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Contributed Paper

Effects of Forest Fragmentation and Habitat Degradation on West African Leaf-Litter Frogs

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Abstract: *Habitat degradation alters the dynamics and composition of anuran assemblages in tropical forests. The effects of forest fragmentation on the composition of anuran assemblages are so far poorly known. We studied the joint influence of forest fragmentation and degradation on leaf-litter frogs. We specifically asked whether the processes structuring leaf-litter anuran assemblages in fragmented forests are the same as those in continuous forests. We analyzed anuran assemblages with respect to habitat characteristics, including fragmentation and degradation parameters. In comparison with continuous forests, species richness and diversity were lower and assemblage composition was altered in forest fragments. These changes seemed to be mainly caused by habitat degradation rather than forest fragmentation. Availability of aquatic sites for breeding, vegetation structure (including those variables indicating degradation), and leaf-litter cover had the most influence on the presence of single species. The comparatively small impact of fragmentation on anurans might be due to the location of the study area; it still possessed large tracts of continuous forest. These forest blocks may stabilize the regional rainforest climate and thus weaken the effects of fragmentation.*

Keywords: forest fragmentation, frog assemblages, habitat degradation, leaf-litter anurans, species assemblages, Taï National Park, tropical rainforest, West Africa

Efectos de la Fragmentación de Bosques y la Degradación del Hábitat sobre Ranas de la Hojarasca en el Oeste de África

Resumen: *La degradación del hábitat altera la dinámica y composición de los ensambles de anuros en los bosques tropicales. Los efectos de la fragmentación del bosque sobre la composición de ensambles de anuros son poco conocidos hasta la fecha. Estudiamos la influencia conjunta de la fragmentación y la degradación sobre ranas de la hojarasca. Específicamente nos preguntamos si los procesos que estructuran a los ensambles de anuros de la hojarasca en bosques fragmentados son los mismos que en bosques continuos. Analizamos los ensambles de anuros con respecto a las características del hábitat incluyendo parámetros de fragmentación y degradación. En comparación con los bosques continuos, la riqueza y diversidad de especies fueron menores y la composición del ensamble se alteró en los fragmentos de bosque. Estos cambios aparentemente fueron causados principalmente por la degradación del hábitat y no por la fragmentación del bosque. La disponibilidad de sitios acuáticos para reproducción, la estructura de la vegetación (incluyendo las variables indicadoras de degradación), y la cobertura de hojarasca tuvieron la mayor influencia sobre la presencia de especies individuales. El comparativamente pequeño impacto de la fragmentación sobre los anuros se puede deber a la localización del área de estudio; aun había grandes extensiones de bosque*

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continuo. Estos bloques de bosque pueden estabilizar el clima de la región y por lo tanto debilitar los efectos de la fragmentación.

Palabras Clave: África Occidental, anuros de la hojarasca, bosque tropical lluvioso, degradación de hábitat, ensambles de especies, ensambles de ranas, fragmentación de bosque, Parque Nacional Taï

Introduction

Tropical forests are not only the most diverse terrestrial ecosystem but they also suffer most in terms of destruction (Bowles et al. 1998; Pineda & Halffter 2004). With a mean annual forest loss of 0.48–0.56% between 1990 and 2005, deforestation rates are exceptionally high in West and Central Africa (FAO 2006). Even in today's core forest regions such as western Côte d'Ivoire, rainforest has decreased by more than 80% since the 1960s (Chatelain et al. 1996). Remaining forests are often highly fragmented and/or degraded. In general, fragmentation causes ecological degradation and ecosystem changes (Tabarelli & Gascon 2005). Nevertheless, the degree of degradation following fragmentation may vary, depending, for example, on the time since a fragment was isolated and the quality of the surrounding landscape. Even when forest fragments stay in nearly pristine conditions fragmentation may directly affect the composition of plant and animal communities (e.g., Benítez-Malvido & Martínez-Ramos 2003; Bickel et al. 2006), for example, through an increase of demographic stochasticity.

It remains largely unknown how fragmentation and degradation affect biodiversity and hence ecosystems on local and regional scales. So far only 2 publications have dealt with the effects of forest fragmentation in West Africa. Hill and Curran (2003) reported a significant species–area relationship for plants and predicted that forest fragmentation would cause local extinction of species. Beier et al. (2002) revealed that overall community composition of birds changed and several forest species disappeared in fragmented forests.

Amphibians are particularly sensitive to habitat degradation (e.g., Wake 1991; Blaustein et al. 1994; Ernst et al. 2006). Surprisingly, the effects of habitat fragmentation on amphibian populations have been tackled only in a few publications, mainly focusing on changes in species diversity and richness (e.g., Marsh & Pearman 1997; Tocher et al. 1997; Pineda & Halffter 2004). Habitat effects have been largely neglected, although it has been suggested that forest fragmentation may indirectly affect amphibians through edge effects (Urbina-Cardona et al. 2006) and a decrease in overall habitat quality (Marsh & Pearman 1997; Pineda & Halffter 2004). Habitat parameters that are expected to be important for amphibians and that are potentially affected by fragmentation are humidity, thickness of the leaf litter, understory density, and canopy cover (Marsh & Pearman 1997; Bell & Donnelly 2006; Urbina-Cardona et al. 2006). Nevertheless, fragment size and distance to the nearest continuous forest are still regarded as being most important for species abundance, species richness, and diversity (e.g., Marsh & Pearman 1997; Tocher et al. 1997; Pineda & Halffter 2004).

In Taï National Park (TNP), Côte d'Ivoire forest degradation has changed the composition of local anuran assemblages and their predictability (Ernst & Rödel 2005). On the basis of the habitat parameters, anuran assemblages in pristine forest were unpredictable, whereas they were highly predictable in selectively logged forest. This difference in predictability was caused by a nonrandom loss of species with particular life histories in degraded forests. Disappearance of these species most likely was due to an altered microclimate (Ernst & Rödel 2005; Ernst et al. 2006, 2007). An alteration of microclimatic conditions is also thought to be of major importance to plants and animals in fragmented forests (Kapos et al. 1997; Harper et al. 2005).

Despite the known effects of forest fragmentation and degradation on amphibians (e.g., Ernst & Rödel 2005; Cushman 2006; Urbina-Cardona et al. 2006), their joint effects are poorly understood. Therefore, we simultaneously tested the effects of forest fragmentation and degradation on the composition of forest amphibian assemblages. We selected the TNP and its surroundings as our study area and leaf-litter anurans as our model system because the regional pool of these species is very well known (Ernst & Rödel 2005) and effects of fragmentation can directly be compared with the effects of degradation in this area and this ecological group (Ernst & Rödel 2005). Sites within TNP represented undisturbed, unfragmented habitats. We compared them with forest fragments in the vicinity, which varied in size and in degrees of isolation.

We define *degradation* exclusively as changes in the vegetation structure. Respective degradation effects are, for example, alteration of the microclimate due to an opened canopy. Hence, degradation, for example, as a consequence of logging, can be observed in continuous and in fragmented forests. We define *fragmentation* as changes in size and connectivity of the forest habitat. Consequently, the increase of edge areas followed by edge effects is regarded as part of the fragmentation process. Hence, fragments cannot a priori be considered as degraded as defined herein. Nevertheless, in our case all fragments showed alteration of the vegetation structure

to differing degrees, ranging from almost pristine to heavily logged. We analyzed the effects of forest fragmentation and degradation on the anuran assemblages and identified those habitat parameters that were most influential to the presence or absence of particular species.

Methods

Study Area

Fieldwork was carried out during the rainy season from June to September 2002 in the western part of TNP, Côte d'Ivoire, and in forest fragments situated between TNP and the Cavally River (5°75.665′–6°02.576′N; 7°19.879′-7°30.125′W). This river marks the Ivorian–Liberian border. In Liberia larger tracts of rainforest still exist, and TNP is the largest remnant of continuous rainforest in West Africa. All fragments were closer to TNP than to the Liberian forests. Hence, we regarded the TNP as the nearest continuous forest. For a more detailed description of the study area, see Riezebos et al. (1994).

Study Design and Data Collection

We established 16 plots (Table 1), 6 within the primary forest of TNP and 1 in each of 10 forest fragments. Plot size was 2 ha except for the Keibly fragment (1.5 ha). The pristine forest plots in TNP were identical to those studied by Rödel and Ernst (2004), Veith et al. (2004), Ernst and Rödel (2005), and Ernst et al. (2006). This allowed us to assess the completeness of our records in the TNP plots and hence the accuracy of our method in general. The forest fragments varied in size, level of degradation, fragmentation age, and distance to TNP (Table 1). We selected the fragment plots as representative subsamples that ideally included all habitat types of the respective fragment. We could not avoid including edge habitat because it was not possible in smaller fragments. The surrounding landscape was mainly under cultivation (coffee, cocoa, banana, corn, rice). In addition, there were some fallow areas.

All data were collected by A.H. and 2 field assistants. Relative searching times summed up to 8 observer-hours/ha/plot. To account for seasonal and daily weather variation, we visited sites 3–8 times, and visits were randomly distributed over the entire investigation period. We visited plots during the day because TNP leaf-litter frogs are best assessed from dawn till dusk (M.-O.R., unpublished data). Species distribution and reproduction modes were categorized following Ernst and Rödel (2006; Table 2). During random walks, we used a combination of visual (VES) and acoustic (AES) encounter surveys to search for frogs. This combination gives the most reliable results in terms of species presences and relative abundance (Rödel & Ernst 2004). Visually encountered frogs were captured, identified, sexed, measured, and released after searching time was completed. For abiotic and biotic plot characterization, we selected 11, 5 × 5 m squares within a 200 × 100 m plot. Four squares were located in the corners, 3 on the line separating the plot into

Table 1. Characteristics of study sites in forest fragments and in Taï National Park (TNP) a species richness, relative abundance, and diversity of frogs in study sites.

Site	*Size (ha)*	*Distance to TNP border (m)*	*Fragmentation date (year)*	*Breeding sites*[a]		S[b]	*Ind./h*[c]	H'[d]	J'[e]
				lentic	*lotic*				
Zaipobly 1		4430	1984	0	1	7	5.54	0.622	0.736
Gahably 2	1.5–3	4656	1984	0	1	3	5.43	0.393	0.823
Keibly		5911	1984	1	1	6	5.74	0.593	0.762
Gahably 1	3–6	4150	1984	0	0	3	2.88	0.330	0.692
Port-Gentil 2		?[f]	?	1	1	6	4.80	0.439	0.564
Gouléako	6–12	1936	1990	0	0	2	3.69	0.296	0.983
Port-Gentil 1		?	?	0	0	5	3.95	0.213	0.305
Ponan	12–24	4538	1990	1	1	6	6.26	0.528	0.679
Zaipobly 2		4927	1990	0	0	4	3.56	0.389	0.646
Zaipobly 3	24–48	6085	1990	1	1	5	4.19	0.511	0.730
TNP 1	>48	−5357	continuous	1	1	10	9.69	0.805	0.805
TNP 2		−5177		0	0	6	3.70	0.564	0.725
TNP 3		−7247		0	1	11	7.05	0.846	0.812
TNP 4		−6957		1	1	12	9.07	0.794	0.736
TNP 5		−7277		1	1	10	7.61	0.861	0.861
TNP 6		−7157		1	0	8	5.88	0.788	0.872

[a] *Presence (1) or absence (0) of potential breeding sites.*
[b] *Number of anuran leaf-litter species.*
[c] *Number of frogs of all species observed per hour.*
[d] *Shannon index.*
[e] *Evenness.*
[f] *Information not available.*

Table 2. Relative abundance, distribution, and reproduction mode of frog species in Taï National Park (TNP) and in forest fragments.

Species (code)[a]	*TNP*	*Fragments*	*Distribution*[b]	*Reproduction*[c]
Arthroleptidae				
Arthroleptis comb. (arthro)	8.25	24.15	C	2
Astylosternus occidentalis (occid)	–[d]	0.06	B	1
Cardioglossa leucomystax (leuco)	0.06	–	A	1
Bufonidae				
Amietophrynus togoensis (togo)	0.51	0.06	C	1
Hyperoliidae				
Kassina lamottei (lamot)	0.13	–	A	1
Phrynobatrachidae				
Phrynobatrachus accraensis (accra)	–	0.06	B	1
P. alleni (all)	12.33	2.83	C	1
P. annulatus (annu)	0.06	–	A	1
P. fraterculus (frater)	0.06	–	A	1
P. guineensis (guine)	0.50	–	A	1
P. gutturosus (guttu)	0.12	–	A	1
P. liberiensis (libe)	6.62	7.30	C	1
P. plicatus (plica)	2.48	0.43	C	1
P. phyllophilus (phyllo)	2.38	0.76	C	1
P. tokba (tokba)	2.68	10.07	C	2
P. villiersi (villi)	5.26	0.20	C	1
Ptychadenidae				
Ptychadena aequiplicata (aequi)	1.50	0.18	C	1
Ranidae				
Hydrophylax albolabris (albo)	0.06	–	A	1

[a] *Nomenclature according to Frost et al. (2006). Species codes as used in Figs. 1 & 2.*
[b] *Distribution of frog species (obtained from NMDS; modified after Ernst & Rödel 2006; Ernst et al. 2006; and our own unpublished data): A, true primary forest species restricted to TNP primary forest; B, species restricted to forest fragments/disturbance indicator; C, ubiquitous species.*
[c] *Reproduction mode of frog species (Ernst & Rödel 2006): 1, larvae with aquatic development; 2, larvae with terrestrial direct development.*
[d] *No record.*

100 × 100 m (1 on each side and 1 in the center), and 4 on the 2 diagonals between each corner and the center. For each of the 11 squares, we recorded habitat parameters at the corners and in the center. Hence, we recorded habitat parameters at 55 points in every plot. We counted the abundances of categories or calculated mean values of counts of a particular parameter set in each plot. Habitat parameters included 16 categories of combinations of substrate type based on 4 main soil types (forest, arenaceous, loamy, and sabulous; Lieberoth 1982); percentage of leaf-litter cover (simplified after Braun-Blanquet 1964; 5 categories divided into 20% steps); and vegetation density (VD) in 4 strata (understory and shrub strata [<1 m] bush stratum [1–4 m], lower-tree stratum [4–15 m], and canopy [>15 m]). For each vegetation-density stratum, there were 7 subcategories (vegetation absent, gaps predominating, predominantly closed, vegetation completely closed, and the 3 transitions between these 4 categories); plant-stem diameter at breast height (dbh) in 5 categories (dbh1 = 0–5 cm, dbh2 = 6–10 cm, dbh 3 = 11–20 cm, dbh 4 = 21–50 cm, and dbh 5 > 50 cm); and presence or absence of potential lentic or lotic breeding sites. Stratum density and dbh quantify habitat degradation, assuming that in comparison with degraded forests, pristine forests have a predominantly closed canopy, more open understory and bush strata, and more trees in higher dbh categories (Chatelain et al. 1996).

Degrees of fragmentation were inferred from satellite images (data from Landsat Thematic Mapper [TM] 1974, Landsat Multispectral Scanner 1984, Landsat TM 1990, Système Probatoire d'Observation de la Terre [SPOT] XS 1997, SPOT XI/2000, 30 × 50 km) composed of fragment size (ha), distance to TNP border (m), and fragmentation date (years). Because determination of the exact fragment size was not possible, we used 6 size categories: 1.5–3 ha, 3–6 ha, 6–12 ha, 12–24 ha, 24–48 ha, and >48 ha. The TNP plots were assigned to category 6. For 2 fragments (Port-Gentil 1 and Port-Gentil 2), fragmentation date and distance to TNP could not be assessed. Plot characteristics are summarized in Table 1.

Statistical Analyses

We calculated relative species abundance corrected for the number of observer hours (Table 2). Because species abundances were not distributed normally (Kolmogorov–Smirnov test), we log-transformed them or used nonparametric tests. Two species of *Arthroleptis* could not be distinguished on the basis of morphology alone (Rödel & Bangoura 2004). Because they have similar microhabitat requirements (Ernst & Rödel 2005), we pooled them into an artificial taxon, *Arthroleptis* comb. The diversity of anuran assemblages in the leaf litter was measured with the Shannon index (H') and its respective evenness

(J') (BioDiversity Pro [version 2], Natural History Museum, London, and Scottish Association for Marine Science, Oban).

Relationships between the degree of fragmentation, forest characteristics, and the composition of anuran assemblages were tested with Mantel tests, nonmetric multidimensional scaling (NMDS; both with PC-ORD for windows [version 4.17], MjM Software Design, Gleneden Beach, Oregon), and regression analyses (Statistica for Windows [kernel version 6.0], StatSoft, Tulsa, Oklahoma). With Mantel tests, we pairwise controlled for the influence of similarity in habitat structure (calculated over all habitat parameters) and plot proximity (real distances in meters as cell entries) on the similarity among species assemblages (on the basis of relative species abundances). The distance matrix of species similarity was based on the Sørensen quantitative (Bray–Curtis) index (Faith et al. 1987; Magurran 2004). For the environmental similarity matrix, we used the relativized Euclidian distance (RED; Legendre & Legendre 1998). Distance matrices were compared among all plots and among primary and fragmented forest plots separately.

To investigate the influence of fragmentation and habitat characteristics on the presence of frog species, we performed NMDS analyses (Kruskal 1964; Van Deun & Delbeke 2000). We minimized the risk of finding a local instead of a global minimum by defining the appropriate dimensionality and statistical significance through the use of a start configuration (Legendre & Legendre 1998). For preliminary runs, Sørensen (Bray–Curtis) distances and the following settings were applied: maximum number of iterations = 400, instability criterion = 0.00001, starting number of axes = 6, number of real runs = 40, and number of randomized runs = 50. Resulting configurations were defined as starting coordinates in subsequent ordinations with application of the suggested dimensionality. In the graphical NMDS representation, species and environmental variables contributed to the ordination axes to different degrees, expressed through linear (Pearson's r = parametric) and rank (Kendall's τ = nonparametric) correlations (Jongman et al. 1995; McCune & Grace 2002). The axes were scaled to the longest axis thus providing accurate representation of distance relationships among points. Vectors represented environmental variables that had the highest correlation with ordination axes; thus, these variables had the most influence on the projection of species and plots. The angles and lengths of the vectors indicated direction and strength of correlations, respectively.

We performed NMDSs with fragment variables, habitat variables, and relative species abundances of every plot. In these NMDSs, plots were arranged along the axes according to the variance of their habitat characteristics and their frog assemblages. We based species arrangements on the variance of habitat characteristics of those plots where they were recorded. To reveal the respective effects of fragmentation and degradation, we also analyzed fragment and habitat variables separately. All NMDSs were followed by a second step in which the analyses were performed without the values of relative species abundances. In this second step we obtained ordination scores for every plot that were influenced only by habitat characteristics and/or fragmentation variables. In the case of fragmentation variables alone, this analysis could not be performed because it was not possible to find a useful NMDS configuration. For the other NMDSs performed without species abundances, the best solution was one-dimensional. With the ordination scores for plots resulting from these NMDSs, we subsequently performed regression analyses to test for species-specific habitat requirements. We chose a quadratic regression model (Jongman et al. 1995) because most frog species had a unimodal rather than an even distribution along habitat parameters. We used NMDS ordination scores as independent variables. Dependent variables were the log-transformed values of relative species abundances.

Results

Species Richness and Diversity

In 252 hours of plot sampling (8 hours/ha), we registered 19 frog species (Table2). We recorded 1065 frogs visually and 328 acoustically. In forest fragments there were 11 species. The 17 species recorded in TNP primary forest represent 85% of the leaf-litter species observed between 1999 and 2002 by Rödel and Ernst (2004) and Ernst and Rödel (2005) in the same plots, indicating sufficient and representative sampling.

Species richness and number of individuals varied among sites, with higher values for TNP plots than for forest fragments (Mann-Whitney U, $Z = -3.012$, $p = 0.003$, $n = 16$, $Z = -2.386$, $p = 0.0016$, $n = 16$, respectively). The Shannon diversity index (H') was significantly higher in continuous forest ($Z = -3.037$, $p = 0.002$, $n = 16$), whereas evenness (J') was not different between continuous and fragmented forests ($Z = -1.682$, $p = 0.092$, $n = 16$; Table 1).

The composition of frog assemblages varied among sites (Table 2). Dominant species were identical in TNP and fragmented forests (*Arthroleptis* comb., *Phrynobatrachus alleni*, *P. liberiensis*, and *P. tokba*), but they ranked differently in terms of abundance. The number and abundance of primary forest species was lower in forest fragments, whereas the number of secondary forest and savannah species increased. The comparison of species composition in fragments with data previously collected in TNP (Ernst & Rödel 2005) revealed that the percentage of primary-forest species compared with disturbance-tolerant species was marginally higher in forest fragments (77.8% and 22.2%) than in TNP secondary

Table 3. Values for nonmetric multidimensional (NMDS) scaling of study sites in Taï National Park and forest fragments performed with relative species abundances of frogs and environmental characteristics (fragmentation parameters and/or habitat parameters): stress in relation to dimensionality (number of axes) and coefficients of determination for the correlations between NMDS ordination distances and distances in the original *n*-dimensional space (explained variance).

		Stress in real data		*Stress in randomized data*[a]				
Ordination	*Axis*	*minimum*	*maximum*	*minimum*	*maximum*	p	*Increment*	*Cumulative*
NMDS 1[b]	1						0.142	0.142
	2	5.968	9.621	8.778	34.954	0.0323	0.803	0.944
NMDS 2[c]	1						0.226	0.226
	2	7.896	26.194	12.154	23.334	0.0323	0.664	0.890

[a] *Randomized data are derived from Monte Carlo simulations (50 randomized runs) (distance measure, Sørensen [Bray–Curtis]).*
[b] *Derived from the relative abundances of species, fragmentation parameters, and habitat parameters.*
[c] *Calculated for relative abundances of species and habitat parameters only.*

forest (73.9% and 26.1%). There was no correlation between the number of species and fragment size (Pearson correlation coefficient, $r = -0.10$, $p = 0.77$, $n = 10$) or between species richness and distance of fragments to the continuous forest block ($r = 0.59$, $p = 0.13$, $n = 8$).

Assemblage Predictability

The comparison of species, environmental, and geographic distance matrices for all plots revealed significant pairwise correlations only for geographic distances and assemblage similarities ($r = 0.3565$, $p = 0.004$): plots that were closer to each other had similar assemblages. Nevertheless, overall habitat similarity was almost paralleled by a similarity in frog assemblages ($r = 0.1683$, $p = 0.054$). When repeating this analysis for TNP plots only, this result did not change (species vs. geographic distances: $r = 0.3910$, $p = 0.037$; species vs. environmental distances: $r = 0.2882$, $p = 0.210$). When only considering plots in fragments, significant correlations were detected between species and geographic ($r = 0.5170$, $p = 0.007$) and species and environmental distances ($r = 0.2392$, $p = 0.047$). Hence, frog assemblages in forest fragments were predictable on the basis of habitat characteristics, whereas this was not the case in continuous forest.

Responses of Species to Fragmentation Level and Habitat Structure

Preliminary NMDS runs produced a 2-dimensional ordination that provided significantly more reduction in stress than expected by chance ($\alpha = 0.05$; Table 3). When considering the level of fragmentation, habitat parameters and species abundances, the 2 axes explained 94.4% of the overall variance (Table 3; NMDS 1). Ten habitat parameters and the 3 fragmentation parameters correlated sufficiently well with ordination axes (Table 4, Fig. 1). Parameters that explained most of species projection along axis 1 were the availability of lentic and lotic breeding sites. Species arrangement along axis 2 was dominated by vegetation density in shrub and bush strata, thickness of leaf-litter layer, openness of the canopy, plant dbh in the lower categories, fragment size, isolation date, and distance to the TNP border. In an overlay on the axes, most frogs showed a unimodal distribution. Nevertheless, no significant relationship between frog species and the most influential environmental variables was found when applying the regression model with the plots' ordination

Table 4. Correlation values of habitat parameters with the 2 axes of nonmetric multidimensional scaling (NMDS) of study sites in Taï National Park and forest fragments performed with relative species abundances of frogs and environmental characteristics (fragmentation parameters and/or habitat parameters).

		Axis 1		*Axis 2*	
	Parameter[a]	r[b]	T[c]	r[b]	T[c]
NMDS	leaf-litter cover	−0.183	−0.161	0.622	0.484
	VD shrub	0.107	0.016	0.821	0.641
	VD bush	0.337	0.168	0.407	0.196
	VD canopy	0.023	0.077	−0.582	−0.465
	dbh 1	−0.044	−0.077	0.810	0.604
	dbh2	0.113	−0.044	0.58	0.398
NMDS 1[d]	dbh3	−0.295	−0.421	0.673	0.489
	dbh4	0.142	−0.101	0.450	0.326
	lotic	0.660	0.564	−0.305	−0.365
	lentic	0.687	0.516	−0.378	−0.328
	surface	0.070	0.099	−0.736	−0.568
	distance	−0.036	−0.077	0.851	0.341
	isolation date	−0.053	−0.105	0.797	0.577
	leaf-litter cover	−0.197	−0.139	0.653	0.481
	VD shrub	−0.646	−0.505	0.687	0.554
	VD canopy	0.513	0.347	−0.473	−0.408
NMDS 2[e]	dbh1	−0.517	−0.367	0.736	0.500
	dbh2	−0.435	−0.252	0.500	0.454
	dbh3	−0.484	−0.224	0.467	0.397
	lotic	−0.207	−0.165	−0.568	−0.471
	lentic	0.006	0.047	−0.470	−0.377

[a] *Abbreviations: VD, vegetation density in different strata; dbh, stem diameter breast height.*
[b] *Pearson correlation.*
[c] *Kendall correlation.*
[d] *Derived from the relative abundance of species, fragmentation parameters, and habitat parameters.*
[e] *Calculated for relative abundance of species and habitat parameters only.*

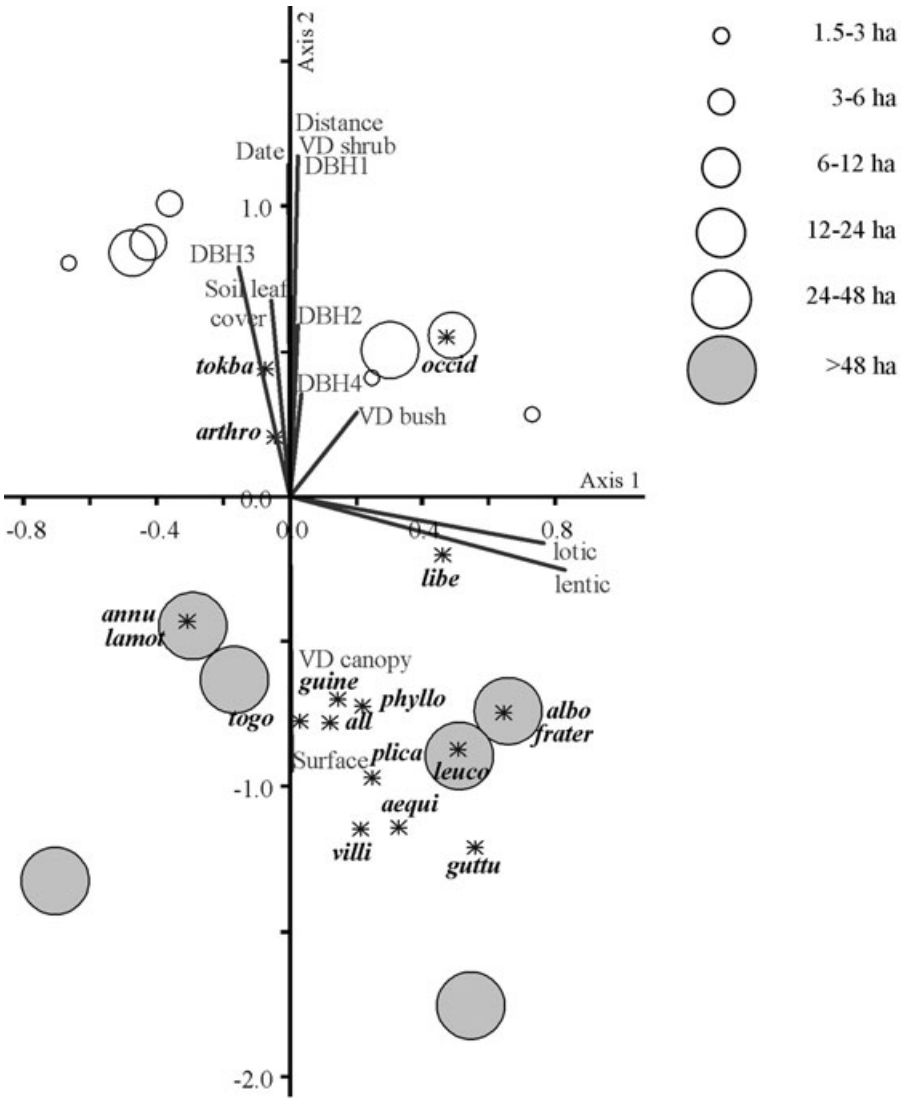

Figure 1. Nonmetric multidimensional scaling (NMDS) ordination of study sites in Taï National Park and forest fragments performed with relative abundances of 17 frog species and environmental parameters (fragmentation and habitat parameters; distance matrix derived from the Sørensen coefficient). Positions of sampling sites (circles) in graphs are determined by the variances of habitat parameters, fragmentation parameters, and by the sampling sites' species assemblages. Position of frog species is determined by the variance of their occurrence in plots along the axes of environmental variables. Vectors describe environmental variables with highest explanatory values for ordination axes. Dominating variables for NMDS 1 are presence of lentic and lotic habitats on axis 1; distance to Taï National Park, vegetation density (VD) shrub, dbh1, and fragmentation date on axis 2. Species codes are defined in Table 2 (DBH, diameter breast height). Continuous forest plots are in gray.

scores from the subsequent one-dimensional NMDS and species abundances.

The first step of the NMDS calculated with fragmentation variables and values for the species abundances explained 94.4% of the variance, suggesting a 2-dimensional solution. Nevertheless, in a second NMDS with fragmentation variables alone it was not possible to find an exercisable NMDS configuration. We therefore could not perform this second step and the subsequent regression analyses.

For the NMDS with habitat parameters and species abundances, but without fragmentation parameters, a 2-dimensional solution still explained 89% of the variance (Table 3, NMDS 2). The observed arrangement in the joint plot was similar to that in the first NMDS (Fig. 2). Nevertheless, axis 1 represented a degradation gradient, whereas axis 2 was mainly influenced by the presence or absence of aquatic breeding sites. Low dbh categories and the vegetation density in the shrub stratum, both indicating disturbance, also significantly influenced axis 2 (Table 4 and Fig. 2). The following NMDS without species abundances showed a one-dimensional solution. The most influential habitat characteristics were the canopy density and the presence or absence of lentic and lotic habitats (on the axis toward 1), the dbh 1, 2, 3, and the shrub-stratum density (on the axis toward 0). The corresponding regression analysis revealed significant correlations between habitat variables and the abundances of *Amietophrynus togoensis*: ($r^2 = 0.347$, $p = 0.038$), *Kassina lamottei*: ($r^2 = 0.516$, $p = 0.009$), *P. alleni* ($r^2 = 0.735$, $p = 0.002$), *P. annulatus* ($r^2 = 0.516$, $p = 0.009$), *P. guineensis* ($r^2 = 0.327$, $p = 0.027$), *P. phyllophilus* ($r^2 = 0.441$, $p = 0.014$), *P. plicatus* ($r^2 = 0.601$, $p = 0.010$), *P. villiersi* ($r^2 = 0.895$, $p = < 0.001$), and *Ptychadena aequiplicata* ($r^2 = 0.566$, $p = 0.037$). The 3 frog species with highest correlations (*P. villiersi*, *P. plicatus*, and *P. alleni*) are typical forest species that depend on small lentic aquatic breeding sitexs.

The a priori affiliation of primary forest species (group A) and species of forest fragments (group B) was

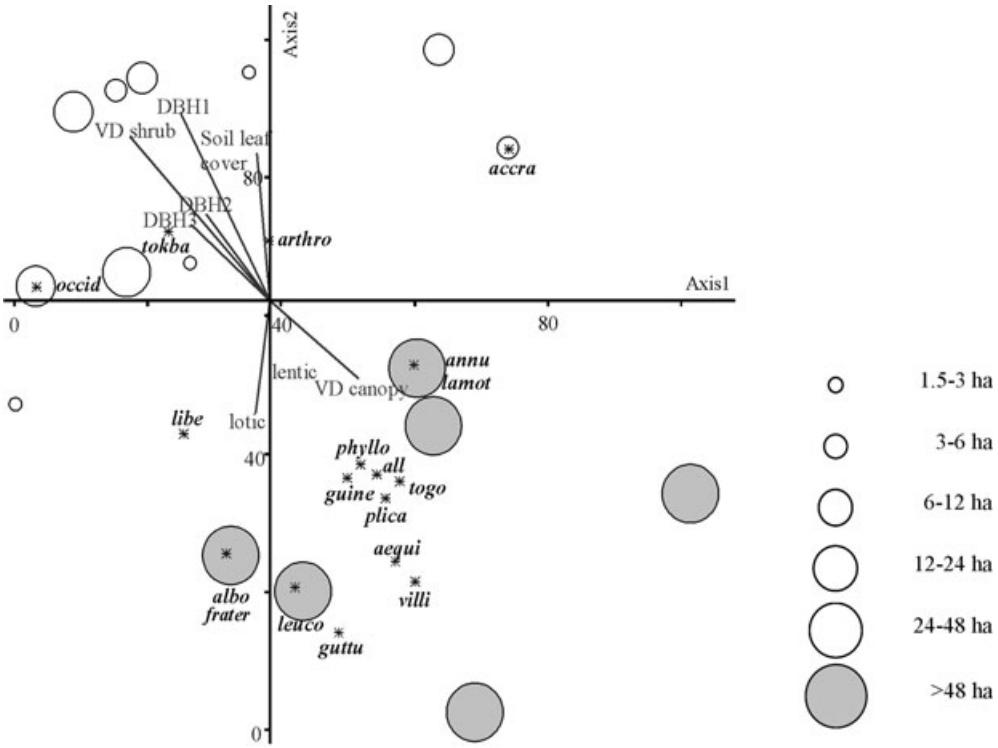

Figure 2. Nonmetric multidimensional scaling (NMDS) ordination of study sites in Taï National Park and forest fragments performed with relative abundances of 18 frog species and habitat parameters (distance matrix derived from the Sørensen coefficient, compare Fig. 1), excluding fragmentation parameters. Dominating vectors for NMDS 2 are vegetation density shrub stratum, vegetation density canopy, and DBH 1, 2, and 3 on axis 1 and DBH1 (DBH, diameter breast height), vegetation density (VD) shrub, leaf-litter cover, and presence of lotic habitats on axis 2. For species codes and acronyms, see Table 2. Continuous forest plots are in gray.

mirrored by both NMDS runs (Figs. 1 & 2). Species of group C with aquatic development (group 1 in Table 2) clustered with TNP species, whereas the 2 species with direct development (group 2 in Table 2) showed more affiliations to group B species due to their high prevalence in fragments.

Discussion

In TNP habitat alteration by selective logging changed the composition and predictability of leaf-litter frog assemblages. Canopy opening resulted in microclimatic changes that most likely posed physiological constraints on several frog species. This led to a nonrandom reduction in functional diversity of amphibian species (i.e., the number of true forest species decreased in logged forests) (Ernst & Rödel 2005; Ernst et al. 2006).

We investigated the combined effect of forest fragmentation and degradation. The comparison of pristine continuous with partly degraded and fragmented forests revealed decreased species richness and diversity in fragments, a loss of several forest species, and a change in assemblage composition. Nevertheless, typical fragmentation parameters could not explain these changes. Neither did we observe a relationship between species richness and fragment size as has been shown in forest fragments for a variety of taxonomic groups (e.g., Laurance et al. 2002; Benedick et al. 2006), including frogs (Tocher et al. 1997; Pineda & Halffter 2004; Bell & Donnelly 2006), nor was species richness influenced by the distance of forest fragments to continuous forest. Hence, we conclude that fragmentation, as defined by our parameters, did not directly affect leaf-litter frogs.

Thus, forest fragmentation may indirectly influence assemblage composition, for example, through increasing edge areas, and thus lead to habitat conditions similar to those in logged forests. This was reflected by species occurrences and the relationships of species with a set of habitat parameters in the NMDS without fragmentation variables. Indirect fragmentation effects are suggested by Marsh and Pearman (1997), who, however, could not identify the habitat factors that specifically influenced the presence or absence of amphibian species. In our study, habitat characteristics, such as the presence or absence of breeding sites and the vegetation structure, including

degradation parameters, were important for species occurrences.

Availability of lentic or lotic habitats is of major importance for the reproduction of most anurans (Zimmermann & Simberloff 1996; Hofer et al. 2000; Pineda & Halffter 2004). In forest fragments of the Brazilian Amazon, the presence of aquatic habitats is a key factor for the maintenance of particular frog species (Neckel-Olivieira & Gascon 2006). Like Pineda and Halffter (2004) we observed that some species survive and reproduce, regardless of fragmentation and disturbance, provided aquatic breeding sites were still available. In our forest fragments the presence or absence of aquatic breeding sites is likely to be independent of fragmentation and degradation itself. Nevertheless, water persistence, at least of stagnant waters, may be influenced by forest degradation following isolation. Higher temperatures and increased evaporation are enhanced by a more open canopy and may reduce pond persistence. This may at least partially explain the loss of pond specialists in degraded forests as observed by Ernst et al. (2006).

In addition, a variety of other parameters were of equally high importance for the presence of species. In particular these parameters were related to habitat degradation, such as vegetation density in different strata (especially in the canopy), dbh categories, and the thickness of the leaf litter. These factors were also identified as major determinants of amphibian occurrence in Mexican rainforest fragments (Urbina-Cardona et al. 2006). By effectively preserving moisture, thick leaf-litter layers may substantially contribute to a higher humidity in forest fragments (Urbina-Cardona et al. 2006) than expected due to edge effects, which support dryer and hotter conditions (Murcia 1995; Harper et al. 2005). A thick layer of leaf litter, probably due to reduced decomposition by microorganisms in fragments, may thus function as a microclimatic buffer that stabilizes microhabitat conditions and hence may partly compensate for edge and degradation effects. This assumption is supported by the fact that species with direct terrestrial development, depositing eggs in moist leaf litter (Table 2), benefit from forest fragmentation. These species show highest abundances in fragments. This mirrors the pattern of degraded forests (Ernst & Rödel 2005; Ernst et al. 2006, 2007), where species with specialized reproductive strategies are more resistant to habitat alteration, being able to maintain stable or even increase populations.

Similar to Ernst and Rödel (2005), we observed a shift in abundances of species and a change in predictability of the assemblages. Frog communities in TNP primary forest were predictable on the basis of geographic distance only. Nearby sites in primary forests hence harbored similar assemblages, whereas similar habitats did not necessarily have similar frog assemblages. In contrast, similarity of frog assemblages among forest fragments was positively correlated with both geographic proximity and habitat similarity. The similarity of neighboring species assemblages in TNP may best be explained by the existence of a forestwide species pool from which local assemblages recruited their members. Prior to fragmentation, today's forest fragments must have been subject to the same similarity–distance relationship as our TNP plots. Therefore, neighboring fragments started with rather similar frog assemblages. Similarity then should be even higher when the separation of fragments is a more recent event and stochastic extinctions of species have not yet yielded large effects. Unfortunately, our data do not allow testing this hypothesis because our fragments were relatively recently separated from TNP during only 2 distinct periods (Table 1). Because extinction likely has a strong random component, the timing of species extinctions following isolation of a forest fragment is usually unknown (Meffe et al. 1997). Tocher et al. (1997) and Pineda and Halffter (2004) did not observe a loss of typical forest anurans during the first 10 years after fragmentation. Our fragments were all older than 10 years, and the observed lack of forest species may thus be interpreted as a negative long-term effect of habitat fragmentation.

Fewer forest species can persist in altered habitats (i.e., several TNP species were absent in forest fragments: *Hydrophylax albolabris*, *P. annulatus*, *P. fraterculus*, *P. guineensis*, *P. gutturosus*, *Cardioglossa leucomystax*, and *K. lamottei*). In contrast, we recorded several savannah and secondary forest species (e.g., *P. accraensis*, *Astylosternus occidentalis*) in the fragments, clearly indicating forest disturbance. We observed almost identical percentages of primary-forest and disturbance-tolerant species in fragments as Ernst and Rödel (2005) in their secondary forest plots, which may be another hint that degradation in both studies was most responsible for the observed changes. Nevertheless, we did not observe several primary forest species that at least occasionally were found in TNP secondary forest (Ernst & Rödel 2005). This may indicate that these species are only able to persist in, or sometimes migrate into, degraded forest if it is still connected to continuous forest.

As for the observed changes in frog assemblage composition, the predominant importance of degradation (i.e., vegetation structure) over the level of fragmentation (size and age of fragments and distance to nearest big forests) may be explained by the geographic location of our fragments. They were between the 2 major extant West African forest regions, the TNP and the Liberian forest block west of the Cavally River. The entire area is probably still dominated by an overall rainforest climate that can weaken potential fragmentation effects. In addition, thicker leaf-litter layers in our fragments may have buffered microclimatic changes following fragmentation. This supports Laurance et al. (2002), who hypothesized differences in the effects of forest fragmentation in different regions. Their fragments were less sensitive to fragmentation effects because of their square shape, the

surrounding landscape with tall vegetation, and the short distances to large tracts of continuous forest. A review of fragmentation studies conducted in different climatic and geographic regions led Harper et al. (2005) to the conclusion that an evaluation of potential edge influences is not possible without considering local and regional conditions, but effects seem to be especially strong for young edges in tropical regions in more open landscapes. Cloudy and rainy climates and regenerating edges potentially reduce these effects.

Nevertheless, in the light of the observed overall negative effect of forest fragmentation on amphibian species richness and diversity, it is evident that further fragmentation and degradation in the Taï area should be avoided in order to maintain the high amphibian diversity of this upper Guinea forest subregion (Rödel et al. 2008). The fact that presence or absence of leaf-litter frogs largely depended on the amount of degradation and not on fragmentation itself underlines the outstanding suitability of these species as indicators for the degradation status and thus the habitat health of tropical rainforests.

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