RESEARCH ARTICLE

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What makes a successful species? Traits facilitating survival in altered tropical forests

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Abstract

Background: Ongoing conversion, disturbance and fragmentation of tropical forests stress this ecosystem and cause the decline or disappearance of many species. Particular traits have been identified which indicate an increasing extinction risk of a species, but traits facilitating survival in altered habitats have mostly been neglected. Here we search for traits that make a species tolerant to disturbances, thus independent of pristine forests. We identify the fauna that have an increasing effect on the ecosystem and its functioning in our human-dominated landscapes.

Methods: We use a unique set of published data on the occurrences of 243 frog species in pristine and altered forests throughout the tropics. We established a forest dependency index with four levels, based on these occurrence data and applied Random Forest classification and binomial Generalized Linear Models to test whether species life history traits, ecological traits or range size influence the likelihood of a species to persist in disturbed habitats.

Results: Our results revealed that indirect developing species exhibiting a large range size and wide elevational distribution, being independent of streams, and inhabiting the leaf litter, cope best with modifications of their natural habitats.

Conclusion: The traits identified in our study will likely persist in altered tropical forest systems and are comparable to those generally recognized for a low species extinction risk. Hence our findings will help to predict future frog communities in our human-dominated world.

Keywords: Forest degradation, Frogs, Life-history traits, Adaptation, Extinction risk, Tropics

Background

The anthropogenic conversion of natural environments, in particular of forest habitats, is a major threat to tropical biodiversity [1]. Beside the intensive loss of forest cover [2], fragmentation of the pristine remnants further affects species [3] and limits their ability to move into adequate areas. Thus the ability to cope with altered landscapes is crucial for the persistence of a species, especially in the face of climate change.

Numerous empirical and comparative approaches on species response to environmental changes and studies relating species properties to their extinction risk were conducted on invertebrates e.g. [4–6] as well as vertebrates e.g. [7–10]. However, the general pattern which

leads to the persistence of some species but the decrease or loss of other species due to forest disturbances is not fully understood. In different taxonomic groups some life-history and ecological traits show parallel patterns in their response to forest alteration, e.g. small range size [8, 10, 11] or low fecundity [12, 13] that lead to higher extinction risks. Whereas other traits, like body size exhibit a fuzzy prediction of a species' risk to decline in fragmented habitats [summary in 14]. The susceptibility of species is not determined by a single trait, but by a combination of properties which lead to a speciesspecific extinction risk [15-17]. So far, the majority of studies have focused on species affected by environmental changes and filter for traits increasing the extinction risk. Species not responding to habitat alterations and the traits required for their persistence in disturbed landscapes are frequently neglected. However, those species remaining are of high interest as they will make up the

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majority of the fauna in our human-dominated world and thus have an increasing effect on ecosystems and their functioning [18, 19].

Frogs are strongly influenced by their environment and the degradation and conversion of natural forests is one major cause for their current global decline [20–22]. However, not all species are affected by degradation or fragmentation [23–25] and a set of life-history or ecological traits is assumed to reduce their susceptibility [8, 26].

In this study, we search for factors allowing a species to be independent of pristine areas and thus permitting their occurrence in degraded and disturbed forests, which are the dominant tropical habitats now and in future [27]. We use a unique data set comprising published records on frog species occurrences in tropical forests, forest fragments and more intense altered landscapes such as plantations or settlements. For these species we gathered life-history (e.g. body size, clutch size) and ecological traits (e.g. habitat use) as well as distribution data, which are known to affect the susceptibility of species in general [8, 26, 28] and thus might likewise influence a species response to forest degradation. We ask whether these candidate traits could predict the forest dependency of tropical frog species and whether a particular set of traits makes species less vulnerable to changes in their natural habitat and decreases their risk of extinction.

Methods

Data acquisition

We combined a comprehensive data set on anuran occurrences across tropical forests and human altered forest habitats with detailed information on species traits. To cover all research published on anuran distribution in pristine versus altered environments in the tropics, we did a comprehensive literature research using Google, Google Scholar, Web of Science and data bases included therein (January to August 2013). Queries using different combinations of appropriate keywords (e.g. frog, amphibian, anuran, disturbance, alteration, fragmentation, logging etc.) were applied to all data bases. Appropriate data sets covered a description of the study sites and information on the presence (and absence) of each species in the different habitat types. In addition to already published studies we added our own data on anuran occurrences from the forest zone of Cameroon (M. Hirschfeld et al. unpublished data). The survey amounted to 61 studies (see Additional file 1: anuran distribution references) covering all continents that include a tropical climate: Africa, Asia, Central- and South-America, and Australia with a total of more than 750 different anuran taxa. For our analysis we only included records with species level identifications. Species names were checked and updated if necessary according to Frost [30]. If a taxonomic name could not be unambiguously assigned to a valid species, i.e. due to cryptic species complexes, the record was not included. This resulted in a data set with 672 species.

For each valid species from the occurrence data set, its life-history and ecological traits (hereafter referred to as traits) were gathered using published literature, suitable data bases reviewed by specialists, and further web resources (see Additional file 2: anuran traits references). Additionally we included our own unpublished data, collected either in the field or from museum specimens (Museum für Naturkunde Berlin, e.g. body size, ripe eggs in female ovaries). Traits collected and used in the analysis comprised information on species distribution, morphology, biology, and ecology. We also noted the geographic (i.e. continent) and phylogenetic (family) origin of each species (see Table 1 for details). As we only considered species for our analysis where at least information on body size (either male or female) was available, the data set was reduced further to 619 species.

Data preparation

Some of the collected trait data required processing for subsequent analysis. We used the elevational range calculated as the difference from the maximum to the minimum elevation where a species is known to occur. Regarding body size, we used the maximum body length known per species and sex or, if not available, mean values plus standard deviation. Only if maximum and/or standard deviation were not available, mean or single values were used. We supplemented the data set with sexual dimorphism, calculated as male divided by female body size. Clutch size was only available for a subset of species (345). The available data on clutch sizes were grouped objectively into ten size classes (A: 4-98, B: 100-265, C: 290–549, D: 563–905, E: 979–1652, F: 1900–3320, G: 3607-6701, H: 8357-12940, I: 17000-25000, J: 36100-40000) and species without information on clutch size were subsequently assigned to a class based on body size (see Additional file 3: clutch size classes for more details).

Studies included in our analyses focused on the comparison of anuran distribution among various landscapes. Hence, broader habitat categories were necessary to combine the results within one analysis. Based on all information available we chose three major habitat categories along a human altered degradation gradient: forest, secondary growth, and non-forest. The habitat category "forest" comprises primary forests, primary forest fragments, and selectively logged or exploited areas; "secondary growth" subsumes secondary forests, edges of primary forests, abandoned plantations (>5 years) and agricultural habitats with remaining forests (e.g. shaded coffee plantations); non-forests comprise simple structured plantations (single strata), pasture or inhabited areas such as villages.

Table 1 Life-history and ecological traits used in the study

Trait	Definition	Scale	Unit/level
Range size ^a	Natural area of occurrence	Ratio	km²
Elevation	Min. and max. elevation in the entire area of occurrence	Ratio	m asl
SVL male/female	Body length, measured as snout vent length	Ratio	mm
Dimorphism	Calculated as male divided by female body size	Ratio	Proportion
Clutch size	Maximal number of total eggs deposited or maximal number of ripe eggs in the uteri of dissected females	Ratio	#
Clutch size class	Clutch sizes assigned to size classes	Ordinal	Ten size classes, see "Methods" for details
Reproduction	Development	Nominal	Direct, indirect
Adult habitat	Habitat where adults are usually encountered, perch height	Nominal	Aquatic, semi-aquatic, fossorial, litter (<1 m), semi-arboreal (1–3 m), arboreal (>3 m)
Larval habitat	Habitat where the larvae develop	Nominal	None (direct development), terrestrial, semi-aquatic, lentic, lentic and lotic, lotic, phytotelmata (plant associated water bodies, e.g. tree holes, bromeliad tank), skin ^b
Egg deposition	Habitat where the eggs are deposited	Nominal	Terrestrial, semi-terrestrial, aquatic, arboreal, skin ^b
Family	Taxonomic origin, affiliation to family	Nominal	Anuran families according to Frost [30]
Region of origin	Broad geographic region (i.e. continent)	Nominal	

Given is the trait, its definition, the scale of measurement, and the unit (ratio) or levels (nominal, ordinal) of the respective trait

Categorization was realized in accordance with comparative studies [4, 31, 32]. However, in consideration of the modified forest types examined in our data set, slight adaptations and a reduction of categories were necessary. We only took species into account which had information on the presence and absences in these major habitat categories. If a species was detected in several studies, its single occurrence per habitat category (although absent in other studies) was crucial to assign the species to that habitat type. Combining this reduced data set with the available trait data, the final data set amounted to 243 different species with only a few gaps for some traits. As multivariate statistics often require complete data sets, missing values in the trait data set were replaced by dummy variables. This prevents a high loss of information by excluding a trait or a species. For traits with a ratio scale we used the mean, and for traits with a nominal scale the level which occurred most often (compare Table 1). Numbers of required dummy variables in the final data set: range size = 2 (mean = $1,795,153 \text{ km}^2$), elevational range: 35 (1217.6 m), snout-vent length (SVL) males: 4 (10.5 mm), SVL females: 21 (18 mm), reproductive mode: 1 (most frequent: indirect development), adult habitat: 2 (litter); larval habitat: 11 (lentic), egg deposition site: 34 (aquatic). All analyses were conducted with the completed data set (see Additional file 4).

Based on the species occurrences in the three major habitat categories, a forest dependency index (FDI) with four levels was established (Fig. 1): dependent species solely detected in forests (D), slightly dependent species occurring in forests and habitats with secondary growth (SD), forest independent species occurring not in primary forests, i.e. only in habitats with secondary growth and/or non-forested habitats (I), and species with no response occurring in all three habitat categories or forest and non-forest habitats (NR).

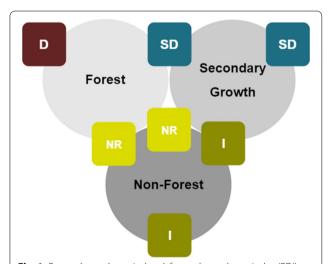


Fig. 1 Forest dependency index. A forest dependency index (FDI) was established based on species occurrences in three major habitat categories (forest, secondary growth, non-forest); FDI: *D* dependent, solely detected in forests, *SD* slightly dependent, species occurring in forests and habitats with secondary growth, *I* forest independent species, occurring not in primary forests, i.e. only in habitats with secondary growth and/or non-forested habitats, *NR* species with no response, occurring in all three habitat categories or forest and non-forest habitats

a Range size according to the IUCN Red List [29] or, if not available, for West African species to the calculated environmental niche model [70]

^b Carried in or on adult male or female

Statistical analysis

The distribution and trait data (ratio scale) were nonnormal distributed (Shapiro-Wilk test, R package 'stats'). We thus applied the non-parametric Kruskal–Wallis test and subsequent pairwise Wilcoxon tests with false discovery rate (fdr) correction for parameter comparison among species with different forest dependency indices (R package 'stats'). To filter for species traits explaining the presence or absence of a species in differently degraded habitats and thus their assignment to a particular FDI we performed a Random Forest (RF) classification [33] where 1000 classification trees on bootstrap samples of the data were grown (randomForest, R package 'randomForest' [34]). The number of candidate variables at each node (*mtry*) was the square root of the total number of variables in the analysis (default setting). To correct for different sample sizes in the training data set, sampsize was adjusted according to the minimum sample size per analysis. RF was performed for the whole data set and four subsets, three comparing forest dependent species (D) with one of the other FDIs and a comparison of the groups NR and I. We incorporated all available information for a species in RF, including species distribution (range size, elevation range, region of origin) and seven traits (see Table 1). As families were evenly distributed among the different FDIs (see Additional file 5), the affiliation to a family was excluded from the analysis. Binomial Generalized Linear Models (GLM) were performed to filter for potential traits explaining the habitat dependency of a species (glm, R package 'stats'). Therefore, species not responding to habitat changes (NR) were defined as '0' and compared to forest dependent species (D) as well as forest independent species (I), both defined as '1'. Numerical variables (body size and sexual dimorphism) were scaled from 0 to 1. To avoid multi-colinearity among explaining variables within one model, generalized variance inflation factors (GVIF) were calculated (vif, R package 'car'). Each model contained the covariates: SVL females, sexual dimorphism, clutch size class, larval habitat, adult habitat, reproductive mode, and egg deposition site. After reducing the co-linearity among the explaining variables and eliminating those with a GVIF higher than five [35], the full model only contained: SVL females, sexual dimorphism, clutch size class, and larval habitat. To test for any influence on the forest dependency of species distribution we fitted Generalized Linear Mixed Effect Models (GLMM) with range size and elevational range (both scaled from 0 to 1) as fixed and the region of origin as random factor (glme, R package 'lme4'). Here, a reduction of covariates due to co-linearity was not necessary. Based on the models, we predicted whether a species is either dependent on forest (non-forest) or occurs in all available habitats (>0.5 for forest, D or non-forest, I; <0.5 for habitat independent species, NR). All statistical analysis were applied using R 3.2.1 [36].

Results

Taxonomy

The 243 anuran species included in the analysis belonged to 26 different families. The most common families were Rhacophoridae and Hylidae, the latter representing 10–30% of the species in all forest dependency indices (FDIs). The families were equally distributed among the different FIDs (see Additional file 5), ruling out any phylogenetic influence in the data.

Species distribution

Range sizes ranged from 6.17 to 12,217,676 km² and varied highly within each FDI (Table 1 for information on gathered traits; see Table 2; Fig. 2 for results). It differed significantly between forest dependent species (D) and species not responding to habitat alteration (NR) as well as between species slightly depending on forests (SD) and NR. All FDIs covered species with limited and wide altitudinal distribution (see Fig. 2). NR species had the broadest distribution and differed significantly from the others (see Table 2). Species in the final data set originated from Africa, Madagascar, America and Asia. The indices NR, I and SD comprised species from all four regions, only D was lacking Malagasy species (Fig. 3). The region of origin did not differ significantly between the FDIs (Pearson's χ^2 test: $\chi^2 = 5.89$, df = 3, p = 0.12).

Habitat

Overall, most species preferred litter as well as shrubs and lower tree strata (1-3 m) as adult habitat (Fig. 3). Almost 75% of the species belonging to D and I live in trees (categories semi-arboreal and arboreal); SD and NR species were mostly found on the ground. Aquatic habitats were not inhabited by SD species, while the other FDIs covered all types. The habitat use differed slightly among the FDIs (Pearson's χ^2 test: $\chi^2=27.28$, df = 15, p = 0.03). Lentic waters constitute 35-60% of the tadpoles' habitat per FDI (Fig. 3). Lotic waters were of high importance in SD species, but less in other FDIs. All other categories were only sparsely presented, apart from no larval habitat, representing direct developing species. The larval habitat differed significantly between species assigned to different FDIs ($\chi^2 = 45.23$, df = 21, p = 0.002).

Body size

Maximum body sizes ranged from 10 to 187 mm for males and from 18 to 287 mm for females, respectively, with a high variation for both sexes within each FDI (see

Table 2 Distribution pattern and life history traits

Trait	General n = 243		D n = 33		SD n = 108		NR n = 83		l n = 19	
	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
р										
Range size (km²)ª	1,795,153 ± 2,784,023	6.17–12,217,676	1,511,311 ± 2,996,433	14.67–12,217,676	1,086,942 ± 2,069,589	6.17–10,932,823	2,850,720 ± 3,163,102	21.62-11,045,631	1,795,153 ± 2,784,023 6.17-12,217,676 1,511,311 ± 2,996,433 14,67-12,217,676 1,086,942 ± 2,069,589 6.17-10,932,823 2,850,720 ± 3,163,102 21,62-11,045,631 1,702,603 ± 2,983,042 305,09-10,415	305.09– 10,419,167
Elevational range (m) ^a	1217.60 ± 591.78 1–3100	1–3100	994.04 ± 582.89	72–3000	1123.0 ± 557.65	1–2500	1446.33 ± 561.84	400–3002	1144.46 ± 652.31	20–3100
SVL males (mm) ^a	47.13 ± 30.25	10.5-187	45.83 ± 26.96	18.4–146	45.90 ± 31.85	10.5-180	50.34 ± 31.29	17.0–187	42.44 ± 21.00	20.0–81
SVL females (mm) ^a	56.37 ± 34.04	18–287	63.06 ± 40.50	24-228.9	50.80 ± 26.95	18-185.0	61.99 ± 40.10	18-287.0	51.90 ± 24.22	23-94.0
Sexual dimorphism ^a	0.86 ± 0.26	0.09-3.19	0.79 ± 0.29	0.09-2.03	0.90 ± 0.31	0.25-3.19	0.83 ± 0.18	0.49-1.99	0.84 ± 0.19	0.41-1.29
Clutch size ^b	1609.62 ± 5186.19	4-40,000	1296.36 ± 3701.47	10-17,000	748.99 ± 1158.77	6-5018	2578.56 ± 7423.93	7-40,000	584.08 ± 823.73	4-2500
Trait	Kruska	Kruskal–Wallis test		Pairwise W	Pairwise Wilcox test (p)					
	X ²	df	ď	D vs SD	D vs. NR	Dvsl	SD vs. NR	SD vs. I	NR vs. I	
q										
Range size (km²)ª	19.72	8	<0.001	0.29	<0.01	0.32	<0.01	0.50	0.07	
Elevational range (m) ^a	21.7	æ	<0.0001	0.26	<0.001	0.46	<0.001	0.82	<0.05	
SVL males (mm) ^a	2.67	æ	0.45	ı	ı	ı	ı	I	ı	
SVL females (mm) ^a	5.72	æ	0.13	ı	I	ı	ı	I	I	
Sexual dimorphism ^a	8.92	æ	<0.05	0.05	0.38	0.38	0.11	0.46	0.71	
Clutch size ^b	6.92	æ	0.07	ı	I	ı	ı	ı	I	

Given are the respective mean, standard deviation (sd), and range in general, and for each dependency index separately (a) and comparisons of traits between species of different forest dependency indices using the Kruskal-Wallis test and a pairwise Wilcox test with fdr correction as posthoc (b); forest dependency index: D = dependent (n = 33), SD = slightly dependent (n = 108), NR = non-responding (n = 83), 1 = forest independent (n = 19)

^a Incorporate calculated dummy variables (see "Methods")

 $^{^{\}rm b}$ Only measured values and therewith differing sample sizes: general = 152, D = 22, SD = 52, NR = 66, I = 12; compare Figs. 2 and 3

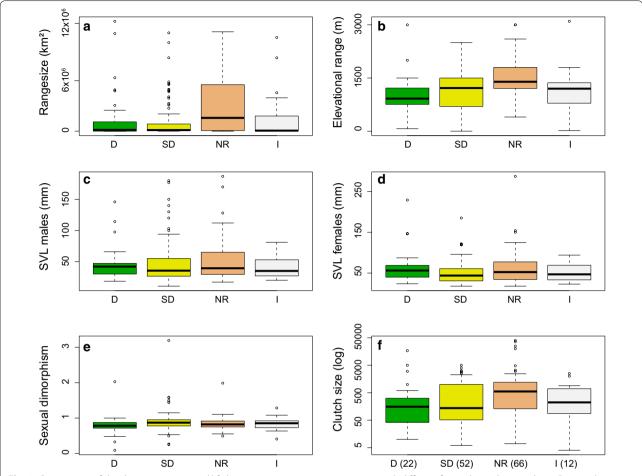


Fig. 2 Comparison of distribution patterns and life history traits among anuran species with different forest dependency indices. Given is the range size (\mathbf{a}) , distribution range along the elevation (\mathbf{b}) , the maximum body length of males (\mathbf{c}) and females (\mathbf{d}) , size dimorphism between sexes (males/females, $\mathbf{e})$ and the maximum clutch size (\mathbf{f}) ; in addition to the available data, dummy variables were calculated (see "Methods") and added $(\mathbf{a}-\mathbf{e})$; forest dependency index: D dependent D dependent

Table 2; Fig. 2). It did not differ between the FDIs (see Table 2). Sexual dimorphism also did not show large differences between the indices, but the comparison between D and SD species showed a trend towards D hosting species with greater dimorphism. As female and male body size were highly correlated (Spearman Rank Correlation: $\rho = 0.88$, p < 0.0001, n = 243), we only used female body size and dimorphism in subsequent analysis.

Reproduction

Clutch size varied between 4 and 40,000 eggs and did not differ between the FDIs (see Table 2; Fig. 2). Independent of the FDI, most clutches were in the first two size classes (4–98 and 100–265 eggs). Species belonging to I did not have clutches greater than 6700 eggs. The clutch size measured in categories likewise did not differ significantly between the FDIs (Pearson's χ^2 test: $\chi^2 = 34.96$,

df = 27, p = 0.14). Most species deposited their eggs in aquatic habitats (see Fig. 3). The second most common habitat was terrestrial, followed by arboreal deposition sites. There were no significant differences in egg deposition site between the FDIs ($\chi^2 = 11.52$, df = 12, p = 0.48). Almost 80% of the investigated species showed a biphasic development with free swimming tadpoles (see Fig. 3); D species had the highest proportion of direct developers (>30%). The reproductive mode did not differ significantly between the FIDs ($\chi^2 = 5.89$, df = 3, p = 0.12).

Classification by RF on the whole data set resulted in an overall error rate of 50.2%, the misclassification per FDI varied between 42.2 and 94.4% (see Table 3). Classification of subsets performed better, with an overall error rate of 20.7% (D vs. NR), 22.0% (D vs. I), 30.4% (NR vs. I), and 40.4% (D vs. I). Range size was important in

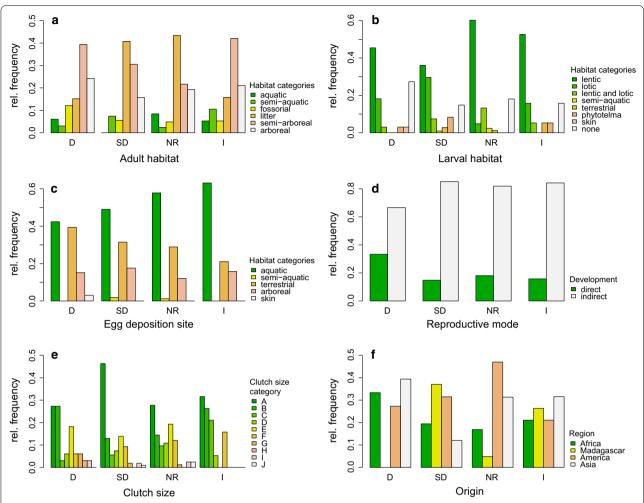


Fig. 3 Comparison of life history traits and species' origin among anuran species with different forest dependency indices. Shown is the relative frequency of a category for adult (**a**) and larval (**b**) habitats, the egg deposition site (**c**), the reproductive mode (**d**), the clutch size (**e**), and the region of origin (**f**); in addition to the available data, dummy variables were calculated (see "Methods") and added to the data set (**a**–**e**); forest dependency index: *D* dependent (n = 33), *SD* slightly dependent (n = 108), *NR* non-responding (n = 83), *I* forest independent (n = 19); see legends for color codes for each plot separately, y-axis are scaled differently; for details on habitat types and definition see "Methods" and Table 1; see "Results" for statistical comparisons of frequencies

all, sexual dimorphism and elevational range in four, and clutch size category in three models (Table 4).

Generalized linear models (Table 5) revealed larval habitat and clutch size class as important factors explaining the dependency to forests (D vs. NR species) with the development in lotic waters being significant and clutches of class G (3607-6701 eggs) being almost significant. Based on this model, 77% of all species could be correctly assigned to the original FDIs (matches: D: 12, n = 33; NR: 77, n = 83; sample size from original data). The model for forest independent species (I vs. NR species) revealed likewise larval habitat as being important with development in lotic waters being significant. The model assigned 82% of all the species correctly to the FDI derived from field observation (I: 4, n = 19; NR: 81,

n = 83). Generalized Linear Mixed Models (Table 5) fitted with species distribution revealed elevational range as being important factors when comparing both, D and NR as well as I and NR species (the latter barely non-significant). The model contrasting D and NR species assigned 78% of the species to correct FDIs (D = 13; NR = 77), based on the model comparing I and NR species 71% were correctly classified compared to the original FDIs (I = 0; NR = 83). Results of the different approaches confirm each other at least partly: RF vs. GLM: forest dependent species (D): classification overlap of 72%, matches: D: 9; NR: 74; forest independent species (I): 75%, I = 5; NR: 71; RF vs. GLMM: D: 84%, D = 16, NR = 81; I: 71%, I = 0, NR = 72; GLM vs. GLMM: D: 77%, D = 5, NR = 84; I: 94%, I = 0; NR = 96.

Table 3 Confusion matrices of Random Forest analysis

	D	I	NR	SD	CE (%)	OE (%)
Complete data set						50.2
D	15	4	9	5	54.5	
1	5	1	7	6	94.4	
NR	12	6	48	17	42.2	
SD	9	12	29	57	47.2	
Subset D vs. SD						22.0
D	17	_	_	16	48.5	
SD	15	-	-	93	12.0	
Subset D vs. NR						20.7
D	21	-	12	=	36.4	
NR	12	-	71	-	14.5	
Subset D vs. I						40.4
D	23	10	=	=	30.3	
1	11	8	=	=	57.9	
Subset I vs. NR						30.4
1	-	9	10	-	52.6	
NR	-	21	62	-	25.3	

Confusion matrices with per class error (CE) rate and overall error (OE) rate per Random Forest analysis (complete data set and different subsets); analysis were performed with ntree = 1000, mtry = 3 and sampsize adjusted to the smallest sample size (R package 'randomForest'); forest dependency index: D dependent (n = 33), SD slightly dependent (n = 108), NR non-responding (n = 83), I forest independent (n = 19)

Table 4 Importance of each variable in Random Forest analysis

Variable	Complete	D vs. SD	D vs. NR	D vs. I	I vs. NR
SVL females	6.73	3.41	3.42	2.15	2.08
Adult habitat	4.70	3.23	3.64	0.91	2.37
Sexual dimorphism	9.02	4.00	2.98	2.63	2.59
Clutch size category	6.15	3.49	3.39	4.20	2.63
Egg deposition site	1.13	1.04	0.46	0.50	0.48
Reproductive mode	0.14	0.47	0.07	0.10	0.14
Larval habitat	3.46	2.63	2.10	0.89	1.12
Region	4.54	4.95	2.62	2.11	1.58
Range size	12.52	5.91	7.52	3.27	3.06
Elevational range	8.59	3.37	6.81	2.23	2.87

Importance of each variable per Random Forest analysis (complete data set and different subsets); the four most important variables contributing to the classification are in italics; analysis were performed with ntree = 1000, mtry = 3 and sampsize adjusted based on the smallest sample size for each analysis respectively (R package 'randomForest'); forest dependency index: D dependent (n = 33), SD slightly dependent (n = 108), NR non-responding (n = 83), I forest independent (n = 19)

Discussion

Geographic range size has been identified as a vital factor predicting a species' susceptibility and extinction risk, including birds [11], mammals [10, 16], and amphibians [8, 37]. Species tolerating a wide range of abiotic factors, different habitats [38], or not responding to forest degradation (this study) likewise have the widest distribution. Here, we assign species to one of four levels of

forest dependency, according to their occurrence in habitats with differently strong disturbance. Species belonging to D (forest dependent) depend on pristine forests, species assigned to the other categories (NR, I, or SD) can cope with habitat disturbances to different extents. We determined the most important traits explaining the forest dependency of a species using RF classification, GLM, and GLMM techniques. Since range size and extinction risk or habitat breadth might directly depend on each other, making it a single criterion to assess species as critically endangered in the IUCN Red List [29], we excluded it in the GLM filtering for species traits, but analyzed it separately (GLMM). Here, however, only elevational range was important for distinguishing NR from D and NR from I species. This is consistent with previous results where a wide altitudinal distribution decreases a species' vulnerability [9, 39, 40], as such species are naturally adapted to varying environmental factors (e.g. vegetation, climate) and hence might also cope better with changes of these factors caused by forest disturbances.

Body size is a central trait, usually correlated with factors such as population size, range size, clutch size or rate of exploitation, all influencing the extinction risk of a species [41–43]. It was thus typically taken into consideration when estimating a species' susceptibility. With increasing body size, studies revealed an increase (amphibians: [39], mammals: [41], birds: [44]), or, as in our data, no change in the extinction risk (amphibians: [28], birds: [40], bats: [45]). These converse results

Table 5 Effects of species traits and distribution on habitat dependency

	Forest deper	ndent species (D	vs. NR)		Non-forest s	pecies (I vs. NR)		
	Estimate	Std. error	z	р	Estimate	Std. error	z	р
GLM on species traits								
Intercept	0.085	1.47	0.058	0.95	-2.98	1.37	-2.18	0.03
SVL females	-0.08	2.70	-0.03	0.98	0.05	4.59	0.01	0.99
Sexual dimorphism	-3.73	3.11	-1.20	0.23	2.71	2.83	0.96	0.34
Larval habitat								
Lentic/lotic	-17.13	1852.28	-0.009	0.99	-1.13	1.30	-0.87	0.38
Lotic	1.66	0.77	2.16	0.03	3.00	1.34	2.23	0.03
None	0.39	0.64	0.61	0.54	0.26	0.91	0.28	0.78
Phytotelma	18.95	6522.64	0.003	0.99	22.54	10,750	0.002	0.99
Semi-terrestrial	-17.22	4611.48	-0.004	0.99	-16.31	6635	-0.002	0.99
Skin	19.79	6522.64	0.003	0.99	-	_	-	-
Terrestrial	-0.08	2.70	-0.03	0.98	2.50	1.67	1.49	0.14
Clutch size class								
В	0.67	0.67	1.01	0.31	1.14	0.86	1.34	0.18
C	-0.57	1.22	-0.47	0.64	1.73	1.07	1.61	0.11
D	-0.19	1.02	-0.19	0.85	0.20	1.36	0.15	0.88
E	-0.02	0.79	-0.03	0.98	-18.48	2343	-0.01	0.99
F	-0.10	1.10	-0.09	0.93	0.85	1.32	0.64	0.52
G	3.16	1.86	1.70	0.09	-17.69	10,750	-0.002	0.99
Н	37.40	6780.54	0.01	0.99				
1	0.59	1.57	0.38	0.71	-17.37	7585	-0.002	0.99
J	-16.74	3995.08	-0.004	0.99	-16.46	7482	-0.002	0.99
GLMM on species distrib	ution							
Fixed effects								
Intercept	1.23	0.68	1.80	0.07	-0.004	0.69	-0.006	0.99
Range size	-1.59	1.13	-1.41	0.16	-1.18	1.38	-0.86	0.39
Elevational range	-4.97	1.45	-3.44	0.0006	-3.03	1.56	-1.85	0.06

Binomial models for forest dependent and non-forest species were conducted and full models (*glm*, R package 'stats'; *glme*, R packages 'lme4') after eliminating multicollinearity (*vif*, R package 'car') are presented; Generalized Linear Model (GLM): variables included: SVL females, sexual dimorphism, clutch size class, larval habitat; removed due to co-linearity: adult habitat, reproductive mode, and egg deposition site; Generalized Linear Mixed Model (GLMM): range size and elevation range as fixed and region of continent random factors (no co-linearity among explaining variables); significant effects are in italics; *D* forest dependent species (n = 33), *NR* non-responding species (n = 83), *I* forest independent species (n = 19)

emphasize the complex effects of body size and explain the variation in its influence on the vulnerability of species, differing with study systems [14] but also with the source of extinction risk [46]. According to our results, neither body size nor sexual size dimorphism seem to influence forest dependency.

Although the number of offspring explains the extinction risk in several taxa [12, 13], traits related to reproduction only had minor effects on degradation susceptibility of a frog species in our data set. Species belonging to I, however, do not deposit bigger clutches (separating I from NR species in RF). This could either be related to the larger number of I species using flowing, not stagnant, waters as larval habitat and the fact that stream breeders tend to have bigger eggs and thus smaller clutches [47], or to the absence of bigger females,

depositing larger clutches (see Figure in Additional file 3) in I. A higher percentage of direct developers among forests dependent species (this study, but see [48, 49]) and an increased extinction risk of ovoviviparous anuran species in general ([8], but see [50]) can be explained by the required moist microhabitat for a direct development [51], available in pristine forests, but not necessarily in degraded or fragmented habitats [52, 53].

A species' microhabitat preferences affect its vulnerability, i.e. the availability of breeding sites, particular soil conditions or vegetation structure can be crucial for the presence of an amphibian species [e.g. 49, 54, 55]. Modified forests are accompanied by an open canopy which facilitates the growth of herbaceous strata and leads to an advantageous humid microclimate for some leaf-litter anurans. This structured understory, including

downed woody debris, has been identified as an important habitat feature for amphibian populations in altered forests [56, 57] and explains the increase of ground dwelling species among degradation tolerant species [25, this study]. Degradation with an accompanying loss of canopy cover generates the most prominent microclimatic shifts in the mid-story, forming the upper strata after disturbances. The resulting decreased humidity, stronger temperature extremes, and increased solar radiation [58–60] have adverse effects on amphibians and explain the high number of semi-arboreal species in our study being forest dependent and the low number being degradation tolerant.

Forest degradation negatively impacts riparian habitats for amphibians by decreasing the amount of woody debris or leaf litter, resulting in less dissolved organic carbon [61] and by a reduction of the canopy cover, leading to higher temperatures and solar radiation [62, 63]. These unfavorable changes explain the higher number of stream breeders among species prone to degradation (this study) and the higher susceptibility of species dependent on lotic breeding sites [54] and riparian species in general [39, 50]. Although forest degradation potentially cause similar changes in lentic habitats, pond breeding amphibians might be less vulnerable or, due to different life-history strategies, even benefit from the consequences: higher temperatures for example increase the developmental rate [64, 65] and higher solar radiation favors the growth of algae [62], the primary food resource for many pond dwelling tadpoles. Compared to species not responding to habitat changes, also a higher number of non-forest species strongly depend on rivers for their tadpole development. These species might be already accustomed to open riparian habitats and thus do not suffer from the prevailing conditions like species occurring in all habitat types.

When contrasting the classification of RF, GLM, and GLMM based on the comparisons D vs. NR, ten species were always wrongly assigned. For example two species, known to occur in strongly degraded habitats [66] and to reproduce in artificial ponds [67] were assigned to D but predicted to belong to NR. Hence the models predicted the species correctly and only the incorporated information from the field was limited and did not cover the occurrences in altered habitats.

Conclusions

Generalist species were identified as the winners in human-dominated landscapes [18, 68], but particular traits facilitating this adaptation were not yet determined. Our pan-tropical approach revealed that the dependency to forested habitats is explained by traits similar to those generally recognized for high species extinction risk. Indirect developing species exhibiting a big range size, wide elevational range, being independent of streams, and inhabiting the leaf litter are less prone to modifications of their natural habitats. As the effect of a particular trait on the vulnerability of a species might differ among threats [17, 69] and study scales (local vs. global), the generality of our results needs to be treated with caution. However, our findings point to the traits persisting in degraded habitats and thus help to identify future frog communities in our human-dominated world.

Additional files

Additional file 1. Anuran distribution references. References to studies appropriate for the study. Respective data were incorporated in the primary data set on anuran occurrence in different habitat types.

Additional file 2. Anuran traits references. References to journal articles, books and web resources containing information on species traits for the species included in the primary data set on anuran occurrence.

Additional file 3. Clutch size classes. Additional methods describing the objective grouping of clutch sizes.

Additional file 4. Final data set. Given is the species, the traits looked at and the forest dependency index (FDI) derived from the occurrence data. Dummy variables are highlighted in grey. See Table 1 for information on the respective traits.

Additional file 5. Affiliation to different anuran families. Number and relative frequency of species belonging to a particular family per forest dependency index.

Authors' contributions

MH collected data and performed statistical analysis; MH and MOR wrote the text. Both authors read and approved the final manuscript.

Acknowledgements

M. Dahmen provided additional data on species occurrence in Cameroon. M. F. Barej, M. Dahmen, M. Emmrich, H. C. Liedtke, J. Penner, and J. C. Riemann contributed to the trait data set. F. Tillack assisted during literature research and L. Sandberger-Loua gave valuable advices analyzing the data set. A. Channing helped with a thorough language check. All supports are gratefully acknowledged.

Competing interests

The authors declare that they have no competing interests.

Availability of data and materials

All data generated or analyzed during this study are included in this published article and its additional information files.

Ethics approval and consent to participate

Only Cameroonian frog data were collected for this study. Research permits covered all areas visited and the entire study protocol. They were issued by the Cameroonian Ministry of Scientific Research and Innovation (MINRESI) and the Ministry of Forestry and Wildlife (MINFOF). This study was not approved by any ethics committee as this was not required by Cameroonian or German law. However, all work complied with the guidelines for the use of live amphibians and reptiles in field research compiled by the American Society of Ichthyologists and Herpetologists (ASIH), The Herpetologists' League (HL) and the Society for the Study of Amphibians and Reptiles (SSAR). During amphibian surveys, individuals were identified to species level and immediately released at the same site.

Funding

Fieldwork of MH in Cameroon was supported by scholarships from the Federal State of Berlin (Elsa-Neumann-Stipendium) and the German Academic Exchange Service (DAAD). The publication of this article was funded by the Leibniz Open Access Publishing Fund.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Received: 8 January 2017 Accepted: 20 June 2017 Published online: 28 June 2017

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Additional file 1. Anuran distribution references

References to studies appropriate for the study. Respective data were incorporated in the primary data set on anuran occurrence in different habitat types.

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Additional file 2. Anuran traits references.

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Amphibia Web http://amphibiaweb.org/

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Animal Diversity Web http://animaldiversity.ummz.umich.edu

Dendroworld http://www.dendroworld.co.uk

Frog Atlas http://www.frogatlas.com.au/

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Frog.org http://talkto.thefrog.org/

Frogs of Borneo http://frogsofborneo.org/

Hepetofauna Costa Ricas http://www.herpetologia.de

IUCN http://www.iucnredlist.org/

Online field guide http://online-field-guide.com/

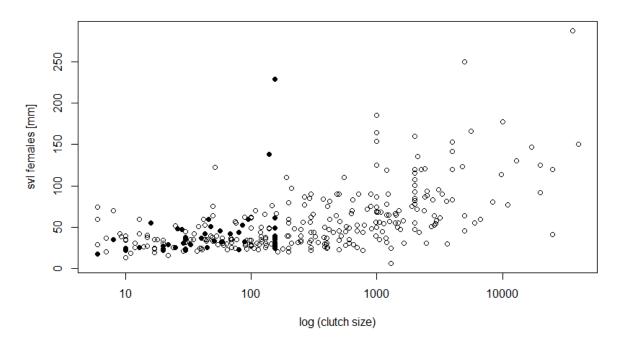
Reptiles http://www.reptilesmagazine.com/

Tropical Herping http://www.tropicalherping.com/default.html

Wikipedia https://en.wikipedia.org

Additional file 3. Clutch size classes

Clutch size was only available for a subset (345 out of 619) of species. An objective grouping by applying Kmeans clustering (kmeans, R package 'stats'; 1000 iterations) on the available data revealed the following clutch size classes (mean, range, sample size = species with this clutch size): A: 38.6, 4-98, n = 121; B: 160.5, 100-265, n = 68, C: 392.0, 290-549, n =37; D: 712.0, 563-905, n = 24; E: 1201.6, 979-1652, n =37; F: 2408.7, 1900-3320, n = 32, G: 4724.5, 3607-6701, n = 13; H: 10420.0, 8357-12940, n = 5; I: 21400.0, 17000-25000, n = 5, J: 38050.0, 36100-40000, n = 2. Ten classes were chosen to achieve a fine scale fractionation but at the same time at least a number of five records per class; except for the biggest size class. Species without information on clutch size were subsequently assigned to a single class based female (or male if female size was not available) body size, as the maximal number of eggs per clutch was significantly correlated with body size (females: rho = 0.58, p < 0.0001, n = 334; males: rho = 0.58, p < 0.0001, n = 341). Crucial was the minimal distance of the body size of a species lacking information to the mean body size of a particular clutch size class. 266 species were assigned based on female, 34 based on male body size. Calculation of clutch size classes and the assignment to a category was conducted independently of the reproductive mode, i.e. direct and indirect developing species together. This was permitted as data distribution of clutch size as well as the data distribution of clutch size related to female body size did not differ between the modes, i.e. data of direct developing species were within the range of clutch sizes of indirect developing species with similar body size (Kolmogorov-Smirnov test: clutch size: D = 0.08, p = 0.23; clutch size / female body size: D = 0.07, p = 0.46; N: direct developing species = 47, indirect developing species = 297; see Figure below).



Given are the maximum clutch size (log transformed) and the maximum female body size (snout vent length, svl) of 344 species. Direct developing species (n = 47) are marked with black, indirect developing species (n = 297) with white dots.

Additional file 4. Final Data set
Given is the species, the traits looked at and the forest dependency index (FDI) derived from the occurrence data. Dummy variables are highlighted in grey. See Table 1 for information on the respective traits.

Family	Genus	Species	Region	Range	Elevational	S	VL	Adult	Larval	Clutch	Clutch	Egg depos.	Develop-	FDI
			of origin		range		f	habitat		size	size class	site	ment	
				size		m			habitat					
Aromobatidae	Allobates	marchesianus	America	1913449,48	1217,6	16,3	26,4	lit	len	14	Α	ter	i	SD
Aromobatidae	Anomaloglossus	stepheni	America	24168,75	1217,6	17,0	18,0	lit	ter	6	Α	ter	i	SD
Arthroleptidae	Arthroleptis	adelphus	Africa	471769,61	2003	29,0	33,1	lit	none	51	Α	ter	d	SD
Arthroleptidae	Arthroleptis	poecilonotus	Africa	738639	1199	27,0	31,0	lit	none	29	Α	ter	d	SD
Arthroleptidae	Arthroleptis	stenodactylus	Africa	2386661,02	1960	33,0	44,0	lit	none	80	Α	ter	d	NR
Arthroleptidae	Arthroleptis	sylvaticus	Africa	1013495,74	1900	21,2	21,9	lit	none	20	Α	ter	d	SD
Arthroleptidae	Arthroleptis	variabilis	Africa	1795153,2	1359	10,5	42,0	lit	none	68	Α	ter	d	SD
Arthroleptidae	Arthroleptis	wahlbergii	Africa	50859,91	1000	18,0	22,0	lit	none	30	Α	ter	d	NR
Arthroleptidae	Arthroleptis	xenodactyloides	Africa	1481,64	2000	17,0	27,0	lit	none	20	Α	ter	d	NR
Arthroleptidae	Cardioglossa	gracilis	Africa	660912,32	1446	37,8	40,0	lit	lot	48	Α	ter	i	SD
Arthroleptidae	Leptopelis	brevirostris	Africa	543127,2	1100	45,0	64,0	s-arb	none	NA	Е	ter	i	SD
Arthroleptidae	Leptopelis	calcaratus	Africa	1884906,04	1500	42,0	57,0	s-arb	len	NA	D	ter	i	SD
Arthroleptidae	Leptopelis	flavomaculatus	Africa	805972,28	1217,6	50,0	70,0	arb	len	NA	E	ter	i	D
Arthroleptidae	Leptopelis	mossambicus	Africa	379280,3	1217,6	52,0	63,0	arb	len	NA	E	ter	i	D
Arthroleptidae	Leptopelis	rufus	Africa	236932,47	1757	55,0	87,0	arb	lot	NA	F	ter	i	SD
Arthroleptidae	Trichobatrachus	robustus	Africa	217523,72	1458	130,0	90,0	lit	lot	721	D	aqu	i	SD
Brevicipitidae	Breviceps	adspersus	Africa	2329163,99	1400	47,0	60,0	fos	none	95	Α	ter	d	D
Brevicipitidae	Breviceps	mossambicus	Africa	1606225,44	1800	33,0	52,0	fos	ter	25	Α	ter	i	- 1
Bufonidae	Adenomus	kelaartii	Asia	4928,03	1670	33,0	50,0	s-arb	lot	1000	E	aqu	i	NR
Bufonidae	Amietophrynus	garmani	Africa	1754477,81	2000	74,0	115,0	lit	len / lot	2000	F	aqu	i	NR
Bufonidae	Amietophrynus	gutturalis	Africa	5933446,92	1800	90,0	120,0	lit	len	25000	I	aqu	i	NR
Bufonidae	Atelopus	pulcher	America	9259,31	300	29,3	35,1	lit	lot	600	D	aqu	i	SD
Bufonidae	Bufoides	meghalayanus	Asia	305,09	20	41,0	56,4	lit	len	NA	С	aqu	i	- 1
Bufonidae	Duttaphrynus	kotagamai	Asia	30,31	920	40,3	62,7	lit	lot	NA	E	aqu	i	D
Bufonidae	Duttaphrynus	melanostictus	Asia	600,82	1800	83,0	150,0	lit	len	40000	J	aqu	i	NR
Bufonidae	Incilius	cristatus	America	100,08	100	54,8	87,3	lit	lot	NA	F	aqu	i	D
Bufonidae	Incilius	valliceps	America	603359,39	1850	76,0	82,0	lit	len	NA	F	aqu	i	NR
Bufonidae	Ingerophrynus	celebensis	Asia	180051,98	1217,6	59,0	80,0	lit	len / lot	NA	F	aqu	i	NR
Bufonidae	Mertensophryne	loveridgei	Africa	56624,03	1217,6	35,0	38,0	lit	len	131	В	aqu	i	NR
Bufonidae	Pedostibes	kempi	Asia	6,17	1	30,0	56,4	arb	lot	NA	Α	aqu	i	SD
Bufonidae	Rhinella	granulosa	America	10992958,86	1217,6	70,0	90,0	lit	len	900	D	aqu	i	NR
Bufonidae	Rhinella	marina	America	9689511,58	3000	187,0	287,0	lit	len / lot	36100	J	aqu	i	NR
Bufonidae	Schismaderma	carens	Africa	2955848,16	1217,6	88,0	92,0	lit	len	20000	1	aqu	i	NR
Centrolenidae	Hyalinobatrachium	fleischmanni	America	405988,89	1800	25,5	32,0	arb	lot	30	Α	arb	i	SD
Centrolenidae	Vitreorana	oyampiensis	America	822656,57	810	21,0	24,0	arb	lot	20	Α	arb	i	D
Ceratophryidae	Ceratophrys	cornuta	America	5285910,29	400	77,0	120,0	lit	len	2270	F	aqu	i	SD
Craugastoridae	Craugastor	alfredi	America	33650,37	600	36,0	45,0	lit	none	NA	В	ter	d	SD
Craugastoridae	Craugastor	berkenbuschii	America	56056,05	1500	69,5	93,0	s-aqu	none	NA	F	ter	d	SD
Craugastoridae	Craugastor	decoratus	America	5298,29	1378	45,0	60,0	s-arb	none	46	Α	ter	d	NR
Craugastoridae	Craugastor	fitzingeri	America	273537,28	1520	35,0	52,5	s-arb	none	85	Α	ter	d	NR
Craugastoridae	Craugastor	mexicanus	America	43635,86	1920	28,1	39,5	lit	none	NA	Α	ter	d	SD
Craugastoridae	Craugastor	pygmaeus	America	16205,21	2000	18,0	18,0	lit	none	NA	Α	ter	d	NR
Craugastoridae	Craugastor	spatulatus	America	85,95	1217,6	23,6	32,0	s-arb	none	NA	Α	ter	d	SD
Craugastoridae	Craugastor	uno	America	321,31	1217,6	47,1	62,5	lit	none	NA	Е	ter	d	SD

Craugastoridae	Craugastor	vulcani	America	1593,35	800	47,1	73,0	lit	none	NA	Е	ter	d	D
Craugastoridae	Pristimantis	achatinus	America	184759	2330	36,0	46,0	s-arb	none	57	Α	ter	d	NR
Craugastoridae	Pristimantis	chloronatus	America	7932,73	1500	30,3	36,9	s-arb	none	40	Α	ter	d	NR
Craugastoridae	Pristimantis	fenestratus	America	3557857,79	1850	39,3	51,0	s-arb	none	48	Α	ter	d	NR
Craugastoridae	Pristimantis	festae	America	1795153,2	1340	21,5	23,0	lit	none	NA	Α	aqu	d	SD
Craugastoridae	Pristimantis	zimmermanae	America	39885,11	50	21,0	26,0	s-arb	none	NA	Α	ter	d	SD
Dendrobatidae	Allobates	femoralis	America	5607495,67	1000	33,0	35,0	lit	len	43	Α	ter	i	NR
Dicroglossidae	Euphlyctis	cyanophlyctis	Asia	4439313,99	2500	45,0	72,0	aqu	len / lot	844	D	aqu	i	NR
Dicroglossidae	Euphlyctis	hexadactylus	Asia	1477319,91	800	86,8	120,0	aqu	len	2000	F	aqu	i	NR
Dicroglossidae	Fejervarya	limnocharis	Asia	8896740,71	2000	52,0	67,0	s-aqu	len / lot	1400	E	aqu	i	NR
Dicroglossidae	Fejevarya	cancrivora	Asia	1342960,13	1300	70,0	82,0	aqu	len	2000	F	aqu	i	- 1
Dicroglossidae	Hoplobatrachus	tigerinus	Asia	3495177,78	1975	80,0	121,0	aqu	len / lot	2400	F	aqu	i	NR
Dicroglossidae	Limnonectes	grunniens	Asia	330324,38	1217,6	146,0	146,0	s-aqu	len / lot	NA	Н	aqu	i	D
Dicroglossidae	Limnonectes	laticeps	Asia	341740,01	1450	47,0	46,0	s-aqu	lot	NA	В	aqu	i	SD
Dicroglossidae	Limnonectes	malesianus	Asia	140359,73	150	150,0	95,0	lit	lot	NA	1	aqu	i	SD
Dicroglossidae	Limnonectes	modestus	Asia	276147,2	1217,6	72,0	70,0	lit	lot	NA	E	ter	i	SD
Dicroglossidae	Occidozyga	laevis	Asia	507731,45	500	31,0	48,0	aqu	len / lot	140	В	aqu	i	NR
Dicroglossidae	Sphaerotheca	breviceps	Asia	3279685,84	1500	55,0	57,0	fos	len	75	Α	aqu	i	NR
Dicroglossidae	Zakerana	kirtisinghei	Asia	8078,04	1430	39,0	44,0	lit	len	NA	В	aqu	i	- 1
Eleutherodactylidae	e Diasporus	diastema	America	109484,13	1619	21,0	25,0	arb	none	10	Α	arb	d	NR
Eleutherodactylidae	e Eleutherodactylus	cystignathoides	America	24906,65	1200	14,0	26,0	lit	none	13	Α	ter	d	SD
Eleutherodactylidae	e Eleutherodactylus	leprus	America	2031,47	795	27,0	30,0	lit	none	NA	Α	ter	d	NR
Hemisotidae	Hemisus	guttatus	Africa	51667,84	1000	51,0	80,0	fos	len	200	В	ter	i	NR
Hemisotidae	Hemisus	marmoratum	Africa	9850888,49	1850	45,0	55,0	fos	len	200	В	ter	i	SD
Hylidae	Charadrahyla	taeniopus	America	7538,77	1217,6	65,9	70,0	s-arb	len	NA	Ε	aqu	i	D
Hylidae	Dendropsophus	brevifrons	America	513088,37	1217,6	21,4	23,2	arb	len	115	В	arb	i	SD
Hylidae	Dendropsophus	ebraccatus	America	232873,74	1600	28,0	37,0	arb	len	155,5	В	arb	i	SD
Hylidae	Dendropsophus	leucophyllata	America	5525350,6	1217,6	36,0	44,0	s-arb	len	771	D	arb	i	NR
Hylidae	Dendropsophus	marmorata	America	4845441,2	1217,6	44,0	56,0	arb	len	979	E	aqu	i	NR
Hylidae	Dendropsophus	microcephalus	America	5570825,86	1300	25,0	32,0	s-arb	len	NA	Α	aqu	i	NR
Hylidae	Dendropsophus	minutus	America	11045630,91	1217,6	23,0	25,0	arb	len	400	С	arb	i	NR
Hylidae	Dendropsophus	nanus	America	8158117,78	1500	20,0	23,0	s-arb	len	NA	Α	aqu	i	
Hylidae	Dendropsophus	parviceps	America	4478924,19	1217,6	21,9	26,1	s-arb	len	385	С	aqu	i	SD
Hylidae	Ecnomiohyla	miotympanum	America	22082,36	1382	38,4	51,0	arb	len / lot	NA	С	aqu	i	NR
Hylidae	Ecnomiohyla	valancifer	America	1241,71	880	77,7	82,0	arb	lot	NA	F	aqu	i	
Hylidae	Hypsiboas	boans	America	6899721,81	1000	128,0	123,0	arb	len	4800	G	aqu	i	NR
Hylidae	Hypsiboas	calcaratus	America	4611334,93	600	44,0	54,0	arb	len / lot	1144	E	aqu	i	SD
Hylidae	Hypsiboas	cinerascens	America	5614933,83	500	35,0	37,0	arb	len	400	С	aqu	i	NR
Hylidae	Hypsiboas	geographicus	America	5190041,24	700	55,0	83,0	arb	len / lot	2797	F	aqu	i	SD
Hylidae	Hypsiboas	lanciformis	America	10419166,83	1217,6	80,0	94,0	arb	len	2500	F	aqu	i	'
Hylidae	Hypsiboas	punctatus	America	4621749,79	1400	30,0	39,0	arb	len	325	С	aqu	i	NR
Hylidae	Megastomatohyla	mixomaculata	America	973,43	600	30,0	35,0	s-arb	lot	NA	Α	aqu	i	D
Hylidae	Osteocephalus	buckleyi	America	4477069,23	1217,6	50,0	69,0	arb	lot	1000	E	aqu	i	D
Hylidae	Osteocephalus	leprieurii	America	3812252,54	860	48,1	64,0	arb	len	2882	F	aqu	i	SD
Hylidae	Osteocephalus	taurinus	America	6116928,89	1217,6	92,0	101,0	arb	len	2000	F	aqu	i	NR
Hylidae	Phyllomedusa	bicolor	America	5230330,94	800	103,0	119,0	arb	len	1202	E	arb	i	SD
Hylidae	Phyllomedusa	tarsius	America	2694953,8	450	90,0	110,0	s-arb	len	549	С	arb	i	NR
Hylidae	Phyllomedusa	tomopterna	America	5475272	500	54,0	62,0	arb	len	89	Α	arb	i	SD
Hylidae	Phyllomedusa	vaillantii	America	4991230,63	450	65,0	83,0	arb	len	645	D	arb	i	NR
Hylidae	Plectrohyla	arborescandens	America	3286,81	1500	38,0	52,0	arb	lot	NA	D	aqu	i	D

Hylidae	Plectrohyla	pentheter	America	2297,22	720	46,0	57,8	s-arb	lot	NA	D	aqu	i	SD
Hylidae	Ptychohyla	leonhardschultzei	America	1123,88	1300	34,9	30,5	lit	lot	60	Α	aqu	i	SD
Hylidae	Scinax	cruentommus	America	2460973,09	1217,6	27,0	32,0	arb	len	1200	E	aqu	i	NR
Hylidae	Scinax	garbei	America	3703694,25	1217,6	46,0	48,0	arb	len	905	D	aqu	i	1
Hylidae	Scinax	ruber	America	8136346	2600	37,0	45,0	arb	len	1105	E	aqu	i	NR
Hylidae	Scinax	staufferi	America	569459,34	1530	29,0	32,0	arb	len	NA	Α	aqu	i	SD
Hylidae	Smilisca	baudinii	America	1050352,67	1925	76,0	90,0	arb	len	3320	F	aqu	i	NR
Hylidae	Tlalocohyla	loquax	America	348680,87	1585	35,0	47,0	s-arb	len	250	В	aqu	i	NR
, Hylidae	Tlalocohyla	picta	America	313559,87	1300	21,4	22,1	s-arb	len	NA	Α	agu	i	SD
, Hylidae	Trachycephalus	resinifictrix	America	4649150,62	450	77,0	88,0	arb	phy	2500	F	arb	i	SD
, Hyperoliidae	Afrixalus .	fulvovittatus	Africa	94244,89	1685	27,0	28,0	s-arb	len	100	В	arb	i	SD
Hyperoliidae	Afrixalus	laevis	Africa	1207641,32	1217,6	23,0	25,0	s-arb	lot	39	Α	arb	i	SD
Hyperoliidae	Hyperolius	argus	Africa	708667,09	300	34,0	37,0	s-arb	len	NA	Α	arb	i	D
Hyperoliidae	Hyperolius	marmoratus	Africa	1212234,73	1600	34,0	34,0	s-arb	len	100	В	aqu	i	NR
Hyperoliidae	Hyperolius	mitchelli	Africa	808554,63	1217,6	27,0	32,0	s-arb	len	290	C	arb	i	
Hyperoliidae	Hyperolius	nasutus	Africa	1828824,27	1217,6	24,0	25,0	s-arb	len / lot	NA	A	agu	i i	SD
Hyperoliidae	Hyperolius	pusillus	Africa	798478,66	800	20,0	25,0	s-arb	len	200	В	aqu	i i	D
Hyperoliidae	Hyperolius	semidiscus	Africa	141664,64	1217,6	25,0	35,0	s-arb	len	17	A	aqu	i	l b
Hyperoliidae	Hyperolius	tuberilinguis	Africa	3091192,54	1000	33,0	35,0 35,0	s-arb	len / lot	NA	A	aqu arb	i	SC
Hyperoliidae	Kassina	senegalensis	Africa	12217676,34	2000	40,0	40,0	lit	len	10	A	agu	i	D
Leiuperidae	Physalaemus	cuvieri	America	7282718,66	1217,6	40,0 28,0	40,0 31,0	lit	len	2465	F	•	i i	NF
Legioperidae				•				lit			•	aqu	! :	
·	Adenomera Leptodactylus	andreae fragilis	America	5976957,43 1433339,34	400 1700	20,0 36,0	27,0 40,0	lit	ter	15 250	A B	ter	! :	NF NF
Leptodactylidae	' '		America			•			len			ter	! :	
Leptodactylidae	Leptodactylus	knudseni	America	5236498,65	1800	170,0	154,0	lit	len	1000	E	ter	!	NF
Leptodactylidae	Leptodactylus	leptodactyloides	America	10932822,52	685	47,9	56,2	lit	len	1053	E	aqu	!	SE
Leptodactylidae	Leptodactylus	mystaceus	America	7133840,42	1217,6	50,0	60,0	lit	len	425	C	ter	!	NF
Leptodactylidae	Leptodactylus	mystacinus	America	5187450,08	1800	65,0	67,0	lit	len	627	D	ter	I .	NF
Leptodactylidae	Leptodactylus	pentadactylus	America	4505396,51	1195	177,0	185,0	lit	len	1000	E	ter	i	SE
Leptodactylidae	Leptodactylus	petersii	America	6056228,71	1217,6	40,0	45,0	lit	len	563	D	ter	İ	NF
Leptodactylidae	Leptodactylus	rhodomystax	America	5152273,6	500	72,0	85,0	lit	len	290	С	ter	i	NF
Leptodactylidae	Leptodactylus	riveroi	America	836714,79	360	58,0	74,0	lit	len	1000	E	aqu	i	SE
Leptodactylidae	Leptodactylus	stenodema	America	4406321,41	1217,6	94,0	96,0	lit	len	NA	l	s-ter	i	SE
Leptodactylidae	Lithodytes	lineatus	America	442,1	1800	43,0	56,0	lit	len	260	В	ter	i	NF
Mantellidae	Aglyptodactylus	madagascariensis	Madagascar	152848,58	2000	41,0	53,0	lit	len	2865	F	aqu	i	SE
Mantellidae	Blommersia	blommersae	Madagascar	17718,31	400	21,0	20,0	s-arb	len	NA	Α	arb	i	NF
Mantellidae	Blommersia	grandisonae	Madagascar	64754,59	800	23,0	20,0	s-arb	lot	NA	Α	arb	i	SD
Mantellidae	Boophis	boehmei	Madagascar	60227,92	1100	30,0	41,0	s-arb	lot	NA	Α	aqu	i	- 1
Mantellidae	Boophis	goudotii	Madagascar	80548,07	1300	70,0	87,0	s-arb	lot	1000	Е	aqu	i	NF
Mantellidae	Boophis	lichenoides	Madagascar	57627,21	850	43,0	56,4	s-arb	len	NA	С	aqu	i	SD
Mantellidae	Boophis	luteus	Madagascar	37505,21	1500	60,0	40,0	s-arb	lot	200	В	aqu	i	SE
Mantellidae	Boophis	madagascariensis	Madagascar	91319,12	1700	62,0	75,0	s-arb	len / lot	405	С	aqu	i	SE
Mantellidae	Boophis	marojezensis	Madagascar	41872,73	700	27,0	33,0	s-arb	lot	NA	Α	aqu	i	SE
Mantellidae	Boophis	picturatus	Madagascar	28014,9	150	33,0	56,4	s-arb	lot	NA	Α	aqu	i	SD
Mantellidae	Boophis	, pyrrhus	Madagascar	30001,38	465	32,0	37,0	s-arb	len	NA	Α	aqu	i	SD
Mantellidae	Boophis	rappiodes	Madagascar	31797,19	600	25,0	34,0	s-arb	lot	300	С	aqu	i	SD
Mantellidae	Boophis	reticulatus	Madagascar	62346,55	850	35,0	44,0	s-arb	len	NA	В	aqu	i	SD
Mantellidae	Boophis	rufioculis	Madagascar	15852,15	300	35,0	47,0	s-arb	lot	NA	В	aqu	i	1
Mantellidae	Gephyromantis	boulengeri	Madagascar	27478,03	1200	30,0	56,4	lit	none	NA	A	ter	d	SD
Mantellidae	Gephyromantis	cornutus	Madagascar	9606,04	350	40,0	39,0	s-arb	len	NA	Α	aqu	i	SD
Mantellidae	Gephyromantis	eiselti	Madagascar	1993,95	400	23,0	35,0	lit	none	4	A	ter	d	

//antellidae	Gephyromantis	luteus	Madagascar	64398,49	700	43,0	47,0	s-arb	none	NA	В	ter	d	SD
⁄lantellidae	Gephyromantis	malagasius	Madagascar	62053,09	1500	23,0	26,0	lit	none	NA	Α	ter	d	SD
⁄lantellidae	Gephyromantis	redimitus	Madagascar	52053,49	850	53,0	56,4	s-arb	len	NA	Ε	aqu	i	SD
/lantellidae	Guibemantis	bicalcaratus	Madagascar	115691,97	1200	26,0	29,0	arb	phy	54,8	Α	arb	i	SD
/lantellidae	Guibemantis	depressiceps	Madagascar	134337,42	1200	45,0	35,0	s-arb	len	70	Α	arb	i	1
//antellidae	Guibemantis	flavobrunneus	Madagascar	62478,52	1000	33,0	38,0	arb	len	NA	Α	aqu	i	SD
⁄Iantellidae	Guibemantis	kathrinae	Madagascar	450,46	340	59,0	56,4	arb	len	NA	Ε	arb	i	SD
/lantellidae	Guibemantis	liber	Madagascar	143658,64	2050	29,0	28,0	arb	len	90	Α	arb	i	NR
/lantellidae	Guibemantis	pulcher	Madagascar	62885,3	1400	25,0	28,0	arb	phy	NA	Α	arb	i	SD
/lantellidae	Mantella	baroni	Madagascar	32886,41	600	29,0	30,0	lit	len	64	Α	ter	i	SD
/lantellidae	Mantella	pulchra	Madagascar	16161,75	650	26,0	28,0	lit	lot	61	Α	ter	i	SD
//antellidae	Mantidactylus	aerumnalis	Madagascar	36593,35	500	27,0	31,0	lit	lot	NA	Α	ter	i	SD
/lantellidae	Mantidactylus	albofrenatus	Madagascar	1848,89	50	23,0	27,0	lit	lot	NA	Α	ter	i	SD
//antellidae	Mantidactylus	argenteus	Madagascar	28417,71	600	27,0	31,0	lit	lot	12	Α	arb	i	SD
/lantellidae	Mantidactylus	betsileanus	Madagascar	87389,03	1500	28,0	37,0	lit	lot	7	A	s-ter	i	NR
//antellidae	Mantidactylus	biporus	Madagascar	88413,28	1600	27,0	34,0	s-aqu	len	, NA	A	ter	i	SD
Mantellidae	Mantidactylus	femoralis	Madagascar	191431,49	2500	27,0 37,0	55,0	s-aqu s-aqu	lot	76	A	ter	i	SD
//antellidae	Mantidactylus	grandidieri	Madagascar	76192,23	1500	180,0	56,4	•	lot	NA	ı		i	SD
fantellidae fantellidae	•	~	_	126158,93	2500		67,0	s-aqu lit	lot	NA NA	7	aqu tor	i	SD
	Mantidactylus Mantidactylus	mocquardi	Madagascar	•		55,0					Δ	ter	:	
lantellidae	Mantidactylus	opiparis tricinatus	Madagascar	74905,08	900	26,0 10.0	33,0	lit	lot	89 NA	A	aqu	! :	SD
lantellidae	Mantidactylus	tricinctus	Madagascar	2229,22	400	19,0	20,0	s-aqu	len / lot	NA	A	aqu	!	SD
lantellidae	Spinomantis	peraccae	Madagascar	100196,03	1500	41,0	42,0	arb	lot	NA	D	arb		SD
legophryidae	Leptobrachium	smithi 	Asia	206534,7	1290	68,2	78,0	lit	lot	NA	F	aqu	. I	SD
licrohylidae	Anodonthyla	boulengerii	Madagascar	80806,46	1300	22,0	21,0	s-arb	phy	NA	Α	arb	İ	SD
licrohylidae	Chiasmocleis	albopunctata	America	2548381,93	1400	32,0	38,0	lit	len	NA	Α	aqu	i	SD
licrohylidae	Chiasmocleis	shudikarensis	America	2910745,4	200	25,0	28,0	lit	len	566	D	aqu	i	SD
licrohylidae	Ctenophryne	geayi	America	5940721,75	600	41,7	49,3	fos	len	600	D	ter	i	D
1icrohylidae	Gastrophryne	elegans	America	10959404,32	952	25,8	28,9	lit	len	NA	Α	aqu	i	NR
licrohylidae	Hypopachus	ustus	America	211031,15	1000	30,6	31,4	lit	len	NA	Α	aqu	i	SD
1icrohylidae	Kalophrynus	pleurostigma	Asia	754159,24	2200	55,0	60,0	lit	len	6	Α	aqu	i	SD
1icrohylidae	Kaloula	baleata	Asia	860868,31	1525	61,0	67,0	fos	len	160	В	aqu	i	NR
1icrohylidae	Kaloula	pulchra	Asia	2438006,6	750	70,0	75,0	fos	len	NA	E	aqu	i	NR
1icrohylidae	Microhyla	berdmorei	Asia	1622527,08	1217,6	28,0	45,0	lit	len	NA	В	aqu	i	NR
1icrohylidae	Microhyla	ornata	Asia	3446277,95	2000	27,0	32,0	lit	len	1200	E	aqu	i	NR
1icrohylidae	Microhyla	rubra	Asia	1178745,31	700	27,5	29,5	lit	len	NA	Α	aqu	i	NR
1icrohylidae	Paradoxophyla	palmata	Madagascar	31237,38	950	22,1	25,6	fos	len	408	С	aqu	i	SD
1icrohylidae	Platypelis	barbouri	Madagascar	37250,33	1100	23,0	56,4	s-arb	phy	NA	Α	aqu	i	ı
, Iicrohylidae	Platypelis	grandis	Madagascar	129138,45	1217,6	88,0	61,0	s-arb	len	100	В	aqu	i	SD
, 1icrohylidae	Platypelis	pollicaris	Madagascar	11501,66	1200	28,0	56,4	s-arb	phy	NA	Α	aqu	i	SD
1icrohylidae	Platypelis	tuberifera	Madagascar	62693,76	800	40,0	56,4	s-arb	phy	NA	С	aqu	i	SD
1icrohylidae	Plethodontohyla	inguinalis	Madagascar	71194,35	700	100,0	63,0	s-arb	phy	NA	Е	arb	i	SD
1icrohylidae	Plethodontohyla	notosticta	Madagascar	102688,81	1200	35,0	38,5	s-arb	phy	120	В	aqu	i	SD
licrohylidae	Rhombophryne	alluaudi	Madagascar	99859,19	1400	60,0	56,4	fos	len	NA	F	ter	i	SD
icrohylidae	Stumpffia	tetradactyla	Madagascar	595,36	100	15,0	56,4	lit	ter	NA	A	ter	i	SD
licrohylidae	Synapturanus	salseri	America	1318002,07	200	30,0	35,0	fos	ter	8	A	ter	ď	SD
etropedetidae	Conraua	crassipes	Africa	555260,86	1758	81,0	76,0		lot	NA	F		i	SD
etropedetidae	Conraua	robusta	Africa	12360,4	650			s-aqu	_	52	Λ	aqu	:	
•						140,0	122,0	s-aqu	lot		A B	ter	:	SD
hrynobatrachidae	Phrynobatrachus	acridoides	Africa	1756215,67	700	27,0	25,0	s-aqu	len	105		aqu	!	"
hrynobatrachidae	Phrynobatrachus	africanus	Africa	713611,07	1758	28,0	30,0	lit	len	NA	A	aqu		SD
hrynobatrachidae	Phrynobatrachus	mababiensis	Africa	4355399,29	2410	19,0	22,0	lit	len	775	D	aqu	I	NR

Phrynobatrachidae	Phrynobatrachus	natalensis	Africa	10456437,35	2200	30,0	31,0	lit	len	1652	E	aqu	i	NR
Pipidae	Pipa	arrabali	America	1038533,62	860	42,0	55,0	aqu	skin	16	Α	skin	d	D
Pipidae	Xenopus	laevis	Africa	4599862,56	3000	97,5	147,0	aqu	len	17000	I	aqu	i	D
Ptychadenidae	Ptychadena	anchietae	Africa	6641710,13	1780	51,0	62,0	lit	len	300	С	aqu	i	NR
Ptychadenidae	Ptychadena	mascareniensis	Africa	590831,48	2000	57,0	68,0	lit	len	1079	Ε	aqu	i	NR
Ptychadenidae	Ptychadena	mossambica	Africa	2867084,3	1000	35,0	44,0	lit	len	315	С	aqu	i	D
Ptychadenidae	Ptychadena	oxyrhynchus	Africa	8160886,06	2000	53,0	64,0	lit	len	5018	G	aqu	i	SD
Pyxicephalidae	Amietia	angolensis	Africa	4274988,92	3100	81,0	90,0	s-aqu	len / lot	500	С	aqu	i	ı
Pyxicephalidae	Pyxicephalus	edulis	Africa	2933976,25	1500	120,0	120,0	fos	len	4000	G	aqu	i	SD
Pyxicephalidae	Tomopterna	cryptotis	Africa	10857651,05	811	45,0	58,0	fos	len	3000	F	aqu	i	D
Pyxicephalidae	Tomopterna	krugerensis	Africa	1209670,06	1500	45,0	46,0	fos	len	5000	G	aqu	i	D
Pyxicephalidae	Tomopterna	natalensis	Africa	494825,84	2000	39,0	44,0	fos	len / lot	NA	В	aqu	i	SD
Ranidae	Clinotarsus	alticola	Asia	152446,47	1217,6	53,0	56,4	s-arb	lot	NA	Ε	aqu	i	SD
Ranidae	Hylarana	albolabris	Africa	3669770,03	1939	56,0	70,0	s-arb	len	636	D	aqu	i	SD
Ranidae	Hylarana	aurantiaca	Asia	12416,56	1395	56,0	63,0	s-arb	lot	NA	Ε	aqu	i	NR
Ranidae	Hylarana	celebensis	Asia	30938,04	1217,6	46,0	56,4	lit	len / lot	NA	D	aqu	i	NR
Ranidae	Hylarana	chalconota	Asia	246684,24	1217,6	45,0	61,0	s-arb	len / lot	3200	F	aqu	i	SD
Ranidae	Hylarana	erythraea	Asia	2091033,97	1200	48,0	75,0	lit	len	1900	F	aqu	i	NR
Ranidae	Hylarana	temporalis	Asia	43280,93	1770	56,1	78,0	lit	lot	1200	Ε	aqu	i	SD
Ranidae	Lankanectes	corrugatus	Asia	9692,15	1495	35,0	71,0	aqu	len	NA	Е	aqu	i	NR
Ranidae	Lithobates	berlandieri	America	1463513,93	3002	112,0	56,4	aqu	len / lot	3000	F	aqu	i	NR
Ranidae	Lithobates	vaillanti	America	507080,67	1097	94,0	125,0	s-aqu	len / lot	1000	Е	aqu	i	NR
Ranidae	Nannophrys	ceylonensis	Asia	5598,28	1140	42,5	52,5	aqu	semi-aquatic	43,2	Α	ter	i	NR
Ranidae	Pterorana	khare	Asia	5211,62	1400	62,0	56,4	lit	lot	900	D	aqu	i	SD
Ranixalidae	Indirana	beddomii	Asia	50217,45	1800	50,0	60,0	lit	semi-aquatic	NA	Е	aqu	i	NR
Ranixalidae	Indirana	leithii	Asia	16246,03	800	38,0	56,4	lit	semi-aquatic	NA	В	s-ter	i	SD
Rhacophoridae	Chiromantis	vittatus	Asia	1279274,39	1500	35,0	32,0	arb	len	NA	Α	arb	i	NR
Rhacophoridae	Chiromantis	xerampelina	Africa	2780951,55	1200	75,0	90,0	arb	len	1226	Е	arb	i	NR
Rhacophoridae	Nyctixalus	pictus	Asia	205915,69	1700	33,0	38,0	s-arb	phy	15	Α	arb	i	SD
Rhacophoridae	Philautus	namdaphaensis	Asia	928,27	200	27,0	56,4	s-arb	len	12	Α	ter	d	D
Rhacophoridae	Polypedates	cruciger	Asia	16005,14	1510	59,8	90,0	arb	len	300	С	arb	i	I
Rhacophoridae	Polypedates	leucomystax	Asia	3926220,27	1500	50,0	75,0	arb	len	900	D	arb	i	NR
Rhacophoridae	Polypedates	longinasus	Asia	97,9	1150	47,0	60,0	s-arb	len	42	Α	arb	i	D
Rhacophoridae	Pseudophilautus	abundus	Asia	402,43	72	31,0	37,0	s-arb	none	155	В	ter	d	D
Rhacophoridae	Pseudophilautus	auratus	Asia	111,54	757	23,3	26,4	s-arb	none	155	В	ter	d	D
Rhacophoridae	Pseudophilautus	cavirostris	Asia	197,21	900	47,1	48,9	s-arb	none	155	В	ter	d	D
Rhacophoridae	Pseudophilautus	cuspis	Asia	130,28	510	20,3	228,9	s-arb	none	155	В	ter	d	D
Rhacophoridae	Pseudophilautus	folicola	Asia	21,62	1240	23,1	29,4	s-arb	none	155	В	ter	d	NR
Rhacophoridae	Pseudophilautus	hoipolloi	Asia	501,92	685	27,6	28,6	s-arb	none	155	В	ter	d	1
Rhacophoridae	Pseudophilautus	mittermeieri	Asia	14,67	90	18,4	56,4	s-arb	none	155	В	ter	d	D
Rhacophoridae	Pseudophilautus	popularis	Asia	3743,31	1067	21,3	24,7	s-arb	none	155	В	ter	d	I
Rhacophoridae	Pseudophilautus	reticulatus	Asia	96,12	1340	44,1	61,1	arb	none	155	В	ter	d	D
Rhacophoridae	Pseudophilautus	silvaticus	Asia	106,27	760	25,3	31,3	s-arb	none	155	В	ter	d	D
Rhacophoridae	Pseudophilautus	sordidus	Asia	6404,69	1519	36,8	39,4	s-arb	none	155	В	ter	d	NR
Rhacophoridae	Pseudophilautus	stictomerus	Asia	230,04	455	23,2	36,0	s-arb	none	155	В	ter	d	NR
Rhacophoridae	Raorchestes	parvulus	Asia	426431,47	1350	19,6	21,0	s-arb	none	NA	Α	aqu	d	NR
Rhacophoridae	Rhacophorus	georgii	Asia	4493,61	1217,6	47,1	70,0	arb	phy	108	В	arb	i	D
Rhacophoridae	Rhacophorus	maximus	Asia	328678,53	1500	114,3	56,4	arb	len	NA	G	arb	i	D
Rhacophoridae	Rhacophorus	monticola	Asia	23126,65	1217,6	36,7	39,9	lit	len	NA	В	arb	i	SD

Additional file 5. Affiliation to different anuran families

Given are number and relative frequency (in color code) of species belonging to a particular family per forest dependency index (higher frequency with darker color, see legend in table); forest dependency index: D = dependent (n = 33), SD = slightly dependent (n = 108), NR = non-responding (n = 83), I = forest independent (n = 19).

Family	Forest	depend	dency I	ndex	
	D	SD	NR	ı	
Aromobatidae	0	2	0	0	
Arthroleptidae	2	9	3	0	
Brevicipitidae	1	0	0	1	
Bufonidae	2	2	10	1	
Centrolenidae	1	1	0	0	
Ceratophryidae	0	1	0	0	
Craugastoridae	1	7	6	0	
Dendrobatidae	0	0	1	0	
Dicroglossidae	1	3	6	2	
Eleutherodactylidae	0	1	2	0	
Hemisotidae	0	1	1	0	
Hylidae	4	13	15	4	
Hyperoliidae	4	4	1	1	
Leiuperidae	0	0	1	0	
Leptodactylidae	0	4	8	0	
Mantellidae	0	31	4	4	
Megophryidae	0	1	0	0	
Microhylidae	1	14	6	1	
Petropedetidae	0	2	0	0	
Phrynobatrachidae	0	1	2	1	
Pipidae	2	0	0	0	
Ptychadenidae	1	1	2	0	
Pyxicephalidae	2	2	0	1	0
Ranidae	0	5	7	0	< 10%
Ranixalidae	0	1	1	0	< 30%
Rhacophoridae	11	2	7	3	> 30% (33%)