0	0	0	0	1	0	1
Incilius aucoinae	85.5	0	1	1	0	1	0	0	0	0	0	1	1
Incilius coniferus	83	0	1	0	1	0	1	0	0	0	0	1	1
Leptodactylus fragilis	38	0	1	1	0	0	1	1	0	0	0	1	1
Leptodactylus insularum	107.5	0	1	1	0	0	0	1	0	0	0	1	1
Leptodactylus savagei	181.5	0	1	1	0	0	1	1	0	0	0	1	1
Lithobates warszewitschii	57.5	1	0	1	0	0	0	1	0	0	0	0	1
Oedipina alleni	150	1	0	1	1	0	0	0	0	0	0	0	0
Phyllobates vittatus	28.5	1	0	1	0	0	0	0	1	0	0	0	1

Species	Resource quantity	Activity		Vertical stratification		Oviposition site						Reproduction	
	BS	D	N	GD	VE	LO	LE	GR	LL	PH	LS	CS	DV
Pristimantis cruentus	35	0	1	1	1	0	0	0	0	1	0	0	1
Rhaebo haematiticus	71	0	1	1	0	0	1	0	0	0	0	1	1
Rhinella horribilis	160	0	1	1	0	1	1	0	0	0	0	1	1
Sachatamia albomaculata	31	0	1	0	1	0	0	0	0	0	1	0	1
Scinax boulengeri	51	0	1	0	1	0	1	0	0	0	0	1	1
Silverstoneia flotator	17.5	1	0	1	0	0	0	0	1	0	0	0	1
Smilisca sila/sordida	59	0	1	1	1	1	1	0	0	0	0	1	1
Teratohyla pulverata	31	0	1	0	1	0	0	0	0	0	1	0	1

Table A6. Trait matrix reptiles: Resource quantity: Body size (BS); activity: day (D), night (N); vertical stratification: ground dwelling (GD), vegetation (VE); diet: herbivorous (HE), eggs (EG), invertebrates (IN), small vertebrates (SV)

Species	Resource quantity	Activity		Vertical stratification		Diet			
	BS	D	N	GD	VE	HE	EG	IN	SV
Anolis aquaticus	190	1	0	1	1	0	0	1	0
Anolis capito	248	1	0	1	1	0	0	1	1
Anolis lemurinus	228	1	0	0	1	0	0	1	0
Anolis limifrons	156	1	0	1	1	0	0	1	0
Anolis polylepis	175	1	0	1	1	0	0	1	0
Basiliscus basiliscus	755	1	0	1	1	1	0	1	1
Bothrops asper	2350	0	1	1	1	0	0	1	1
Bothriechis schlegelii	820	0	1	0	1	0	0	0	0
Caiman crocodilus	2500	1	1	1	0	0	0	1	1
Chironius flavopictus	2000	1	0	1	1	0	0	0	1
Coniophanes fissidens	715	1	0	1	1	0	1	0	1

Species	Resource quantity	Activity		Vertical stratification		Diet			
	BS	D	N	GD	VE	HE	EG	IN	SV
Corytophanes cristatus	360	1	0	0	1	0	0	1	1
Holcosus festivus	350	1	0	1	0	0	0	1	0
Holcosus leptophrys	439	1	0	1	0	0	0	1	1
Holcosus quadrilineatus	283	1	0	1	0	0	0	1	0
Iguana iguana	2000	1	0	0	1	1	0	0	0
Imantodes cenchoa	1280	0	1	0	1	0	0	0	1
Leptodeira septentrionalis	1000	0	1	1	1	0	1	0	1
Loxopholis southi	100	1	0	1	0	0	0	1	0
Marisora unimarginata	255	1	0	1	0	0	0	1	0
Mastigodryas melanolomus	140	1	0	1	1	0	0	0	1
Micrurus alleni	1320	0	1	1	0	0	0	0	1
Oxybelis aeneus	1700	1	0	0	1	0	0	0	1
Porthidium porrasi	370	0	1	1	0	0	0	0	1
Scincella cherriei	178	1	0	1	0	0	0	1	0
Sibon nebulatus	850	0	1	0	1	0	0	1	0
Siphlophis compressus	1170	0	1	0	1	0	0	0	1
Tantilla supracincta	600	1	1	1	0	0	0	1	0
Thecadactylus rapicauda	225	0	1	0	1	0	0	1	0

Table A7. Changes in relative abundance for all amphibian species. Changes in forest interior (FI), forest margin (FM) and oil palm plantations (OP) between 2013 and 2018 (n/a - no individual found).

Amphibians			
Species	FI	FM	OP
Agalychnis callidryas	n/a	n/a	0.11%
Allobates talamancae	-0.72%	-2.60%	n/a
Boana rosenbergi	-0.48%	-0.18%	0.05%
Bolitoglossa lignicolor	-0.18%	0.11%	0.11%
Craugastor crassidigitus/fitzingeri	3.55%	5.65%	1.57%
Craugastor stejnegerianus	3.34%	-3.14%	-0.18%
Dendrobates auratus	n/a	-0.88%	n/a
Dendropsophus microcephalus	-0.18%	n/a	0.69%
Diasporus diastema	-0.59%	0.11%	0.11%
Diasporus vocator	-0.95%	-0.35%	n/a
Engystomops pustulosus	-0.41%	0.57%	-12.17%
Espadarana prosoblepon	-0.41%	0.78%	0.34%
Hyalinobatrachium colymbiphyllum	-0.35%	-0.06%	n/a
Hyalinobatrachium valerioi	-0.06%	-2.76%	0.00%
Incilius aucoinae	0.62%	-0.34%	-2.59%
Incilius coniferus	0.34%	0.39%	0.92%
Leptodactylus fragilis	n/a	n/a	-3.24%
Leptodactylus insularum	n/a	-0.18%	-0.41%
Leptodactylus savagei	1.23%	-0.19%	-1.50%
Lithobates warszewitschii	0.43%	0.05%	n/a
Oedipina alleni	-0.06%	n/a	n/a
Phyllobates vittatus	-0.18%	n/a	n/a
Pristimantis cruentus	0.51%	-0.18%	n/a
Rhaebo haematiticus	n/a	0.17%	-0.18%
Rhinella horribilis	0.11%	-0.18%	-0.54%
Sachatamia albomaculata	-0.06%	0.23%	n/a
Scinax boulengeri	0.34%	0.11%	n/a
Silverstoneia flotator	0.09%	0.47%	n/a
Smilisca sordida/sila	2.34%	4.02%	5.48%
Teratohyla pulverata	n/a	1.49%	n/a

Table A8. Changes in relative abundance for all reptile species. Changes in forest interior (FI), forest margin (FM) and oil palm plantations (OP) between 2013 and 2018 (n/a - no individual found).

species long	FI	FM	OP
Anolis aquaticus	0.19%	1.13%	n/a
Anolis capito	0.55%	-0.38%	n/a
Anolis lemurinus	n/a	n/a	-0.77%
Anolis limifrons	-0.21%	1.31%	5.66%
Anolis polylepis	-3.70%	4.74%	1.67%
Basiliscus basiliscus	-0.21%	3.14%	-3.87%
Bothrops asper	-0.19%	0.55%	-0.59%
Botriechis schlegelii	n/a	0.19%	n/a

Caiman crocodilus	n/a	-0.38%	n/a
Chironius flavopictus	n/a	n/a	0.19%
Coniophanes fissidens	-0.01%	-0.77%	0.19%
Corytophanes cristatus	-0.78%	1.51%	n/a
Holcosus festivus	-0.77%	-0.20%	-0.38%
Holcosus leptophrys	-4.79%	-4.99%	n/a
Holcosus quadrilineatus	n/a	0.38%	n/a
Iguana iguana	-0.38%	n/a	n/a
Imantodes cenchoa	-0.20%	-0.38%	n/a
Leptodeira septentrionalis	0.75%	0.57%	-1.54%
Loxopholis southi	0.94%	0.94%	n/a
Marisora unimarginata	n/a	-0.77%	0.19%
Mastigodryas melanolomus	n/a	-0.38%	n/a
Micrurus alleni	n/a	n/a	-0.38%
Oxybelis aeneus	n/a	0.19%	n/a
Porthidium porrasi	0.18%	n/a	n/a
Scincella cherriei	0.37%	0.57%	n/a
Sibon nebulatus	n/a	0.19%	0.19%
Siphlophis compressus	0.19%	n/a	n/a
Tantilla supracincta	n/a	0.19%	n/a
Thecadactylus rapicauda	0.19%	n/a	n/a

Table A 9. Functional diversity indices: functional richness (FRic), functional evenness (FEve), functional divergence (FFiv), functional dispersion (FDis)

Habitat	Site	FRic		FEve		FDiv		FDis	
		2013	2018	2013	2018	2013	2018	2013	2018
Amphibians (*qual.FRic* = 0.83)									
FI	FI1	0.00469	0.00012	0.82255	0.63844	0.95346	0.93192	0.22681	0.18883
	FI2	0.00218	0.00268	0.48465	0.30738	0.89351	0.83423	0.26003	0.27588
	FI3	0.00192	0.01138	0.58625	0.68204	0.94422	0.87951	0.24455	0.29548
	FI4	0.00003	0.00009	0.62734	0.44643	0.74216	0.98670	0.21365	0.18820
	FI5	0.00835	0.00282	0.60493	0.63186	0.77863	0.92090	0.23854	0.25909
FM	FM1	0.00275	0.00265	0.58616	0.56724	0.83775	0.94607	0.21673	0.29345
	FM2	0.00353	0.00093	0.75706	0.52864	0.91208	0.91841	0.25023	0.29600
	FM3	0.00004	0.00324	0.66247	0.50477	0.75377	0.69896	0.28725	0.23932
	FM4	0.00188	0.00136	0.63608	0.56316	0.94293	0.88796	0.27481	0.19545
	FM5	0.00207	0.00255	0.66044	0.52574	0.95451	0.93342	0.25757	0.26719
OP	OP1	0.00011	0.00030	0.43933	0.61400	0.56490	0.60046	0.10412	0.13650
	OP2	0.00017	0.00237	0.60261	0.54733	0.64267	0.59135	0.16730	0.14805
	OP3	0.00009	0.00046	0.42850	0.47013	0.52896	0.64074	0.08808	0.20480
	OP4	0.00001	0.00009	0.65330	0.60309	0.57654	0.64189	0.04715	0.11645
	OP5	0.00000	0.00005	0.67892	0.71347	0.66922	0.64838	0.22008	0.19541
Reptiles (*qual. FRic* = 0.58)									
FI	FI1	0.14363	0.21138	0.49810	0.50915	0.76678	0.83184	0.10899	0.07380
	FI2	0.18998	0.10324	0.47845	0.51749	0.67677	0.65287	0.16845	0.15931
	FI3	*NA*	0.15972	*NA*	0.63056	*NA*	0.56617	0.05064	0.06094
	FI4	0.13483	0.20822	0.39813	0.39158	0.62360	0.87245	0.10655	0.10661
	FI5	0.16807	0.21517	0.48690	0.38223	0.65466	0.81619	0.09382	0.05012
FM	FM1	0.10504	0.23738	0.51779	0.49105	0.77599	0.75629	0.12387	0.10615
	FM2	0.00009	0.12728	0.19267	0.30087	0.68366	0.51511	0.06403	0.06862
	FM3	0.01536	0.20466	0.87802	0.46215	0.74666	0.62475	0.04886	0.09916
	FM4	0.11259	0.15775	0.50355	0.45433	0.76081	0.79578	0.13135	0.06506
	FM5	0.19581	0.16233	0.50068	0.55913	0.75503	0.63072	0.13071	0.11280
OP	OP1	0.04397	0.14781	0.84766	0.61348	0.93282	0.54363	0.26678	0.15722
	OP2	0.01961	0.06132	0.68305	0.39330	0.60861	0.90294	0.15102	0.09441
	OP3	0.09079	0.01876	0.44911	0.51976	0.82279	0.84811	0.15984	0.13379
	OP4	0.01203	0.06232	0.97342	0.51723	0.65650	0.79728	0.16459	0.15433
	OP5	*NA*	0.01965	*NA*	0.50357	*NA*	0.86366	0.20579	0.20998