Does selective wood exploitation affect amphibian diversity? The case of An'Ala, a tropical rainforest in eastern Madagascar

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Abstract The diversity of amphibians before and after low-level forest exploitation in An'Ala forest in central-eastern Madagascar was compared over the course of 4 years. Neither abundance nor diversity of amphibians generally were significantly affected by low-level selective logging, although the abundance of individual species differed. Mantelline anurans were the most sensitive, in contrast to the tree frogs of the subfamily Boophinae (Mantellidae) and Cophylinae (Microhylidae). The abundance of Mantellinae anurans decreased by 15.8% after logging, whereas Boophinae and Microhylidae anurans increased by 12.1% and 3.7%, respectively. In general, species strongly tied to rainforest habitat showed a non-significant 10.1% decrease in abundance after logging. It appears therefore that amphibians are relatively resilient to a low-level of forest exploitation and their diversity is apparently not affected, at least in the short-term. This and other studies have, however, shown that logging commonly results in a shift in species composition, with species typical of pristine rainforests being replaced by species adapted to secondary habitats.

Keywords Amphibian, Boophinae, Cophylinae, diversity, Mantellinae, rainforest, selective wood exploitation.

Introduction

Tropical rainforests worldwide are cleared and exploited for many reasons, and trees are often felled selectively, especially if the aim is to remove the most valuable timber rather than clear felling for pasture and/or crop fields. Such felling produces diffuse disturbance, but even relatively low levels of anthropogenic (e.g. harvest) pressure leads to damage. Below a certain threshold of disturbance a forest can regenerate, although it can take many centuries for an exploited tropical rainforest to attain climax following disturbance (Terborgh, 1992).

The natural vegetation of eastern Madagascar is tropical rainforest (Nicoll & Langrand, 1989) and the country is one of the areas of the world where deforestation has been particularly severe. It is generally agreed that only *c.* 11% of the original forest cover remains (Benstead *et al.*, 2000) and information about the effects of deforestation upon natural animal communities is urgently needed.

Despite the existence of 16 protected areas in the eastern rainforests (ANGAP, 2001), the vast majority of the remaining natural vegetation does not have legal protection. The region around Andasibe, including the Special Nature Reserve of Analamazaotra and the National Park of Mantadia, has been identified as a key area for maintaining habitat continuity and biodiversity within the eastern region (Lees, 1996). However, conservation management in the region faces numerous problems and often does not integrate natural habitats outside protected areas (Dolch, 2004). One of these natural habitats is the forest of An'Ala (also known as Forêt de Sity) to the east of Andasibe.

From 1995 to 1997 zoological inventories were conducted in the forest of An'Ala (literally meaning 'the forest' in Malagasy) and several nearby habitats to evaluate the consequences of human activities on amphibians (Vallan, 2002). For many years local communities have undertaken low-level exploitation of the An'Ala forest for hunting, cattle pasture and timber extraction. During 1995–1997 the forest was being exploited at a low level for timber, with only traces of a few trees felled during previous years visible, and forest habitat in the valley was more or less intact. A subsequent visit in 1999 indicated that timber exploitation had increased considerably, with sizeable gaps from the felling of large trees. Resting places for woodcutters, where logs are cut into planks, had been established in the valley, and the

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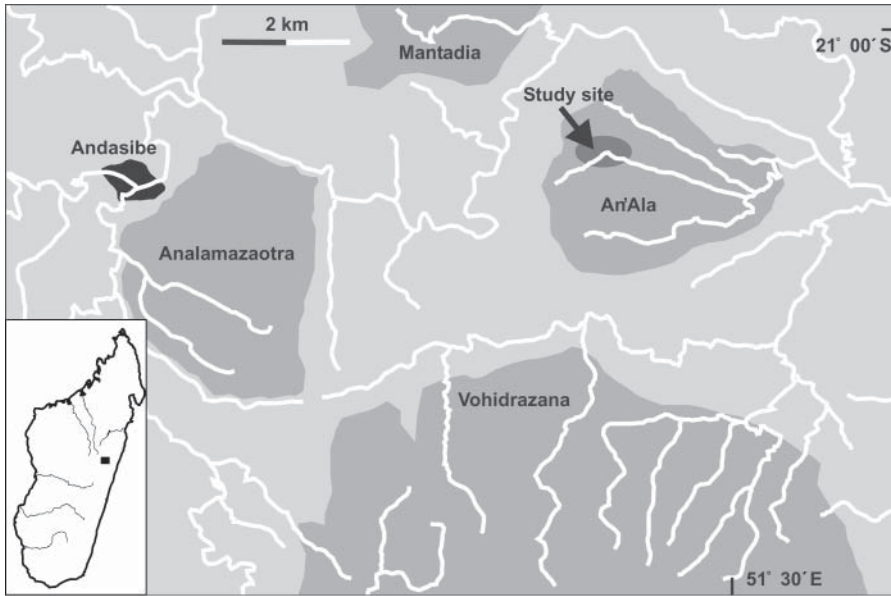
Fig. 1 Location of the forests of Andasibe and An'Ala. Based upon an FTM (Foiben-Taosarintanin'i Madagascar/Institut Géographique et Hydrographique National) map and aerial photographs. Dark grey: rainforest; light grey: man-made landscape; white lines: rivers and streams.

network of trails used by farmers, woodcutters and cattle had increased. The anthropogenic pressure was, however, still low and <10 trees per ha had been felled.

Anthropogenic habitat alteration (degradation or fragmentation) can have a strong negative influence on both tropical and temperate amphibian communities (Demaynadier & Hunter, 1998; Vallan, 2000, 2002; Krishnamurthy, 2003). Other studies have, however, shown a low or even positive influence on amphibian diversity, mainly if the disturbance level is relatively low (Lemckert, 1999; de Lima & Gascon, 1999; Vonesh, 2001), with the most adaptable taxa, the generalists, benefiting (Pearman, 1997). These species, able to live in both pristine and degraded habitats, have better chances of reproduction in a degraded environment than specialist species that are strongly tied to a pristine habitat. In this context, anthropogenic disturbance may lead to biotic homogenization (McKinney & Lockwood, 1999), with only a few species surviving and spreading. These apparently contradictory results illustrate the need for further studies to elucidate how anthropogenic activities such as logging affect amphibian guilds and species.

Taking advantage of the results of an earlier research project on amphibian diversity at An'Ala prior to forest disturbance (Vallan, 2002), we repeated data collection using the same methods and at the same site after selective logging had occurred. Our aim was to examine the influence of low levels of timber exploitation on amphibian diversity and guilds. There have been several recent studies of the influence of logging on amphibians (e.g. Pearman, 1997; Demaynadier & Hunter, 1998; Lemckert, 1999; Vonesh, 2001), mostly based on the

simultaneous comparison of sites with different degrees of exploitation. In this study we had the opportunity to look at a single site before and after selective logging had taken place.

Study site

An'Ala is a *c.* 600 ha forest island located in central-eastern Madagascar (48°29′E, 18°55′S), *c.* 6 km east of Andasibe at an altitude of *c.* 900 m (Fig. 1). The region is located on the border between the eastern region and the highlands (Battistini & Richard-Vindard, 1972). The original vegetation is mid-altitude dense rainforest (Koechlin, 1972), which is characterized by a canopy layer in one stratum, with a lower tree height (20–25 m) and species diversity than in lowland formations. A large part of the original vegetation was cleared for slash-and-burn agriculture, rice fields, *Eucalyptus* plantations and firewood harvesting. Two larger rainforest fragments (Mantadia and Vohidrazana) of several thousand ha and many small forest islands of <1000 ha remain in this region.

The An'Ala forest stretches along a valley open to the east. *Eucalyptus* plantations, degraded secondary vegetation, roads and railways constitute the borders of this forest. The study site lies in a valley where a small, slow running brook forms a network of small ponds and extensive swamps. The predominant plants in the valley are screw pine (*Pandanus* sp.). Valuable woods such as varongy (*Ocotea* sp.) and Madagascar rosewood (*Dalbergia* sp.) are found mainly on the slopes. Species present in the secondary vegetation, mainly introduced guava (*Psidium* sp.), shrub verbena *Lantana camara* and

Ceylon blackberry *Rubus moluccans*, penetrate into the forest following the gaps created by felled trees.

Mean monthly maximum temperatures are 20.2–27.5°C between November and March, and 9.8–16.0°C from June to September (data from the meteorological station of the Réserve Spéciale d'Analamazaotra, near Andasibe, for 1985–1994). The mean annual precipitation is 1,680 mm, falling over 163 days of the year on average, with a peak from December to February.

Methods

Data were collected using the visual encounter survey method described by Crump & Scott (1994). Special attention was paid to amphibian biotopes (Zimmerman & Simberloff, 1996) such as tree holes, *Pandanus* leaf axils and places in streams and swamps suitable for spawning. Searches for amphibians were carried out both during the day and at night, with headlamps and torches used at night. Data were collected exclusively in the rainy season (15 January–11 April 1997 and 17–23 March 2001). To ensure that most of the species present in An'Ala were located, the search continued until the species accumulation curve reached a plateau (Fig. 2). In 1997 and 2001 a total of 55.9 and 75.3 man-hours searching, respectively, were carried out by the same three people.

Single animals that could not be identified in the field were euthanized with injection of chlorobutanol, fixed in 90% and preserved in 70% ethanol. We collected specimens only if absolutely necessary. Voucher specimens are held at the University of Antananarivo (Madagascar), and the Natural History Museum of Berne (Switzerland). Frog calls were recorded for subsequent analysis. In cases where the presence of a species at a study site was only identified by its call, the species was registered as a single individual.

Not all amphibian species found in An'Ala are strongly tied to pristine habitat. Data from Vallan (2002), who analysed amphibian diversity in rainforest,

Eucalyptus plantations, rice fields and secondary vegetation in the region of Andasibe, were used to classify species preferences. If a species was found in one habitat in >95% of cases, this was defined as its preferred habitat. If no habitat reached the 95% level then all habitats in which the species was found in >5% of all cases were considered as the assemblage of its habitats. Accordingly, two classes were established: (1) species strongly tied to rainforest habitat (rainforest specialists), and (2) species occurring in both rainforest and secondary habitats (generalists).

To test the abundance of individuals in different families, subfamilies and species, the observed values were tested against the expected values by a χ^2 test, with Yates correction where necessary. The expected values after logging (in 2001) are calculated as $n_e = n_b \, T_a \, / \, T_b$, where n_b is the observed number of individuals before logging (in 1997) of each family or subfamily, T_a is the search time after logging and T_b is the search time before logging.

To quantify the effect of habitat change on the vertical distribution of animals, three strata classes were used: class 1, terrestrial; class 2, up to 50 cm above ground; and class 3, >50 cm above ground. For species where one to two thirds of all individuals found belonged to class 1 and 2 or 2 and 3 they where classified as intermediate between arboreal and terrestrial (semi-arboreal). Statistical analysis of diversity were performed using the software BIODIV (Baev & Penev, 1995). To test differences between diversities, measured with the Shannon Index (H'), the Hutcheson test (Magurran, 1988) was used. To calculate the expected number of species for a given number of individuals found the rarefaction method was used (Krebs, 1989).

For analyses of taxonomic composition the Mantellidae subfamilies Boophinae and Laliostominae were pooled (for taxonomy see Vences & Glaw, 2001) as they are closely related and only two individuals of one species of the latter family were observed during the study.
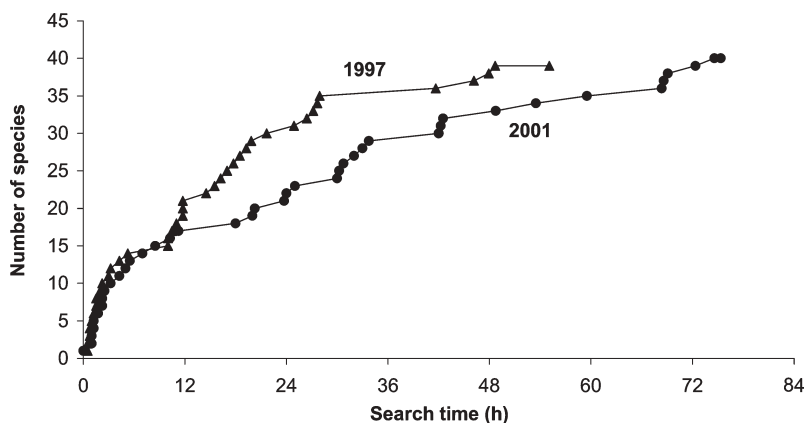

Fig. 2 Species accumulation curve for time spent searching, for the period before (1997) and after (2001) logging.

Table 1 Percentage of the 51 anuran species found in the rainforest of An'Ala before (39 species, 251 individuals) and after (40 species, 238 individuals) low-level selective logging, with the habitat preference and vertical distribution of each species.

Species (by Family & Subfamily)	% before low-level logging (1997)	% after low-level logging (2001)	Habitat perference[1]	Vertical distribution[2]
Mantellidae, Mantellinae				
Mantidactylus aerumnalis	2.4	5.0	F	T
Mantidactylus albofrenatus	4.0	2.5	F	T
Mantidactylus opiparis	0.8	4.2	FS	T
Mantidactylus femoralis	14.3	8.8	FS	T
Mantidactylus mocquardi	2.4	5.0	FS	T
Mantidactylus zolitschka	0.8	1.3	F	T
Mantidactylus grandidieri	0.4	0.0	F	A
Mantidactylus betsileanus	12.0	4.6	FS	T
Mantidactylus biporus	5.6	1.7	F	T
Mantidactylus tricinctus	4.8	3.4	F	T
Mantidactylus boulengeri	0.4	2.1	FS	S
Mantidactylus eiselti	0.0	0.4	FS	T
Mantidactylus luteus	0.8	0.4	F	A
Mantidactylus cornutus	0.8	0.0	F	A
Mantidactylus redimitus	4.0	2.1	F	A
Mantidactylus aglavei	1.2	1.3	F	A
Mantidactylus argenteus	8.4	8.8	F	A
Mantidactylus blommersae	3.2	0.0	FS	T
Mantidactylus grandisonae	0.4	0.4	F	T
Mantidactylus liber	8.8	8.0	FS	A
Mantidactylus depressiceps	0.0	0.8	FS	A
Mantidactylus kathrinae	0.4	0.4	F	A
Mantidactylus bicalcaratus	1.2	0.0	FS	A
Mantidactylus flavobrunneus	1.2	0.0	F	A
Mantidactylus pulcher	0.4	2.1	F	A
Mantella baroni	0.8	0.4	F	T
Mantella pulchra	1.2	0.8	F	T
Mantellidae, Laliostominae				
Aglyptodactylus madagascariensis	0.0	0.8	FS	T
Mantellidae, Boophinae				
Boophis luteus	0.0	0.4	FS	A
Boophis rappiodes	1.2	0.0	FS	A
Boophis tasymena	0.8	0.0	F	A
Boophis pyrrhus	2.0	6.7	FS	A
Boophis marojezensis	0.8	2.9	F	A
Boophis picturatus	2.4	0.8	F	A
Boophis boehmei	0.0	0.4	F	A
Boophis goudoti	0.0	0.4	FS	S
Boophis madacascariensis	1.6	1.3	FS	A
Boophis reticulatus	4.0	6.7	F	A
Boophis rufioculis	0.0	4.6	F	A
Boophis lichenoides	0.4	0.0	F	A
Microhylidae, Scaphiophryninae				
Paradoxophyla palmata	0.4	0.0	F	T
Microhylidae, Cophylinae				
Plethodontohyla inguinalis	0.4	0.4	FS	T
Plethodontohyla alluaudi	0.0	0.8	F	T
Plethodontohyla mihanika	0.0	0.8	FS	T
Stumpffia tetradactyla	0.4	0.0	F	T
Stumpffia cf. *roseifemoralis*	0.0	0.4	F	T
Stumpffia sp. A	0.4	0.0	FS	T
Platypelis barbouri	0.0	0.8	FS	A
Platypelis pollicaris	0.0	0.4	F	A
Platypelis tuberifera	3.6	5.0	F	A
Anodonthyla boulengeri	1.2	1.3	F	A

[1]After Glaw & Vences (1994) and Vallan (2002); F, rainforest; FS, rainforest and secondary habitats.
[2]T, terrestrial; A, arboreal; S, semi-arboreal.

Results

Although the tree felling in 1999 was at a low level the damage caused by falling trees left large gaps, but by 2001 these gaps were almost completely covered by heliophilous vegetation. The vegetation did not suffer additional damage from wood removal, as the trees were cut up *in situ* rather than being dragged out of the forest for processing. Planks were carried out without the help of machines or cattle.

Of the total 51 species found, a similar number of species was found before and after logging (39 vs 40) (Tables 1 & 2), and similarly diversity before and after logging was not significantly different (H′ = 3.09 vs H′ = 3.24). Using rarefaction analysis, with the number of individuals found in 1997 as the reference, <39 species should have been found after logging, close to the

40 species that were actually found (Table 2). However, amphibian abundance decreased significantly after logging from 4.49 to 3.16 individuals located per hour (Table 2). Details of species richness, diversity and abundance by family and subfamily are also given in Table 2.

The number of species found only in rainforest showed a non-significant 10% decrease after logging, and there was also no evidence that the abundance of rainforest specialist species decreased after logging (Table 3). Some species (*Mantidactylus betsileanus*, *M. blommersae*, *M. opiparis*, *M. albofrenatus*, *M. femoralis* and *M. mocquardi*), regarded by Vallan (2002) as a single species, probably form several species complexes (Glaw & Vences, 2002; Vences & Glaw, 2004), and were therefore omitted from this analysis.

Table 2 Observed number of species, expected number of species, diversity (Shannon Index, H′), number of individuals, search time and abundance per unit effort of anuran species found in the rainforest of An'Ala before and after low level selective logging, by Family and/or Subfamily. Figures in parentheses are percentages of the total at each time period (1997 and 2001).

	Mantellidae (Mantellinae)			Mantellidae (Boophinae & Laliostominae)			Microhylidae			Total		
	Before	After	Test	Before	After	Test	Before	After	Test	Before	After	Test
Observed number of species	25 (64.1)	22 (56.4)	$\chi^2 = 0.19$, $P > 0.05$	8 (20.5)	10 (25.6)	$\chi^2 = 0.22$, $P > 0.05$	6 (15.4)	8 (20.5)	$\chi^2 = 0.29$, $P > 0.05$	39	40	$\chi^2 = 0.01$, $P > 0.05$
Expected number of species*	25	23.5		8.17	10		6.67	8		39	38.5	
Diversity (H′)	2.66	2.70	T = 0.42 $P > 0.05$	1.88	1.85	T = 0.18 $P > 0.05$	1.33	1.62	T = 0.856 $P > 0.05$	3.09	3.24	T = 1.51 $P > 0.05$
Number of individuals	202 (80.5)	154 (61.4)		33 (13.1)	60 (23.9)		16 (6.4)	24 (9.6)		251	238	
Search time (h:m)	55:55	75:20		55:55	75:20		55:55	75:20		55:55	75:20	
Abundance (individuals h^{-1})	3.61	2.05	$\chi^2 = 16.24$, $P < 0.001$	0.59	0.80	$\chi^2 = 0.96$, $P > 0.05$	0.29	0.32	$\chi^2 = 0.04$, $P > 0.05$	4.49	3.16	$\chi^2 = 8.15$, $P < 0.005$

*Calculated using rarefaction method; the smaller number of species is the calculated expected value based on the larger sample (see text for details).

Table 3 Number and percentage (in parentheses) of anuran species and individuals occurring in rainforest and secondary vegetation or rainforest only and in three vertical strata in An'Ala before and after low level selective logging (see text for details), with χ^2 test for differences between habitats and vertical strata.

	Species			Number of individuals		
Habitat and vertical stratification	Before low-level logging	After low-level logging	χ^2 test	Before low-level logging	After low-level logging	χ^2 test
Rainforest and secondary vegetation species	8 (24.2)	12 (34.3)	0.83, P > 0.05	40 (25.2)	55 (30.9)	1.37, P > 0.05
Rainforest species	25 (75.8)	23 (65.7)		119 (74.8)	123 (69.1)	
Arboreal	21 (53.8)	20 (50.0)	0.05, P > 0.05	114 (45.4)	132 (55.5)	6.15, P < 0.05
Semi-arboreal*	1 (2.6)	2 (5.0)		1 (0.4)	6 (2.5)	
Terrestrial	17 (43.6)	18 (45.0)		136 (54.3)	100 (42.0)	

*For the χ^2 test this category was not considered.

A significant decrease in the number of terrestrial individuals located per unit effort was observed after logging, whereas the number of terrestrial species increased non-significantly following logging (Table 3). Because only a few semi-arboreal species and individuals were found, they were omitted for the χ^2 analysis (Table 3).

The selective logging did not significantly influence richness at the family or subfamily level. However, the abundance of Mantellinae decreased significantly after logging (Table 3).

Discussion

Amphibian populations at the An'Ala forest appeared to be resilient to low-level logging, as neither species richness nor species diversity of rainforest specialist species changed significantly following logging. The subfamily Mantellinae (genus *Mantidactylus*), which are known to be typical rainforest specialists (Andreone, 1994; Vallan, 2002; Andreone & Luiselli, 2003), were the predominant taxa in An'Ala both before and after logging. Several *Mantidactylus* species present in 1997 were not located in the post-logging surveys in 2001: *M. cornutus*, *M. grandidieri*, *M. bicalcaratus*, *M. blommersae,* and *M. flavobrunneus* (Table 1). With the exception of *M. bicalcaratus* and *M. blommersae*, these species are mainly restricted to rainforest habitat in the region of Andasibe. In other regions these species may also adapt to secondary and degraded habitats (F. Andreone, pers. obs.). The large and semi-aquatic *M. grandidieri*, which is usually an abundant species along forest streams, was not found after logging. We presume that its absence was a consequence of direct hunting, as this frog is actively targeted for food by local people (Andreone, 1999).

Various studies (Andreone, 1994; Vallan, 2000, 2002) have shown that species richness of the family Microhylidae decreases in fragmented habitats and in secondary vegetation. However, we found that neither microhylid species richness nor the number of microhylid individuals changed following logging, and this may be related to the climatic conditions in An'Ala (see below).

There were no changes in the richness of either terrestrial or arboreal amphibian species as a result of logging. However, after logging, significantly more individuals of arboreal species were found, and fewer individuals of terrestrial species. It is known that terrestrial species of the genus *Mantidactylus* are sensitive to habitat changes (Andreone, 1994; Vallan, 2000). The decrease in the number of *Mantidactylus* individuals after logging may be explained by the warmer and drier microclimate that results from the creation of forest gaps and other open areas during selective logging. Similar conclusions

regarding the decline of Mantellinae in habitats altered by human activity were reached by Vallan (2002).

The number of arboreal individuals increased after logging. Tree frogs are known to have a comparatively lower sensitivity to logging than terrestrial species (Andreone, 1994; Pearman *et al.*, 1995; Pearman, 1997; Lemckert, 1999; Andreone & Luiselli, 2003). The skin of arboreal frog species is probably less permeable than that of terrestrial species (Pough *et al.*, 1998). Furthermore, living in the upper layers of the forest, arboreal species are preadapted to climatic changes (higher temperature variations, wind, and exposure to the sun), and thus have an advantage compared with terrestrial amphibians, at least during the first phase of forest alteration.

Several studies have shown that amphibians respond in a variety of ways to logging (Pearman, 1997; Demaynadier & Hunter, 1998; Lemckert, 1999; Vonesh, 2001; Krishnamurthy, 2003). The diversity of some taxa or guilds increases in logged forests, in others it decreases. There are many factors influencing such reactions, with microclimate, vegetation type and presence of water being key factors for amphibian diversity and abundance. The present study does not provide any evidence that species of the family Microhylidae react to selective logging, although in regions with a more accentuated seasonal climate, Microhylidae occur only in rainforest patches of a certain size (Vallan, 2000). How an amphibian species or a guild reacts to disturbance depends not only on its characteristics but also on the local climate.

We did not find marked changes in amphibian diversity as a result of selective logging. However, diversity of all groups, with the exception of the Boophinae/ Laliostominae, tended to increase as logging continues (Table 2). Vonesh (2001) and Inger (1980) made similar observations of terrestrial amphibians in tropical Africa and Malaysia, and Lemckert (1999) found an increase in species diversity after logging in a subtropical Australian forest. These results indicate that disturbance such as logging positively influences the richness of amphibian species in the rainforest, at least in the short-term. Generalist and tree frog species react positively to logging (Lemckert, 1999). Two main questions arise: what happens in the long-term to specialized species, and what is the influence of different logging techniques? Traditional logging techniques, as adopted in An'Ala, lead to only moderate habitat disturbance. In contrast, the mechanized extraction of timber leads to significant damage in rainforests (Johns, 1988). If logging rate, and consequently forest disturbance, increases, or mechanized techniques are adopted, then the amphibian diversity also decreases (Vallan, 2002). Logging or other disturbances will seldom lead to a total loss of amphibian diversity. More commonly, as in this study, there is a

shift in species composition (Robins & Robins, 1999; Kalif *et al.*, 2001). Species typical of pristine rainforests (specialists) are therefore replaced by species adapted to secondary habitats (often generalists). Biological homogenization is the result (McKinny & Lockwood, 1999).

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