

Deforestation and the Structure of Frog Communities in the Humedale Terraba-Sierpe, Costa Rica

Dario Furlani^{1†}, Gentile Francesco Ficetola^{1§*}, Giorgio Colombo¹, Murat Ugurlucan² and Fiorenza De Bernardi¹

¹Dipartimento di Biologia, Università degli Studi di Milano, V. Celoria 26, Milano 20133, Italy

²Medizinische Fakultät, Universität Rostock, Schillingallee 69, Rostock 18057, Germany

Loss of tropical forests is a major cause of biodiversity loss worldwide. Although drastic modification of the habitat has been shown to negatively affect amphibians, we are far from a complete understanding of the response of amphibian communities to deforestation. We studied frog assemblages in a gradient of forest modification in a humid area of Costa Rica, where the primary forest has been partially converted into pasture. The study area is a mosaic of primary palm forest, abandoned pasture covered by secondary forest, and pasture. Species richness was assessed by randomized walk surveys and audio strip transects. We also measured ecological features to evaluate the relationship between landscape alteration and amphibian distribution. The study area hosted a large number of amphibian species. We focused our monitoring on six anurans: *Leptodactylus labialis*, *Eleutherodactylus fitzingeri*, *E. diastema*, *Hyla rosenbergi*, *H. microcephala*, and *Cochranella granulosa*. Three species (*L. labialis*, *H. rosenbergi*, and *H. microcephala*) were most abundant in pasture areas with livestock presence, while *E. fitzingeri*, *E. diastema*, and *C. granulosa* were associated with primary forest. Most of the variation in community structure was explained by the joint effect of forest alteration and presence of livestock. Whereas forest specialists suffer direct negative effect from deforestation, generalist species can take advantage of forest alteration and the presence of farm animals. Species that are able to take advantage of the new environmental characteristics associated with human modifications of landscapes will come to prevail in the new communities.

Key words: Amphibian community, amphibian conservation, audio strip transects, *Eleutherodactylus diastema*, *Eleutherodactylus fitzingeri*, *Leptodactylus labialis*, *Hyla rosenbergi*, *Hyla microcephala*, *Cochranella granulosa*, tropical forest, habitat alteration

INTRODUCTION

The Neotropics host nearly 50% of known amphibian species, and Neotropical forests are thus considered one of the most important areas for amphibian diversity at the global scale (Stuart et al., 2004; Grenyer et al., 2006). However, tropical forests are under serious human pressure, and the loss and alteration of habitat is a major cause of the loss of amphibian diversity (Stuart et al., 2004; Gardner et al., 2007). Even though the negative effects of habitat alteration on amphibians have generally been acknowledged, we are far from a complete understanding of the response of amphibian communities to deforestation (Tocher et al., 2002). Moreover, most studies evaluating the effects of habitat alteration on amphibian assemblages have been

performed in temperate areas (Gardner et al., 2007). It is therefore urgent to increase our knowledge of the response of amphibian communities to the loss of tropical forests.

In this study, we analysed frog communities in a gradient of forest alteration in the Humedale Terraba-Sierpe, Costa Rica. In this area, primary forest was partially converted to pasture in the 1970s (Alvarez et al., 1999). The area is currently a mosaic of flooded areas, primary forest, pasture, and abandoned deforested areas where the regrowth of vegetation is ongoing. This environmental complexity makes the area an ideal site for studying the modifications of communities following deforestation.

The aim of this study was to evaluate the relationship between the distribution of frog species and environmental gradients created by the human alteration of landscapes. Moreover, we evaluated the modification of community structure (i.e., the composition of communities and the abundance of species) along these gradients. Our results highlight strong interspecific differences in the response to environmental gradients, and the complex role of environmental factors in structuring communities.

STUDY AREA AND METHODS

We studied an area of about 500 ha within the Humedale

* Corresponding author. Phone: +39-(0)2-6448-2945;
Fax : +39-(0)2-6448-2945;
E-mail: francesco.ficetola@unimi.it

† Present address: Medizinische Fakultät, Universität Rostock, Schillingallee 69, Rostock, 18057, Germany

§ Present address: Dipartimento di Scienze dell'Ambiente e del Territorio, Università degli Studi di Milano-Bicocca. Piazza della Scienza 1, 20126 Milano Italy
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Terraba Sierpe, Southern Costa Rica (8°48'N, 84°24'W; overall surface about 30,000 ha). The Humedale is a partially flooded wetland, originally occupied by palm swamp forests; in the 1970s, the primary forest was partially cleared for pasture (Alvarez et al., 1999). Further details on the study area were reported by Ficetola et al. (2008). Approximately 150 ha of the study area are covered by primary palm forest, and constitute one of Costa Rica's private wildlife refugia (Langholz et al., 2000); about 33 ha are abandoned pasture covered by secondary forest, and 140 ha are currently exploited pasture. The remaining areas consist of the Sierpe River and areas flooded nearly permanently. It is thus possible to distinguish three main levels of forest alteration: (1) primary forest (no alteration); (2) secondary forest; (3) pasture. Permanently flooded areas were not investigated. See Ficetola et al. (2008) for a map of the study area.

Recent phylogenetic analyses based on molecular data suggested taxonomic changes for some of the species found in the study area (e.g., Frost et al., 2006). However, the taxonomy is currently under debate, and many of the species found in the study area were not included in the molecular studies; thus, we followed the nomenclature of Savage (2002).

Sampling of amphibians

The study area was monitored during the late dry season and the beginning of the rainy season in 2002 (3 February to 5 May). At the beginning of the sampling period (February to early March), we performed randomized walk surveys to obtain preliminary information on the species present within the study area. Species were generally captured by hand and were identified by using existing keys (Leenders, 2001; Savage, 2002). Federigo Bolaños (Instituto de Biología Tropical, Universidad de Costa Rica, San José) confirmed our identifications.

After these preliminary surveys, we established 14 linear transects to compare amphibian communities along the existing environmental gradients. Transect length was 200 m. Transects were selected on the basis of stratified random sampling, in order to cover the habitat types present in the study area, although accessibility partially constrained the location of transects in primary forest.

From 27 March to 29 April 2002 (the beginning of the rainy season), we used audio strip transects (Zimmerman, 1994) to monitor the presence of amphibians in the different environments, on the basis of species-specific vocalizations (Leenders, 2001; Savage, 2002); we repeated each transect 8–10 times. For each transect, calling males were counted in 10 consecutive point counts spaced 20 m apart. Each point count lasted 1 minute (Zimmerman, 1994); therefore, during each transect listening lasted 10 minutes. See Ficetola et al. (2008) for further details.

The audio strip transects were focused on six species that can be reliably identified on the basis of calls (Leenders, 2001; Savage, 2002) and that were found in at least four transects (see Results): *Leptodactylus labialis*, *Eleutherodactylus fitzingeri*, *E. diastema*, *Hyla rosenbergi*, *H. microcephala*, and *Cochranella granulosa*. We limited our analyses to these six species, because it is difficult to obtain reliable relationships when presence localities are very few. The identification of calling males was confirmed by morphological examination of several males for each species. Of these six regularly monitored species, the males of *E. fitzingeri*, *E. diastema*, *H. microcephala*, and *C. granulosa* tended to be well spaced, and it was thus possible to obtain counts. For *Leptodactylus labialis* and *H. rosenbergi*, which formed large choruses, we only recorded abundance classes (five classes: 1, 2, 3–5, 6–10, >10).

Sound transmission and thus detection distances can vary with vegetation structure. We therefore measured the maximum distance at which calling frogs could no longer be heard clearly (detection distance) in each transect (Zimmerman, 1994) and calculated the area covered by each transect; the density of calling males was equal to the average number of calling males / area covered. Further details on transect calibration are provided by Ficetola et al. (2008).

Habitat features

For each transect, we measured seven environmental variables to relate amphibian distribution to habitat features: grass cover, canopy cover, number of large trees, litter thickness, percent flooded, water permanence, and distance from the river. Grass cover, canopy cover, and percent flooded were visually estimated in a 50×200 m strip along the transect (Ficetola et al., 2004), as the average of the habitat features observed at each observation point (every 25 m). The number of large trees was recorded in a 20×200 m strip as the number of trees of diameter >50 cm at 1.5 m above the ground (Pearman, 1997). Litter thickness was measured with a ruler at two points (50 and 150 m from the beginning, eight measurements per distance point) and averaged for each transect. Water permanence was recorded by using a rank scale: 1, ephemeral (only after rain); 2, temporary (depending on daily tide), 3, permanent. We also recorded whether livestock was present in the proximity of a transect. Livestock was present on four transects located in pasture. Despite clear differences among the three levels of forest alteration, there was overlap in environmental features among the habitat types (Table 1a).

Data analysis

Some of the environmental variables were strongly correlated (Table 2). The presence of intercorrelated independent variables could bias the results of multiple regression analyses (Berry, 1985). We therefore used principal component analysis (PCA) to reduce environmental variables to a smaller number of unrelated factors.

Table 1. Environmental features and average abundance of six amphibians in transects in pasture, secondary forest and primary forest. In parenthesis, the range of variation observed.

	Pasture	Secondary forest	Primary forest
	Mean (min–max)		
a) environmental features			
litter thickness	1.4 (1.0–1.5)	3.4 (2.0–4.5)	5.5 (4.0–6.5)
% flooded	0.32 (0.05–0.50)	0.25 (0.05–0.80)	0.48 (0.05–0.90)
water permanence	2.3 (1–3)	2.5 (2–3)	3 (3–3)
grass cover	0.89 (0.80–1.0)	0.18 (0–0.60)	0.03 (0.00–0.10)
wood cover	0.07 (0.05–0.10)	0.61 (0.05–1.0)	1.0 (1.0–1.0)
b) amphibians			
<i>Leptodactylus labialis</i> *	1.0 (0.0–1.9)	0.2 (0–0.6)	0.0
<i>Eleutherodactylus fitzingeri</i>	0.2 (0.1–0.3)	6.44 (0.22–12.22)	15.1 (3.3–28.6)
<i>Eleutherodactylus diastema</i>	0.2 (0.02–0.5)	3.5 (1.0–5.3)	45.2 (18.8–79.7)
<i>Hyla rosenbergi</i> *	0.4 (0.0–1.2)	0.1 (0–0.5)	0.0
<i>Hyla microcephala</i>	0.9 (0.0–2.7)	0.4 (0.0–1.5)	0.0
<i>Cochranella granulosa</i>	0.0	0.0	0.6 (0.1–0.9)

*, abundance recorded on a rank scale (see Methods).

Table 2. Pearson's pairwise correlations among environmental variables. $n=14$ for all correlations.

		Water perman.	Distance to river	litter thickness	grass cover	wood cover	N large trees
% flooded	<i>r</i>	0.534	0.518	0.060	0.021	–0.061	0.061
	<i>p</i>	0.049	0.058	0.839	0.945	0.837	0.835
water permanence	<i>r</i>		0.475	0.264	–0.248	0.160	0.069
	<i>p</i>		0.086	0.363	0.392	0.584	0.814
distance to river	<i>r</i>			–0.196	0.216	–0.283	–0.269
	<i>p</i>			0.501	0.459	0.327	0.353
litter thickness	<i>r</i>				–0.920	0.978	0.864
	<i>p</i>				<0.001	<0.001	<0.001
grass cover	<i>r</i>					–0.940	–0.679
	<i>p</i>					<0.001	0.008
wood cover	<i>r</i>						0.810
	<i>p</i>						<0.001

PCA extracted two components with eigenvalues greater than 1; altogether, these components explained 82% of the variation. PCA1 (hereafter, *alteration*) was negatively related to litter thickness, wood cover, and the number of large trees, and was positively related to grass cover (for all correlations, $|r| \geq 0.88$ and $p < 0.001$). Alteration was not correlated with other environmental variables (all $r < 0.2$). Forest alteration therefore represents a gradient from the primary forest to the most altered pasture sites. Alteration was significantly different among the three environmental types (ANOVA: $F_{2,11} = 36.031$, $P < 0.001$); it was higher in pasture than in secondary forest, and higher in secondary forest than in primary forest (Tukey's post-hoc test; all $p < 0.007$). PCA2 (hereafter, *flooding*) was positively related to percent flooded, water permanence, and distance from the river (all $r \geq 0.8$, all $p < 0.001$), while it was not correlated with the other variables. Flooding was not different among the three environmental types (ANOVA: $F_{2,11} = 0.337$, $p = 0.721$).

The presence of livestock was obviously associated with pasture, and hence with the most altered areas; however, it should be noted that, during the study period, livestock was not present in all the open areas surveyed. We preferred not to include livestock presence in the PCA to evaluate its independent effect after taking into account habitat features, because cattle footprints could be used by some species for reproduction (Hobel, 1999; see discussion).

We used multiple linear regression to relate the abundance of each species to environmental features. We used the abundance of species in each transect as dependent variables, averaged over the times a transect was monitored; we used alteration, flooding, and livestock presence as independent variables. We then performed hierarchical partitioning, to identify the causal variables having the largest independent effect on amphibian abundance (Chevan and Sutherland, 1991; Werner et al., 2007). Hierarchical partitioning allows partitioning the explanatory power of each independent variable into independent effects and those due to joint effects with other variables (i.e., effects that cannot be unambiguously related to the variable) (Werner et al., 2007).

We used complementary techniques to relate the variation in community structure to environmental features. First, we performed two-dimensional nonmetric multidimensional scaling (NMDS), based on Bray-Curtis distances among communities (Legendre and Legendre, 1998), to visualize differences among environmental types. An iterative search with random configurations confirmed that two dimensions corresponded to the best solution. We then used Mantel test to relate the Bray-Curtis dissimilarity among communities to habitat differences among localities (measured using Euclidean distances) (Legendre and Legendre, 1998; Ernst and Rödel, 2005). The significance of the Mantel test was assessed by using 10,000 permutations.

Second, we used canonical correspondence analysis (CCA) (Legendre and Legendre, 1998) to relate variation in community structure to environmental features. CCA allowed us to relate a multivariate matrix representing species abundance to a second multivariate matrix (e.g., environmental features). We evaluated the significance of the relationship between community structure and each environmental variable by performing 5,000 permutations (Legendre and Legendre, 1998). We then performed variance partitioning (Cushman and McGarigal, 2002) to calculate the percentage of variation explained by each independent variable. Variance partitioning allowed us to decompose the independent and the joint effects of variables, and to rank them according to their explanatory power. Statistical analyses were performed by using the packages Vegan 1.6 (Oksanen et al., 2005) and Hier.part 1.0 (Walsh and Mac Nally, 2005) in the R 2.2 environment (R Development Core Team, 2005).

RESULTS

Combining the preliminary walk surveys and the stan-

dardized transects, we observed 22 anuran species within the study area (Table 3). The most speciose genera were *Eleutherodactylus* and *Hyla* (four species each). No previous records on amphibian distribution were available for the study area. Savage (2002) reported 51 species of anurans for the region surrounding the study area; therefore, we found 43% of the regional species richness in an area of about 500 ha.

Six species were observed calling consistently in at least four transects: *Leptodactylus labialis*, *Eleutherodactylus fitzingeri*, *E. diastema*, *Hyla rosenbergi*, *H. microcephala* and *Cochranella granulosa*. The following analyses focus on these six species.

Species abundance

The six species analysed showed different responses to environmental features. Three species (*L. labialis*, *H. rosenbergi*, and *H. microcephala*) were present only in the most disturbed areas (Table 1b) and were positively related to areas with livestock present (Table 4). Conversely, *E. fitzingeri*, *E. diastema*, and *C. granulosa* were negatively related to forest alteration (Table 1b, Table 4). We did not find any significant relationship between species abundance and flooding.

In all cases, the significant variables were the variables with the largest independent contribution to the model. For example, the independent effect of forest alteration explained 37–43% of the variance in the distribution of *Eleutherodactylus* frogs, while the independent effect of livestock presence explained 42–48% of the variance for the *Hyla* tree frogs. For all models, the independent contribution of variables was much larger than their joint contribution. Even though livestock presence was positively related to forest alteration ($r = 0.60$, $p = 0.023$), its high independent contribution sug-

Table 3. Species observed in the study area.

Species	Family
<i>Bufo marinus</i>	Bufoidea
<i>B. melanochlorus</i>	Bufoidea
<i>Leptodactylus bolivianus</i>	Leptodactylidae
<i>L. labialis</i>	Leptodactylidae
<i>Eleutherodactylus fitzingeri</i>	Leptodactylidae
<i>E. bransfordi</i>	Leptodactylidae
<i>E. caryophyllaceus</i>	Leptodactylidae
<i>E. diastema</i>	Leptodactylidae
<i>Hyla rufitela</i>	Hylidae
<i>H. rosenbergi</i>	Hylidae
<i>H. ebraccata</i>	Hylidae
<i>H. microcephala</i>	Hylidae
<i>Scinax elaeochroa</i>	Hylidae
<i>Sc. stauferi</i>	Hylidae
<i>Smilisca phaeota</i>	Hylidae
<i>Sm. sordida</i>	Hylidae
<i>Cochranella granulosa</i>	Centrolenidae
<i>Colostethus flotator</i>	Dendrobatidae
<i>Colostethus talamancae</i>	Dendrobatidae
<i>Dendrobates auratus</i>	Dendrobatidae
<i>D. granuliferus</i>	Dendrobatidae
<i>Phyllobates vittatus</i>	Dendrobatidae

Table 4. Results of multiple linear regressions relating the abundance of six anuran species to environmental variables. Effect signs are reported only for variables with significant coefficients. In bold, significant variables and the variables explaining the largest proportion of variation. Negative joint effects are possible for variables that act as suppressors of other variables (Chevan and Sutherland, 1991). I, independent contribution of the variable to the variance explained by the model; J, joint contribution of the variable to the variance explained by the model.

Species		r^2	Forest alteration	Flooding	Livestock
<i>L. labialis</i>	Effect sign				+
	$F_{1,10}$		1.943	1.422	47.256
	p		0.194	0.261	<0.001
	I		0.12	0.05	0.49
	J	0.928	0.09	0.03	0.14
<i>E. fitzingeri</i>	Effect sign		-		
	$F_{1,10}$		12.600	3.087	0.796
	p		0.005	0.109	0.393
	I		0.43	0.08	0.07
	J	0.646	0.03	-0.02	0.06
<i>E. diastema</i>	Effect sign		-		
	$F_{1,10}$		7.754	0.190	0.261
	p		0.019	0.672	0.620
	I		0.37	0.01	0.05
	J	0.516	0.04	0.00	0.04
<i>H. rosenbergi</i>	Effect sign				+
	$F_{1,10}$		0.351	0.957	10.204
	p		0.567	0.351	0.010
	I		0.06	0.02	0.42
	J	0.586	0.05	-0.02	0.04
<i>H. microcephala</i>	Effect sign				+
	$F_{1,10}$		0.929	1.603	10.655
	p		0.358	0.234	0.039
	I		0.06	0.04	0.48
	J	0.564	0.02	-0.04	0.00
<i>C. granulosa</i>	Effect sign		-		
	$F_{1,10}$		7.258	0.078	0.270
	p		0.023	0.786	0.614
	I		0.37	0.00	0.05
	J	0.495	0.04	0.00	0.04

gested that it had an important role in the distribution of some species, after taking into account forest alteration.

Community structure

Nonmetric multidimensional scaling showed that pasture, secondary forest, and primary forest had distinct communities (Fig. 1). Dissimilarity among the communities was strongly related to habitat differences (Mantel test, $r=742$, $p<0.0001$).

Canonical correspondence analysis showed a clear community structure, with a distinction of species in two homogeneous groups (Fig. 2). *Leptodactylus labialis*, *H. microcephala*, and *H. rosenbergi* showed similar habitat preferences and were associated with the areas with highest alteration and livestock presence (see also Table 1b). Conversely, *E. fitzingeri*, *E. diastema*, and *C. granulosa* were associated with the sites with low alteration and thus the absence of livestock. Permutation tests showed that both livestock presence and alteration explained a significant proportion of inertia for community structure (both $P<0.001$). Conversely, flooding did not explain a significant proportion

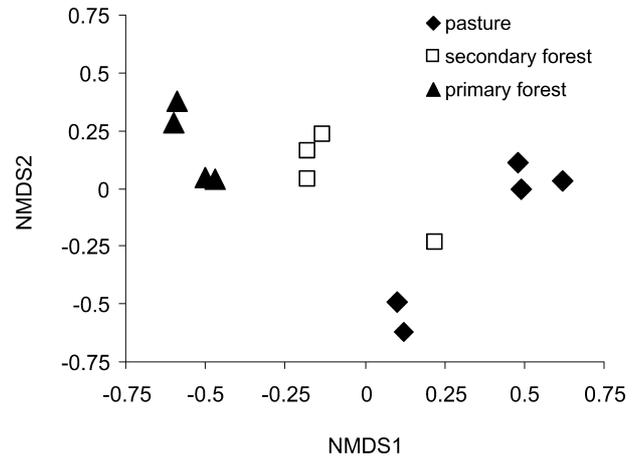


Fig. 1. Nonmetric multidimensional scaling, based on Bray-Curtis dissimilarities, showing differences in amphibian communities among pasture, secondary forest, and primary forest.

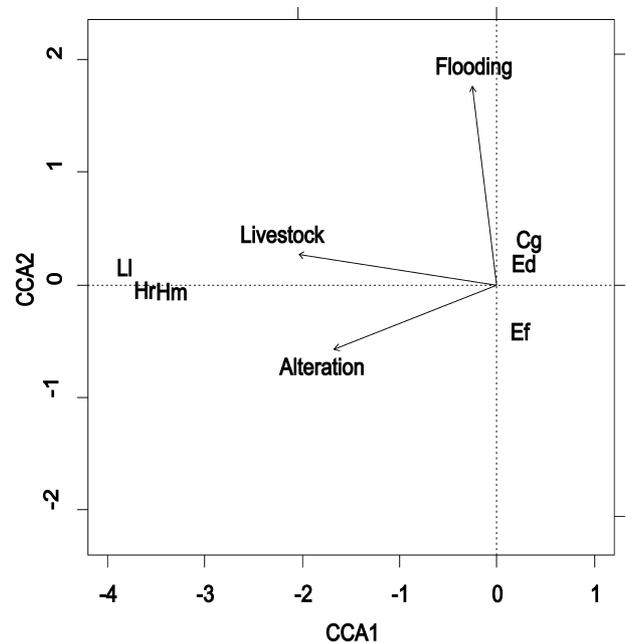


Fig. 2. Canonical correspondence analysis, relating community structure to environmental variables. LI, *Leptodactylus labialis*; Ef, *Eleutherodactylus fitzingeri*; Ed, *E. diastema*; Hr, *Hyla rosenbergi*; Hm, *H. microcephala*; Cg, *Cochranella granulosa*.

of inertia ($P=0.209$). CCA explained 89% of inertia of community structure.

To assess the independent role of the three environmental factors, we performed variance decomposition (Fig. 3). Most of the variation was explained by the joint effect of forest alteration and livestock presence (52% of inertia), while livestock presence was the variable with the largest independent effect (24%). The independent effects of the other variables, and the joint effects of the other variable combinations, explained only a small proportion of the variation (Fig. 3).

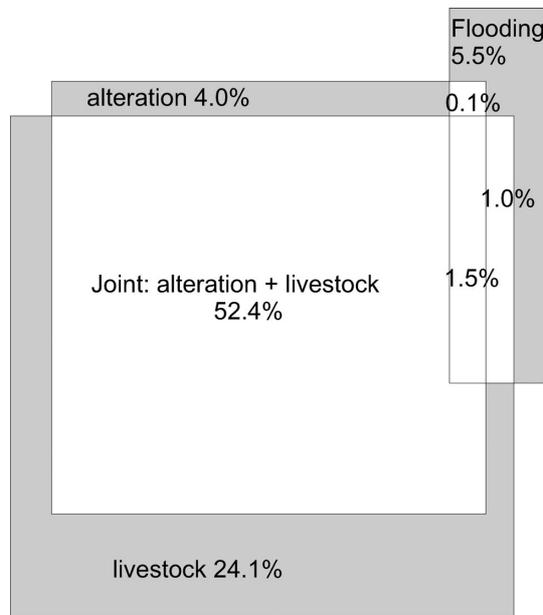


Fig. 3. Results of variance partitioning of the influence of forest alteration, flooding, and livestock presence on frog community structure. The area of each rectangle is proportional to the variance explained for that independent variable. The numbers in the rectangular cells indicate the percent of variance explained by each variable.

DISCUSSION

In tropical forests, amphibians can have complex responses to environmental alterations caused by human activities (Pearman, 1997; Tocher et al., 2002; Pineda and Halfpeter, 2004; Ernst and Rödel, 2005). Our study shows that amphibian distribution and abundance are strongly influenced by habitat modifications caused by human activities. However, the response was greatly different among species. Some amphibians (*E. fitzingeri*, *E. diastema*, and *C. granulosa*) were negatively affected by forest alteration, and were associated with the most natural areas of primary forest. Conversely, other species were associated with pasture with livestock present (Table 3). Interspecific differences in the response to land alteration were strong; this pattern can arise when different species have different species-specific needs, and when these differences drive the differential responses of the species to habitat alteration (Tocher et al., 2002; Ficetola et al., 2007).

Our study focused mostly on calling males. This allowed us to obtain reliable abundance estimates also for arboreal species living in the canopy (e.g., *E. diastema*, *C. granulosa*; Savage, 2002), which are difficult to study using other methods (Driscoll, 1998). Moreover, calling males during the breeding season suggest the presence of areas suitable for reproduction, especially for territorial species such as *Eleutherodactylus* and *H. rosenbergi*. Nevertheless, it should be noted that the presence of calling males does not always imply successful reproduction, especially for species with metapopulation dynamics (Sjogren, 1991). Further studies will be required to evaluate whether fitness is different among the areas where species are present (Neckel-Oliveira and Gascon, 2006; Todd and Rothermel,

2006; Ernst et al., 2007), but differences in density probably reflect differences in suitability for the various species.

Flooding did not have significant effects on amphibian distributions. Flooded areas were present all across the study area. Although the flooding extent strongly varied among transects, at least 5% of all transects were flooded. It is therefore possible that the high water availability in the study area reduced the preponderance of water as a limiting factor.

The gradient of forest alteration was the most important environmental variable influencing the distribution of anurans in the study area. Three forest specialists (*E. fitzingeri*, *E. diastema*, and *C. granulosa*) were most abundant in the least altered forest. Work on the habitat of these species is scarce, but studies on other species belonging to the genera *Eleutherodactylus* and *Cochranella* classified them as forest specialists (Pearman, 1997; Alzevedo-Ramos and Galatti, 2002). Nevertheless, individuals of these species (particularly *E. fitzingeri*) have been observed also in secondary forest or pasture (Table 1b; see also Ficetola et al. 2008). Other studies found that several primary-forest species are able to survive also in the most altered landscapes (Tocher et al. 2002; Hillers et al. 2008). Even though some primary-forest species can be observed also in altered areas, the clear gradient and the strong differences among communities (Figs. 1, 2) confirm the suitability of some amphibians as indicators of degradation of tropical rainforests (Hillers et al. 2008).

Conversely, three species (*L. labialis*, *H. rosenbergi*, and *H. microcephala*) were strongly associated with the pasture areas where livestock was present. These species often breed in wetlands within open areas, and are probably well adapted to more open areas (Savage, 2002). Studies analyzing the effects of deforestation and fragmentation on community structure have shown that matrix-tolerant species are the ones more likely to survive in fragmented landscapes, and are therefore the most resistant to forest alteration (Laurance, 2008). However, it should be noted that livestock presence was the variable with the strongest independent effect on the abundance of these species (Table 4). The relationship between livestock presence and these species cannot therefore be explained simply by their association with open areas. Livestock tracks create small pools that can be used as breeding sites by anurans breeding in wetlands (Hobel, 1999); this increase in microhabitat heterogeneity can therefore have positive effects for some species. Though we did not directly observe deposition, we found several unidentified egg masses laid within livestock tracks, confirming the importance of these areas for some amphibians.

This study shows how complex the relationships between landscape alteration and community structure can be. In addition to the direct negative effect of deforestation, which causes the loss of forest specialists (Tocher et al., 2002), forest alteration can also have indirect effects with profound consequences for the structure of the whole community: most of the variation in community structure was indeed explained by the joint effect of forest alteration and livestock presence (Fig. 3). Deforestation produces a more open landscape, and generalist species can take advantage of these conditions and quickly colonize the most altered

areas and the secondary forest (Tocher et al., 2002), where they can become much more abundant than the forest species. Moreover, the presence of livestock in the deforested areas can create novel environmental features, such as small pools in livestock tracks. Species that are able to exploit the environmental features associated with these areas shaped by human activities will become dominant in the new communities.

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