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Effects of topography on structure and composition of the understorey herpetofauna of a lowland rainforest in the Golfo Dulce Region, Costa Rica

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1. Introduction

Analyzing the main forces affecting species richness and composition in different ecosystems is one of the most challenging and complex fields in biology. Different studies revealed that topographic gradients are one of the crucial factors having a significant influence on those biodiversity measurements (Basnet 1992; MacArthur 1965; Castilho et al. 2006; Duellmann 1999; Parris & McCarthy 1999; van Rensburg et al. 2002; Vasconcelos et al. 2010; Webb et al. 1999; Yu et al. 2015). For example forest habitat variables such as soil moisture, microclimate, leaf-litter layer and vegetation structure, all influenced by topography, proved being capable of affecting the occurrence of species (Fauth et al. 1989; Urbina-Cardona et al. 2006). Moreover, besides having effects on a regional scale (Coblentz & Riitters 2004; Davies et al. 2007; Kerr & Pecker 2001; Kerr & Packer 1997; Scott 1976; Zerm et al. 2001) topography can shape biodiversity already on small spatial scales (Everson & Boucher 1998; Kubota et al. 2004; Pearman 1997; Webb et al. 1999). Tropical rainforests are proven to contain the highest biodiversity of all ecosystems, especially in lowland areas with high annual rainfall distribution (Gentry 1992). As many rainforest species appear to be characterized by particularly small ecological niches a transition from ridge to creek forests can result in a significant change of species assemblages within a small area, as documented for tropical butterflies (Binz et al. 2014).

Tropical amphibians and reptiles already proved to be highly sensitive to environmental changes caused by human activities (Brooks et al. 2002; Collins & Crump 2009; Fischer et al. 2005; Gallant et al. 2014; Sodhi et al. 2008; Urbina-Cardona et al. 2006). However, also natural heterogeneity of environmental conditions on small spatial scales can affect the occurrence of amphibian as demonstrated for changes in leaf litter thickness, the amount of dead wood, leaf litter cover and shrub cover, which all proved to influence herpetofaunal richness (Wanger et al. 2010). Nevertheless the relationship between topography and biodiversity in herpetofauna is still poorly understood, although first studies indicate that the occurrence of individual leaf litter frog species can be explained by topography (Heinen 1992; Menin et al. 2007; Zhou et al. 2015). Currently amphibians and reptiles belong to one of the most threatened groups of terrestrial vertebrates (Collins & Crump 2009; Stuart et al. 2004). Considering the current situation of massive species loss during the last few decades, a deeper understanding of essential factors influencing species composition is highly recommended (Brooks et al. 2002; Gibbon et al. 2000). A study from La Selva Biological Station in Costa Rica has already shown that the population density of terrestrial amphibians and common reptiles declined by nearly 75% during the last 30 years. In this case scientists suggest that climatic shifts influenced the amount of standing leaf litter and this led to a rapid decline of herpetofaunal species (Whitfield et al. 2007).

This study assessed effects of small-scale topography on the herpetofauna of a lowland forest area in southwestern Costa Rica. The Golfo Dulce Region, where the study took place, is an important biological hotspot with 145 known species of amphibians and reptiles (Campbell 1998; Höbel 2008; Leenders 2001; Myers et al. 2000; Savage 2002). The region's lowland ridge forests are typically characterized by lower humidity, higher insolation and higher plant species richness compared to creek forest sites. The latter are extremely humid throughout the year, most likely due to being closely situated to small forest streams flowing at the center of the creeks. Slope forests are intermediate between these two forest types in terms of plant richness and microclimate (Weissenhofer et al. 2008). First studies reported conspicuous effects of topography on the structure and composition of forest butterflies (Binz et al. 2014) and birds (Schulze unpublished). The aim of this study was to use amphibians and reptiles as model organisms to investigate how local biodiversity is shaped by small-scale topographical heterogeneity.

In particular, the following hypotheses were tested:

(1) Investigated forest types differ in species richness, abundance and species composition of reptiles and amphibians. In frogs, highest abundance and species richness may be found in creek forest due to a more humid microclimate and permanent access to freshwater sites for oviposition. Differences between forest types may be less pronounced in reptiles. Besides, the composition of species assemblages may differ between forest types due to different biotic and abiotic conditions.

(2) The occurrence of individual species is affected by habitat characteristics, such as leaf litter volume and understorey vegetation structure, all differing between forest types. For example, certain species, such as small leaf litter frogs, may reach particularly high abundances at forest sites with a high leaf litter ground cover, while other amphibians depend on the presence of small forest streams at creeks for oviposition. Certain lizards occupying sunspots on the forest floor may be more abundant at ridge forest sites where the sunlight can more easily penetrate the upper vegetation layers.

2. Methods

2.1. Study area and study sites

This study was carried out in proximity of the Tropical Research Station La Gamba (N 8°42'61", W 83°12'97") located at the margin of the Esquinas Forest (Piedras Blancas National Park and "Regenwald der Österreicher") on the Pacific slope of southern Costa Rica. It's one of the wettest lowland forests in Costa Rica and even in the whole of Central America with an average annual

precipitation of 5,836 mm. Precipitation peaks are in September and October, the driest months are January till March – but still precipitation is not much lower than in adjacent months. The average yearly temperature is 28.2°C (Huber & Weissenhofer 2008). Relative humidity is with 88.3 % equally high throughout the year and with 97.7 % even higher within the forest (Aschan 1997). During our study period climate data were recorded every day and highest amount of rainfall and humidity was measured in November. Highest temperatures occurred in December (compare Appendix Table A1).

The area's high topographical heterogeneity facilitates different forest types due to varying microclimate and soil parameters (Weissenhofer et al. 2008). Six study sites were sampled in ridge (sites RF1-6), slope (SF1-6) and creek forest (CF1-6) forest, respectively (Fig. 1). So in total data were collected on 18 different transects. Study sites were situated at elevations between 80m a.s.l. in creek and 290m a.s.l. on ridge forest, represent (near-) primary forest sites and are located within a large forest block. Hence, they are no obvious dispersal barriers between sites. All study sites were already selected in the course of a study on butterflies, based on an available vegetation map of the area (Weissenhofer et al. 2008). Selected sites were distributed over approximately 1.5 km²; distances between sampled forest sites ranged between 110 and 1,390 m. The spatial distribution of study sites is not spatially autocorrelated (compare Binz et al. 2014).

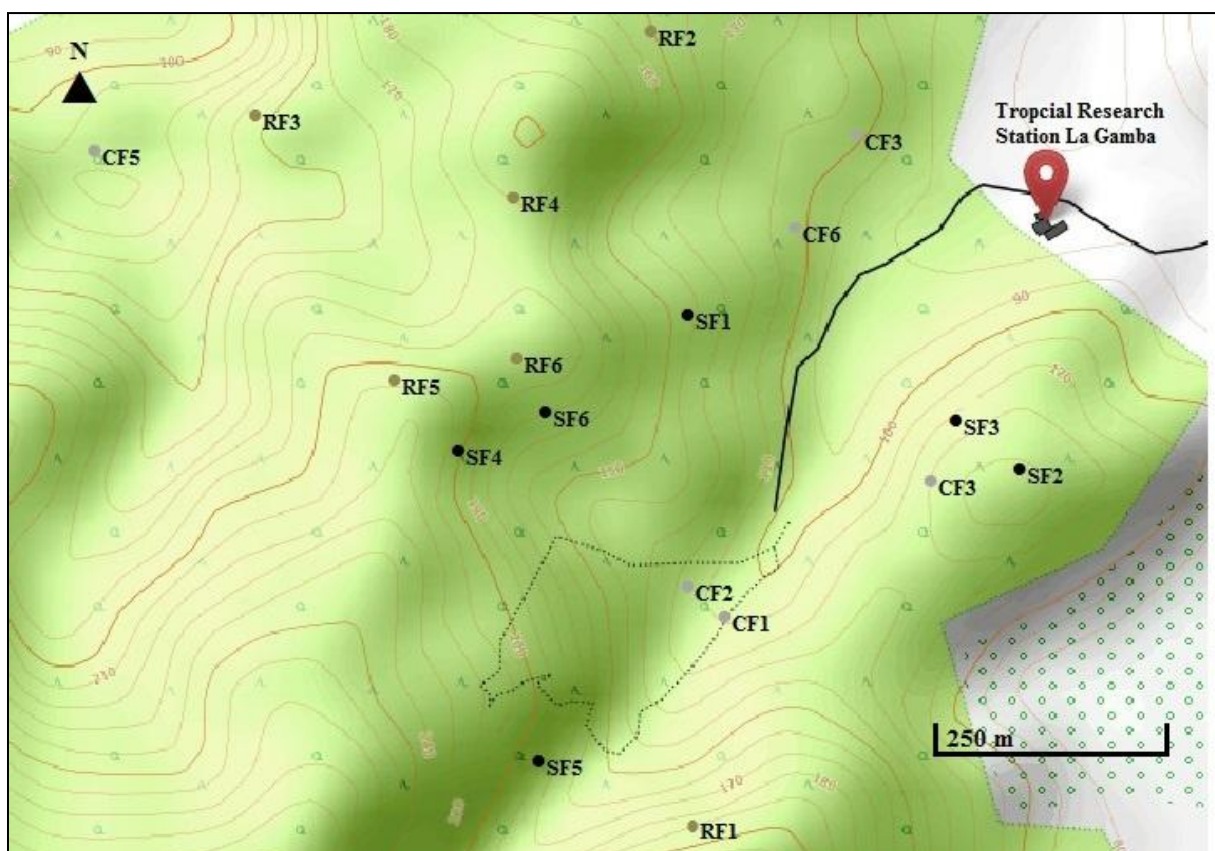


Fig. 1: Map of the 18 study sites located in ridge forest (RF), slope forest (SF) and creek forest (CF) near the Tropical Research Station La Gamba.

2.2. Sampling of amphibians and reptiles

At each study site reptiles and amphibians were recorded along a 100 m transect by visual surveys (Heyer et al. 1994; Veith et al. 2004). Each transect was sampled seven times during the day (between 9:00 and 16:00) and at night (between 19:00 and 06:00), respectively, between 01 November 2015 and 31 January 2016 (compare Appendix Table A2). Randomized sampling time of each plot and habitat category prevented repeated sampling of the same plot at the same time. During one sampling unit all reptiles and amphibians were recorded which could be detected within a band of 2 m at both sides of the transect in understory vegetation as well as leaf litter and dead wood (Doan 2003; Gallmetzer & Schulze 2015; Wanger et al. 2010). Each transect census lasted for one entire hour if working alone and half an hour, if two people were searching. Night surveys were conducted using a head torch (Gallmetzer & Schulze 2015). Specimens found were photographed and – when necessary for identification – caught and measured. Animals were identified in the field or in the laboratory using a microscope and referring to published monographs and internet sources (AmphibiaWeb 2014; Chacón & Johnston 2013; Leenders 2001; Savage 2002; Uetz & Hošek 2014).

2.3. Habitat variables

Various habitat variables were measured, which proved to be important for explaining differences in amphibian and reptile assemblages in tropical forest understory (Vonesh 2001; Wanger et al. 2010). For each of the 18 study sites the number of lying and standing deadwood, understory density and canopy cover were recorded (compare Appendix Table A3). But just the amount of lying and standing deadwood was measured during this three month survey period. The quantity of deadwood was defined as the total number of logs and branches with a diameter of >10 found within a buffer of 2m around each transect. Data for canopy cover and understory density were taken from Binz (2010), because the same transects were used in that research. To measure understory density, a range finder was pointed randomly into the understorey 5 times (once every ca. 20 m) at each site of the trail. Understorey density was then quantified as the mean of the 10 measured values. A higher mean distance then indicates a lower understory density. For measuring canopy cover, canopy photographs were taken along each transect every ca. 20 m. Pictures were then all adjusted to an identical size of 1050 x 788 pixels using the software PIXresizer 2.0.4. Subsequently, the software ImageJ 1.42 was used to convert the photographs into black and white pictures. The percentage of black pixels was then taken as measure for canopy cover. For each transects the mean of all five photographs was calculated.

2.4. Data analysis

All statistical tests were, unless stated otherwise, calculated with R 1.9-2 (R Core Team, University of Auckland, New Zealand) and valuated as significant when $p < 0.05$. Specimens that could not be identified at species level were excluded from further analysis (reptiles: 0, amphibians: 11).

To measure the influence of habitat type on habitat variables analyses of variance (ANOVAs) were conducted. If habitat variables proved to differ significantly between habitat types, subsequently Tukey's Honest Significant Difference Tests were calculated. Also multicollinearity of habitat variables was tested by creating a correlation matrix with R 1.9-2.

One way analyses of variance (ANOVAs) were conducted to test for differences in total species richness and species abundance of sampling sites between forest types. If species richness or abundance proved to differ significantly between habitat types, subsequently Tukey's Honest Significant Difference Tests were calculated and results illustrated in a boxplot. To assess sampling completeness and compare total species richness among habitat types sample-based species accumulation curves were calculated with EstimateS 9.1.0 (Robert K. Colwell, University of Connecticut, USA) by carrying out 100 random re-orderings of sampling units; curves were extrapolated to double sampling amount for every forest type (Colwell et al. 2012; Magurran 2004). Accumulation curves were calculated for amphibians and reptiles separately. Generalized linear mixed models (GLMMs) were used to test for the influence of habitat variables and forest type on total species richness and for both taxonomic groups separately. To test for relationships between total abundance and occurrence frequency (= total number of sites at which a species was recorded) of amphibians and reptile species, respectively, correlations were calculated in R 1.9-2.

Bray-Curtis similarities were calculated for all pairwise comparisons of sampling sites to quantify similarities of species compositions. Subsequently, similarity relationships were visualized using non-metric multidimensional scaling (NMDS) ordinations. Resulting stress values < 0.20 were considered as reliable (Clarke 1993). This analysis was conducted in PAST 2.17c (Øyvind Hammer, Natural History Museum, University of Oslo). In advance, abundances were square root transformed to reduce the influence of highly dominant species. To test for differences in species composition between forest types one-way analyses of similarity (ANOSIMs) with 999 random permutations of the similarity matrix were conducted for reptiles and amphibians separately (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 of the habitat variables (Gallmetzer & Schulze 2015).

With a Canonical Correspondence Analyses (CCAs) conducted in R 1.9-2 the influence of environmental factors on species composition was calculated. Species represented with less than 5 individuals were excluded from this analysis (31 species excluded, 28 species included).

For all sampled species relevant literature (AmphibiaWeb 2004; Savage et al. 2002) was used to classify if they are (a) water-dependent or not and if they (b) dependent on direct sunlight or not. Subsequently we calculated the relative abundance and richness of species depending on water and direct sunlight for each sampling site and calculated one-way ANOVAs to test for differences between forest types.

3. Results

3.1. Habitat characteristics

All analyzed habitat variables achieved normal distribution. The test for multicollinearity showed no inter-correlation between all measured habitat variables (compare Appendix Table A4). Hence, they were considered being independent from each other.

Significant differences of habitat variables between forest types could only be found for lying deadwood (one-way ANOVA, $F_{2,15} = 4.088$, $p = 0.0383$). The amount of lying deadwood was highest in CF (2.9 ± 0.33) followed by RF (2.6 ± 0.30) and lowest in SF (2.5 ± 0.27) (Fig. 2). However, subsequently calculated HSD-tests only indicate a significant difference between CF and SF ($p = 0.047$) but no for the other pairwise combinations (RF-CF: $p = 0.086$; RF-SF: $p = 0.944$).

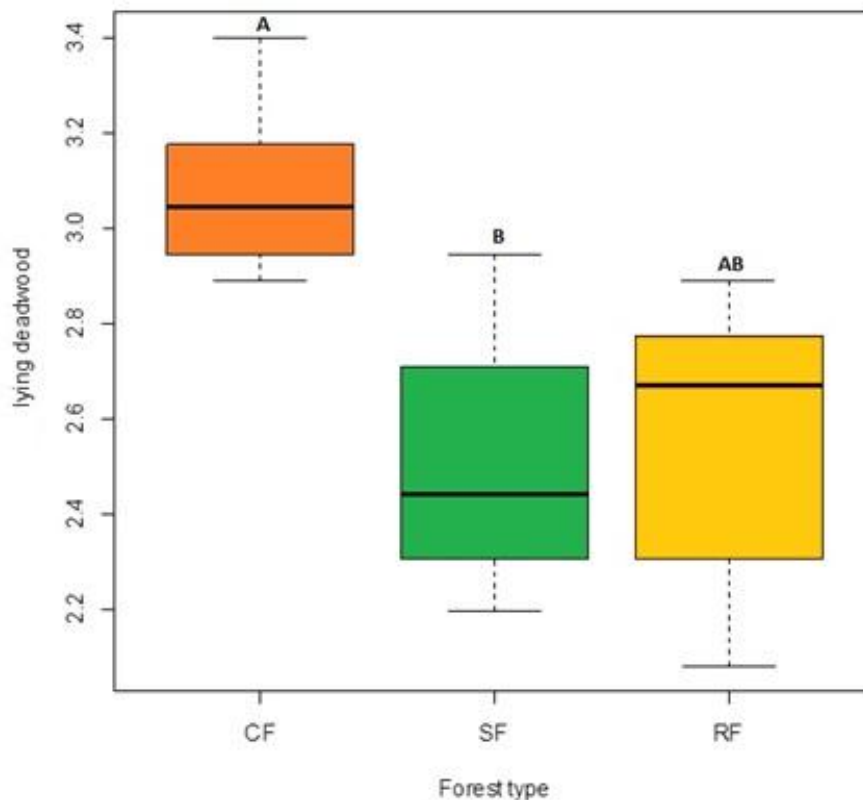


Fig. 2: Mean amount of lying deadwood $\pm$ SE (box) and 95% CI for creek forest (CF), slope forest (SF) and ridge forest (RF). Different letters indicate significant differences between habitats (Tukey's Honest Significant Difference Test).

3.2. Species richness and abundance

A total of 59 different species, 26 amphibians and 33 reptile species could be found during 252 transect runs. We counted a total of 1580 individuals, 840 reptiles and 740 amphibians. Except of one freshly dead *Caiman crocodilus* (not further considered in subsequent analyses), all recorded reptile species represented snakes and lizards. Most amphibians represented toads and frogs, just six individuals belonged to two different salamander species (Appendix Table A5 & A6).

Total species richness was highest in CF (total: 44 species; reptiles: 21 species; amphibians: 23 species) and lowest in RF (total: 32 species; reptiles: 18 species; amphibians: 14 species). SF was similar to RF in terms of species richness (total: 34 species, reptiles: 15 species, amphibians: 19 species). Considering the calculated species-assimilation curves (Fig. 3) similar conclusions can be drawn. The highest number of amphibian species was expected in CF, followed by SF and RF. Estimated numbers of reptiles were almost equal for CF and RF transects, with a slightly positive trend for RF sides though. SF had the lowest expected number of species for reptiles.

Calculated GLMs could not detect a any significant influence of considered habitat variables on species richness of amphibians or reptiles.

Total species abundance was highest in CF (total: 704 individuals; reptiles: 384 individuals; amphibians: 320 individuals) and lowest in RF (total: 410 individuals; reptiles: 217 individuals; amphibians: 193 individuals) for both taxa. Also here SF was intermediate between these two forest types (total: 466 individuals; reptiles: 239 individuals; amphibians: 227 individuals). However, mean total species richness didn't differ between forest types (one-way ANOVA: $F_{2,15} = 1.226$, $p = 0.321$). In contrast, the mean number of individuals per sampling site was significantly affected by forest type (one-way ANOVA: $F_{2,15} = 8.037$, $p = 0.0040$). Subsequently calculated HSD-tests indicate a significant difference between CF and the other two forest types SF (CF- SF: $p = 0.02$) and RF (CF-RF: $p = 0.005$), but not between SF and RF (SF-RF: $p = 0.755$) (Fig.4). The same analysis for both taxonomic groups separately showed no significant difference between habitats for amphibians in relation to species richness (one-way ANOVA: $F_{2,15} = 1.653$, $p = 0.2246$) and abundance (one-way ANOVA: $F_{2,15} = 2.592$, $p = 0.1079$). For reptiles we found significant differences in species abundance between forest types (one-way ANOVA: $F_{2,15} = 8.092$, $p = 0.0041$). The HSD-tests indicate a significant difference between CF and the other two forest types SF (CF- SF: $p = 0.015$) and RF (CF-RF: $p = 0.005$), but not between SF and RF (SF-RF: $p = 0.689$) (Fig.4). Species richness for reptiles didn't differ between forest types (one-way ANOVA: $F_{2,15} = 1.375$, $p = 0.2829$).

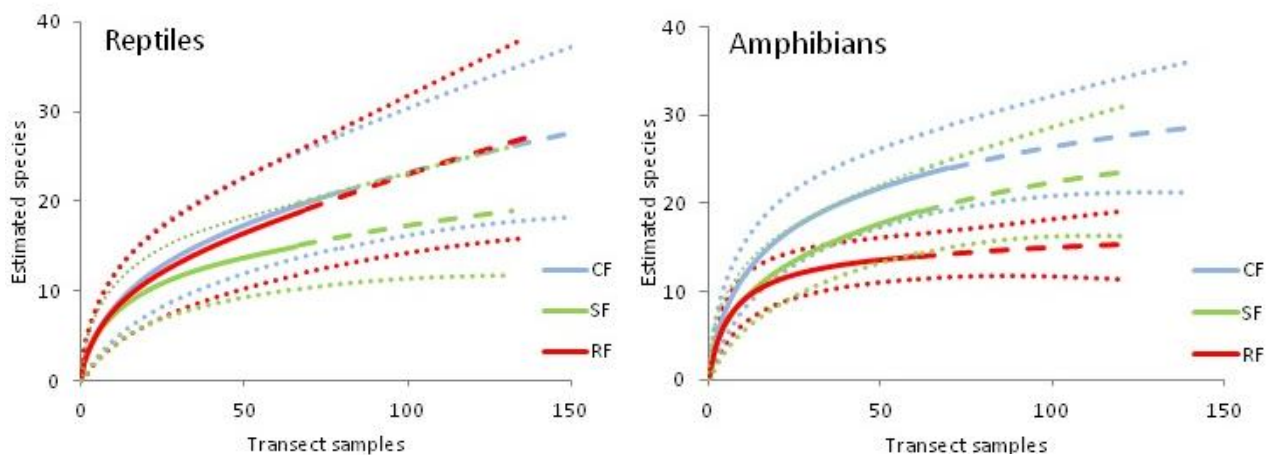


Fig.3: Rarefaction curves ($\pm$ 95% CI) demonstrating species accumulation for reptiles and amphibians sampled in three different forest types (CF= Creek Forest, SF= Slope Forest, RF= Ridge Forest). Broken lines indicate extrapolated parts of the curves; dotted lines represent 95% CIs.

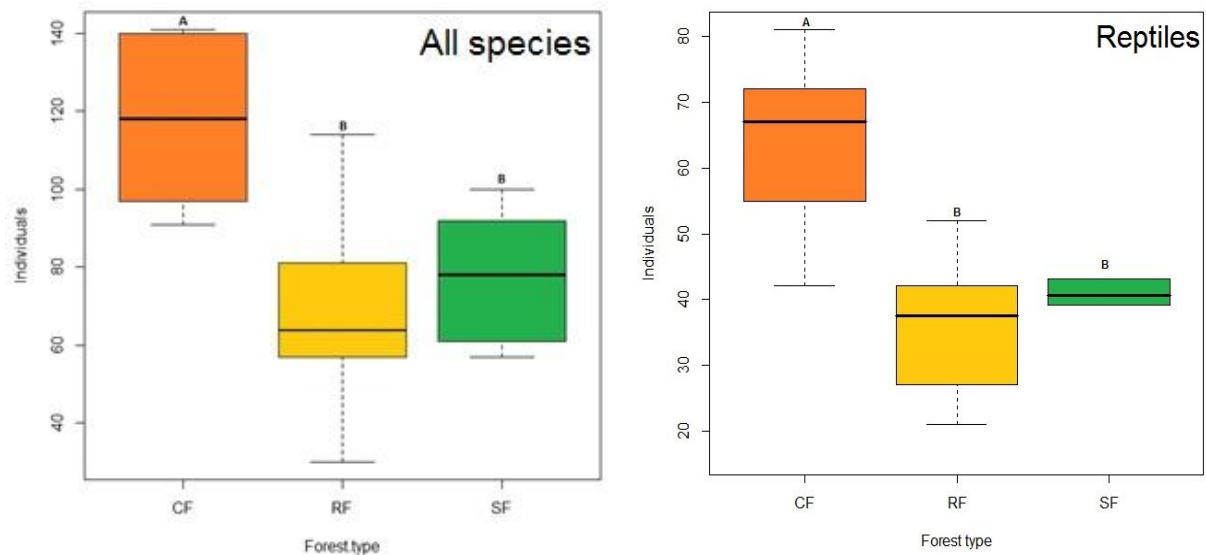


Fig.4: Mean number of individuals $\pm$ SE (box) and 95% CI per transect in three different forest types for all species and reptiles. Different letters indicates significant differences between means (Tukey's Honest Significant Difference Test).

Only few species could be recorded at the majority of sampling sites. Such species also proved to be highly abundant (Fig. 5), e.g. *Anolis polylepis* and *Craugastor fitzingeri* recorded with a total of 575 and 211 individuals respectively were sampled on all 18 transects, *Craugastor stejnegerianus* (174 individuals) and *Anolis capito* (43 individuals) on 16 sample sites. On the contrast, many species could be recorded only once, for example *Anolis lemurinus* and *Bothriechis schlegelii*.

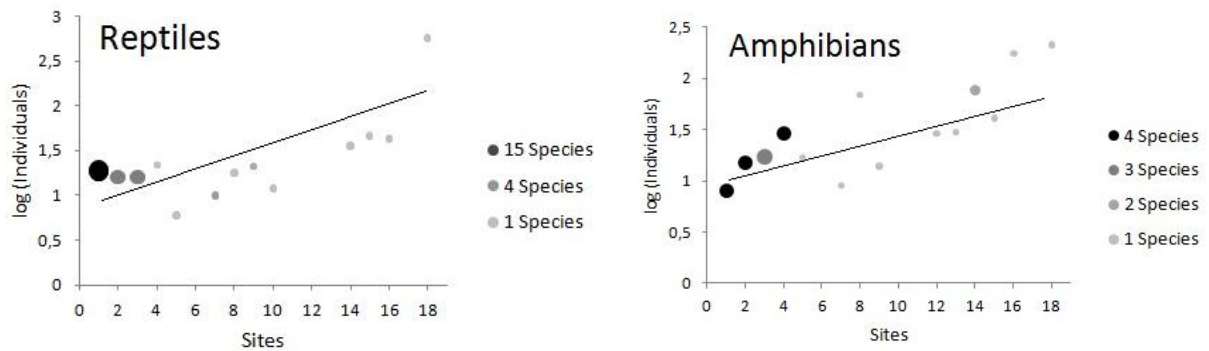


Fig. 5: Relationship between total abundance of species and their occurrence frequency (number of transects with records) for reptiles and amphibians.

3.3. Species composition

Species composition in our three forest types differed significantly for both taxa (reptiles: one-way ANOSIM: $R = 0.327$, $p = 0.004$; amphibians: one-way ANOSIM: $R = 0.269$, $p = 0.023$). And even the NMDS ordination (based on Bray-Curtis similarities) calculated separately for amphibians and reptiles indicate distinct species assemblages between forest types, particularly in amphibians (Fig. 6). For the latter CF can clearly be separated from the other two forest types, while constructed polygons for species assemblages recorded at RF and SF sites, respectively, do slightly overlap. These observations could be confirmed by subsequently calculated pairwise ANOSIMs. CF differed significantly from both RF and SF in both taxonomic groups; in contrast, differences between the latter two did not achieve a significant level neither in amphibians nor in reptiles (Tab. 1)

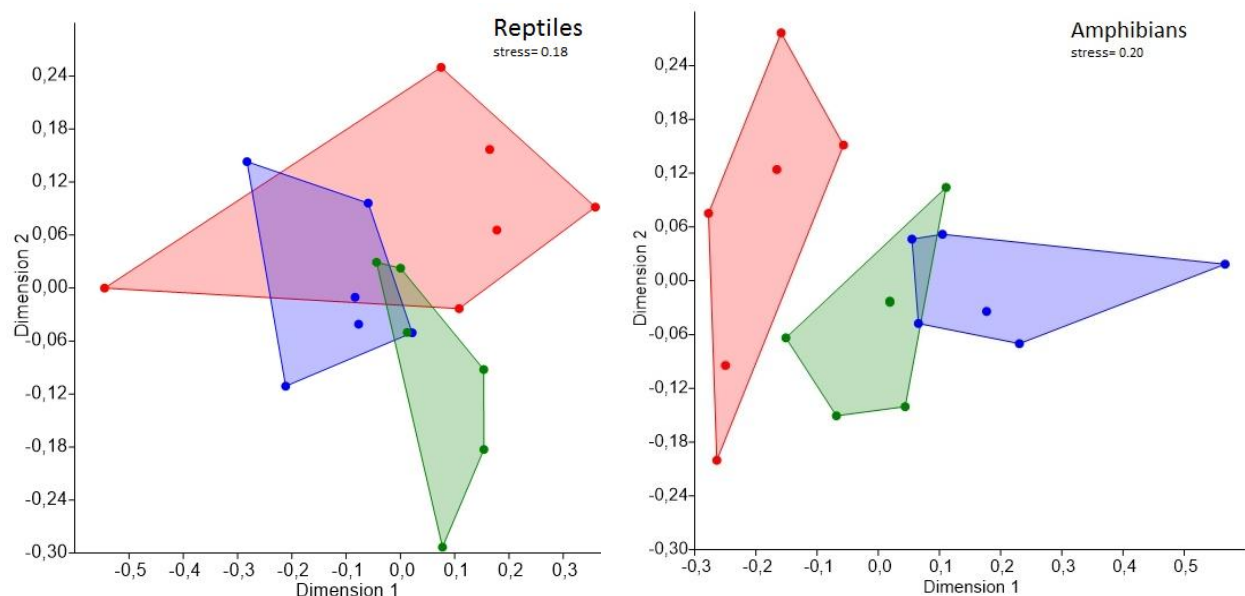


Fig. 6: NMDS ordinations (based on Bray-Curtis similarities with $\sqrt{x}$ transformed abundances) for reptile and amphibian species assemblages recorded at creek forest (CF ●), slope forest (SF●) and ridge forest (RF ●) sites.

Tab. 1: Results of one-way ANOSIMs testing for effects of forest type on species composition separately for amphibians and reptiles. Based on square-root transformed abundances, Bray Curtis similarities were used to measure similarity relationships.

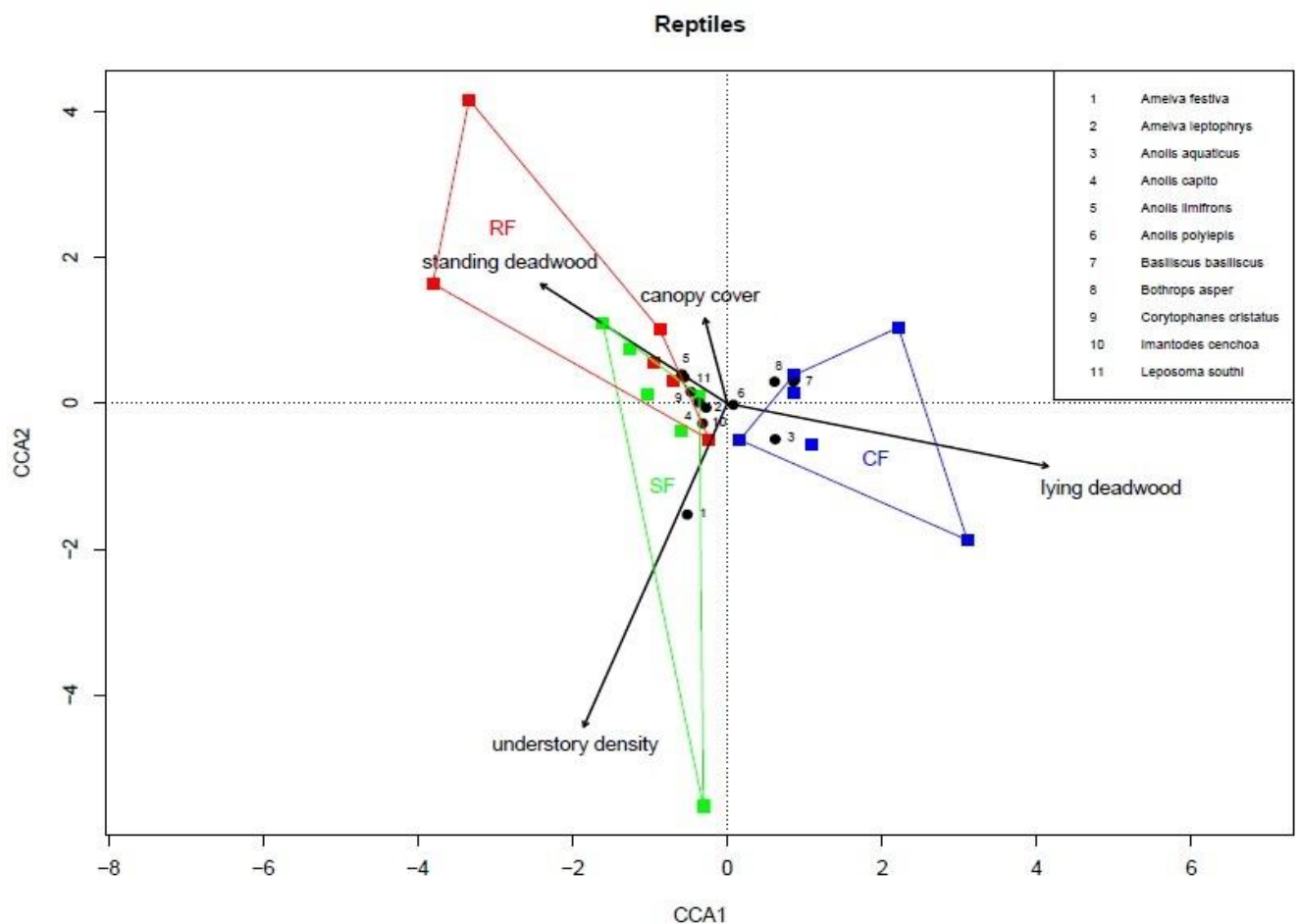
Pairwise test	Results of one-way ANOSIMs	
	R	p
Amphibians		
CF vs. RF	0.6093	0.0051
CF vs. SF	0.4463	0.0081
RF vs. SF	0.113	0.2487
Reptiles		

CF vs. RF	0.3963	0.0207
CF vs. SF	0.2685	0.0195
RF vs. SF	0.1815	0.1797

Dimension 1 and Dimension 2 values extracted from the NMDS ordinations showed no correlations with any of the measured habitat variables. Thus besides the forest type our habitat variables cannot explain differences in species composition between transects.

3.4. Habitat preferences of species

The calculated CANOCO segregated the three forest types in distinct clusters. Furthermore it clear visualizes, that some species show a high affinity to a particular habitat type. For example *Basiliscus basiliscus*, *Rhaebo haematiticus*, *Smilisca sordida* and *Anolis aquaticus* to CF sites, *Anolis limifrons* to RF transects, *Ameiva festiva* and *Engystomops pustulosus* to SF sites. (Fig. 7)



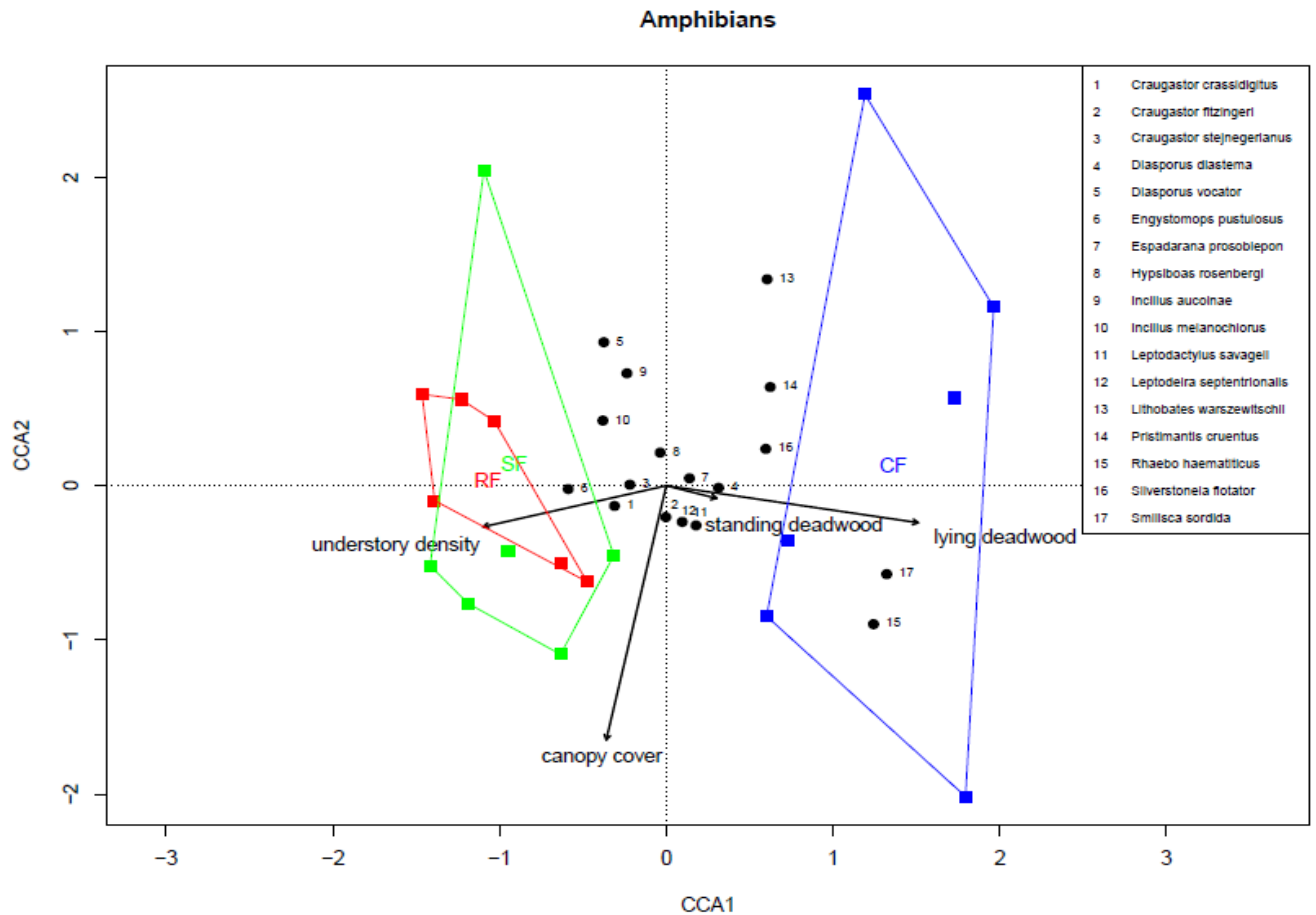


Fig. 7: Results of CCA for amphibians and reptiles. Sampled sites can be divided into the three forest types (CF, SF, RF) and single species show affinities to certain habitats.

CCA was conducted with the combination of CCA1 and CCA2 values which explained most of the variance of habitat variables for both taxonomic groups (amphibians: 73.6%, reptiles: 80.2%) (Tab.2). For amphibians CCA1 accounted for 42.8 % of variance and was negatively related to canopy cover and understory density. CCA2 explained 30.8% of variance and was negatively related to all habitat variables. For reptiles CCA1 accounted for 54% of variance and was negatively correlated to standing deadwood, understory density and canopy cover. CCA2 explained 26% of variance and was negatively correlated to lying deadwood and understory density.

Tab. 2: Factors loadings of Canonical Correspondence Analysis for amphibians and reptiles.

Habitat variables	CCA1	CCA2	CCA3	CCA4
Amphibians				
Lying deadwood	0.8807	-0.13992	0.4007	0.19364
Standing deadwood	0.1760	-0.04784	-0.6483	0.74060

Canopy cover	-0.2102	-0.96090	-0.1601	0.08196
Understory density	-0.6404	-0.15547	0.5787	0.48747
Reptiles				
Lying deadwood	0.80221	-0.1672	0.4269	0.3825
Standing deadwood	-0.46633	0.3170	0.5769	0.5912
Canopy cover	-0.05627	0.2257	0.7221	-0.6512
Understory density	-0.35938	-0.8586	0.3032	-0.2025

Classification of recorded species showed, that water-dependent species had a significant higher relative abundance (CF = 24.8%, RF = 3.1%, SF = 4%; one-way ANOVA: $F_{2,54}=5.6$, $p = 0.005$) and relative richness (CF = 38.8%, RF = 27.3%, SF= 35.2%; one-way ANOVA: $F_{2,54} = 11.3$, $p < 0,0001$) on CF sites than on RF and SF transects. For sun-dependent species neither relative abundance (CF = 2.3%, RF = 14.8%, SF = 5.1%; one-way ANOVA: $F_{15,17}=0.2$, $p = 0.79$) nor relative species richness (CF = 7.4%, RF = 15.2%, SF = 11.7%; one-way ANOVA: $F_{2,9}= 3.6$, $p = 0.06$) did change significantly between forest types.

4. Discussion

Species richness and abundance

Our recorded total species richness is comparable with other lowland forest sites in Central America like the Atlantic side of Panama or parts of Southeast Asia as Borneo and Malaysia (Höbel 2008; Inger 1980). And it easily exceeds numbers of species found during studies on the Philippines (19 species, plot size 610 or 930 m²) and in Uganda (18 species, 50 plots each 5m × 5m) (Scott 1976; Vonesh 2001). For amphibians specifically, numbers found in our study area were higher than in dry forests of Central America (6-22, mean = 14.4, N=5, considered sites encompassing fewer than 10,000 hectares) (Duellman 1988), higher than the number found in a study from Brazil with just 12 different amphibian species (498 plots each 5m × 5m) (Allmon 1991) and similar to some parts of South America like the Guianan Region (32 species, considered sites encompassing fewer than 10,000 hectares) (Duellman 1988). But number was still much lower than for other comparable habitats in South America. For example greatest number of anurans was found in the equatorial part of Amazonian Ecuador with 84 detected species (considered sites encompassing fewer than 10,000 hectares) (Duellman 1988).

The species-abundance structure of the species assemblages recorded by this study is typical for the New World tropics (and other tropical regions): there are a few extremely abundant species and a very large number of rare ones (Fauth et al. 1989; Leenders 2001). The ubiquitous *Anolis polylepsis* was the most abundant species in our study with 575 counted individuals and represented 68.4 % of all reptile individuals that were sampled during three months of survey time. In contrast 33.8% of all species were only recorded as singletons or doubletons in our samples.

Results of this study suggest that total herpetofaunal species richness and abundance is sensitive to topographic factors even on small spatial scales as already reported by the study of Vonesh (2001). Although mean species richness per study site failed differing significantly between CF, SF and RF in amphibians and reptiles, the species assimilation curves for all sites pooled per habitat type indicate a distinct decline of herpetofaunal richness from CF towards SF and RF sites. This importance of CF for herpetofaunal species richness and abundance can be explained by several reasons. The thin, moist skin of amphibians causes rapid escape of fluids, what can result in dehydration and ultimately death. Ridge forests with high insolation may therefore not be an adequate habitat for many members of this taxon. Furthermore, amphibians can replenish their internal water supply by absorbing water through their skin, from the ground, the air, or bodies of water. For that reason, amphibians are mostly found in places with high humidity or with access to water bodies (such as small forest streams at the bottom of creeks) (Duellman & Trueb 1994; Donnelly & Guyer 1994; Leenders 2001; Qian et al. 2007; Wells 2007). Moreover, many anuran members depend on water for egg deposition and therefore are bonded to aquatic habitats (Höbel 2008). Considering the fact that our sampling time corresponded to an intensive breeding period for many anurans, for example *Hylidae* (Amphibia Web; Höbel 2008; Savage 2002), their need for water and wet underground is even more important. Creek forest sites in the study region are extremely humid throughout the year and hence offer optimal climatic conditions for amphibians to live (Weissenhofer et al. 2008).

While the close relationship of amphibians to creek sites with constantly high humidity was predictable, the amount of reptile species and significantly higher abundance of individuals in this habitat was unexpected. Many reptiles, especially lizards, are extreme solar ectotherms and thus need sunny dry spots to heat up and absorb enough energy to stay active (Wanger et al. 2010). Normally they bask around during day, because their impermeable scaly skin prevents evaporation and allows them to stay in the sun (Leender 2001; Qian et al. 2007; Rodríguez et al. 2005). According to that, RF would provide better conditions for reptiles due to higher insolation and relatively dry climatic conditions (Weissenhofer et al. 2008). However, other studies suggested that low humidity and an increased temperature difference between day and night can have negative impact on reptiles (Glor et al. 2001). These climatic circumstances may generate less suitable conditions at RF.

Another reason could be that the diet of many snake species recorded in this study consists of tree frogs and their eggs (Guyer 1994; Solórzano 2004). Hence, the higher food and resource availability in CF may explain increased abundances of snakes, such as *Leptodeira septentrionalis*, *Imantodes cenchoa* and *Bothrops asper*, in CF). Also seasonal differences in the availability of frog species may affect the abundance of active snake species as demonstrated by a study from Brazil's Atlantic forest (Marques et al. 2000). Another explanation for the importance of CF for reptiles could be that most lizards and all oviparous snakes have flexible eggs either without a calcareous layer or a very thin one. As a consequence, the eggs are highly sensitive to changes in humidity, and have higher hatchling success when adequate moisture is available (Höbel 2008).

The importance of creek forest sites for herpetofauna can thus be explained with the life history, ecology and behavioral requirements of amphibian as well as reptile species. RF sites play an important role for reptiles though, as also demonstrated in our species accumulation curve, where the number of expected reptiles was equally high in CF and RF. Based on our own observations in the field we can confirm that commonly encountered diurnal lizards are often basking at sunny spots, which can represent an important habitat requisite for many heliothermic reptiles (Vitt et al. 1997). Such sun spots may occur at higher densities at hill tops, where light can more easily penetrate the forest up to the ground (Weissenhofer et al. 2008).

Nevertheless, our results correspond to observations from other Neotropical Regions with higher species densities in wet areas than on dry sites and on flat terrains compared to slopes (Duellman 1988; Scott 1976).

4.2. Species composition and habitat preferences

Our results provide clear evidence that small-scale differences in the composition of amphibian and reptile species assemblages are affected by topography. Also other studies documented that topography is an important factor shaping the species composition of plants (Itoh et al. 2003; Zhang et al. 2013), ants (Vasconcelos et al. 2003) and small mammals (Adler 1987). For the herpetofauna the crucial impact of small-scale geographic features as topography on local communities was emphasized already by a study from Peru (Doan & Arriaga 2002). Microclimatic conditions, plant composition and other biotic and abiotic factor determining a forest type may be responsible for small-scale differences in habitat suitability for individual amphibian and reptile species. Comparable results were obtained by Binz *et al.* (2014) for butterflies recorded at the same transects used in this study. Also here species composition was significantly influenced by forest type.

Our study indicates that forest types differ in suitability particularly for water-dependent species. CF with its humid climate and permanent availability of water offers good conditions for a considerable number of such species and thus shows a distinct species composition from SF and RF sites. A huge amount of tropical anura need water bodies for reproduction (Crump 1974) and thus have a specifically high affinity to this habitat. Hence, richness and abundance of water-dependent species was significantly higher at CF sites than on RF and SF transects. For example *Smilisca sordida* is depending on water for reproduction as it breeds along streams and the benthic larvae live in shallow, clear water (AmphibiaWeb 2014). Other species recorded at CF in our study, such as the glass frog *Hyalinobatrachium valerioi*, live next to water bodies. Males of *H. valerioi* brood eggs on leaves overhanging streams and release their offspring directly to the water. Two other species just found on CF sites, *Lithobates warszewitschii* and *Silverstoneia flotator*, tend to concentrate near stream courses and are commonly observed along slow-moving creeks and little brooks in the forest (Höbel 2008; Savage 2002). *Leptodactylus savagei* prefers forest habitat near swamps and slowly flowing streams (Guyer and Donnelly 2005). Also some reptiles prefer creek sides along streams and water bodies, e.g. *Anolis aquaticus*, a lizard restricted to stream courses within Lowland Wet Forests (Savage 2002), was just sampled at CF sites. Furthermore snakes like *Leptodeira* and *Imantodes* prefer habitats along streams, where they find their favorite prey (frogs/their eggs and lizards). *Bothrops asper* is another reptile commonly found along streams, where it is often curled up and resting on logs or rocks (Höbel 2008). But while CF shows a distinct species composition, RF and SF sites didn't differ significantly from each other and also the relative number of sun-dependent species is not significantly higher at ridge locations. Possible explanations could be, first, that plant species compositions and forest structure at slope sites are often similar to ridge forests and thus offer similar habitat conditions for species (Weissenhofer et al. 2008). Second, RF sites offer more sunspots to warm up-a habitat characteristic, that is important for some heliothermic species, e.g. *Anolis limifrons*, a gap species with highest population densities in relatively open areas which prefers basking in direct sunlight (Savage 2002). These observations suggest that life history, food availability and other biotic and abiotic factors have a crucial influence on how species are literally forced to use specific habitats and thus are dependent on suitable topographic circumstances to survive. Species often react to a particular set of physiological constraints imposed by particular features of environment (Ernst & Rödel 2006), resulting in a high extent of habitat specificity. However, a certain proportion of species recorded in our study appeared to be very ubiquitous in terms of forest type affinities, such as *Craugastor* species exhibiting direct development and don't need water for reproduction (Doan & Arriaga 2002; Höbel 2008). We found them in all three forest types in similar abundances, while other species had more specified habitat relations. A study from Urbina-Cardona et al. (2006) in Mexico also reported that tropical herpetofauna is characterized by

habitat specialists as well as habitat generalists. The latter tolerated all the environmental gradients that occurred between a pasture and the forest interior, while strictly forest interior species were more affected by changes in structure and loss of specific habitat conditions (e.g., leaf litter cover, understorey density and temperature).

Additionally, the possible occurrence of seasonal shifts in species composition within a habitat has to be considered. A seasonal change in water sources can affect the frog fauna because of lacking spawning grounds (Scott 1976). So, seasonal reproductive cycles can influence activity patterns and be a decisive factor affecting the detectable species composition. Also seasonal changes in the local litter arthropod abundance may affect their spatio-temporal distribution (Toft 1980, Vonesh 2001). As demonstrated in a study in Costa Rica the amount of litter arthropods influenced species richness of leaf-litter frogs (Lieberman 1986). Also Ryan and Poe (2014) demonstrated a season shift of *Anolis polylepsis* densities between forest and riparian macrohabitats. During dry season individuals moved to riparian locations looking for water to avoid desiccation and to find more prey. Studies from La Selva Biological Station (Costa Rica) demonstrated that greatest diversity and abundance of herpetofaunal species can be recorded between the end of the dry season and the onset of the rainy season (Leenders 2001).

Our CCA analysis did not only show, that species compositions varies between forest types but also that habitat preferences of single species are influenced by the presence of specific habitat components. For example, some species responded positively to the amount of lying deadwood. *Basiliscus basiliscus* is associated with riparian habitats and vegetation along streams and adults tend to prefer perches near or above a watercourse (AmphibiaWeb 2014; Höbel 2008), often on lying deadwood (personal observation). *Bothrops asper* can hide beneath deadwood and couch for bypassing prey. *Smilisca sordida* is a stream-breeding tree frog and can use lying deadwood next to water bodies for egg depository (AmphibiaWeb 2014). Moreover this habitat variable could also be of high importance for nocturnal species like *Rhaebo haematiticus*. They hunt and reproduce at night and often spend the day hiding below logs (Höbel 2008; Savage 2002). Hence, lying deadwood appears to be an important habitat requisite for several species. More habitat variables have to be considered when aiming to explain more species-specific variation. Here, just forest type proved to be a significant explanatory variable for changes in species compositions. Nevertheless, our data can confirm the importance of small-scale differences in topography for shaping local species assemblages (Catling & Burt 1995; Parris 2004; Parris & McCarthy 1999; Schwarzkopf & Rylands 1989; Vasconcelos et al. 2003)

5. Conclusion

The results of our study clearly demonstrate the importance of topography for shaping the structure and composition of amphibian and reptile assemblages even on a small spatial scale. They also indicate that tropical rain forest species inventories are not homogeneous entities but differ significantly between forest types situated at ridges, slopes and creeks. These results have to be considered when future studies want to obtain full species inventories of an area (Binz et al. 2014). But also conservation programs should consider these results when trying to maintain and protect a comprehensive range of local biodiversity (Binz et al. 2014). Determining the variables influencing herpetofaunal richness, abundance and composition is a crucial duty to obtain reliable information about the actual status quo. Topographic heterogeneity must therefore definitely be taken into consideration.

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Appendix

Table A1: Average climate dates during sampling time from November 2015 - January 2016 in La Gamba. Highest values marked grey.

Climate data			
	Rain [mm]	Temperature [°C]	Air humidity [%]
November	13.3 (±SD 22)	24.2-28.2	77.8-90.7
December	7.4 (±SD 16)	25.2-29.4	73.6-89.1
January	6.9 (±SD 13.8)	24.5-29.3	75.7-90.3

Table A2: Sampling dates for every single transect. Night surveys are marked grey.

Site	Sampling dates
RF1	02 Nov. 2015, 04 Nov. 2015, 10 Nov. 2015, 18 Nov. 2015, 25 Nov. 2015, 29 Nov. 2015, 11 Dez. 2015, 16 Dez. 2015, 22 Dez. 2015, 25 Dez. 2015, 05 Jan. 2016, 08 Jan. 2016, 22 Jan. 2016, 24 Jan. 2016
RF2	04 Nov. 2015, 06 Nov. 2015, 12 Nov. 2016, 17 Nov. 2015, 23 Nov. 2015, 06 Dez. 2015, 13 Dez. 2015, 15 Dez. 2015, 25 Dez. 2015, 30 Dez. 2015, 17 Jan. 2016, 22 Jan. 2016, 28 Jan. 2016, 28 Jan. 2016
RF3	03 Nov. 2016, 06 Nov. 2015, 12 Nov. 2016, 14 Nov. 2015, 27 Nov. 2015, 06 Dez. 2015, 11 Dez. 2015, 13 Dez. 2016, 30 Dez. 2016, 31 Dez. 2015, 04 Jan. 2016, 17 Jan. 2016, 27 Jan. 2016, 28 Jan. 2016
RF4	04 Nov. 2015, 06 Nov. 2015, 12 Nov. 2015, 14 Nov. 2015, 20 Nov. 2015, 23 Nov. 2015, 6 Dez. 2015, 13 Dez. 2015, 21 Dez. 2015, 22 Dez. 2015, 03 Jan. 2016, 06 Jan. 2016, 22 Jan. 2016, 29 Jan. 2015
RF5	04 Nov. 2015, 06 Nov. 2015, 12 Nov. 2015, 14 Nov. 2015, 21 Nov. 2015, 06 Dez. 2015, 08 Dez. 2015, 14. Dez. 2016, 21 Dez. 2015, 22 Dez. 2015, 04 Jan. 2016, 06 Jan. 2016, 23 Jan. 2016, 25 Jan. 2016
RF6	05 Nov. 2015, 09 Nov. 2015, 09 Nov. 2015, 21 Nov. 2015, 25 Nov. 2015, 28 Nov. 2015, 08 Nov. 2015, 14 Dez. 2015, 18 Dez. 2015, 20 Dez. 2015, 06 Jan. 2016, 22 Jan. 2016, 25 Jan. 2016, 26 Jan. 2016
SF1	05 Nov. 2015, 09 Nov. 2015, 09 Nov. 2015, 13 Nov. 2015, 17 Nov. 2015, 01 Dez. 2015, 07 Dez. 2015, 09 Dez. 2015, 25 Dez. 2015, 31 Dez. 2015, 03 Jan. 2016, 13 Jan. 2016, 22 Jan. 2016, 30 Jan. 2016
SF2	04 Nov. 2015, 08 Nov. 2015, 13 Nov. 2015, 18 Nov. 2015, 26 Nov. 2015, 29 Nov. 2015, 09 Dez. 2015, 16 Dez. 2015, 25 Dez. 2015, 30 Dez. 2015, 02 Dez. 2015, 08 Jan. 2016, 22 Jan. 2016, 28 Jan. 2016
SF3	04 Nov. 2015, 06 Nov. 2015, 08 Nov. 2015, 15 Nov. 2015, 18 Nov. 2015, 29 Nov. 2015, 15 Dez. 2015, 16 Dez. 2015, 25 Dez. 2015, 31 Dez. 2015, 05 Jan. 2016, 08 Jan. 2016, 22 Jan. 2016, 24 Jan. 2016
SF4	03 Nov. 2015, 05 Nov. 2015, 09 Nov. 2015, 13 Nov. 2015, 18 Nov. 2015, 28 Nov. 2015, 05 Dez. 2015, 14 Dez. 2015, 17 Dez. 2015, 22 Dez. 2015, 04 Jan. 2016, 16 Jan. 2016, 24 Jan. 2016, 30 Jan. 2016
SF5	06 Nov. 2015, 10 Nov. 2015, 10 Nov. 2015, 25 Nov. 2015, 25 Nov. 2015, 05 Dez. 2015, 08 Dez. 2015, 20 Dez. 2015, 22 Dez. 2015, 31 Dez. 2015, 13 Jan. 2016, 18 Jan. 2016, 22 Jan. 2016

	2016, 25 Jan. 2016
SF6	04 Nov. 2015, 09 Nov. 2015, 09 Nov. 2015, 13 Nov. 2015, 17 Nov. 2015, 28 Nov. 2015, 01 Dez. 2015, 09 Dez. 2015, 20 Dez. 2015, 25 Dez. 2015, 03 Jan. 2016, 14 Jan. 2016, 23 Jan. 2016, 25 Jan. 2016
CF1	02 Nov. 2015, 07 Nov. 2015, 10 Nov. 2015, 10 Nov. 2015, 25 Nov. 2015, 25 Nov. 2015, 01 Dez. 2015, 10 Dez. 2015, 22 Dez. 2015, 23 Dez. 2015, 03 Jan. 2016, 05 Jan. 2016, 23 Jan. 2016, 25 Jan. 2016
CF2	03 Nov. 2015, 05 Nov. 2015, 10 Nov. 2015, 13 Nov. 2015, 18 Nov. 2015, 28 Nov. 2015, 05 Dez. 2015, 10 Dez. 2015, 17 Dez. 2015, 31 Dez. 2015, 03 Jan. 2016, 14 Jan. 2016, 26 Jan. 2016, 30 Jan. 2016
CF3	03 Nov. 2015, 09 Nov. 2015, 11 Nov. 2015, 15 Nov. 2015, 21 Nov. 2015, 01 Dez. 2015, 04 Dez. 2015, 11 Dez. 2015, 20 Dez. 2015, 23 Dez. 2015, 14 Jan. 2016, 16 Jan. 2016, 26 Jan. 2016, 28 Jan. 2016
CF4	02 Nov. 2015, 07 Nov. 2015, 08 Nov. 2015, 14 Nov. 2015, 25 Nov. 2015, 08 Dez. 2015, 11 Dez. 2015, 12 Dez. 2015, 20 Dez. 2015, 30 Dez. 2015, 03 Jan. 2016, 13 Jan. 2016, 25 Jan. 2016, 26 Jan. 2016
CF5	03 Nov. 2015, 06 Nov. 2015, 12 Nov. 2015, 14 Nov. 2015, 27 Nov. 2015, 06 Dez. 2015, 11 Dez. 2015, 13 Dez. 2015, 30 Dez. 2015, 31 Dez. 2015, 15 Jan. 2016, 17 Jan. 2016, 22 Jan. 2016, 28 Jan. 2016
CF6	01 Nov. 2015, 06 Nov. 2015, 11 Nov. 2015, 15 Nov. 2015, 21 Nov. 2015, 04 Dez. 2015, 09 Dez. 2015, 12 Jan. 2016, 20 Dez. 2015, 22 Dez. 2015, 04 Jan. 2016, 05 Jan. 2016, 27 Jan. 2016, 29 Jan. 2016

Table A3: Recorded habitat characteristics and coordinates for every single study site.

Site	Coordinates	Amount of standing deadwood	Lying deadwood	Canopy cover (%)	Understory density
CF1	N 08°41.788' W 083°12.325'	2	20	80	3.488
CF2	N 08°41.828' W 083°12.373'	2	18	79	2.971
CF3	N 08°42.242' W 083°12.225'	6	17	71	2.485
CF4	N 08°41.867' W 083°12.213'	2	10	83	2.028
CF5	N 08°42.092' W 083°12.780'	4	23	84	3.56
CF6	N 08°42.125' W 083°12.270'	3	29	83	3.164
RF1	N 08°41.517' W 083°12.395"	0	15	78	4.022
RF2	N 08°42.267' W 083°12.367"	13	12	85	2.827
RF3	N 08°42.128' W 083°12.627"	0	15	78	2.827
RF4	N 08°42.113' W 083°12.458"	3	9	81	1.615
RF5	N 08°41.968' W 083°12.455"	1	7	80	1.508

RF6	N 08°41.925' W 083°12.550'	14	17	83	2.356
SF1	N 08°41.998' W 083°12.362'	6	8	86	4.113
SF2	N 08°41.862' W 083°12.133'	3	9	86	3.592
SF3	N 08°41.908' W 083°12.172'	6	10	74	2.259
SF4	N 08°41.882' W 083°12.500'	4	14	83	4.798
SF5	N 08°41.722' W 083°12.432'	4	18	84	3.792
SF6	N 08°41.934' W 083°12.438'	4	11	83	2.636

Table A4: Pearson correlation matrix between single habitat variables

	(1)	(2)	(3)
(1) Canopy cover			
(2) Lying deadwood	r= - 0.11 p= 0.6525		
(3) Standing deadwood	r= 0.24 p= 0.3404	r= 0.00 p= 0.9897	
(4) Understory density	r= 0.31 p= 0.2146	r= - 0.11 p= 0.6648	r= - 0.02 p= 0.9367

Table A5: Total counts for the number of species and individuals over three months of surveys

November				
	Amphibians			
	CF	SF	RF	Total
Number of species	17	14	11	42
Number of individuals	86	59	57	202

Reptiles				
Number of species	10	8	12	31
Number of individuals	108	77	75	260
December				
Amphibians				
	CF	SF	RF	Total
Number of species	15	10	11	36
Number of individuals	133	94	83	310
Reptiles				
Number of species	15	13	11	39
Number of individuals	149	82	85	316
January				
Amphibians				
	CF	SF	RF	Total
Number of species	14	12	10	36
Number of individuals	101	74	53	228
Reptiles				
Number of species	14	11	11	36
Number of individuals	127	80	57	264

Table A6: Detected species on the 18 different study sites. Nomenclature as in Savage (2002) with updates on classification according to AmphibiaWeb (2014) and Uetz & Hošek (2014).

Species	Ridge Forest						Slope Forest						Creek Forest					
	RF 1	RF 2	RF 3	RF 4	RF 5	RF 6	SF 1	SF 2	SF 3	SF 4	SF 5	SF 6	CF 1	CF 2	CF 3	CF 4	CF 5	CF 6
AMPHIBIANS																		
Bufonidae																		
<i>Incilius melanochlorus</i>	+	-	+	+	+	+	+	-	+	-	+	+	-	+	-	+	-	-
<i>Incilius aucoinae</i>	+	-	-	+	-	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Incilius coniferus</i>	-	+	-	-	-	-	-	+	+	-	-	-	-	-	-	-	-	+
<i>Rhaebo haematiticus</i>	-	-	-	-	-	-	-	-	-	-	+	-	+	-	-	-	+	-
<i>Rhinella marina</i>	-	-	-	-	-	-	-	-	-	+	-	-	+	-	-	-	-	-
Rhinophrynidae																		
<i>Pristimantis ridens</i>	-	-	-	-	-	-	-	-	-	+	-	-	+	-	-	-	-	-
<i>Pristimantis cruentus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+	+	-	+
Leptodactylidae																		
<i>Leptodactylus bolivianus</i>	-	-	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-
<i>Leptodactylus savagei</i>	+	+	-	+	+	-	+	-	-	+	+	+	+	-	+	+	-	+
Dendrobatidae																		
<i>Silverstoneia flotator</i>	-	-	-	-	-	-	-	+	-	+	-	-	+	+	+	+	+	+
Centrolenidae																		
<i>Espadarana prosoblepon</i>	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-
<i>Hyalinobatrachium valerioi</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
<i>Hyalinobatrachium colymbiphellum</i>	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
Hylidae																		
<i>Hypsiboas rosenbergi</i>	+	+	+	+	+	+	-	+	-	-	-	-	-	-	+	-	-	+
<i>Smilisca sordida</i>	-	-	-	-	-	-	-	-	-	-	-	-	+	-	+	-	+	+
<i>Scinax elaeochroa</i>	-	-	-	-	-	-	-	-	-	+	-	-	-	+	+	-	-	-
Eleutherodactylidae																		
<i>Diasporus diastema</i>	+	-	+	+	-	+	+	+	+	+	-	-	+	-	+	+	+	+
<i>Diasporus vocator</i>	+	-	-	+	-	-	-	+	+	+	-	-	+	-	+	-	-	-
Craugastoridae																		
<i>Craugastor fitzingeri</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Craugastor crassidigitus</i>	+	-	+	+	+	+	+	+	+	+	+	+	+	+	-	+	+	-
<i>Craugastor</i>	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-

Species	Ridge Forest						Slope Forest						Creek Forest					
	RF	RF	RF	RF	RF	RF	SF	SF	SF	SF	SF	SF	CF	CF	CF	CF	CF	CF
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
<i>noblei</i>																		
<i>Craugastor stejnegerianus</i>	+	-	+	+	+	-	+	+	+	+	+	+	+	+	+	+	+	+
Ranidae																		
<i>Lithobates warszewitschii</i>	-	-	-	+	+	-	-	-	+	-	-	-	-	-	+	-	-	+
Leiuperidae																		
<i>Engystomops pustulosus</i>	+	+	-	+	+	+	+	+	+	+	+	+	+	+	+	-	-	-
Plethodontidae																		
<i>Oedipina alleni</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-
<i>Bolitoglossa lignicolor</i>	-	+	+	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-
REPTILES																		
Alligatoridae																		
<i>Caiman crocodilus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
Dactyloidae																		
<i>Anolis polylepis</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Anolis capito</i>	+	+	+	+	+	+	+	-	+	-	+	+	+	+	+	+	+	+
<i>Anolis aquaticus</i>	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	-	-
<i>Anolis lemurinus</i>	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Anolis limifrons</i>	+	+	+	-	+	+	-	-	-	-	+	+	-	-	-	+	+	-
<i>Anolis biporcatus</i>	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-
Corytophanidae																		
<i>Basiliscus basiliscus</i>	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	+	+	-
<i>Corytophanes cristatus</i>	+	-	-	+	+	+	+	+	+	+	-	+	+	+	+	+	-	+
Teiidae																		
<i>Ameiva festiva</i>	-	-	-	-	-	-	-	-	-	+	-	-	+	+	-	-	-	-
<i>Ameiva leptophrys</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	-	+	-	+	-
Gymnophthalmidae																		
<i>Leposoma southi</i>	+	-	-	+	+	+	-	-	+	-	+	+	-	-	-	-	-	+
Scincidae																		
<i>Sphenomorphus cherriei</i>	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Mabuya unimarginata</i>	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Alopoglossidae																		
<i>Ptychoglossus plicatus</i>	-	-	-	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-
Sphaerodactylidae																		
<i>Lepidoblepharis xanthostigma</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-
Colubridae																		

Species	Ridge Forest						Slope Forest						Creek Forest					
	RF	RF	RF	RF	RF	RF	SF	SF	SF	SF	SF	SF	CF	CF	CF	CF	CF	CF
	1	2	3	4	5	6	1	2	3	4	5	6	1	2	3	4	5	6
<i>Coniophanes fissidens</i>	-	-	-	-	+	-	-	-	-	-	-	-	+	-	-	-	-	-
<i>Imantodes cenchoa</i>	+	-	+	-	-	+	+	+	-	+	-	+	+	-	+	-	+	-
<i>Leptodeira septentrionalis</i>	-	-	+	-	+	-	-	-	-	-	-	+	+	-	-	+	-	-
<i>Mastigodryas melanolomus</i>	+	-	-	+	-	+	-	-	-	-	-	-	-	-	-	-	-	-
<i>Rhadinaea decorata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Ninia maculata</i>	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	-
<i>Oxybelis aeneus</i>	-	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Siphlophis compressus</i>	-	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-	+	-
<i>Sibon nebulatus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-
<i>Sibon dimidiatus</i>	-	-	+	-	-	-	-	-	+	-	-	-	-	-	-	-	-	+
<i>Leptophis ahaetulla</i>	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Geophis hoffmanni</i>	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-
Elapidae																		
<i>Micrurus clarki</i>	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
Viperidae																		
<i>Bothrops asper</i>	-	-	-	+	-	-	+	-	-	-	-	-	+	+	-	+	+	+
<i>Porthidium nasutum</i>	-	-	-	-	-	-	-	+	-	+	-	-	-	-	-	-	-	-
<i>Bothriechis schlegelii</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-

Abstract

Topography can shape biodiversity already on small spatial scales and thus it has a crucial influence on richness, composition and abundance of species. In this study we investigated this effect on herpetofaunal biodiversity in a tropical lowland forest in southwestern Costa Rica. Amphibians and reptiles were sampled on six different transects in ridge (RF), slope (SF) and creek (CF) forests, respectively, between November 2015 and January 2016. In total 740 amphibians and 840 reptiles representing 26 and 33 species, respectively, could be found during 252 transect runs. Total herpetofaunal abundance but not species richness differed between forest types with most individuals found at CF sites. Also species abundance of reptiles (but not amphibians) proved to be significantly higher at CF sites. Moreover CF was characterized by distinct species assemblages, while composition of SF and RF sites was similar. Water-dependent species were significantly more abundant at CF sites. Thus forest type has a crucial influence on species-specific habitat use because of differences biotic and abiotic conditions. Our results underline the importance of small-scale topographic heterogeneity for local herpetofaunal species richness. Hence small-scale topography has to be considered in conservation measures aiming to protect the entire species richness of amphibians and reptiles of tropical lowland rainforests.

Zusammenfassung

Topographische Faktoren können die Biodiversität auf kleinster räumlicher Ebene beeinflussen und daher einen entscheidenden Einfluss auf Artenreichtum, -zusammensetzung und –abundanz haben. In unserer Studie haben wir diesen Effekt auf die Biodiversität der Herpetofauna in einem Tiefland-Regenwald in Costa Rica untersucht. Amphibien und Reptilien wurden auf jeweils 6 verschiedenen Transekten im Kammwald (RF), Hangwald (SF) und Schluchtwald (CF) zwischen November 2015 und Januar 2016 erfasst. Während insgesamt 252 Transektbegehungen konnten 58 verschiedene Arten gefunden werden, 26 Amphibien- und 33 Reptilienarten. Es wurden 1580 Individuen dokumentiert, 840 Reptilien und 740 Amphibien. Die Abundanz der gesamten Herpetofauna variiert zwischen den drei Waldtypen, wobei die meisten Individuen an CF-Standorten gefunden wurden. Für den Artenreichtum konnten solche signifikanten Unterschiede nicht festgestellt werden. Im Detail konnte auch für Reptilien (jedoch nicht für Amphibien) alleine eine signifikant höhere Abundanz an CF-Transekten nachgewiesen werden. Auch zeichnete sich CF durch eine signifikant unterschiedliche Artenzusammensetzungen im Vergleich zu den beiden anderen Waldtypen SF und RF aus. so konnte an CF-Standorten eine erhöhte Anzahl an von Fließgewässern abhängigen Arten gefunden werden.

Dies zeigt eindeutig, dass aufgrund unterschiedlicher biotischer und abiotischer Bedingungen artspezifische Präferenzen für einzelne durch die Topografie bedingte Waldtypen bestehen. Unsere Ergebnisse betonen die Bedeutung von kleinräumiger topographischer Heterogenität für den lokalen Artenreichtum der Herpetofauna. Daher muss kleinräumige Topographie bei Schutzbemühungen für den gesamten Artenreichtum von Amphibien und Reptilien in tropischen Tieflandregenwäldern berücksichtigt werden.