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Impact of oil palm agriculture on amphibians and reptiles: a Neotropical perspective

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Abstract

In the last decades, oil palm plantations expanded rapidly in many tropical regions, including the Neotropics. In this study from the Pacific lowlands of Costa Rica, we quantified the impact on the region's herpetofauna. Amphibians and reptiles were sampled along transects at five sites in forest interior (FI), at forest margins (FM) and in oil palm plantations (OP), respectively. Besides assessing species richness, we calculated four different functional diversity (FD) measures (FRic – functional richness, FEve – functional evenness, FDiv – functional divergence, FDis – functional dispersion). While no significant differences in species richness were found between FI and FM, OP was characterized by a strongly impoverished fauna. Total species richness of amphibians (28 species) and reptiles (19 species) was reduced to 45.3% and 49.8% compared to FI, respectively. Only 31.8% of amphibian and 30.8% of reptile species found in FI were also found in OP. In both taxa, species composition of OP sites differed significantly from both forest habitats. Species recorded in OP were predominantly disturbance-tolerant species. We did not find differences in FD measures between the FI and FM but a dramatic decline of FRic, FDiv and FDis in amphibians towards OP indicating a decrease in ecological function of amphibian communities in this land-use system. Further, we found a severe loss of endemic species in OP. The almost complete absence of leaf litter, understory vegetation and woody debris as well as the more open canopy may be important drivers for reducing herpetofauna species richness in oil palm plantations. Enhancing understory vegetation could help making plantations a less hostile environment for some species. Still, those management measures might not be enough to promote the occurrence of forest specialists in OP. Therefore, to complement such efforts and prevent losing the majority of

the tropical herpetofauna in human-modified landscapes, it is essential to protect any kind of forested habitat ranging from secondary forests to strips of gallery forests and remnants of old-growth forests.

Keywords

Costa Rica, forest specialists, functional diversity, Herpetofauna, oil palm cultivation, species richness, species composition, range-restricted species

Zusammenfassung

In den letzten Jahrzehnten breiteten sich Palmölplantagen in den vielen Regionen der Tropen rapide aus, unter anderem auch in den Neuwelttropen. In dieser Studie aus dem pazifischen Tiefland Costa Ricas wurde ihr Einfluss auf die regionale Herpetofauna untersucht. Amphibien und Reptilien wurden entlang von Transekten an je fünf Standorten im Waldinneren (FI), am Waldrand (FM) und in Palmölplantagen (OP) erfasst. Neben der Erfassung des Artenreichtums wurden Veränderungen der funktionellen Diversität (FD) mittels vier Kenngrößen (FRic – *functional richness*, FEve – *functional evenness*, FDiv – *functional divergence*, FDis – *functional dispersion*) untersucht. Hinsichtlich Artenvielfalt waren FI und FM nicht signifikant unterschiedlich, OP waren jedoch durch eine stark verarmte Fauna gekennzeichnet. Die Zahl der Arten an Amphibien (28 Arten) und Reptilien (19 Arten) war hier im Vergleich zu FI um 45,3 bzw. 49,8% geringer und nur 31,8 bzw. 30.8% der Arten aus FI konnten auch in OP nachgewiesen werden. In beiden Taxa unterschied sich die Artenzusammensetzung von OP Standorten signifikant von beiden Waldhabitaten und war in erster Linie von störungstoleranten Arten dominiert. FD-Maße der beiden Waldhabitate erwiesen sich als sehr ähnlich. In OP Hingegen waren FRic, FDiv und FDis von Amphibien jedoch dramatisch reduziert in OP. Dies weist auf einen deutlichen Rückgang funktionellen Diversität von Amphibiengemeinschaften in diesem Landnutzungssystem hin. In den Palmölplantagen kam es zudem zu einem erheblichen Verlust an endemischen Arten. Das komplette Fehlen von Streuschicht, Unterwuchsvegetation und Totholz sowie ein verringerter Baumkronenschluss stellen vermutlich die Hauptursache für den Rückgang der Artenvielfalt der Herpetofauna in Palmölplantagen dar. Eine Förderung der Unterwuchsvegetation könnte hier helfen,

Plantagen zumindest für einige Arten zu einem geeigneteren Lebensraum zu machen. Für wahre Waldspezialisten reichen solche Maßnahmen jedoch vermutlich nicht aus. Daher ist der Schutz jeglicher Art verbleibender Waldhabitate in der Kulturlandschaft, seien es Sekundärwälder, Galeriewaldstreifen oder Reste naturnaher Waldfragmente, essentiell, um den Verlust eines Großteils der tropischen Herpetofauna in vom Menschen geprägten Landschaften zu verhindern.

Introduction

Loss and fragmentation of tropical rainforests are widely recognized as major driving forces of global biodiversity decline (Wilcox & Murphy 1985; Sala et al. 2000; Brooks et al. 2002; Gallant et al. 2007; Sodhi et al. 2008). During the last decades across the tropics more than half of the new cropland came primarily on the expense of tropical forests (Gibbs et al. 2010) and often resulted in large-scale landscape homogenization (Koellner & Scholz 2008). This development poses a serious threat for tropical biodiversity as such habitats lack the complexity the previous habitats provided. The following decrease in many narrowly distributed species, coupled with an increase in a small number of cosmopolitan species, also leads to an increasing homogenization of the biota (McKinney & Lockwood 1999).

Huge parts of those expanding croplands are oil palm plantations (Koh 2007), currently representing the largest perennial cropland in the tropics (Sheil et al. 2009; Meijaard & Sheil 2013). The exponential growth of oil palm cultivation is partly driven by their ability to produce three to eight times more oil per area unit than any other oil crop (Corley 2009; FAO 2014). Unfortunately, those oil palm plantations are characterized by an extremely reduced species richness and shifts in community composition towards disturbance tolerant species (beetles: Chung et al. 2000, Davis & Philips 2005; ants: Brühl & Eltz 2010, Fayle et al. 2010; birds: Aratrakorn et al. 2006, Koh & Wilcove 2008, Edwards et al. 2010, Azhar et al. 2011) and a strongly declined functional diversity (Edwards et al. 2013a, 2013b). Typically, oil palm plantations are monocultures dominated by only one plant species (*Elaeis guineensis*). They are structurally less complex than natural forests, with a uniform tree age structure, a more open canopy, little understory vegetation, stronger temperature fluctuations and lower humidity (Danielsen & Heegaard 1995; Fitzherbert et al. 2008).

Amphibians are proven particularly sensitive to environmental change due to their complex life history and their need for both wetland and terrestrial habitats (Alford & Richards 1999). Having suffered unprecedented rates of decline in recent decades, they are considered the most threatened animal groups globally (Gibbons et al. 2000; Stuart et al. 2004). However, few studies have examined the impact of forest alteration on tropical amphibian communities (e.g. Vitt & Caldwell 2001, Gardner et al. 2007, Wanger et al. 2009, 2010) and

only two have studied the impact of conversion to oil palm plantations (Gillespie et al. 2012; Faruk et al. 2013). Both studies indicate that common habitat generalists of little conservation concern dominate amphibian communities in oil palm plantations. Just as amphibians, reptile species are declining on a global scale and are among the most threatened animal groups worldwide (Gibbons et al. 2000). The only existing study on the impact of oil palm cultivation on reptiles was conducted in the Dominican Republic and exclusively considered lizards, which showed a reduced species richness in oil palm plantations compared to forests and most other land-use systems (Glor et al. 2001).

In the last decades, oil palm plantations have also been rapidly expanding in the Neotropics, where they already covered about 860,000 ha in 2012 (FAO 2014). Between 2002 and 2012 the expansion rate has been approximately 4.9% per year on average (FAO 2014). In all Mesoamerica, Costa Rica has one of the largest areas of oil palm plantations, ranking only second after Honduras. With Costa Rica being one of the most biodiverse countries in the world (Myers et al. 2000) and oil palm monoculture expanding exponentially (FAO 2014, Fig. 1), the importance of determining the effects of these plantations on the neotropical herpetofauna and finding the environmental triggers behind it becomes obvious.
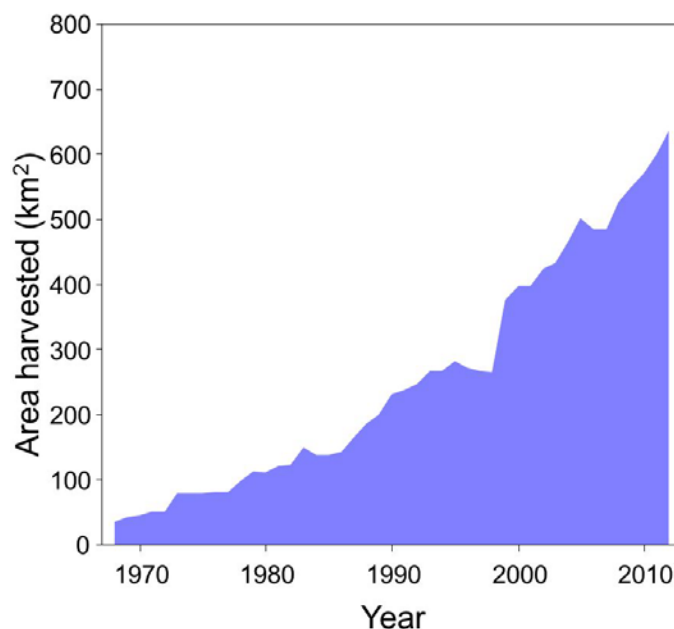

Fig. 1. Increase of the area of harvested oil palm plantations in Costa Rica between 1968 and 2012 (based on data from FAO 2014).

This is the first case study from the Neotropics trying to quantify the impact of oil palm cultivation on amphibians and reptiles for the Pacific lowlands of Costa Rica. We particularly addressed the following hypotheses:

(1) Oil palm plantations are characterized by a dramatically decreased structural complexity compared to forest habitats resulting in a reduced canopy cover and a decline of available microhabitats (e.g. leaf litter, deadwood) (Gillespie et al. 2012; Faruk et al. 2013). These changes most likely transfer into a decrease of species richness. To reduce additional negative effects on the herpetofauna, that were not in the focus of this study, caused by isolation of plantations from the source habitat forest, all plantation sites selected for this study were located adjacent to the forest margin. However, the forest edge may represent an important transition zone already reducing the number of true forest interior species available for the colonization of adjacent plantations.

(2) Further, we expect that the strong environmental filtering from forest sites towards oil palm plantations is reducing functional diversity of amphibian and reptile communities, as demonstrated for other taxa (Edwards et al. 2013a, 2013b). We used several functional diversity measures (functional richness, functional evenness, functional divergence and functional dispersion; Villéger et al. 2008; Mouchet et al. 2010; Laliberté & Legendre 2010) to quantify changes in ecological functions of the herpetofauna from forest interior towards forest margin and oil palm plantations.

(3) As reported for amphibians from Southeast Asia (Gillespie et al. 2012; Faruk et al. 2013) and lizards from the Caribbean region (Glor et al. 2001), we expect that oil palm plantations in the Neotropics are also characterized by a species composition distinct from forest habitats caused by changes in habitat structure.

(4) Most likely species assemblages shift from forest specialists depending on specific microhabitats in forest habitats towards common and disturbance tolerant species in oil palm plantations as documented for other regions (Gillespie et al. 2012) and other taxonomic groups (birds: Edwards et al. 2013a; dung beetles: Edwards et al. 2013b).

(5) Range-restricted forest species of high conservation relevance should be particularly prone to habitat disturbance and hence largely absent in oil palm plantations as demonstrated by studies on lizards (Glor et al. 2001) and birds (Edwards et al. 2013a).

Methods

Study area and study sites

This study was carried out in proximity of the Tropical Research Station La Gamba (8°42′61″ N, 83°12′97″ W, 70 m ASL) on the Pacific slope of southwestern Costa Rica (Fig. 2). Beside the remaining large block of primary forest (located in the Piedras Blancas National Park) and a variety of old-growth secondary forests, the forest margin zone next to the village of La Gamba is an agro-mosaic increasingly dominated by oil palm plantations (Höbinger et al. 2012). La Gamba has an average annual precipitation of about 6,000 mm with a distinct rainy season from May to November. Mean annual temperature is 28.5°C (Weissenhofer & Huber 2008).

We selected five replicate sites in each of the three following habitat types (Fig. 2): forest interior (sites FI1, FI2, FI3, FI4 and FI5), forest margin (FM1, FM2, FM3, FM4 and FM5) and oil palm plantation (OP1, OP2, OP3, OP4 and OP6) (Appendix Table A1).

For a preliminary selection of study sites we used a vegetation map of the Piedras Blancas National Park and adjacent areas (Weissenhofer & Huber 2008). The final selection of study sites was made after a visit of all sites before starting the herpetofaunal surveys. Selected FI sites were pristine or old-growth secondary forests situated at least 200 m away from the nearest forest edge. All FM sites were adjacent to strongly human-modified habitats (e.g. fallows, pastures, gardens, oil palm plantations). Sampled OP sites were situated adjacent to a forest margin and had an area of ca. 10-50 ha. All study sites were at least 300 m apart from each other.
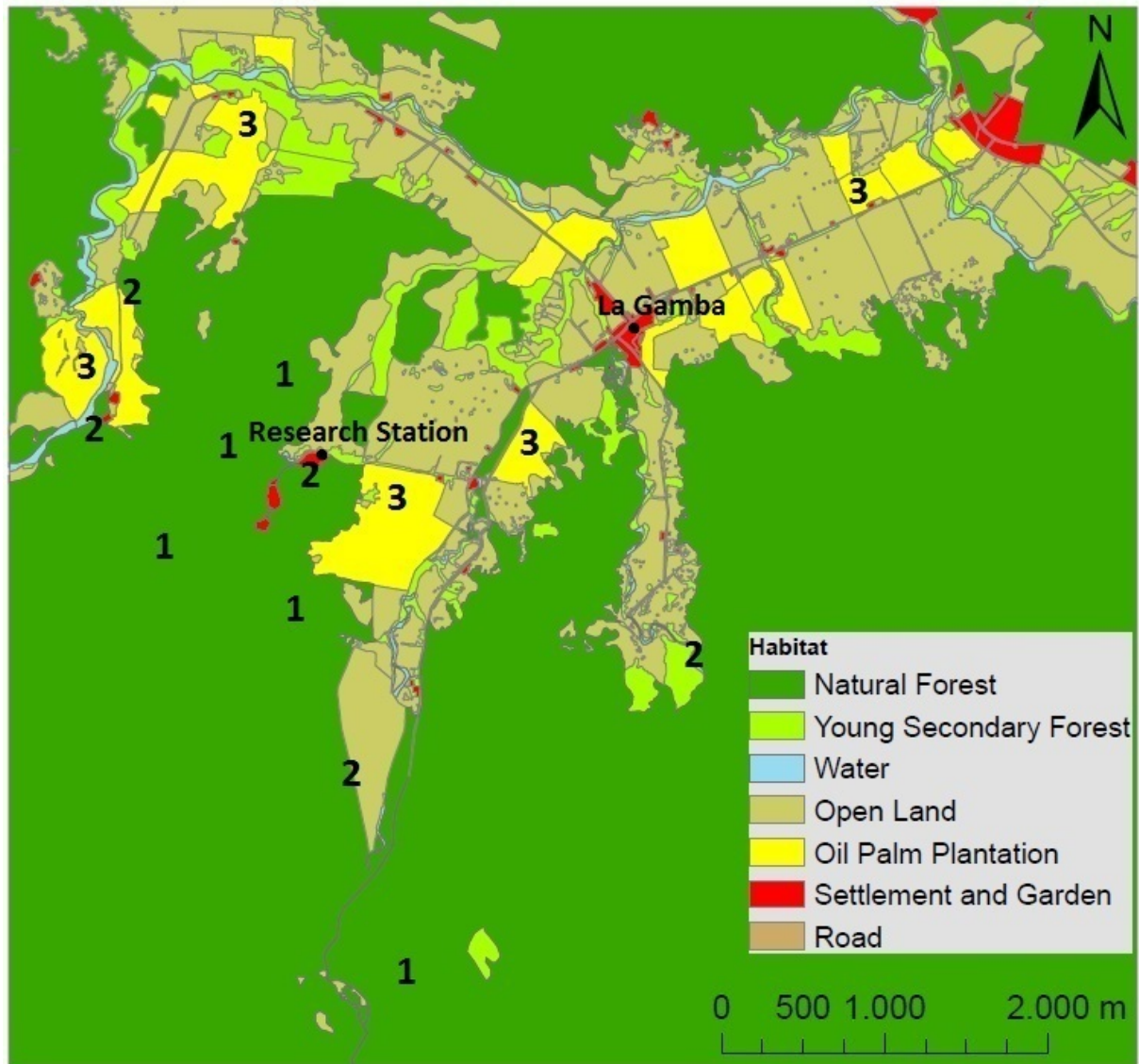
Fig. 2. Map of the study area indicating the 15 study sites (1 - forest interior, 2 - forest margins, 3 - oil palm plantations) in proximity to the Tropical Research Station La Gamba (8°42′61″ N, 83°12′97″ W).

Sampling of amphibians and reptiles

Fieldwork was conducted during the rainy season between 03 July and 27 September 2013, when activity of terrestrial amphibians and reptiles is particularly high (Marques et al. 2000; Veith et al. 2004). At each sampling site all visually detected reptiles and amphibians were recorded along two 100 m transects (Fig. 2). Each transect census lasted between 1 and 2 h to complete and was rather constrained by transect length (2x 100 m) than time. Each

transect was sampled 9-10 times, five times during the day (between 09:30 and 16:30) and four to five times at night (between 18:45 and 01:30) (Appendix Table A2). Censuses at night were conducted using a head torch. Seven transects (FI2, FM2, FM4, FM5, OP2, OP4 and OP6) could only be sampled four times at night due to heavy rainfalls in the afternoon and resulting flooding in late September. During one sampling unit all reptiles and amphibians were recorded which could be detected within a band of 2 m at both sides of each transect. Specimens found during sampling were photographed. Individuals were identified in the field, but all photographs were reexamined to confirm identities (Wanger et al. 2010; Faruk et al. 2013). Some frog species difficult to identify in the field (e.g. genus *Craugastor*) were caught for later identification in the laboratory using a microscope. Various published monographs on amphibians and reptiles were used for identification (Leenders 2001; Savage 2002; Chacón & Johnston 2013; AmphibiaWeb 2014; Uetz & Hošek 2014). Nomenclature in general follows that of (Savage & Bolaños 2009) with updates on classification according to AmphibiaWeb (2014) and Uetz & Hošek (2014).

Habitat variables

To quantify the differences between the three habitat types, five habitat characteristics were recorded at each plot: leaf litter cover, herb cover, understory shrub cover, canopy cover and the amount of deadwood (e.g. Wanger et al. 2009, Kudavidanage et al. 2012). The amount of deadwood was quantified as the total number of logs and branches with a diameter of >10 cm lying on the ground at each transect within a buffer of 2m. Leaf litter, herb and understory shrub cover were estimated at 10 points along the two 100 m transects (Fig. 3) as 0, 10, 20 … 100 % within a radius of 2 m at each point. Canopy cover was assessed using canopy pictures shot at four spots along each transect (Fig. 3). The four canopy pictures per plot were analyzed in ImageJ 1.48p (Wayne Rasband, National Institutes of Health, Bethesda, Maryland, USA) to get percentage of canopy cover. Pictures were first converted into binary black-and-white images, which denotes canopy as black and open sky as white. Afterwards, we calculated the percentage of black pixels, representing the percentage of canopy cover. As measures for leaf litter, herb and understory shrub cover for each site the mean values were calculated (n = 10 measurements per study site). To reduce the effect of strong outliers in canopy cover, we calculated the median values (n = 4 estimates) for each study site.
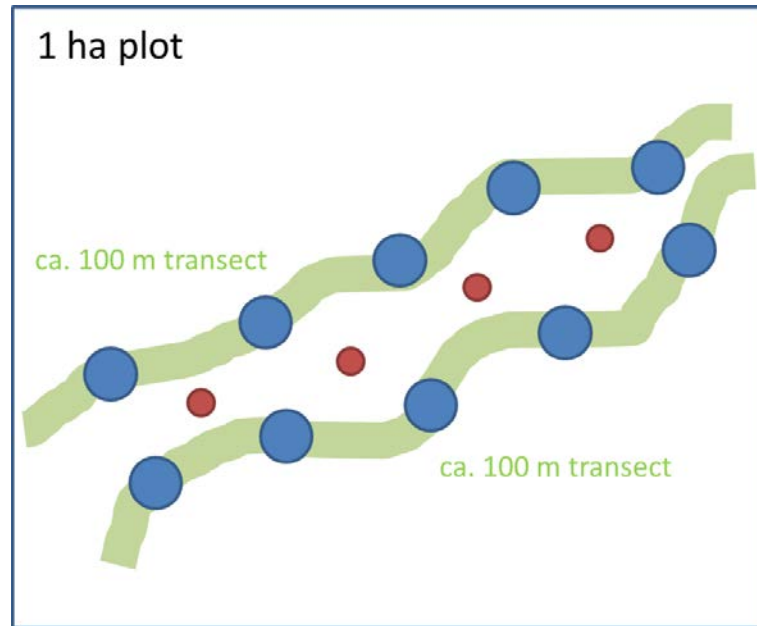
Fig. 3. At each study site amphibians and reptiles were sampled along two 100 m transects. Additionally, the total amount of deadwood (diameter of >10cm) was recorded along each transect. Leaf litter cover, herb cover and understory shrub cover were estimated at 5 points (filled blue circles; 20 m distance between neighboring points) along each of the two transects. Four canopy pictures were taken at each site (filled red circles).

Data analysis

All analyzed variables achieved normal distribution. Unless stated otherwise, statistical tests were executed in STATISTICA 7.1 (StatSoft, Tulsa, OK 74104, USA) and considered being significant if $p < 0.05$. Analyses of variance (ANOVAs) were used to test for differences in habitat variables between habitat types. If habitat type proved to have a significant effect, subsequently calculated Tukey's Honest Significant Difference Tests were used to identify which habitats differed significantly from each other. Due to a high multicollinearity of the five habitat variables, a principal component analysis (PCA) was calculated. Resulting factors were again tested for differences among habitat types.

Due to their vastly different biology, amphibians and reptiles were analyzed separately (Laurencio & Fitzgerald 2010). Specimens that could not be identified to species level either because they escaped or were juveniles too young for reliable identification (28 amphibians and 87 reptiles, representing 4.7 and 25.0 % of the total number of counted individuals, respectively) were excluded from further analyses.

To assess sampling completeness and compare total species richness among habitat types, sample-based species accumulation curves were constructed for amphibians and reptiles in EstimateS 9.1.0 (Robert K. Colwell, University of Connecticut, USA). The accumulation curves were calculated by carrying out 100 random re-orderings of sampling units and were extrapolated to 75 samples (compare Colwell et al. 2012). Additionally, total species richness was estimated from the survey data using the Jack 1 non-parametric species richness estimator, which is considered one of the most accurate estimators to predict actual species richness (Walther & Moore 2005).

To analyze differences in functional diversity (FD) measures between habitat types a species-trait-matrix was compiled for amphibians and reptiles (Appendix Table A4 and A5) containing twelve and nine trait categories, respectively (Table 1 and Table 2). We used traits that influence ecosystem functioning of a species including body size, time of activity during the day, microhabitat use (vertical stratification), oviposition site, size of their egg clutches, and diet (Flynn et al. 2009). Information on traits was extracted from various sources (Leenders 2001; Savage & Bolaños 2009; IUCN 2013; Vitt & Caldwell 2013; AmphibiaWeb 2014; Uetz & Hošek 2014).

Table 1. Functional traits used for calculating functional diversity indices of amphibians.

Trait	Trait category	Type
Resource quantity	Mean of maximum body length of male and female [mm]	continuous (range: 17.0 - 181.0)
Time of activity	Diurnal	binary (yes, no)
	Nocturnal	
Vertical stratification	Ground-dwelling	binary (yes, no)
	Vegetation	
Oviposition site	Lotic systems	binary (yes, no)
	Lentic systems	
	Ground	
	Leaf litter	
	Bromeliads or crevices of tree trunks	
	Surface of leaves	
Egg clutches	Clutch size	binary (single eggs to small egg clumps, explosive breeders)

Table 2. Functional traits used for calculating functional diversity indices of reptiles.

Trait	Trait category	Type
Resource quantity	Mean of maximum body length of male and female [mm]	continuous (range: 156 - 2,475)
Time of activity	Diurnal	binary (yes, no)
	Nocturnal	
Vertical stratification	Ground-dwelling	binary (yes, no)
	Vegetation	
Diet	Herbivorous	binary (yes, no)
	Eggs	
	Invertebrates	
	Small vertebrates	

Those matrices were then related to species-site-matrices in R 2.15.1 (R Core Team 2012), using the package "FD" (Laliberté & Legendre 2010) to calculate four different multidimensional FD indices. Functional richness (FRic) quantifies trait diversity in a community by constructing a convex hull volume as the total space of occupied niches. Functional evenness (FEve) measures evenness of niches occupation or regularity of species abundances within the hull volume. Functional divergence (FDiv) describes the divergence of abundances of species within this volume. Functional dispersion (FDis) accounts for relative abundances of species by shifting the position of the centroid towards the most abundant species (Laliberté & Legendre 2010). Effects of habitat types on FD measures were tested by one-way ANOVAs. Subsequently, false discovery rate (FDR) adjusted p values were computed to correct for multiple comparisons (Pike 2011).

Similarity relationships in species composition between study sites were visualized using non-metric multidimensional scaling (NMDS) ordinations based on Bray-Curtis similarities calculated in PRIMER 5.2.9 (Primer-E Ltd., 3 Meadow View Lutton Ivybridge PL21 9RH UK). Abundances were square root transformed to reduce the influence of highly dominant species. Ordinations with stress values <0.20 were considered to reliably visualize differences in species composition (Clarke 1993). One-way analyses of similarity (ANOSIMs) with 999 random permutations of the similarity matrix were calculated to test for differences in species composition between habitat types (Clarke & Warwick 2001). To test for effects of habitat variables on changes in species composition, Dimension 1 and 2

values extracted from the NMDS ordinations were related to the 1st and 2nd factor of a principal component analysis on the habitat variables (see above).

Canonical Correspondence Analyses (CCAs) calculated in CANOCO 4.5 (Plant Research International, Wageningen, Netherlands) were used to analyze the influence of environmental variables on species distribution among habitat types. Due to multicollinearity among the original environmental variables, PC1 and PC2 were used for the CCA analyses and plotted as vectors. We excluded all species with less than five counted individuals in total or that occurred at only one site from analysis.

To analyze habitat preferences of range-restricted species, all recorded species were classified as either (a) endemic to Costa Rica and Panama or (b) widespread, based on available distribution maps (AmphibiaWeb 2014, Uetz & Hošek 2014). Based on this classification we calculated the percentage of species and individuals that endemics comprised at each site. Effects of habitat types on relative richness and abundance of endemics were then examined by one-way ANOVAs.

Results

Habitat characteristics

Except of herb cover, all estimated habitat variables differed between habitats (one-way ANOVAs; leaf litter cover: $F_{2,12} = 34.35$, $p < 0.0001$; herb cover: $F_{2,12} = 0.65$, $p = 0.5379$, shrub cover: $F_{2,12} = 25.34$, $p < 0.0001$; canopy cover: $F_{2,12} = 11.54$, $p = 0.0016$; deadwood: $F_{2,12} = 23.99$, $p < 0.0001$). Leaf litter, shrub and canopy cover were significantly higher at FI and FM than at OP sites (Fig. 4a, c-d). Deadwood decreased significantly from FI (25.6 ± 9.56) to FM (12.2 ± 3.35) and was completely absent in OP (Fig. 4e).

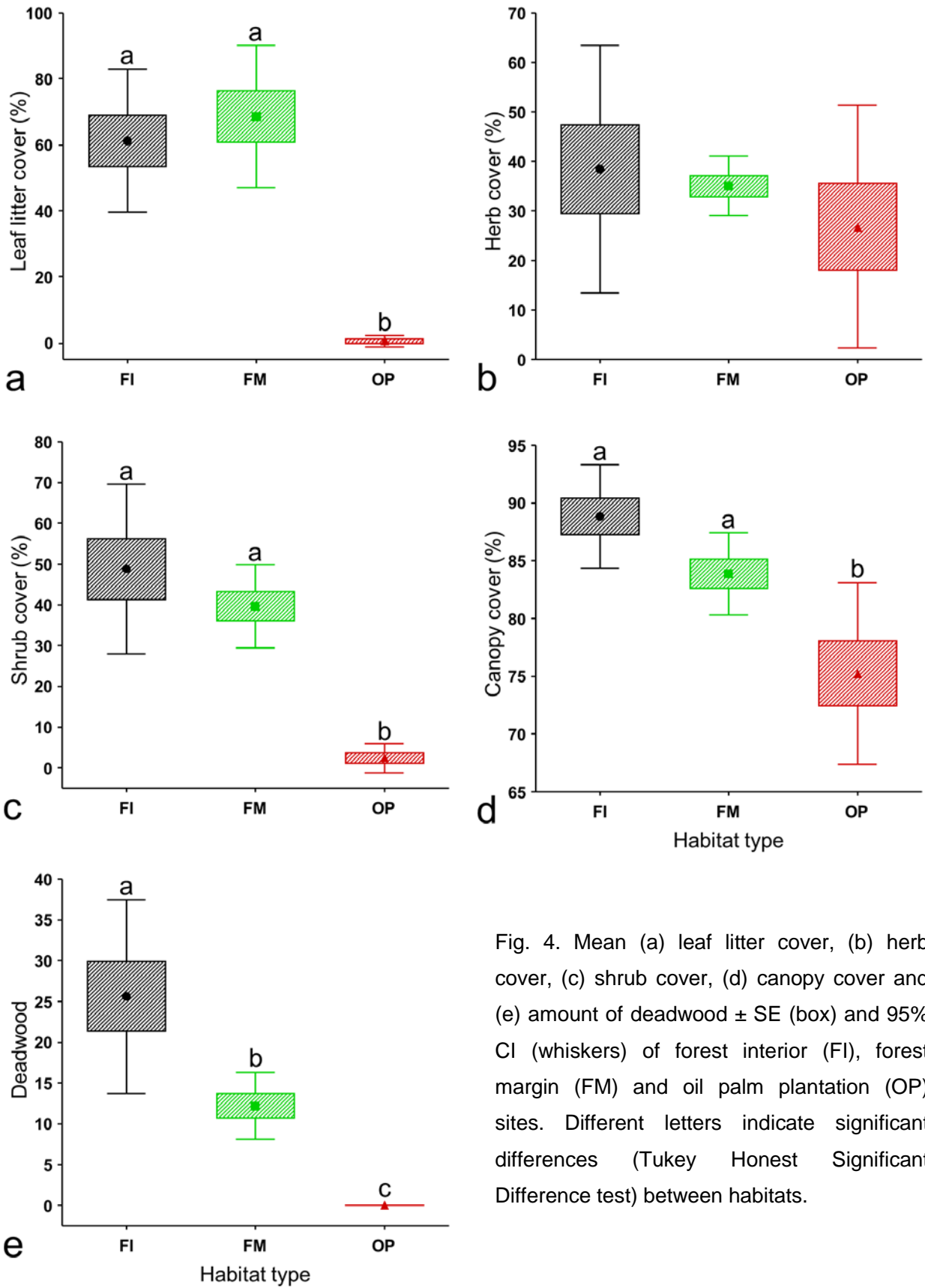Fig. 4. Mean (a) leaf litter cover, (b) herb cover, (c) shrub cover, (d) canopy cover and (e) amount of deadwood ± SE (box) and 95% CI (whiskers) of forest interior (FI), forest margin (FM) and oil palm plantation (OP) sites. Different letters indicate significant differences (Tukey Honest Significant Difference test) between habitats.

Due to a high multicollinearity of habitat variables (compare Appendix Table A3), a principal component analysis was calculated (Table 3). The first two factors explained most of the total variance (82.7%) of the habitat variables, with factor 1 (PC 1) accounting for 64.2% of the variance and being related negatively to leaf litter, shrub and canopy cover and the amount of deadwood. The second factor (PC 2) accounted for 18.5% of the variance and was negatively related to herb cover (Table 4). Of all five factors only PC 1 differed significantly between habitats (one-way ANOVA: $F_{2,12} = 96.63$, $p < 0.0001$), increasing from pristine to disturbed habitats (Fig. 5).

Table 3. Principal component analysis on five habitat variables.

Factors	Eigenvalue	% total variance	Cumulative eigenvalue	Cumulative %
1	3.21	64.19	3.21	64.19
2	0.92	18.47	4.13	82.65
3	0.44	8.81	4.57	91.46
4	0.27	5.46	4.85	96.92
5	0.15	3.08	5.00	100.00

Table 4. Factor loadings of principal component analysis on five habitat variables. High factor loadings are indicated by grey cells.

Habitat variables	PC 1	PC 2	PC 3	PC 4	PC 5
Mean leaf litter cover	-0.88	0.20	-0.26	0.23	-0.23
Mean herb cover	-0.42	-0.90	-0.04	-0.07	-0.08
Mean shrub cover	-0.87	0.13	-0.37	-0.26	0.17
Mean canopy cover	-0.84	0.21	0.42	-0.25	-0.12
Mean deadwood	-0.90	-0.10	0.24	0.29	0.22
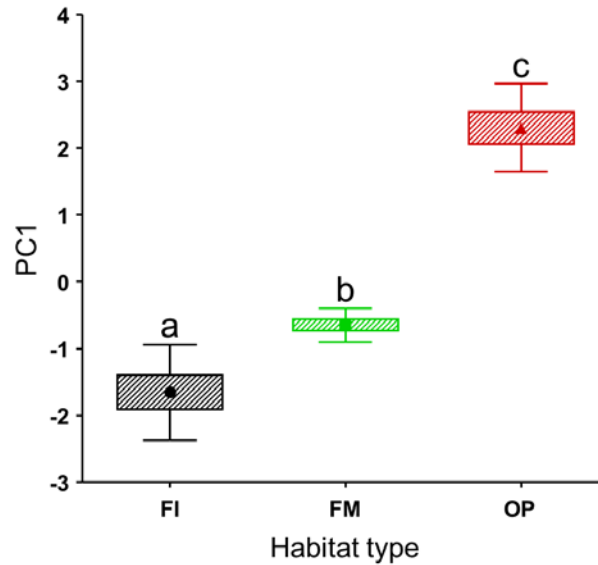
Fig. 5. Mean factor 1 (PC 1) values of a principal component analysis on habitat variables ± SE (box) and 95% CI (whiskers) for forest interior (FI), forest margin (FM) and oil palm plantation (OP) sites. Different letters indicate significant differences (Tukey Honest Significant Difference test) between habitats.

Species richness

In total, we documented 568 amphibians of 28 species and 261 reptiles of 19 species during 143 surveys (Table 5). Recorded amphibian species richness ranged from five species at OP6 to 12 at FI5, with a mean (± SD) of 8.5 (± 2) species per site. With the exception of two single individuals belonging to two different species of caudates (salamanders), anurans (frogs and toads) made up the entire spectrum of amphibian species at all sites (compare Appendix Table A6). Species richness of reptiles ranged from two species at FI3 and OP6 to eight at FI5 and FM4, with a mean (± SD) of 4.5 (± 1.9) species per site. Except of one observed *Caiman crocodilus* (crocodylia), all documented species represented squamantes (snakes and lizards) (compare Appendix Table A6).

Overall, total recorded species richness was similar in FI and FM, but lower in OP in both amphibians (FI: 22 species, FM: 20, OP: 11) and reptiles (FI: 13, FM: 12, OP: 7). This conclusion can also be drawn from the respective species accumulation curves (Fig. 6).

Table 5. Summary of amphibian and reptile sampling.

	FI	FM	OP	All habitats
No. of transect walks	49	47	47	143
Amphibians				
Recorded species (% of total)	22 (78.6)	20 (71.4)	11 (39.3)	28
Jack 1 (% of total)	30.8 (93.4)	26.8 (81.4)	13.9 (42.3)	33.0
Sampling coverage[1]	71.5	74.5	79.0	85.0
Number of individuals	133	146	289	568
Reptiles				
Recorded species (% of total)	13 (68.4)	12 (63.2)	7 (36.8)	19
Jack 1 (% of total)	17.9 (71.7)	15.9 (63.8)	8.9 (35.7)	25.0
Sampling coverage[2]	72.7	75.4	78.6	76.2
Number of individuals	123	102	36	261

[1, 2] % of recorded species in comparison to total number of amphibian and reptile species, respectively, estimated by Jack 1 method.

Differences between forest habitats and OP are even more pronounced when total richness of amphibians is estimated by Jack 1. While Jack 1 estimates 30.8 and 26.8 species for FI and FM, respectively, the estimated species number drops to just 13.9 species in OP. For reptiles, Jack 1 estimates predict 17.9 species for FI, 15.9 for FM and 8.9 for OP. The mean number of species recorded per site, however, did not differ between habitats in both amphibians and reptiles but was slightly lower at OP in both taxa (Table 6).
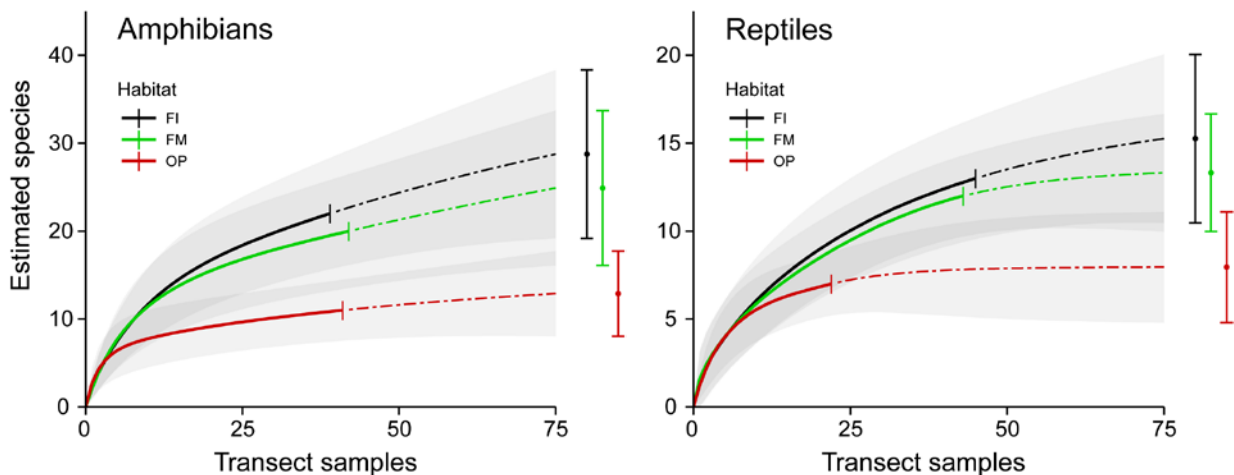

Fig. 6. Species accumulation curves for amphibians and reptiles recorded at forest interior (FI), forest margin (FM) and oil palm plantation (OP) sites.

Functional richness, functional evenness, functional divergence and functional dispersion

While FD measures did not differ between the three habitat types in reptiles, all except of FEve showed a strong response to the human impact in amphibians (Table 6). FRic, FDiv and FDis decreased significantly from the two forest habitats (both characterized by very similar values) towards OP.

Table 6. Mean species richness, functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) and functional dispersion (FDis) ± SD per habitat type. FEve and FDiv are bound between 0 and 1. Additionally, results of one-way ANOVAs testing for differences between habitats, including FDR adjusted p values are provided. Different superscript letters indicate significant differences in pairwise testing between habitats (Tukey Honest Significant Difference Test).

Variables	Habitat types			ANOVA		FDR adjusted p
	FI	FM	OP	$F_{2,12}$	P	
Amphibians						
Species richness	9.40 ± 2.41	9.20 ± 1.48	7.00 ± 1.41	2.66	0.1106	0.1383
FRic	11.78 ± 5.20[a]	12.46 ± 5.34[a]	3.47 ± 1.67[b]	6.43	0.0126	0.0210
FEve	0.58 ± 0.15	0.60 ± 0.06	0.56 ± 0.17	0.09	0.9148	0.9148
FDiv	0.87 ± 0.06[a]	0.82 ± 0.10[a]	0.58 ± 0.12[b]	12.98	0.0010	0.0025
FDis	2.81 ± 0.29[a]	3.05 ± 0.28[a]	2.09 ± 0.29[b]	15.13	0.0005	0.0025
Reptiles						
Species richness	5.20 ± 2.28	5.20 ± 1.92	3.20 ± 0.84	2.08	0.1672	0.2787
FRic	5.98 ± 4.59	5.23 ± 4.46	1.51 ± 1.35	1.57	0.2551	0.3189
FEve	0.38 ± 0.17	0.47 ± 0.26	0.71 ± 0.15	2.88	0.1028	0.2570
FDiv	0.80 ± 0.07	0.78 ± 0.08	0.72 ± 0.10	1.00	0.4013	0.4013
FDis	1.20 ± 0.71	1.32 ± 0.57	2.34 ± 0.36	6.14	0.0146	0.0730

Species composition

Similarities of species assemblages between sampled sites visualized in an NMDS plot indicate a distinct species composition at OP sites and forest habitats (FI and FM sites) for amphibians and reptiles (Fig. 7). Significant differences in assemblage structure between the habitat types could be confirmed by one-way ANOSIMs (amphibians: Global R = 0.755, p = 0.001; reptiles: Global R = 0.458, p = 0.001). In both taxa, species composition of OP sites differed significantly from both forest habitats. In amphibians, even the pairwise test for FI vs. FM achieved a significant level (Table 7).
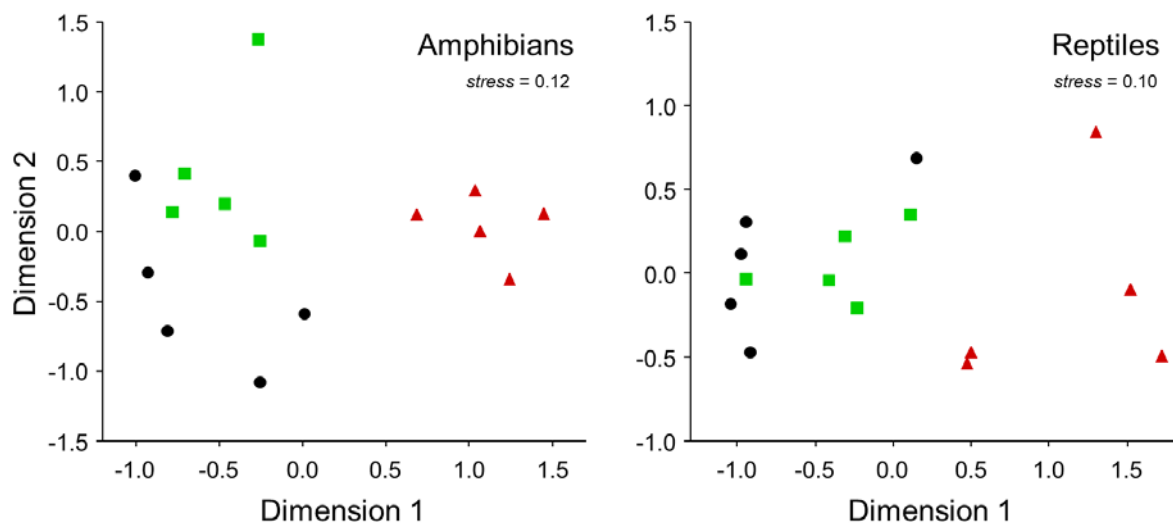
Fig. 7. NMDS ordinations based on Bray-Curtis indices (with √x transformed abundances) visualizing similarity relationships in species composition between forest interior (FI ●), forest margin (FM ■) and oil palm plantation (OP ▲) sites for amphibians and reptiles.

Table 7. Results of pairwise tests (one-way ANOSIMs) for differences in species composition between habitat types for amphibians and reptiles.

Pairwise test	Results of one-way ANOSIMS	
	R	*p*
Amphibians		
FI vs. FM	0.276	0.040
FI vs. OP	0.904	0.008
FM vs. OP	0.924	0.008
Reptiles		
FI vs. FM	0.056	0.317
FI vs. OP	0.816	0.008
FM vs. OP	0.654	0.008

Dimension 1 values extracted from the NMDS ordinations visualizing similarity relationships of amphibian and reptile assemblages between sites (Fig. 7) proved to be highly related to PC1 values of a PCA on habitat variables in both taxonomic groups (Table 8). This indicates that changes in species composition are strongly related to changes in woody vegetation complexity (canopy cover, shrub cover) and the availability of microhabitats (leaf litter, deadwood). In contrast, PC2 values (representing herb cover) were neither related to Dimension 1 nor Dimension 2 values of the respective NMDS ordinations.

Table 8. Correlations between PC1 and PC2 values quantifying changes in vegetation structure and microhabitat availability (compare Table 4) and Dimension 1 and 2 values extracted from NMDS ordinations visualizing similarity relationships of amphibian and reptile assemblages (Fig. 7). n.s. = non-significant ($p < 0.05$).

NMDS plots for	Dimensions	PC 1	PC 2
Amphibians	Dim 1	$r = 0.868$, $p < 0.0001$	n.s.
	Dim 2	n.s.	n.s.
Reptiles	Dim 1	$r = 0.829$, $p = 0.0001$	n.s.
	Dim 2	n.s.	n.s.

Habitat preferences of species

In a CANOCO ordination, the habitat types segregate clearly into three distinct clusters (Fig. 8). The distribution of species in the CANOCO ordination illustrates strong affinities of certain species with particular habitat types, such as *Engystomops pustulosus*, *Leptodactylus bolivianus*, *L. fragilis* or *Leptodeira septentrionalis* with OP, and *Diasporus vocator*, *Lithobates warszewitschii*, *Silverstoneia flotator* and *Corytophanes cristatus* with FI (Fig. 8).

Species

1. *Allobates talamancae*
2. *Craugastor bransfordii*
3. *Craugastor fitzingeri*
4. *Craugastor stejnegerianus*
5. *Diasporus vocator*
6. *Engystomops pustulosus*
7. *Espadarana prosoblepon*
8. *Hyalinobatrachium valerioi*
9. *Hypsiboas rosenbergi*
10. *Incilius aucoinae*
11. *Leptodactylus bolivianus*
12. *Leptodactylus fragilis*
13. *Leptodactylus savagei*
14. *Lithobates warszewitschii*
15. *Rhinella marina*
16. *Silverstoneia flotator*
17. *Smilisca sila*

Species

1. *Holcosus festiva*
2. *Holcosus leptophrys*
3. *Norops limifrons*
4. *Norops polylepis*
5. *Basiliscus basiliscus*
6. *Bothrops asper*
7. *Corytophanes cristatus*
8. *Leptodeira septentrionalis*

Habitats
- ● FI
- ■ FM
- ▲ OP

Fig. 8. Responses of (a) amphibian and (b) reptile communities and species to measured habitat variables (combined in the two factors PC1 and PC2, compare Table 4) visualized in canonical correspondence analysis ordinations. The sampled sites segregate clearly into three groups representing oil palm plantations (OP – filled, red up-triangles), forest margin (FM – filled, green squares) and forest interior (FI – filled, black circles) sites. Several species are closely associated with one of the three sampled habitat types.

Range-restricted species

Considering the range size of species revealed a severe loss of endemic amphibians in oil palm plantations (Fig. 9). Mean relative numbers of species per site that were endemic to Costa Rica and Panama dropped significantly from 33.1% at FI and 29.9% at FM sites to 10.8% at OP sites (one-way ANOVA: $F_{2,12}$ = 8.17, *p* = 0.0058). A similar pattern emerged when comparing the relative abundance of endemics between the three sampled habitat types (FI: 28.2%, FM: 22.6%, OP: 6.5%; $F_{2,12}$ = 5.05, *p* = 0.0257). In reptiles, relative richness of endemic species did not change significantly between habitats (one-way ANOVA: $F_{2,12}$ = 1.67, *p* = 0.2300), but the relative abundance of endemics dropped even sharper ($F_{2,12}$ = 17.52, *p* = 0.0003) than in amphibians from 65.8% at FI and 61.9% at FM sites to only 10.3% at OP sites (Fig. 9).
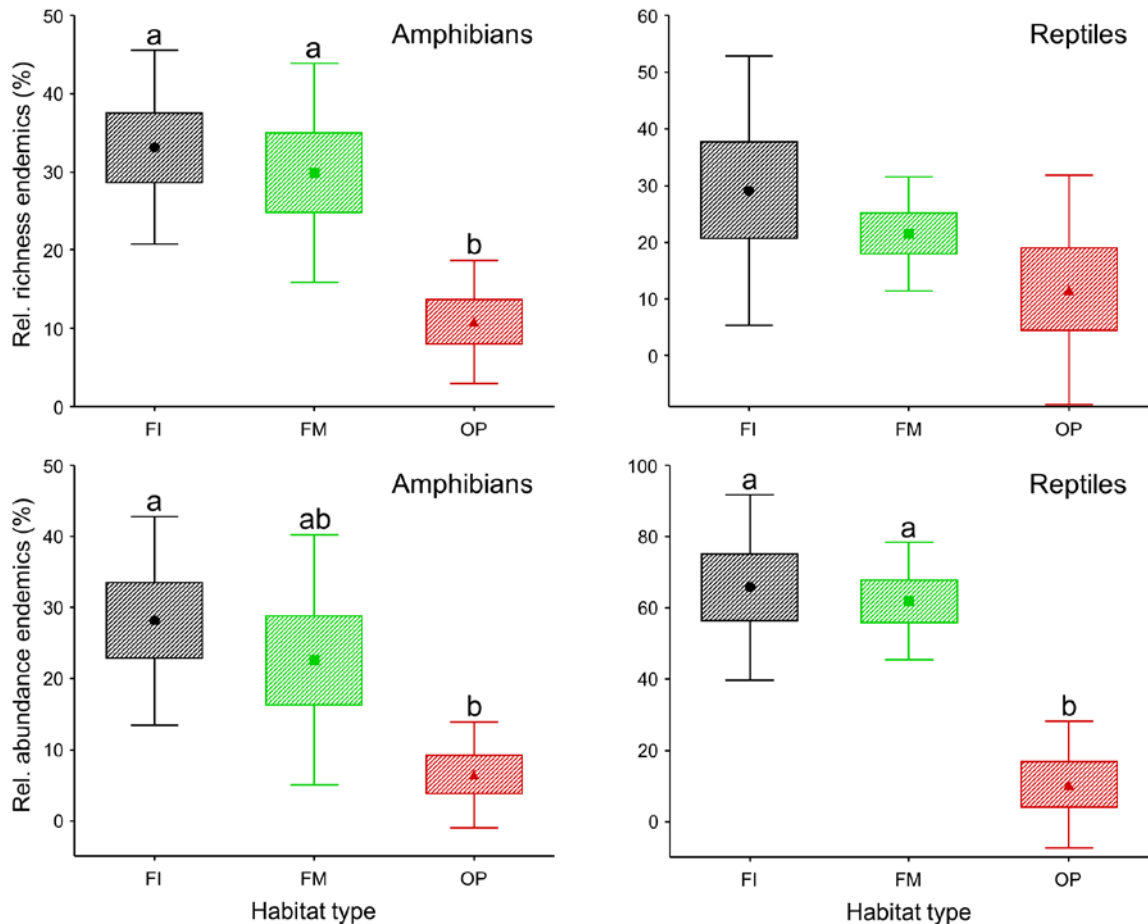

Fig. 9. Mean relative richness and abundance of amphibian and reptile species endemic to Costa Rica and Panama ± SE (box) and 95% CI (whiskers) of forest interior (FI), forest margin (FM) and oil palm plantation (OP) sites. Different letters indicate significant differences (Tukey Honest Significant Difference test) between habitats.

Discussion

Species richness

This first study from Mesoamerica on richness of amphibians and reptiles in oil palm plantations reports a strongly impoverished fauna in this land use system compared to forest habitats. Although species richness in amphibians and reptiles recorded per study site did not differ significantly between FI, FM and OP, the species accumulation curves for the overall habitats show a significant decline in species richness from the two forest habitats to OP on a larger spatial scale. This indicates a similar alpha diversity at study sites independent of the sampled habitat type but lower beta diversity in OP compared to FI and FM. This is most likely the result of the lower heterogeneity of OP sites. Indeed, the plantations in our study area are extremely uniform and characterized by very simple vegetation structure consisting of a single canopy layer provided by oil palms and an herb layer dominated by grasses. Woody understory vegetation, woody debris and a leaf litter layer are largely absent. The very low structural complexity of this land-use system was also emphasized by other studies (Fitzherbert et al. 2008; Luskin & Potts 2011; Gillespie et al. 2012; Faruk et al. 2013). The decreased structural complexity and the low canopy closure of OP can result in lower humidity and an increased temperature flux between day and night (Luskin & Potts 2011). Such conditions can negatively affect a substantial proportion of forest amphibians (Kudavidanage et al. 2012).

A meta-analysis of published studies on various animal groups (including lizards, birds and mammals) from different regions reported a dramatically reduced species richness in OPs. Total vertebrate species richness of OPs was only 38% of that recorded for natural forests and only 23% of the forest vertebrate species were found in OPs (Danielsen et al. 2009). Another analysis considering multiple vertebrate and invertebrate taxa reports that only a mean of 15% of the species found in primary forest can be recorded in OPs (Fitzherbert et al. 2008). This corresponds to our data from Costa Rica, where total species richness of amphibians and reptiles in OPs was reduced to 45.3% and 49.8% compared to the interior of natural forest, respectively, and only 31.8% of amphibian and 30.8% of reptile species found in primary forest were also found in OPs.

Sampled forest margins in our study did not represent natural but artificial forest margins adjacent to cultivated open areas. Therefore, forest species assemblages of such forest margins are not only affected by edge effects but additionally by human disturbance. However, our forest margin sites proofed to support still a higher total number of species than oil palm plantations (20 vs. 11 and 12 vs. 7 species in amphibians and reptiles, respectively). Also two previously conducted studies found significantly more species (amphibians as well as reptiles) in disturbed (logged or secondary) forests when compared to oil palm plantations (Gillespie et al. 2012; Glor et al. 2001; but see Faruk et al. 2013).

Comparing forest margins to primary forests, our study found no significant differences in species richness. Previous studies evaluating the value of disturbed forest habitats came to different conclusions. Gardner et al. (2007) examined the herpetofauna in the northeastern Brazilian Amazon and found that primary forests supported a significantly higher number of species than secondary forests. Wanger et al. (2010) analyzed amphibians and reptiles in Sulawesi, Indonesia and found differences in species richness between primary and secondary forest in reptiles but none in amphibians. Two other studies on amphibians in the wet zone of Sri Lanka (Kudavidanage et al. 2012) and in northeastern Costa Rica (Hilje & Aide 2012) however found a similar mean species richness of pristine and disturbed forests. It remains to be unknown if this reflects regional differences in the sensitivity of amphibian communities to human disturbance or if it is the result of confounding factors. For example, the ability of secondary forests to act as valuable habitat for forest species might depend on the surrounding landscape matrix (Gardner et al. 2007). The high richness of amphibians and reptile species at our disturbed FM sites is most likely caused by their close connection to remaining pristine forest, thus allowing species to migrate freely between FM sites and closed forest remaining unaffected by edge effects.

Functional diversity

To our knowledge, this represents only the third study globally and the first study from the Neotropics using different FD measures (here: FRic, FEve, FDiv and FDis) to evaluate changes in the ecological function of animal communities from pristine forest into oil palm plantations. The first two studies were conducted in Malaysian Borneo on dung beetles (Edwards et al. 2013b) and birds (Edwards et al. 2013a). In bird communities, they found

no difference in FD between degraded and primary forest. In contrast, conversion of forests (unlogged or once logged) to oil palm plantations resulted in a dramatic decrease of FD. Also in dung beetles, three calculated FD measures (FRic, FDiv and FEve) did not differ between primary and disturbed forest, while FRic and FDiv (but not FEve) were all much lower in OPs.

As in the aforementioned studies from Borneo, we also did not find differences in functional diversity measures between the interior of pristine forests and disturbed forest margins but the conversion of forest to oil palm had a strong effect on amphibians. While reptile functional diversity apparently remained stable, amphibians exhibited a dramatic decline in FRic, FDiv as well as FDis. The sharp decline of FRic in amphibians indicates that a high number of different niches occupied by them in forest habitats remain either empty or are missing in oil palm plantations. Most frog species found in OP show a very similar ecology and life history, being nocturnal, ground-dwelling explosive breeders that built foam nests on the ground or in shallow water, e.g. *Engystomops pustulosus*, *Leptodactylus bolivianus* or *Leptodactylus fragilis*. Conversely, the forests we studied were inhabited by species with a wide range of different life histories and biological traits. This becomes apparent when looking at some species encountered at forest sites such as *Dendrobates auratus*, *Diasporus diastema*, *Espadarana prosoblepon* and *Silverstoneia flotator*, all documented exclusively in forest habitats. While *E. prosoblepon* and *D. diastema* are nocturnal, *D. auratus* and *S. flotator* are predominantly diurnal species. They use different microhabitats and show different reproductive behavior. *D. auratus* is often encountered near large, buttressed trees. After the female lays a clutch of three to 13 eggs upon the leaf litter, the male cares for their offspring. After hatching, males carry the tadpoles into the canopy deposit them into the phytotelmata of bromeliads and guard them. *D. diastema* is an arboreal species with direct development that deposits its eggs in bromeliads. *E. prosoblepon* inhabits the forest understory vegetation, where it exhibits strong site fidelity and lays its eggs on leaves overhanging the water. *S. flotator* may also be found in secondary forests and generally lives and breeds in the leaf litter. After hatching, the tadpoles are transported to forest streams by the male (IUCN 2013).

A decline of FDiv as found for amphibians can indicate a decrease in niche differentiation. Such communities with a low FDiv may have a decreased ecosystem function as result of less efficient resource use (Mason et al. 2005). This may be illustrated by the loss of

abundant forest-dependent specialists such as *Hyalinobatrachium valerioi*, *Diasporus vocator* or *Allobates talamancae* towards our OP sites. *A. talamancae* is a ground-dwelling frog requiring leaf litter as habitat and oviposition site. *D. vocator* needs leaf litter as well as understory vegetation and *H. valerioi* lays its eggs on the undersurface of leaves along small streams, where its tadpoles drop into the water after hatching. These structural components of forest sites are largely or completely absent in OPs. In contrast, the most abundant species in our sampled plantations were generalists (e.g. *Engystomops pustulosus*, *Leptodactylus bolivianus* and *L. fragilis*) with a low extent of niche differentiation.

Furthermore, FDis decreased significantly towards OP. An increased FDis should be visible when niche complementarity enhances either occurrence probabilities of species, abundances of species or both (Mason et al. 2013). In contrast, decreased FDis indicates an increase of environmental stress and a decrease of ecosystem function. Hence, our data provide evidence for a strong environmental filtering of the regional amphibian species pool in oil palm plantations with its potentially associated negative effects on provided ecosystem functions.

Surprisingly, FEve did not respond to the dramatic changes in vegetation structure and microhabitat availability in OPs, although simulated communities proved to be sensitive to environmental filtering (Mouchet et al. 2010).Also, empirical data showed that functional evenness was negatively affected by habitat fragmentation and environmental gradients of disturbance, respectively (Pakeman 2011; Ding et al. 2013). However, also FEve in dung beetles did not differ between forest and OPs in Borneo (Edwards et al. 2013b).

Species composition and habitat preferences

The changes in species composition from forest habitats towards OP as recorded in our study area are similar to patterns documented for amphibian communities in other regions (Gillespie et al. 2012; Faruk et al. 2013). This study reports for the first time, that also species composition of reptiles appear to respond in a very similar way to oil palm cultivation, which was characterized by very distinct reptile communities. In amphibians as well as reptiles oil palm plantations appear to attract predominantly disturbance-tolerant species, while being a hostile environment for most forest species (Gillespie et al. 2012;

Faruk et al. 2013). The majority of species encountered at forest interior or forest margin sites were missing in oil palm plantations (amphibians: 68.2% and 55.0%, respectively; reptiles: 69.2% and 66.7%, respectively). Reptile species proofed to be particularly sensitive as oil palms provide a habitat for only 25% (four species) of the species encountered at both forest habitats.

In amphibians, the dramatically reduced diversity of microhabitats may be a key factor explaining the decreased overall anuran richness in OP compared to forest habitats. This may be even worse for arboreal species only covered incompletely by our sampling. Particularly leaf litter accumulations and phytotelmata for oviposition as provided by tank bromeliads or tree holes play an important role in the reproduction of many tropical forest amphibians (Gardner et al. 2007). Oil palm plantations lack most of these microhabitats due to the almost complete absence of forest plant species (Donald 2004). This might be the reason why common forest species like *Allobates talamancae*, *Diasporus diastema*, *Diasporus vocator* or *Silverstoneia flotator*, depending on either phytotelmata or leaf litter as oviposition site, are completely missing in oil palm plantations.

The shift in species composition in reptiles is primarily based on a decreasing abundance as well as species number of lizards in oil palms, which could be explained by the lack of understory microhabitats reptiles use for perching (Glor et al. 2001). As in amphibians, forest dependent species were mostly absent in plantations (e.g. *Holcosus leptophrys* or *Norops polylepis*) while remaining abundant reptile species were primarily disturbance-tolerant snakes (e.g. *Bothrops asper* and *Leptodeira septentrionalis*) and one herbivorous lizard (*Basiliscus basiliscus*).

Conservation implications

With 145 species of amphibians and reptiles known to occur in the Golfo Dulce region (Höbel 2008), representing a substantial proportion (36.6 %) of the Costa Rican herpetofauna (396 species; Savage & Bolaños 2009), the region can be classified as biodiversity hotspot for amphibians and reptiles, including many range-restricted species.

In our study, we documented ten species endemic to Costa Rica and Panama, two of which can be found only in the Golfo Dulce region in southwestern Costa Rica (*Phyllobates*

vittatus and *Porthidium porrasi*). Both, abundance (in amphibians and reptiles) and richness (in amphibians only) of endemic species decreased from forest habitats towards OPs. Of eight endemic amphibians, seven species were completely restricted to forest habitats with four being rare (n ≤ 2 observed individuals) and three common (n ≥ 10). The only endemic amphibian species (*Incilius aucoinae*) occurring in oil palm monocultures showed an increase in abundance towards plantations which might be due to its ability reproduce even in highly degraded habitats (IUCN 2013). In reptiles, *Porthidium porrasi* was found only once at one FI site. *Norops polylepis* which presented a highly abundant species in forest habitats (n= 153; 58.6% of all individuals in reptiles) was encountered only five times in oil palm plantations.

Besides preventing further conversion of natural and secondary forests to oil palm plantations, an increase of structural heterogeneity in oil palm plantations should be promoted to decrease their potential function as barrier for dispersal movements of reptiles and amphibians between forest fragments. This would most likely also result in higher abundances of species such as *Norops* spp., which are able to suppress populations of herbivorous insects (Dial & Roughgarden 1995) and therefore could play an important role as biological control agent of pest insects in oil palm plantations.

The extensive use of palm frond mounds by amphibians and reptiles (pers. obs.) also emphasizes the need for increasing structural complexity of oil palm plantations. The majority of the herpetofauna inhabiting oil palm plantations most likely finds shelter in those structures during the day and many individuals of different species (e.g. *Micrurus alleni*, *Incilius aucoinae*, *Engystomops pustulosus*) immediately sought shelter in those mounds when encountered during surveys (pers. obs.).

To date, suggestions on how to increase the value of oil palm plantations for amphibians and reptiles are still scarce but as previous studies on butterflies, birds and mammals have proven (Koh 2008; Nájera & Simonetti 2010a, 2010b; Ramírez & Simonetti 2011), enhancing the structural complexity of plantations might mitigate the vastly negative effect oil palm monocultures have on biodiversity. In our study, the almost complete absence of leaf litter, understory vegetation and woody debris as well as the more open canopy appeared to represent an important driver for reducing herpetofauna species richness in oil palm plantations. Enhancing understory vegetation could help making plantations a less

hostile environment for some amphibians and reptiles. Still, as discussed in Faruk et al. (2013), plantations present a human-modified and frequently disturbed habitat and even those management measures might not be enough to promote the occurrence of forest specialists. Therefore, to complement such efforts and prevent losing the majority of the tropical herpetofauna in human-modified landscapes, it is essential to protect any kind of forested habitat ranging from secondary forests to strips of gallery forests and remnants of old-growth forests.

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Appendix

Table A1. Coordinates and habitat characteristics of study sites.

Site	Coordinates	Mean leaf litter cover (%)	Mean herb cover (%)	Mean shrub cover (%)	Median canopy cover (%)	Amount of deadwood
FI1	N 8.696130° W 83.203659°	57	11	72	88	11
FI2	N 8.670956° W 83.198562°	38	54	42	92	22
FI3	N 8.702917° W 83.205308°	62	62	59	83	29
FI4	N 8.699113° W 83.207890°	87	33	42	92	36
FI5	N 8.704233° W 83.203474°	62	32	29	89	30
FM1	N 8.700300° W 83.203112°	91	30	38	83	12
FM2	N 8.683977° W 83.198558°	65	42	40	83	18
FM3	N 8.689779° W 83.180629°	70	37	53	81	10
FM4	N 8.702217° W 83.213737°	43	35	36	89	11
FM5	N 8.709846° W 83.212481°	74	31	31	84	10
OP1	N 8.698166° W 83.198537°	3	29	3	82	0
OP2	N 8.705249° W 83.215272°	0	2	0	80	0
OP3	N 8.701415° W 83.190139°	0	12	0	67	0
OP4	N 8.719463° W 83.206079°	0	48	7	76	0
OP6	N 8.715599° W 83.172103°	0	43	2	70	0

Table A2. Sampling dates for each study site. Night surveys printed bold.

Site	Sampling dates
FI1	6-Jul, **10-Jul**, 16-Jul, **27-Jul**, 9-Aug, **18-Aug**, 23-Aug, 7-Sep, **11-Sep**, 13-Sep
FI2	4-Jul, **4-Jul**, 20-Jul, **2-Aug**, **21-Aug**, **30-Aug**, 4-Sep, 10-Sep, 21-Sep
FI3	3-Jul, **5-Jul**, **17-Jul**, **26-Jul**, 1-Aug, 24-Aug, **25-Aug**, 7-Sep, **8-Sep**, 14-Sep
FI4	7-Jul, **13-Jul**, 2-Aug, **4-Aug**, **17-Aug**, **25-Aug**, 2-Sep, 9-Sep, **16-Sep**, 22-Sep
FI5	6-Jul, **11-Jul**, 18-Jul, **8-Aug**, **17-Aug**, 27-Aug, **31-Aug**, 8-Sep, 14-Sep, **23-Sep**
FM1	3-Jul, **5-Jul**, 16-Jul, **28-Jul**, **18-Aug**, 1-Sep, 13-Sep, 22-Sep, **22-Sep**, **25-Sep**
FM2	4-Jul, **11-Jul**, 20-Jul, **2-Aug**, **30-Aug**, 4-Sep, 10-Sep, **13-Sep**, 21-Sep
FM3	8-Jul, **11-Jul**, 6-Aug, **16-Aug**, **19-Aug**, 20-Aug, **1-Sep**, 12-Sep, 23-Sep, **23-Sep**
FM4	9-Jul, **14-Jul**, 4-Aug, 22-Aug, **27-Aug**, **28-Aug**, **7-Sep**, 15-Sep, 25-Sep
FM5	9-Jul, **14-Jul**, **12-Aug**, 18-Aug, **28-Aug**, 11-Sep, 16-Sep, **21-Sep**, 27-Sep
OP1	7-Jul, **7-Jul**, **16-Jul**, 19-Jul, 26-Jul, 6-Aug, **6-Aug**, **23-Aug**, **14-Sep**, 21-Sep
OP2	9-Jul, **14-Jul**, 26-Aug, **27-Aug**, **28-Aug**, **7-Sep**, 11-Sep, 15-Sep, 25-Sep
OP3	8-Jul, **11-Jul**, 17-Jul, **1-Aug**, 16-Aug, **16-Aug**, **1-Sep**, 12-Sep, **22-Sep**, 23-Sep
OP4	9-Jul, **14-Jul**, **12-Aug**, 18-Aug, **29-Aug**, 11-Sep, 16-Sep, **21-Sep**, 27-Sep
OP6	7-Jul, **12-Jul**, **19-Jul**, 5-Aug, **6-Aug**, **23-Aug**, 30-Aug, 12-Sep, 24-Sep

Table A3. Results of correlations between habitat variables.

	(1)	(2)	(3)	(4)
(1) Leaf litter cover (%)				
(2) Herb cover (%)	$r = 0.200$, $p = 0.4753$			
(3) Shrub cover (%)	$r = 0.787$, $p = 0.0005$	$r = 0.265$, $p = 0.3392$		
(4) Canopy cover (%)	$r = 0.642$, $p = 0.0098$	$r = 0.170$, $p = 0.5444$	$r = 0.640$, $p = 0.0102$	
(5) Deadwood	$r = 0.728$, $p = 0.0021$	$r = 0.412$, $p = 0.1267$	$r = 0.639$, $p = 0.0103$	$r = 0.731$, $p = 0.0020$

Table A4. Trait matrix used to calculate functional diversity measures for amphibians. Unless mentioned otherwise: 0…no, 1…yes (BS - mean max. body size [mm], D – diurnal, N – nocturnal, GW – ground-dwelling, VE – vegetation, LOS – lotic systems, LES – lentic systems, GR – ground, LL – leaf litter, PH – phytotelmata, LS – surface of leaves, CS – clutch size [0 = single eggs to small egg clumps, 1 = explosive breeders])

Species	Resource quantity	Activity		Vertical stratification		Oviposition site						Egg clutches
	BS	D	N	GD	VE	LOS	LES	GR	LL	PH	LS	CS
Allobates talamancae	24.50	1	0	1	0	0	0	0	1	0	0	0
Bolitoglossa lignicolor	143.27	0	1	1	1	0	0	0	0	1	0	0
Craugastor bransfordii	24.50	1	1	1	0	0	0	1	0	0	0	0
Craugastor fitzingeri	44.00	1	1	1	1	0	0	0	1	1	0	0
Craugastor stejnegerianus	20.20	1	1	1	0	0	0	1	0	0	0	0
Dendrobates auratus	41.00	1	0	1	1	0	0	0	1	0	0	0
Dendropsophus microcephalus	28.00	0	1	1	1	0	1	0	0	0	0	0
Diasporus diastema	22.50	0	1	1	1	0	0	0	1	1	0	0
Diasporus vocator	17.00	0	1	1	1	0	0	0	1	1	0	0
Engystomops pustulosus	34.50	0	1	1	0	0	1	0	0	0	0	1
Espadarana prosoblepon	29.50	0	1	0	1	0	0	0	0	0	1	0
Hyalinobatrachium colymbiphyllum	28.00	0	1	0	1	0	0	0	0	0	1	0
Hyalinobatrachium valerioi	25.00	0	1	0	1	0	0	0	0	0	1	0
Hypsiboas rosenbergi	80.50	0	1	1	1	0	1	0	0	0	0	1
Incilius aucoinae	84.00	0	1	1	0	1	0	0	0	0	0	1
Incilius coniferus	83.00	0	1	0	1	0	1	0	0	0	0	1
Leptodactylus bolivianus	107.50	0	1	1	0	0	1	0	0	0	0	1

Species	Resource quantity	Activity		Vertical stratification		Oviposition site						Egg clutches
	BS	D	N	GD	VE	LOS	LES	GR	LL	PH	LS	CS
Leptodactylus fragilis	38.00	0	1	1	0	0	0	1	0	0	0	1
Leptodactylus savagei	181.00	0	1	1	0	0	0	1	0	0	0	1
Lithobates warszewitschii	52.50	1	1	1	0	1	0	0	0	0	0	1
Oedipina alleni	129.27	0	1	1	0	0	0	0	1	0	0	0
Phyllobates vittatus	28.50	1	0	1	0	0	0	0	1	0	0	0
Pristimantis cruentus	35.00	0	1	1	1	0	0	0	0	1	0	0
Rhaebo haematiticus	61.00	0	1	1	0	0	1	0	0	0	0	1
Rhinella marina	160.00	0	1	1	0	0	1	0	0	0	0	1
Sachatamia albomaculata	30.50	0	1	0	1	0	0	0	0	0	1	0
Silverstoneia flotator	17.25	1	0	1	0	0	0	0	1	0	0	0
Smilisca sila	53.50	0	1	1	1	0	1	0	0	0	0	1

Table A5. Trait matrix used to calculate functional diversity measures for reptiles. 0…no, 1…yes (BS - Mean max. body size [mm], D – diurnal, N – nocturnal, GW – ground-dwelling, VE – vegetation, HE – herbivorous, EG – eggs, IN – invertebrates, SV – small vertebrates)

Species	Resource quantity	Activity		Vertical stratification		Diet			
	BS	D	N	GD	VE	HE	EG	IN	SV
Basiliscus basiliscus	755	1	0	1	1	1	0	1	1
Bothrops asper	2350	0	1	1	1	0	0	1	1
Caiman crocodilus	2475	1	0	1	0	0	0	1	1
Coniophanes fissidens	715	1	0	1	0	0	1	0	1
Corytophanes cristatus	381	1	0	1	1	0	0	1	1
Holcosus festiva	397	1	0	1	0	0	0	1	1
Holcosus leptophrys	403	1	0	1	0	0	0	1	0
Iguana iguana	1725	1	0	1	1	1	0	0	0
Imantodes cenchoa	1250	0	1	0	1	0	0	0	1
Leptodeira septentrionalis	1010	0	1	1	1	0	1	0	1
Marisora unimarginata	249	1	0	1	1	0	0	1	0
Mastigodryas melanolomus	1500	1	0	1	0	0	1	1	1
Micrurus alleni	983	1	1	1	0	0	0	0	1
Norops capito	248	1	0	1	1	0	0	1	1
Norops lemurinus	228	1	0	1	1	0	0	1	0
Norops limifrons	156	1	0	1	1	0	0	1	0
Norops polylepis	169	1	0	1	1	0	0	1	0
Porthidium porrasi	568	0	1	1	1	0	0	0	1
Scincella cherriei	159	1	0	1	0	0	0	1	0

Table A6. Species recorded at our sampling sites. Nomenclature as per (Savage & Bolaños 2009) with updates on classification according to AmphibiaWeb (2014) and Uetz & Hošek (2014).

Species	Forest interior					Forest margin					Oil palm plantation				
	FI1	FI2	FI3	FI4	FI5	FM1	FM2	FM3	FM4	FM5	OP1	OP2	OP3	OP4	OP6
Amphibians															
Plethodontidae															
Bolitoglossa lignicolor	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Oedipina alleni	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
Rhinophrynidae															
Pristimantis cruentus	-	-	+	-	-	-	-	-	+	-	-	-	-	-	-
Centrolenidae															
Espadarana prosoblepon	-	+	+	-	+	-	+	-	+	+	-	-	-	-	-
Hyalinobatrachium colymbiphyllum	-	+	-	-	-	-	-	-	-	+	-	-	-	-	-
Hyalinobatrachium valerioi	-	-	+	-	-	+	-	-	+	+	-	-	-	-	-
Sachatamia albomaculata	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Leiuperidae															
Engystomops pustulosus	+	-	-	+	-	-	-	-	-	-	+	+	+	+	+
Leptodactylidae															
Leptodactylus bolivianus	-	-	-	-	-	-	-	-	-	+	+	+	+	+	+
Leptodactylus fragilis	-	-	-	-	-	-	-	-	-	-	+	+	+	+	+
Leptodactylus savagei	+	+	+	-	+	+	+	+	+	+	+	+	+	+	-
Aromobatidae															
Allobates talamancae	-	+	-	-	+	+	+	-	-	-	-	-	-	-	-

Species	Forest interior					Forest margin					Oil palm plantation				
	FI1	FI2	FI3	FI4	FI5	FM1	FM2	FM3	FM4	FM5	OP1	OP2	OP3	OP4	OP6
Dendrobatidae															
Dendrobates auratus	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
Phyllobates vittatus	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Silverstoneia flotator	-	+	+	-	+	+	+	-	-	-	-	-	-	-	-
Bufonidae															
Incilius aucoinae	-	-	-	+	-	+	+	+	+	+	+	+	+	+	-
Incilius coniferus	-	-	-	-	-	-	+	-	+	-	-	-	-	-	-
Rhaebo haematiticus	-	-	-	-	-	-	-	-	+	-	-	-	+	-	-
Rhinella marina	-	-	-	-	-	-	-	+	-	-	+	-	-	-	+
Hylidae															
Dendropsophus microcephalus	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hypsiboas rosenbergi	+	-	+	-	+	-	-	+	-	-	-	-	+	-	-
Smilisca sila	-	+	-	-	-	-	-	+	-	-	+	+	-	-	-
Eleutherodactylidae															
Diasporus diastema	-	-	+	+	+	-	-	-	-	-	-	-	-	-	-
Diasporus vocator	+	-	+	+	+	-	+	-	+	-	-	-	-	-	-
Craugastoridae															
Craugastor bransfordii	-	+	-	-	+	+	+	+	+	+	-	+	-	-	-
Craugastor fitzingeri	+	+	+	+	+	+	+	-	+	+	+	+	+	+	+
Craugastor stejnegerianus	-	+	-	+	+	+	+	+	+	-	-	-	-	-	-
Ranidae															
Lithobates warszewitschii	+	-	+	-	+	+	-	-	-	-	-	-	-	-	-

Species	Forest interior					Forest margin					Oil palm plantation				
	FI1	FI2	FI3	FI4	FI5	FM1	FM2	FM3	FM4	FM5	OP1	OP2	OP3	OP4	OP6
Reptiles															
Alligatoridae															
Caiman crocodilus	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
Scincidae															
Marisora unimarginata	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-
Scincella cherriei	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
Teiidae															
Holcosus festiva	-	+	-	-	-	-	-	+	+	-	-	-	-	+	-
Holcosus leptophrys	+	-	+	+	+	+	+	-	+	+	-	-	-	-	-
Iguanidae															
Iguana iguana	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
Corytophanidae															
Basiliscus basiliscus	-	+	-	-	-	+	-	+	+	+	+	+	+	+	+
Corytophanes cristatus	+	-	-	+	+	-	-	-	-	-	-	-	-	-	-
Dactyloidae															
Norops capito	+	-	-	-	+	-	-	-	+	-	-	-	-	-	-
Norops lemurinus	-	-	-	-	-	-	-	-	-	-	+	-	-	+	-
Norops limifrons	+	+	-	-	+	-	+	-	+	-	-	-	-	-	-
Norops polylepis	+	+	+	+	+	+	+	+	+	+	-	+	+	-	-
Viperidae															
Bothrops asper	+	-	-	-	-	+	-	-	+	-	+	+	+	-	-
Porthidium porrasi	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-

Species	Forest interior					Forest margin					Oil palm plantation				
	FI1	FI2	FI3	FI4	FI5	FM1	FM2	FM3	FM4	FM5	OP1	OP2	OP3	OP4	OP6
Colubridae															
Coniophanes fissidens	-	-	-	-	+	+	-	-	+	-	-	-	-	-	-
Imantodes cenchoa	-	+	-	-	+	-	-	-	-	+	-	-	-	-	-
Leptodeira septentrionalis	-	-	-	-	-	-	-	-	-	-	+	-	-	-	+
Mastigodryas melanolomus	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-
Elapidae															
Micrurus alleni	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-

Curriculum Vitae

Persönliche Information

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Ausbildung

1998 – 2006	Bundesrealgymnasium „Gröhrmühlgasse" in Wiener Neustadt mit naturwissenschaftlich-ökologischem Schwerpunkt. Matura mit gutem Erfolg bestanden.
2006 – 2011	Bachelorstudium Biologie/Zoologie an der Universität Wien. Bachelorarbeit: „Blütenbesuchende Vögel in La Gamba, Costa Rica"
2007 – 2011	Bachelorstudium Koreanologie an der Universität Wien
Seit 2011	Masterstudium Naturschutz und Biodiversitätsmanagement an der Universität Wien
Seit 2013	Masterarbeit „Effects of oil palm agriculture on reptiles and amphibians in the Pacific lowlands of Costa Rica"

Auslandsaufenthalte zu Studienzwecken

2009	3-wöchiges Projektpraktikum „Tropenbiologie in Costa Rica" in der Forschungsstation Estacíon Tropical La Gamba, Costa Rica
2010	4-monatiger Sprachaufenthalt in Seoul, Südkorea
2011	6-wöchiges Projektpraktikum zum Schutz der Unechten Karettschildkröte (Caretta caretta) in Fethiye, Türkei
2013	3-monatiger Aufenthalt in Costa Rica zur Datenaufnahme im Rahmen der Masterarbeit

Ehrenamtliche Tätigkeiten & Praktika

Seit 2011	Mithilfe an diversen Restaurationsprojekten des Naturschutzbundes Niederösterreich
2014	6-wöchiges Praktikum bei BirdLife Österreich

Sprachkenntnisse

Deutsch	Muttersprache
Englisch	Sehr gute Kenntnisse (mündlich wie schriftlich)
Französisch	Matura-Niveau
Koreanisch	Grundkenntnisse
Japanisch	Grundkenntnisse