# Recovery of amphibian species richness and composition in a chronosequence of secondary forests, northeastern Costa Rica

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## ABSTRACT

In some tropical regions, following the abandonment of agriculture and pastures, secondary forests can recover plant species richness and forest structure (e.g. canopy cover, biomass); however, the importance of these secondary forests for fauna is not clear. Secondary forests can benefit fauna by providing suitable habitats, connecting forests fragments, and increasing gene flow. Previous studies of forest regeneration have showed different levels of amphibian recovery. In Puerto Rico, 1–5 years old secondary forests achieved similar amphibian species richness and composition in comparison with old-growth forests, while in Brazil secondary forests from 14 to 19 years of recovery only recovered 60% of the species of old-growth forests. We evaluated amphibian recovery in secondary forests in northeastern Costa Rica, by assessing amphibian recovery in 12 secondary forests that vary in age of recovery and in three old-growth forests using visual and acoustic surveys. Our sites varied in terms of their landscape (e.g. amount of surrounding forest) and forest characteristics (e.g. forest age, aboveground biomass, basal area, number of tree species, number of stems, leaf-litter depth), but there was no relationship between these characteristics and amphibian species richness or species composition. We found that amphibians are recovering rapidly in secondary forests in Costa Rica, and even young forests (10–16 years) had similar species richness and composition in comparison with old-growth forests. These forests are providing suitable microhabitats conditions for amphibians. In addition, this study highlights the importance of landscape characteristics. The abundance of amphibian species sources (e.g. forest patches) and connections between forests appear to be helping the species colonize these sites. Worldwide, the area of secondary forests is increasing, and our results show that these habitats are suitable for a diversity of amphibian species, suggesting that these forests can help reduce amphibian population and species decline.

## 1. Introduction

Species richness and structure (e.g. canopy cover, biomass) of tropical forests can recover from different human activities such as deforestation, agriculture or pasture in 20–40 years (Aide et al., 2000; Janzen, 2002; Letcher and Chazdon, 2009). In some tropical regions the rates of deforestation are decreasing and the rates of reforestation are increasing (Aide and Grau, 2004; Rudel et al., 2005). For example, in Dominican Republic and Puerto Rico secondary forests have emerged from abandoned agriculture lands (Rivera et al., 2000; Grau et al., 2003, 2007; Lugo and Helmer, 2004). Secondary forests have also emerged from abandoned pastures for cattle in Puerto Rico, Dominican Republic and Costa

Rica (Aide et al., 1996; Rivera et al., 2000; Janzen, 2002); and there are examples of forests recovery from forest plantations (Mayaux et al., 2005), and following slash and burn agriculture (Rudel et al., 2005) in other neotropical ecosystems. Most of this recovery has occurred due to changes in socioeconomic patterns that involve rural–urban migration, increasing industrialization, and modern agriculture practices (Aide and Grau, 2004; Wright and Muller-Landau, 2006). These secondary forests can be important reservoirs for mature forest plant species (Wright and Muller-Landau, 2006; Chazdon et al., 2009), although their value for fauna is still poorly understood (Dunn, 2004; Gardner et al., 2007).

Secondary forests can benefit fauna by providing suitable habitats (Faria et al., 2009), connecting forests fragments (Faria, 2006), and increasing gene flow (Pardini et al., 2005). For example, secondary forests from 25 to 30 years old have similar ant species composition in comparison with 60 years old secondary forests in Puerto Rico, because they provide similar microhabitats (Osorio-Pérez et al., 2007). Similarly, the diversity, abundance and trophic structure of amphibians and reptiles increased as forest complexity and

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microclimate diversity increased during secondary succession (Heinen, 1992; Williams et al., 2002; Gardner et al., 2007; Ríos-López and Aide, 2007; Ficetola et al., 2008; Herrera-Montes and Brokaw, 2010). Birds and mammals also increase in diversity and abundance as the habitat structure complexity increases during secondary succession (Johnston and Odum, 1956; Barlow et al., 2007; Jayat et al., 2008).

Furthermore, it has been shown that secondary forests can provide corridors between old-growth forests and plantations for bat populations in the Atlantic rainforest of Brazil (Faria, 2006); and small mammal total abundances and levels of gene flow are higher in forests connected by secondary forests than in isolated forests fragments (Pardini et al., 2005).

Because amphibians are sensitive to environmental changes (Collins and Storfer, 2003; Ríos-López and Aide, 2007; Blaustein and Bancroft, 2007), and are less mobile than other vertebrates (Sinsch, 1990; Semlitsch et al., 2009), it is important to understand how amphibian species richness and species composition vary in secondary forests. Since habitat degradation and habitat loss are major causes of the current amphibian decline (Blaustein, 1994; Collins and Storfer, 2003; Stuart et al., 2004; Todd et al., 2009), forest recovery can be especially important for tropical species. A restoration project in Puerto Rico showed that all the amphibian species from the surrounding forests had recolonized an abandoned pasture in only 3 years (Ríos-López and Aide, 2007). However, this site was less than 1 ha in area and was surrounded by older forests, which were sources for amphibian species. In another study of secondary forests in Puerto Rico, young (1–5 years), intermediate (10–20 years) and advanced secondary forests (>40 years) shared six species of amphibians (two exotic), but their abundances varied with forest age (Herrera-Montes and Brokaw, 2010). Although this study covered a greater number of sites (n = 12) and a larger region (24 km$^2$), most sites occurred within 0–100 m of an old-growth forest (i.e. sources of amphibians). These examples of rapid amphibian species recovery in Puerto Rico occurred in a region with low amphibian diversity and in a landscape that often included nearby sources of amphibians (i.e. patches of old-growth forest).

In contrast, in other tropical regions land use often occurs at a larger scale, and, thus the distance to sources of fauna can be much greater. For example, a study in Amazonia, Brazil, covered 15 sites across a larger region (3900 km$^2$) and the distance between the sites and old-growth forests varied between 650 and 2800 m (Gardner et al., 2007). In this study, secondary forests and plantations had lower species richness in comparison with high amphibian diversity old-growth forests. These secondary forests shared only 60% of the species observed in old-growth forests (Gardner et al., 2007). These findings suggest that the landscape characteristics and the spatial scale of analysis are important factors influencing amphibian species recovery in secondary forests.

In the present study, we evaluated amphibian species richness and composition recovery in tropical secondary forests of different age in northeastern Costa Rica. This region has a diverse amphibian community (Guyer and Donnelly, 2005), and the landscape is a mosaic of mature forests, secondary forests, agricultural and pastures (Sánchez-Azofeifa et al., 1999; Bell and Donnelly, 2006, Letcher and Chazdon, 2009). We assessed amphibian recovery in 12 secondary forests that vary in age of recovery and in three old-growth forests. We sampled amphibians' species richness and composition using visual and acoustic surveys. We hypothesized that (1) amphibian species richness will increase as forest age increases, and if amphibian species respond like they did in Puerto Rico, older secondary forests (30–40 years old) will have similar species richness in comparison with old-growth forests; and (2) amphibian species composition in older secondary forests will be more similar with old-growth forests than with younger forests, because specialist species will need microhabitats that will only be available in older

secondary and old-growth forests. Because of the high amphibian diversity in this region, we do not expect species richness and composition to recover as fast as in the studies in Puerto Rico (Ríos-López and Aide, 2007; Herrera-Montes and Brokaw, 2010). But, we do expect amphibian recovery to be more rapid in our sites in comparison with the Brazil study (Gardner et al., 2007), because our sites are not as isolated from old-growth forests. The results from the present study provide valuable information on the suitability of secondary forests as habitat for amphibian species recovery; habitats that can potentially mitigate the negative effects of deforestation and habitat loss that are causing amphibian population and species decline.

## 2. Methods

### 2.1. Study sites and sampling design

The study was carried out in the northeastern region of Costa Rica (10°26′N, 86°59′W), Sarapiquí, Heredia. This region has been characterized by deforestation for agriculture, mainly banana plantations, and cattle for pastures since 40 years ago (Butterfield, 1994). By 1994, forest area was reduced to 34% (Sánchez-Azofeifa et al., 1999), and the major current land uses in this region are cattle pastures, banana and pineapple plantations (Butterfield, 1994; Sánchez-Azofeifa et al., 1999; Bell and Donnelly, 2006; Letcher and Chazdon, 2009). More recently, some of these agricultural areas have been abandoned, and have transformed into secondary forests (Chazdon et al., 2003).

We selected a series of secondary forests that are recovering following cattle pasture abandonment and that vary in age of recovery (Fig. 1, see Appendix A). Specifically, we selected three sites within each of five age classes: 10–16 years old, 17–23 years old, 24–28 years old, 36–48 years old, and old-growth forests as controls (see Appendix A). Seven of these 15 sites were located within La Selva Biological Station (LSBS). Two of these forests sites were adjacent to old-growth forests, but the other sites were located between 700 and 2500 m away from old-growth forest. Two of the old-growth forests sites were located in LSBS. None of the sites included rivers, creeks or ponds, because water sources could be a potential confounding factor (de Souza et al., 2008; Ficetola et al., 2008).

LSBS covers 1536 ha, and approximately 75% is forested. The majority of the forest is old-growth, with secondary forests in areas recovered from abandoned pastures and plantations (McDade and Hartshorn, 1994). LSBS receives approximately 4 m of precipitation per year, and it is included in the tropical wet forest Holdridge's life zone (McDade and Hartshorn, 1994). There are approximately 50 species of amphibians documented for LSBS, 46 of them are frogs (Guyer and Donnelly, 2005).

### 2.2. Visual survey

We established three transects (2 × 50 m) in each site to census amphibian species richness, composition and abundance during the day and night. We used the visual encounter survey (VES) (Crump and Scott, 1994), and each transect was censused by two people for 20 min. Transects were censused in 2010 during the dry season (February and March), transition period (April–May), and wet season (October and November). During each of the three sampling periods, each of the three transects per site were sample by two people for 20 min during the day and night. In total, we spent 12 person hours per site conducting visual censuses.

### 2.3. Acoustic survey

We used acoustic surveys to increase species detection, particularly of species that are difficult to observe (e.g. arboreal, cryptic).

**Fig. 1.** Location of the 15 study sites in northeastern Costa Rica. $\Delta$ = 10–16 years old forests, $\diamond$ = 17–23 years old forests, $\square$ = 24–28 years old forests, $\star$ = 36–48 years old forests, $\bigcirc$ = old-growth forests. See Appendix A for more details.

During each census period one automated recorder, developed by our research group Automated Remote Biodiversity Monitoring Network (ARBIMON, arbimon.net), was placed at each site ($n$ = 15) for 2 weeks. We recorded 1-min every 10 min between 1800 h and 0600 h. Although the detection will vary depending on the power of each species, in general, amphibians will be detected at a radius of 50 m (i.e. 7850 m$^2$ sampling area). For each site, during each of the three census periods we listened to 60 1-min recordings (total 180 per site). We used the first recording of each of the 12 h during the first 5 days. In total, we listened to 2700 1-min recordings. Recordings were analyzed using the ARBIMON-Visualizer software the permits the user to visualize and listen to recordings. All recordings have been archived at arbimon.net. The catalogue for Panama frog species calls (Ibañez et al., 1999) and a catalogue of Costa Rican frogs (Costa Rican Frogs, 2011) were used as references for species identification.

### 2.4. Forest characteristics

To characterize each site we used aboveground biomass (Mg/ha), stem density (stems $\geqslant$ 10 cm DBH), basal area and tree species richness from Letcher and Chazdon (2009), who studied these same sites. In addition, we measured leaf-litter depth using a ruler every 5 m along each 50 m transect, obtaining the mean for each transect. We also measured understory shrub cover using the visual obstruction (VO) measurement method (Robel et al., 1970) every 5 m along each 50 m transect. With this method, we obtained categories of cover from 0 to 10, with 10 being the maximum value.

### 2.5. Landscape characteristics

We estimated the percentage of forest cover around each site based on a 2009 land use classification of this region (Clark et al. pers. com.). We established four buffers from a point between the three transects within each site: 0–250 m, 0–500 m, 0–750 m, and 0–1000 m. We also measured the distance of the secondary forests from the closest old-growth forest. In addition, we measured the area of each forest site. We use ArcGIS 9.0 to perform these analyses.
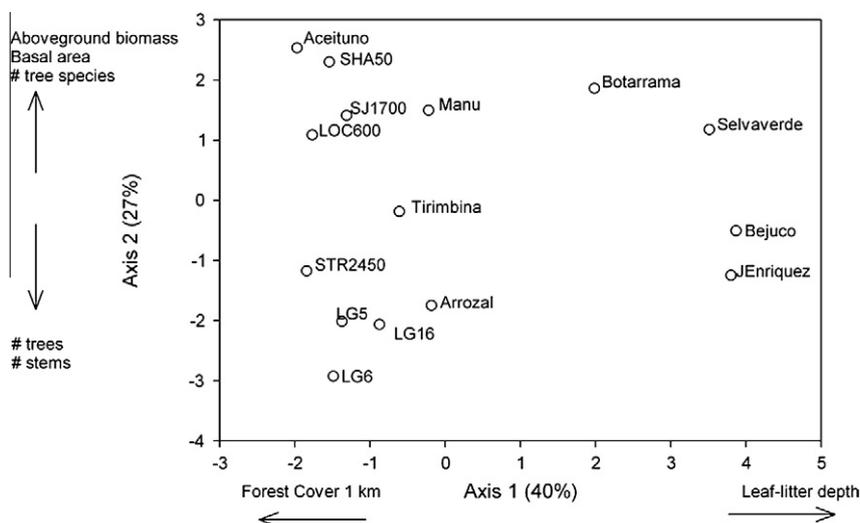
### 2.6. Statistical analysis

Rarefaction curves were used to determine if we detected the total number of species expected in the visual and acoustic surveys for each forest site (EstimateS 8.2.0) (Colwell, 2009). We obtained an average of the expected species using an abundance-based non-parametric estimator, Chao 1, and an incidence-based nonparametric estimator, ICE, to compare with the species detected in our surveys (Colwell, 2009). We performed a multiple regression model in R (version 2.12.2) (R Development Core Team, 2005) to predict which forest characteristics (age, aboveground biomass, stem density, basal area, plant species richness, leaf-litter depth, and understory shrub cover) best explained species richness. We performed another multiple regression model to determine which landscape variables (forest cover, distance to old-growth forest, forest area) best explained species richness.

We performed non-metric multidimensional scaling (NMDS) analyses to relate species presence and abundances within the different forest ages (Clarke, 1993; McCune et al., 2002). These analyses were performed with the program PC-Ord version 5. For the presence–absence data we used both visual and acoustic surveys information. Two separate analyses were done with species abundance data. From the visual survey we used the number of individuals of each species observed. From the recordings we used the relative frequency of species calls in the total number of recordings from each site. We performed NMDS analyses including and removing singletons. Forest and landscape characteristics were included as a secondary matrix.

## 3. Results

### 3.1. Forest characteristics

The first two axes of the PCA analysis based on forest characteristics explained 67% of the variance (Fig. 2, see Appendix A). The first axis separated the sites primarily based on landscape variables (i.e. forest cover around each site), and the amount of leaf-litter. Sites with low values in axis 1 had >50% forest cover within 1 km. The sites with high values in axis 1 had less than <50% forest cover within 1 km, and they were surrounded by agricultural and

**Fig. 2.** Ordination of a principal components analysis of the 15 forest sites based on forest characteristics and landscape variables (Appendix A). The variables with the highest weighting are listed along each axis.

cattle uses. The sites with less forest cover also tended to have high values of leaf-litter depth, and these sites were the younger secondary forests. Older secondary and old-growth forests at LSBS that were dominated by understory palms tended to have less leaf-litter accumulation. The second PCA axis separated sites based on variables associated with age. Older sites tended to be located higher on axis 2 and had higher aboveground biomass, basal area and number of tree species, while younger sites tended to have higher number of stems and were located lower on axis 2 (Fig. 2).

### 3.2. Species richness

We detected a total of 29 of the 46 frog species reported for LSBS (Guyer and Donnelly, 2005) using both visual and acoustic surveys (Table 1). *Craugastor bransfordii*, *Craugastor mimus*, *Oophaga pumilio* and *Diasporus diastema* were present and highly abundant in most of the forest sites and they did not show a preference for a specific forest age (Table 1). Although species richness varied from 7 to 15 species per site, this variation was not related with site age (Table 1). Furthermore, there was no significant relationship between amphibian species richness and forest characteristics ($F_{2,12} = 0.557$, $P = 0.79$) or landscape characteristics ($F_{7,7} = 1.806$, $P = 0.23$).

The Guarias sites (LG5, LG6, and LG16) and LOC600 had the lowest species richness, and common forest-dwelling species (e.g. *C. mimus*, *Craugastor noblei*, *Craugastor talamancae*, and *Pristimantis cruentus*) were absent in most of these sites (Table 1). Most hylid species (i.e. *Agalychnis saltator*, *Smilisca puma*, *Smilisca sordida*, and *Smilisca baudinii*) were observed once and exclusively in young forests sites (Table 1). Three species were detected exclusively with the acoustic survey. The rarefaction curves showed that we detected 86% (Chao 1) and 82% (ICE) of the species expected with the acoustic survey; and 76% (Chao 1) and 70% (ICE) of the species expected using the visual survey.

### 3.3. Species composition

There was not sufficient variation in species composition among sites for the NMDS analyses to ordinate the sites in two dimensions. Similar non-significant results were obtained when the analyses were done including species presence–absence, species abundances and including and removing singletons in both visual and acoustic surveys.

## 4. Discussion

### 4.1. Species richness and composition

Amphibian species richness and composition are recovering rapidly in secondary forests of northeastern Costa Rica. Although we expected older secondary forests to have similar species richness and composition in comparison with old-growth forests, we found that even young forests (10–16 years) had similar assemblages. The rarefaction curves suggest that we are detecting most of species in our sites. However, eight species were only detected once in a site, indicating that they are rare or cryptic species or species that normally do not use understory habitats. We detected 29 of the 46 species reported for the region in secondary forests without permanent water sources. This is a high proportion of the amphibian community, given that we did not sample creeks or ponds, which are important habitats for this group (Savage, 2002; Guyer and Donnelly, 2005).

Our analysis separated forest sites based on the area of forest around each site, leaf-litter depth, and variables associated with forests age, which could be important factors influencing amphibian recovery (Fig. 2). But, there was no relationship between forest characteristics and amphibian species richness or species composition. Several amphibian species were present in most of the forests sites, showing that these forests are providing suitable habitats for them. Regardless of their age, forests with closed canopy, high humidity, deep leaf-litter, and abundant arthropods, provide microhabitat conditions for perching, feeding, mating, and nesting. Hence, the forest sites evaluated here are reaching favorable microhabitat conditions for amphibians as early as 10–16 years following abandonment.

Although site age was not associated with species richness, some sites had very low species richness (⩽8 species) (e.g. the Guarias and LOC600). The Guarias sites (LG5, LG6 and LG16) are young and intermediate forests that emerged from pastures isolated from a forest matrix by the Sarapiquí River and by a major road (Fig. 1). These barriers appear to be limiting the colonization of some forest species specialists. For example, *C. mimus*, *C. noblei*, *C. talamancae*, and *P. cruentus*, occurred in similar aged sites, but they were absent from the Guarias sites. The LOC600 site also had low diversity, but it was surrounded by forest. This is a steep site, and it had the lowest leaf-litter depth of all sites. We believe that runoff is removing the leaf-litter, reducing food resources (e.g. leaf-litter arthropods), which may explain the low amphibian diversity in this site.

**Table 1**

Species detected in the visual or recording surveys in the 15 forest sites organized by time since abandonment. *Total* represents the sum of the observations from all sites, *R* represents species detected only in recordings, and *ND* represents species that were not detected, but are reported for LSBS (Guyer and Donnelly, 2005).

| Species | 10–16 yr | | | 17–23 yr | | | 24–28 yr | | | 36–48 yr | | | old-growth | | | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Bejuco | JEnriquez | LG6 | Arrozal | LG16 | STR2450 | LG5 | LOC600 | Tirimbina | Botarrama | Aceituno | Manu | Selvaverde | SHA50 | SJ1700 | |
| *Craugastor bransfordii* | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 307 |
| *Oophaga pumilio* | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 289 |
| *Pristimantis ridens* | X | X | X | X | X | X | X | X | X | X | X | X | X | | X | 37 |
| *Craugastor mimus* | X | X | | X | | X | | | X | X | X | X | X | X | X | 31 |
| *Pristimantis cerasinus* | X | X | X | X | | X | | X | | X | X | X | | X | X | 27 |
| *Diasporus diastema* | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X | 26 |
| *Craugastor noblei* | | X | | X | | | | | X | X | X | X | X | X | X | 22 |
| *Pristimantis cruentus* | X | X | | X | | X | | | X | | X | X | | X | | 20 |
| *Craugastor fitzingeri* | X | X | | X | X | X | X | | X | X | X | X | X | X | | 13 |
| *Dendrobates auratus* | X | X | | | | | | | | | | | | | | 11 |
| *Rhaebo haematiticus* | | | | X | | X | | | | X | | X | | | | 7 |
| *Craugastor megacephalus* | X | | | | | | | | | | | | | X | | 4 |
| *Leptodactylus savagei* | | | | | | X | | | | | X | X | | X | X | 4 |
| *Lithobates warszewitschii* | | | | | | | | | | X | | | X | X | | 4 |
| *Craugastor talamancae* | | X | | | | X | | X | | | | | | X | X | 3 |
| *Hypsiboas rufitelus* | | X | | | | | | | | | | | | X | | 2 |
| *Incilius melanochlorus* | | | X | X | | | X | | X | | X | | | | | 2 |
| *Teratohyla spinosa* | | | | X | | | | | | | | | | | X | 2 |
| *Agalychnis callidryas* | | | | | | | | | | | | | | | | |
| *Agalychnis saltator* | | | | X | | | | | | | | | | | | 1 |
| *Craugastor crassidigitus* | | X | X | | | | | X | | X | | | X | X | X | 1 |
| *Cruziohyla calcarifer* | | | | | | | | | | | | | | X | | 1 |
| *Dendropsophus ebraccatus* | | | | | | | | | | | | | | | | |
| *Espadarana prosoblepon* | | | | X | | | | X | | | | | X | | | 1 |
| *Gastrophryne pictiventris* | | | | | | X | | | | | | | | | | 1 |
| *Leptodactylus melanonotus* | | | | | | | | | | | | | | | | |
| *Lithobates vaillanti* | | | | | | | | | | | | | | | | |
| *Scinax elaeochroa* | | | | | | | | | | | | | | | | |
| *Leptodactylus poecilochilus* | | | | | | | | X | | | | | | | | 1 |
| *Smilisca puma* | | X | | | | | | | | | | | | | | 1 |
| *Smilisca sordida* | X | | | | | | | | | | | | | | | 1 |
| *Rhinella marina* | | | X | | | | X | | | | | | | | | R |
| *Smilisca baudinii* | | | | | | | | | | X | | | | | | R |
| *Smilisca phaeota* | | | | | | | | | | | | X | | | | R |
| *Bufo coniferus* | | | | | | | | | | | | | | | | ND |
| *Tlalocohyla loquax* | | | | | | | | | | | | | | | | ND |
| *Dendropsophus phlebodes* | | | | | | | | | | | | | | | | ND |
| *Scinax boulengeri* | | | | | | | | | | | | | | | | ND |
| *Sachatamia albomaculata* | | | | | | | | | | | | | | | | ND |
| *Cochranella granulosa* | | | | | | | | | | | | | | | | ND |
| *Hyalinobatrachium fleischmanni* | | | | | | | | | | | | | | | | ND |
| *Teratohyla pulverata* | | | | | | | | | | | | | | | | ND |
| *Hyalinobatrachium valerioi* | | | | | | | | | | | | | | | | ND |
| *Pristimantis altae* | | | | | | | | | | | | | | | | ND |
| *Pristimantis caryophyllaceus* | | | | | | | | | | | | | | | | ND |
| *Craugastor ranoides* | | | | | | | | | | | | | | | | ND |
| *Phyllobates lugubris* | | | | | | | | | | | | | | | | ND |
| **Total species richness** | **18** | | | **17** | | | **15** | | | **16** | | | **18** | | | **819** |

**Table A1**
Age and forest characteristics of the 15 study sites.

| Forest sites | Age | # of trees | # of stems | # of tree species | Aboveground biomass (Mg/ha) | Tree basal area (m²/ha) | Understory shrub cover | Mean leaf-Litter depth (cm) | Forest cover 0–250 m (%) | Forest cover 0–500 m (%) | Forest cover 0–750 m (%) | Forest cover 0–1000 m (%) | Distance to OG forest (m) | Area (ha) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Bejuco | 14 | 288 | 340 | 70 | 117.4 | 22.2 | 3 | 2.5 | 65.7 | 42.8 | 26.1 | 34.2 | 1203.7 | 16.8 |
| JEnriquez | 14 | 261 | 357 | 72 | 50.8 | 10.8 | 2 | 2.4 | 74.0 | 44.7 | 32.4 | 34.2 | 1203.7 | 34.3 |
| LG6 | 15 | 330 | 570 | 61 | 99.7 | 18.3 | 4 | 2.3 | 100.0 | 100.0 | 100.0 | 100.0 | 983.5 | 2.4 |
| Arrozal | 20 | 431 | 431 | 92 | 108.5 | 19.9 | 3 | 3.7 | 93.6 | 92.4 | 87.3 | 83.7 | 4393.1 | 6.4 |
| LG16 | 22 | 268 | 346 | 48 | 129 | 18.7 | 4 | 2.9 | 100.0 | 100.0 | 100.0 | 100.0 | 1425.9 | 17.8 |
| STR2450 | 22 | 335 | 473 | 69 | 158.5 | 24.6 | 3 | 1.4 | 100.0 | 100.0 | 100.0 | 100.0 | 0 | 30.7 |
| LOC600 | 25 | 260 | 299 | 69 | 223.2 | 32.8 | 3 | 1.0 | 100.0 | 100.0 | 100.0 | 100.0 | 0 | 50.9 |
| LG5 | 27 | 337 | 468 | 85 | 119.6 | 20.2 | 4 | 2.5 | 100.0 | 100.0 | 100.0 | 100.0 | 881.1 | 2.7 |
| Tirimbina | 28 | 331 | 403 | 84 | 149.6 | 23.6 | 2 | 2.4 | 100.0 | 99.8 | 85.8 | 75.2 | 5078.3 | 8.2 |
| Aceituno | 36 | 286 | 366 | 105 | 311.6 | 46.7 | 3 | 2.5 | 100.0 | 100.0 | 100.0 | 100.0 | 4216.7 | 6.1 |
| Manu | 46 | 351 | 401 | 136 | 253.3 | 39.6 | 3 | 2.9 | 97.8 | 75.5 | 73.3 | 70.4 | 5000.2 | 20.9 |
| Botarrama | 48 | 306 | 351 | 101 | 251.3 | 38.1 | 3 | 3.1 | 67.5 | 63.0 | 53.3 | 56.4 | 5432.7 | 13.2 |
| Selvaverde | Old-growth | 243 | 261 | 91 | 142.5 | 24.3 | 2 | 3.5 | 62.6 | 63.7 | 49.5 | 37.6 | - | 129.3 |
| SHA50 | Old-growth | 245 | 264 | 104 | 216.7 | 32.2 | 2 | 1.4 | 100.0 | 100.0 | 100.0 | 100.0 | - | 10197.6 |
| SJ1700 | Old-growth | 269 | 285 | 104 | 168.1 | 26.2 | 2 | 1.7 | 100.0 | 100.0 | 100.0 | 100.0 | - | 8158 |

## 4.2. The role of the landscape characteristics on amphibian recovery

Our study, along with others (Gardner et al., 2007; Ríos-López and Aide, 2007; Herrera-Montes and Brokaw, 2010), highlights the importance of landscape characteristics in determining amphibian recovery in tropical forests. The most important landscape factor appears to be the degree of isolation of the secondary forests. In Puerto Rico, amphibian recovery was rapid, and all sites were close (<100 m) to sources of amphibians (Ríos-López and Aide, 2007; Herrera-Montes and Brokaw, 2010). Very young secondary forests (1–5 years of recovery) had similar species richness and composition in comparison with older secondary forests. Furthermore, Puerto Rico has low amphibian diversity in comparison with the mainland tropics, and these species are generalists that occur at high densities (Beard et al., 2003; Ríos-López and Aide, 2007; Delgado-Acevedo and Restrepo, 2008), and these factors could help to accelerate the recovery time. At the other extreme, secondary forest sites in the Amazon in Brazil that were more isolated from amphibian sources (>1 km) recovered only 60% of the old-growth forest species following 14–19 years of recovery (Gardner et al., 2007). Furthermore, the species composition of the secondary forest sites was very different in comparison with the old-growth forest sites. Most of the species in the secondary forests were generalists, while the species that did not colonize these sites were old-growth forest specialists (Gardner et al., 2007). Although species recovery in Costa Rica is slower than in Puerto Rico, young forests (10–16 years of recovery) had similar species richness and species composition in comparison with old-growth forests. This relatively rapid recolonization in our sites occurred even though the average distance to amphibian sources (e.g. old-growth forests) was approximately 500 m, intermediate between Puerto Rico and Brazil studies. We believe that corridors and other land uses in the region have contributed to the rapid recovery. Our study sites are connected with larger areas of forests by riparian vegetation, live fences and/or young forests, and these connections can facilitate amphibian dispersal among sites (Ficetola et al., 2008). In addition, this region includes areas of agroforestry and plantations, and these land uses tend to enhance amphibian gamma diversity (Pearman, 1997; Gardner et al., 2007).

## 5. Conclusions

Our results suggest that secondary forests in northeastern Costa Rica are playing an important role in amphibian species recovery and conservation by providing the minimum conditions for colonization. The landscape context is important, and secondary forests with connections to older and larger forests areas are capable of supporting similar amphibian species richness and composition. Worldwide, the area of secondary forests is increasing (FAO, 2007), and our results show that these habitats are important for amphibians and can help to mitigate amphibian population and species decline.

## Appendix A

See Table A1.

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