

Assessing the value of secondary forest for amphibians: *Eleutherodactylus* frogs in a gradient of forest alteration

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Abstract Secondary forests constitute a growing portion of forested areas worldwide. They might have a substantial role for the conservation of biodiversity in tropical areas, but there is little information on their potential to support forest species and the recovery of faunal communities. We studied two forest frogs (*Eleutherodactylus diastema* and *E. fitzingeri*) in an area of Costa Rica composed of a mosaic of primary forest, young secondary forest and pasture, and we compared the density of calling males in areas with different forest alteration. Autoregressive models were used to compensate for potentially undesired effects of spatial autocorrelation and pseudoreplication. Both species were most abundant in riparian, primary forest. However, *E. fitzingeri* was also abundant in riparian secondary forests, and its density far from the river was similar in primary and secondary forest, suggesting that river proximity can influence the recovery of secondary forest for amphibians. Conversely, the density of *E. diastema* was similar in secondary forest and pasture, stressing interspecific differences for recovery rate. These frogs have a keystone role in nutrient cycling and food webs, and their prompt recovery might represent an important step for the functional recovery of forests. Nevertheless, the strong interspecific differences stress the complexity of these processes.

Keywords Abundance · Amphibian conservation · Audio strip transects · Costa Rica · Deforestation · *Eleutherodactylus diastema* · *Eleutherodactylus fitzingeri* · Tropical forest

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Introduction

The loss of tropical forest is considered one of the most important causes of biodiversity loss at global scale (Wright and Muller-Landau 2006a). After deforestation, landscapes become a complex patchy mosaic composed of agricultural land and primary forest fragments. However, in recent years, some agricultural land has been abandoned, allowing the regrowth of natural vegetation. The outcome of this process is the growth of secondary forests, which are forests where the effects of past human activities on fauna or vegetation are still recognisable (Corlett 1994). Secondary forest covers >40% of forested areas worldwide (Brown and Lugo 1990; Wright and Muller-Landau 2006b), and recent projections predict that in the near future the majority of tropical forest will be secondary, particularly in Asia and the Americas (Wright and Muller-Landau 2006a). Secondary forests might therefore play a pivotal role for the conservation of tropical biodiversity, as suggested by studies showing that animal communities can recover after 20–40 years of natural regrowth (Lawton et al. 1998; Medellin and Equihua 1998; Dunn 2004; Quintero and Roslin 2005). Nevertheless, primary and secondary forest frequently have different species composition, and the time required for recovery probably varies among taxa (Dunn 2004; Lugo and Helmer 2004). To date, most work on the recovery of faunal communities has focused on insects and birds, while only 14% of datasets reviewed by Dunn (2004) analysed the response of non-flying vertebrates. Small mammals (excluding bats), reptiles and amphibians have less mobility than birds, and this might reduce their capacity for recolonization. Therefore, more study of these taxa is needed for better understanding of the recovery process and of the potential of secondary forest for biodiversity conservation.

Tropical forests constitute the habitat of most amphibian species, and deforestation is thus a major cause of amphibian decline (Stuart et al. 2004). Secondary forests might represent an important alternative habitat for amphibians, but their importance for tropical amphibians has only seldom been investigated (Heinen 1992; Neckel-Oliveira 2004; Ernst and Rödel 2005; Neckel-Oliveira and Gascon 2006). In this study, we investigated and compared the abundance of *Eleutherodactylus diastema* and *E. fitzingeri* in primary forest, secondary forest and pasture in an area of Costa Rica, and we evaluated whether secondary forest can be an alternative habitat for these forest frogs. Furthermore, we tested whether the recovery is different in riparian and non-riparian areas, because river proximity influences water availability and vegetation growth (Naiman et al. 2005). *Eleutherodactylus* is the most speciose genus of vertebrates, and these frogs are generally considered forest specialists (Pearman 1997). In neotropical forests, *Eleutherodactylus* frogs constitute a major portion of biomass (Stewart and Woolbright 1996) and have a primary role in ecosystem functioning, enhancing nutrient cycling, decomposition, and primary productivity through multiple interactions (Beard et al. 2002, 2003). Therefore, these frogs might have an important role in the regeneration and the dynamics of secondary forest. This issue may be particularly important in Costa Rica, where secondary forests already constitute a significant proportion of protected forests (Sanchez-Azofeifa et al. 2003).

Methods

Study species

Eleutherodactylus are direct developing frogs that are found throughout the Neotropics. This genus traditionally includes more than 600 species, but recent studies based on

molecular data showed that *Eleutherodactylus* is a paraphyletic taxon composed of several entities (Frost et al. 2006). Nevertheless, the sampling density of Frost et al. (2006) was small when compared to the diversity of this “genus” (about 2% of species), and the proposed taxonomic changes cannot be applied to most of species previously ascribed to *Eleutherodactylus* (Frost et al. 2006). For this reason, we preferred to apply the traditional nomenclature.

Eleutherodactylus diastema is a small frog (up to 24 mm snout-urostile length) living in lowland and premontane moist forest and rainforest, from Nicaragua to Western Ecuador (Savage 2002). It lives on trees, from 1.5 to 35 m above ground (Miyamoto 1982; Leenders 2001). During the wet season, males are territorial, have exclusive home ranges and emit species-specific calls from perching sites on trees or within bromeliads; eggs are frequently laid within bromeliads (Savage 2002). *Eleutherodactylus fitzingeri* is a larger species (up to 53 mm), which is widespread in lowland and premontane humid forests, from Honduras to Colombia. *Eleutherodactylus fitzingeri* can be particularly frequent in riparian areas and is more terrestrial than *E. diastema*; males call from perching sites up to 1.6 m above ground (Miyamoto 1982; Hobel 1999). Breeding probably occurs at the beginning of the wet season and eggs are laid in small nests on the ground (Hobel 1999; Mendoza-Quijano et al. 2002).

Study area

The *Humedale Terraba-Sierpe* (8°48' N, 84°24' W; S Costa Rica, Fig. 1) has a surface of about 30,000 ha, includes the drainages of the Terraba and Sierpe rivers, and it is recognised by the RAMSAR Convention as a wetland of international importance (Alvarez et al. 1999). Annual precipitation is 4,000–6,000 mm/year; average temperature is 24–27°C; the rainy season lasts from April to November. The altitude is 0–3 m, and part of the *Humedale* is constantly flooded and occupied by hygrophilous herbaceous vegetation. The soils that are only temporarily flooded were originally occupied by palm swamp forests, dominated by *Raphia taedigera* (Alvarez et al. 1999; Bravo 1999). In the 1970s, the primary palm swamp forest was partially cleared for pasture; to date, palm forest covers 41% of the *Humedale*. However, since the early 1990s, human population is decreasing, and secondary forest is growing in some areas that were previously pasture (Alvarez et al. 1999).

We studied an area of about 500 ha within the *Humedale*, at a distance of about 45 km from the Pacific Ocean (Fig. 1). Approximately 150 ha of this area are covered by primary palm forest, and constitute a Costa Rica's Private Wildlife Refugium (Langholz et al. 2000); about 33 ha are covered by secondary forest and 140 ha are exploited as pasture. The remaining areas consist of the Sierpe river and by almost permanently flooded areas (Fig. 1). Informal interviews with local people suggested that the secondary forest started growing after the pasture abandonment in 1992.

Permanently flooded areas were not investigated, since *Eleutherodactylus* frogs are terrestrial. We distinguished three main levels of forest alteration: (1) primary forest (no alteration); (2) young secondary forest (age: about 10 years); (3) pasture. Moreover, along the banks of the Sierpe river, the vegetation tends to be more dense, with a higher abundance of shrubs, bromeliads and lianas than in forested areas. We therefore distinguished between riparian (along the river banks) and non-riparian areas (>100 m from the river banks).

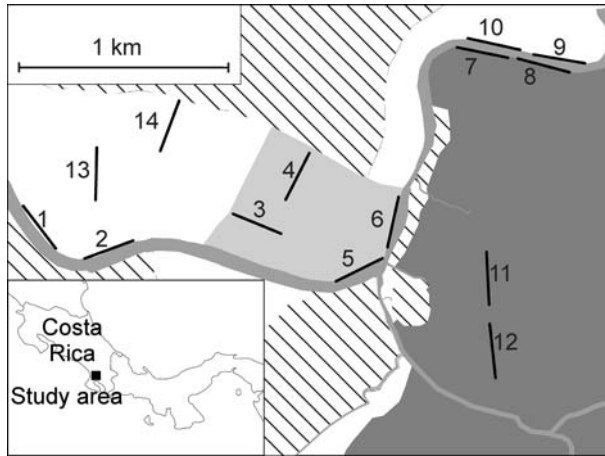


Fig. 1 Study area, and distribution of linear transects. Dark grey: primary forest; pale grey: secondary forest; white: pasture; shaded: flooded areas

Sampling protocol

To evaluate differences between secondary forest, primary forest and pasture we repeatedly monitored 14 linear transects; transect length was 200 m. Transects were selected on the basis of a stratified random sampling, but accessibility partially constrained the location of transects in primary forest. The distance between transects varied from 55 to 2150 m. The smallest distances were for transects on different sides of the Sierpe river. Six transects were located in pasture, four in secondary forest and four in primary forest (Fig. 1, Table 1). Therefore, we recognised six different combinations of forest alteration and distance from the river, giving to six different transect typologies replicated 2–4 times (Table 1). To confirm the structural differences of vegetation among the levels of forest alteration, we measured the canopy cover and the number large trees (trees with diameter >50 cm at 1.5 m above ground level) for each transect (Pearman 1997).

From 27 March to 29 April 2002 (beginning of the rainy season), we monitored the presence of *E. fitzingeri* and *E. diastema* calling males using audio strip transects (Zimmerman 1994), on the basis of species-specific vocalizations (Leenders 2001; Savage 2002); we repeated each transect 8–10 times. The average time interval between sampling of particular transects was 3.4 days (SE = 0.3). The identification of calling males was confirmed by the morphological examination of several males of both species. This technique gives a good estimate of population size for territorial frogs (Driscoll 1998). Capture-mark-recapture techniques might allow to obtain better estimates of densities for species living on the ground (Funk et al. 2003), but the capture of individuals on trees is generally impossible, and it is therefore difficult to apply capture–recapture to arboreal species. Transect surveys were performed after dusk, between 16.45 and 20.45, when calling activity is high (Savage 2002). Every day, we randomly selected the transects to be surveyed; we surveyed 2–7 transects per day, depending on their accessibility. For each transect, the calling males were counted in 10 consecutive point counts at a distance of 20 m apart; each point count lasted 1 min (Zimmerman 1994), therefore, during each transect listening lasted 10 min. The males of both species are territorial and usually well spaced (Hobel 1999; Savage 2002). It was generally possible to estimate the approximate location of perching sites, therefore we are confident that each male was counted

Table 1 Detection distance of calling males in two *Eleutherodactylus* frogs in 14 audio transects, and surface monitored in each transect

Transect	Typology	Detection distance (mean \pm SD)		Surface monitored (ha)	
		<i>E. diastema</i>	<i>E. fitzingeri</i>	<i>E. diastema</i>	<i>E. fitzingeri</i>
1	Pasture, riparian (A)	93 \pm 5	83 \pm 5	1.86	1.66
2	Pasture, riparian (A)	93 \pm 5	83 \pm 5	1.86	1.66
3	Secondary forest, not riparian (B)	53 \pm 5	52 \pm 8	2.12	2.08
4	Secondary forest, not riparian (C)	105 \pm 8	83 \pm 10	4.2	3.32
5	Secondary forest, riparian (D)	18 \pm 3	15 \pm 3	0.36	0.3
6	Secondary forest, riparian (D)	18 \pm 3	15 \pm 3	0.36	0.3
7	Primary forest, riparian (E)	20 \pm 3	14 \pm 4	0.4	0.28
8	Primary forest, riparian (E)	20 \pm 3	14 \pm 4	0.4	0.28
9	Pasture, riparian (A)	93 \pm 5	83 \pm 5	1.86	1.66
10	Pasture, riparian (A)	93 \pm 5	83 \pm 5	1.86	1.66
11	Primary forest, not riparian (F)	50 \pm 6	43 \pm 5	2	1.72
12	Primary forest, not riparian (F)	50 \pm 6	43 \pm 5	2	1.72
13	Pasture, not riparian (G)	103 \pm 5	93 \pm 8	4.12	3.72
14	Pasture, not riparian (G)	103 \pm 5	93 \pm 8	4.12	3.72

For transects with the same letter, the same average detection distance was used

only once. In riparian areas, we counted males on only one side of the transect, while for non-riparian transects we counted males on both sides.

To calibrate the transect strip width, prior to starting the sampling, we measured the maximum distance at which calling frogs could no longer be heard clearly (detection distance), by moving away from males calling from perching sites at a known position. We measured the detection distance for six different males per each species to obtain mean detection distances. Sound transmission and thus detection distances can vary with vegetation structure, therefore mean detection distance was determined for each transect typology (Zimmerman 1994). On the basis of detection distances, we calculated the area covered by each transect (Table 1); calling male density per transect was equal to average number of calling males/covered area. The same observers performed all the transect surveys and all the detection distance estimates together.

Data analysis

Univariate ANOVAs followed by Tukey's post hoc tests were used to evaluate the effect of distance from river and forest alteration on the average density of *E. diastema* and *E. fitzingeri*. Distance from river was a two-level factor (riparian/not riparian), while forest alteration was a three level factor (pasture/secondary forest/primary forest). The density of species in each transect, averaged over the times it was monitored (individuals/ha per transect), was used as a dependent variable.

Due to logistical constraints, transects in the same environment were closer than expected by chance; in particular the transects in primary and secondary forest were performed in the

same forest patch and were sometimes in close proximity. This violates the assumptions of independence of ANOVA and leads to a partially pseudoreplicated design, mainly due to the spatial autocorrelation (Hurlbert 1984; Lichstein et al. 2002; Segurado et al. 2006). Therefore, we used spatial simultaneous autoregressive lag model estimation (LagSAR) to perform linear models after taking into account the spatial dependence of data. LagSAR includes a maximum likelihood estimation of the spatial autoregressive coefficient ρ in linear models. These models are therefore suitable when spatial distribution of observations violates the assumptions of independence of observations (Anselin 2001). We used the UTM coordinates of the midpoint of each transect for the Lag estimate and the likelihood ratio test to evaluate the significance of factors.

LagSAR analyses were performed using `spdep` 0.3–12 (Bivand 2005); all statistical analyses were performed under the R 2.2 environment (R Development Core Team 2005). The residuals of all models were normally distributed (Kolmogorov–Smirnov test, all $P > 0.4$).

Results

Canopy cover and the number of large trees were significantly different among transect typologies (ANOVA: canopy cover, $F_{2,8} = 17.989$, $P < 0.001$; number of large trees, $F_{2,8} = 27.318$, $P < 0.001$). Primary forest had higher canopy cover and more large trees than pasture (Tukey's test, both $P < 0.001$). The canopy cover in secondary forest was higher than in pasture ($P = 0.014$), and not significantly different from primary forest ($P = 0.11$). Conversely, the number of large trees in secondary forest was much lower than in primary forest ($P < 0.001$) and similar to pasture ($P = 0.76$). These results confirm our a priori classification of transects. Secondary forest was clearly distinct from pasture but still different from primary forest; its canopy cover was high, but the forest was composed of young trees.

Both species were detected at least once in each transect. Maximum values of detection distance were recorded in non-riparian pasture and secondary forest (about 100 m for *E. diastema*), while the minimal values were recorded in riparian primary and secondary forest (about 15 m for *E. fitzingeri*). Detection distance tended to be shorter for *E. fitzingeri* through all environments (Table 1).

For *E. diastema*, we observed the highest density in riparian primary forest (up to 80 calling males/ha), while density in pasture and secondary forests was lower (5 males/ha or less) (Fig. 2a). Maximum density of *E. fitzingeri* (28 males/ha) was observed in riparian primary forest too, but density in riparian areas of secondary forest (up to 12 males/ha) was larger than that observed in non-riparian primary forest (about 3 males/ha) (Fig. 2b). For both species, the lowest average density (less than 0.1 males/ha) was observed in non-riparian transects located in pasture (transects 13–14). In these areas, frogs called on the ground or from the few, isolated trees still present.

The results of both traditional ANOVAs and of spatial autoregressive models were similar. Distance from river, forest alteration and their interaction had significant effects on the distribution of both species (Table 2, Fig. 2). For *E. diastema*, average density for riparian transects was larger than that in non-riparian transects. Furthermore, transects in primary forest had higher *E. diastema* density than those in both secondary forest and pasture (Tukey's test: both $P < 0.001$). Conversely, density was not significantly different between secondary forest and pasture ($P = 0.627$). The significant interaction between forest

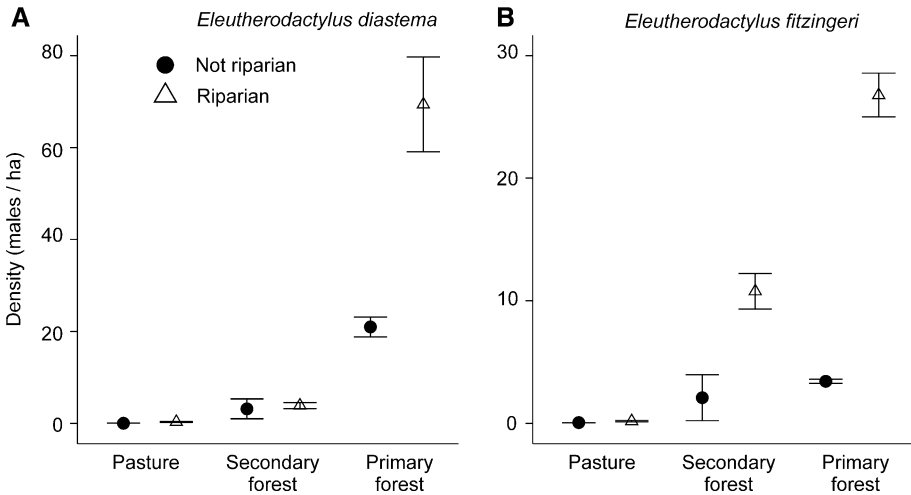


Fig. 2 Average density of (A) *E. diastema* and (B) *E. fitzingeri* in linear transects located in a gradient of forest alteration and at different distances from the river. Error bars represent standard errors

Table 2 Effects of forest alteration and distance from river on the density of calling males of two *Eleutherodactylus* frogs

Dependent	Factor	ANOVA			LagSAR linear model ^a		
		<i>F</i>	df	<i>P</i>	χ^2	df	<i>P</i>
<i>E. diastema</i>	Forest alteration	100.43	2,8	<0.0001	20.04	2	<0.0001
	Distance from river	25.29	1,8	0.001	4.87	1	0.027
	Forest × Distance	27.67	2,8	0.0003	28.81	2	<0.0001
<i>E. fitzingeri</i>	Forest alteration	229.68	2,8	<0.0001	16.90	2	0.0002
	Distance from river	219.85	1,8	<0.0001	10.68	1	0.001
	Forest × Distance	109.51	2,8	<0.0001	50.79	2	<0.0001

Results obtained using traditional ANOVA models and of Lag spatial autoregressive linear models

^a Likelihood ratio test

alteration and distance from the river shows that riparian areas only support higher densities in primary forest (Fig. 2a).

Riparian transects in secondary and primary forest also supported the highest density of *E. fitzingeri*. Its density in primary forest was higher than in both secondary forest and pasture (Tukey’s test: both $P < 0.001$), but for this species secondary forest supported higher density than pasture ($P < 0.001$), and non-riparian primary and secondary forest supported similar densities. The significant interaction between forest alteration and distance from river shows that the differences in density of *E. fitzingeri* between riparian and non-riparian transects are larger in primary forest and secondary forest than in pasture (Fig. 2b).

Discussion

We found strong differences in the density of *Eleutherodactylus* frogs among areas having different degrees of forest alteration and distance from river. The density in secondary forest was lower than in primary forest, but the significant effect of interaction between forest

alteration and distance from the river on frog density suggests that proximity to river can influence the habitat suitability for these species. Riparian areas host the largest densities, and forests with flowing water can be a better habitat for these frogs than forests without rivers. Moreover, the two species showed distinct responses to combinations of forest alteration and distance to river. *Eleutherodactylus diastema* was abundant in primary forest, while in secondary forest this frog was scarce and found at densities not significantly different than in pasture. Conversely, in the riparian areas of secondary forest *E. fitzingeri* was more abundant than in the non-riparian areas of primary forest (Fig. 2). This confirms that interspecific differences in the recovery of populations can be strong, even among closely related taxa (Dunn 2004; Lugo and Helmer 2004). The relatively high density of *E. fitzingeri* in riparian secondary forest suggests a recovery of this species in secondary forest 10 years after the abandonment of pasture. These areas might quickly become an alternative habitat for *E. fitzingeri*, which can lay eggs also on the ground and may take advantage of the dense, low vegetation close to the river banks. Moreover, the significant interaction effect between forest alteration and distance from river suggests that location of secondary forest (i.e., close or far from the river banks) can influence its recovery rate. Several factors might increase the recovery of riparian areas, such as higher water availability and lower disturbance by human activities, as they should promote faster vegetation growth.

The secondary forest investigated in our study is not directly connected to primary forest, but is isolated by pasture, flooded areas and the Sierpe River. This river separates secondary and primary forest, is about 50 m wide, and probably constitutes an effective barrier to the dispersal of terrestrial frogs (see Lampert et al. 2003), suggesting that the males recorded in the secondary forest are not transient individuals. However, we measured the density of calling males, and not reproductive success. In more disturbed areas fitness may be lower, and differences between primary and secondary forest might be magnified (e.g., Neckel-Oliveira 2004; Junca and Rodrigues 2006; Neckel-Oliveira and Gascon 2006; Ernst et al. 2007). Further studies are required to evaluate not only differences in density, but also in turnover, survival and reproductive success among habitats (Neckel-Oliveira 2004; Neckel-Oliveira and Gascon 2006; Todd and Rothermel 2006; Ernst et al. 2007).

Rapid recovery by some *Eleutherodactylus* frog might be considered good news for recovery of secondary forest. Firstly, the metabolism of these species promotes nutrient availability for plants, increases foliage development and primary productivity, and accelerates decomposition (Beard et al. 2002, 2003). Moreover, these frogs have a central role in tropical food webs, may regulate the density of invertebrates and are prey for larger vertebrates (Stewart and Woolbright 1996; Beard et al. 2003). Therefore, their presence constitutes an important step toward the functional reconstitution of ecological networks during forest regeneration.

It might be argued that the differences in density could be a consequence of differences in detection distances among transects. Higher densities were observed for the transects with short detection distances (riparian primary forest), suggesting the possibility that the lower observed densities in pasture or in non-riparian transects were caused by an higher detection failure in the broader transects. However, detection distances in primary and secondary forest were very similar (Table 1), but the frog densities differed (Fig. 2). Moreover, density varied among transects over 2–3 orders of magnitude, and can hardly be explained by differences in operative detection distances of less than one order of magnitude.

Due to logistical constraints, the number of transects was quite small, and in some instances transect pairs were close to each other. For example, four riparian transects (transects 7–10) were in close proximity (Fig. 1). It is therefore possible that factors other than those considered influenced frog distribution. However, riparian transects had higher

densities also in secondary forest, and were located far from transects 7–10. Moreover, ANOVA and LagSAR provided nearly identical results. These considerations support the robustness of our conclusions.

The significance of ANOVA was generally stronger than that of LagSAR, probably because the ANOVA overestimates the significance in presence of strong spatial structure of the data, a commonly observed effect of pseudoreplication (Hurlbert 1984). In tropical areas, logistical constraints and problematic accessibility frequently reduce the possibility of a balanced design and of the selection of truly independent sampling points. The application of models incorporating the spatial structure of the data is still rare in ecological studies (Lichstein et al. 2002; Wagner and Fortin 2005; Piorecky and Prescott 2006), but can compensate for the undesired effects of spatial pseudoreplication (Segurado et al. 2006) and can therefore help increasing the robustness of analyses in studies performed in partially inaccessible areas (Ficetola 2007).

In his review of studies on recovery of secondary forest, Dunn (2004) concluded that a few decades can be sufficient for recovery of faunal communities after deforestation, but that some species can be particularly sensitive and might require a longer period of time. Our results are in agreement with these conclusions: one species (*E. fitzingeri*) was quite abundant in some areas of young secondary forest, while *E. diastema* probably needs a longer period to recover. In the absence of information on all species, “surrogate” and “substitute” species are sometimes used for planning conservation efforts, on the assumption that targeting the few species for which data are available will benefit other species sharing similar requirements, and possibly the whole community (Caro and O’Doherty 1999; Caro et al. 2005). This approach might be particularly important for tropical areas, where information only exists for a small fraction of the biodiversity. However, when closely related species show very different responses to environmental modification, the usefulness of surrogates may be lost (e.g., Lawton et al. 1998; Caro et al. 2005; Denoël and Ficetola 2007), and this can be particularly true in areas subjected to strong human disturbance (Lawton et al. 1998; Anand et al. 2005; Ficetola et al. 2007). This poses a formidable challenge to the study of recovery of secondary forest. Strong interspecific differences make it very difficult to predict the response of taxa that are not directly studied, but unfortunately the monitoring of the whole of biodiversity is not feasible for practical and economical reasons (Lawton et al. 1998). Therefore, the response to questions such as “what is the importance of secondary forest for the conservation of biodiversity”, or “how old does a secondary forest need to be before it recovers its function” can be influenced by which taxa are the focus of the study. Targeting keystone species (such as *Eleutherodactylus* frogs) or species threatened by extinction can be an option, but we should always be aware that the complexity of these systems precludes broad generalizations. Finally, geographic factors such as the presence of flowing water can strongly influence the recovery rate, and these differences should be considered in the analysis of secondary forests.

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