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Research Article

# Small changes in vegetation structure create great changes in amphibian ensembles in the Colombian Pacific rainforest.

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## Abstract

This study determines the composition of amphibian ensembles along a vegetation gradient in the coastal Pacific rainforests in Colombia. Eight environmental and structural variables were measured to characterize the species' habitats and to determine which was most important in structuring amphibian patterns. After a total of 432 man-hours sampling effort, 513 individuals from 32 amphibian species were found. Although the species richness was similar among the vegetation cover types, the composition of the ensembles and total amphibian abundance were different in each case. In addition, a strong relationship was found between changes in the vegetation structure and the amphibian pattern, with the canopy cover being the key variable in the composition of the ensembles for each cover type. Habitats with over 76% canopy cover, combined with a high density of individual woody plants (> 176 individuals per 500 m$^2$) and a high depth of leaf litter (> 16 cm), provide the necessary habitat conditions for typical rainforest composition of amphibian species. However, for amphibian ensembles to have a mature forest composition, the habitat must have a canopy cover over 89%, a density of woody plants exceeding 231 individuals per 500 m$^2$, and a leaf litter depth above 23 cm. Therefore, future studies of amphibian succession and restoration in tropical forests must determine the changes in vegetation structure, rather than the possible direct effect of microclimatic variables.

**Key words:** Frogs, land use gradients, leaf litter, vegetation structure, secondary forest, mixed farming.

## Resumen

Este estudio determina la estructura y composición de ensamblajes de anfibios a lo largo de un gradiente de vegetación en bosques de la Costa Pacífica de Colombia. Ocho variables ambientales y estructurales fueron medidas para caracterizar los habitats de las especies y relacionarlos con la estructura del ensamblaje. Luego de un esfuerzo de muestreo total de 432 horas/hombre, 513 individuos de 32 especies de anfibios fueron encontrados. Aunque la riqueza de especies fue similar entre los tipos de cobertura vegetal, la composición del ensamblaje y la abundancia total de anfibios fue diferente en cada caso. Adicionalmente, una fuerte relación fue detectada entre los cambios en la estructura de la vegetación y la composición de los anfibios, siendo la cobertura de dosel, la variable que jugó un papel clave en la estructuración de los ensamblajes para cada tipo de cobertura. Los habitats con más del 76% de la cobertura de dosel, combinado con un alto número de individuos de plantas leñosas (>176 individuos por 500 m$^2$) y una mayor profundidad de hojarasca (>16 cm), brindan las condiciones necesarias para que las especies de anfibios presenten una estructura típica de selvas. Sin embargo, para que los ensamblajes de anfibios tengan una estructura acorde a un bosque maduro el hábitat debe tener una cobertura de dosel superior a 89%, una densidad de plantas leñosas mayor a 231 individuos por 500 m$^2$ y una profundidad de hojarasca mayor a 23 cm. Por lo tanto, estudios futuros que quieran profundizar en la sucesión y restauración de anfibios en bosques tropicales deben entender los cambios en la estructura de la vegetación, más que el posible efecto directo de las variables microclimáticas.

**Palabras claves**: gradientes de uso de la tierra, hojarasca, estructura de plantas, bosque secundario, bosque tropical, cultivo mixto.

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## Introduction

It is estimated that tropical forests comprise approximately 52% of all forests existing on the planet. The tropical forests with the greatest biodiversity and ecological complexity are found in Latin America and the Caribbean [1]. In Colombia, the forests along the Pacific coast have been deforested by the introduction of livestock, mining activity, the extraction of non-timber products such as rubber (*Hevea brasiliensis*) and tagua (*Phytelephas macrocarpa*), and the introduction of exotic African palm (*Elaeis oleifera*) [2]. Although the Pacific region has a low human population density (5 - 17 individuals/Km$^2$) and 66.5% remaining natural vegetation, the forest-agricultural edge continues to grow due to the arrival of settlers and the planting of illicit crops such as coca (*Erythroxylum coca*) [3, 4].

Anthropogenic habitat disturbance generates changes in the dominance of amphibian species and, at the level of ensemble, diminishes the species composition through homogenization [5]. In disturbed areas, many species that are registered in the ensemble are generalists, capable of withstanding some degree of disturbance; moreover, the distribution is more influenced by the temperature gradient in the microhabitat than by the vegetation structure [6]. However, it is possible that changes in soil characteristics and primary farming production, which can be presented as disturbances and changes in soil use, affect the abundance of amphibians in tropical forests [7]; this process may disturb the reproductive rate of the most abundant anuran species in the rainforest, affecting, in turn, the trophic chains and the ensemble composition [8].

The landscape structure, specifically in the context of the anthropogenic matrix, influences the habitat quality for amphibian species in the remaining forests [9]. Therefore, the recovery of the species composition inside ensembles during the regeneration of forests is inherent to each species; furthermore, to correctly focus management and conservation activities, it is crucial to identify the groups of species that are capable of recolonizing the recovering environments [10]. Certainly, other species that are typical to the forest interior and reflect habitat quality, require an extensive natural coverage that is protected from edge effects [11, 12]. These species are unlikely to colonize environments in successional stages.

Among the vertebrate group, amphibians are critical to ecosystems because they are very abundant [13, 14] and have specific physiological and ecological characteristics that sensitize them to environmental modifications; this fact has led to the proposal that amphibians can be used as good indicators of the habitat quality [15]. As a group, amphibians have a highly permeable skin, which makes them vulnerable to physical and chemical changes in the habitat. Many of these animals have complex life cycles that require aquatic and terrestrial habitats during different stages of development. Amphibians exhibit a great diversity of reproductive modes (approximately 39 modes have been described worldwide) [16] that determine when the microhabitat is selected and when displacement occurs [17]. In general, these animals exhibit low vagility and strong philopatry. Thus, amphibians respond differently to habitat fragmentation and edge effects in remnant forests [18, 19].

In this study, changes in the amphibian ensembles were evaluated in terms of their composition and their relative abundance of species [20], because the effects of habitat changes cannot be quantified solely in terms of the species count [11]. Following Fauth et al. [21], we use the term ‘‘ensemble’’ to identify a group of species belonging to a particular taxon and exploiting a common resource. The goal was to determine the amphibian ensemble changes relative to the environmental and structural variables along a vegetation gradient composed of mature forests, secondary forests, and abandoned mixed farming areas in the Colombian Pacific coast.

## Methods

### *Study Site*

This study was conducted within the Afroamerican collective territory of the Community Council of the Upper and Middle Dagua River. This area is located on the western slope of the Western Colombian mountain range, which is an integral part of the Colombian Pacific platform known as the Tumbes-Choco-Magdalena Forest and is considered one of the mega-diversity centers of the planet [22]. With an approximate area of 7,375 ha, it comprises the transitional ecotone that spans from the subxerophytic Dagua forest to the edge of the Pacific coastal plane. The region includes rainforests and rainy tropical life zones. Its altitude ranges from 100 to 1,800 m, with average monthly precipitation between 6,500 and 6,700 mm and with median monthly temperatures from 24°C to 26°C. The precipitation regime is bimodal, with rainy periods from March to May and from August to November.

### *Research Design*

Using Google Earth version 6 [23], satellite images, and direct field corroboration, three types of vegetation cover and use (i.e., mature forest, secondary forest, and abandoned mixed farming areas) were selected and defined as follows:

*Mature forest*, 3°51'46" N, 76°48'49" W: Forests characterized by high species richness and large trees with an average circumference at breast height (DBH) of 23.5 cm. This vegetation coverage does not have a history of intense disturbance in over 40 years and contained plant species such as Carrá (genus *Huberodendron*, family Bombacaceae), Arenillo (genus *Perygota*, family Sterculliaceae), Cuángare (genera *Virola, Otoba,* and *Iryanthera;* family Myristicaceae), and Cargadero (genus *Guatteria*, family Annonaceae).

*Secondary succession forest,* 03°50’54” N and 76°47’2” W: Forests characterized by 12 to 15 years of natural regeneration after successive events of selective logging of trees for timber. This cover exhibited a forest homogeneity that was reflected in two strata: the lowest, which is dominated mainly by palms, and the canopy, which is dominated by zapotillo (genus *Gloeospermun*, family Violaceae), pacó (genus *Cespedesia,* family Ochnaceae), neme palm (genus *Geonoma*, family Arecaceae), and cuángare trees (genera *Iryanthera*, *Virola,* and *Osteophloeum*; family Myristicaceae). The tallest woody trees have an average CBH of 23.5 cm.

*Abandoned mixed farming areas,* 3°50'1" N, 76°46'50" W: An area with productive systems abandoned for approximately 3 years, with arboreal elements of borojó (genus *Borojoa*, family

Rubiaceae), plantain (genus *Mussa*, family Musaceae), and yuca (genus *Manihot*, family Euphorbiaceae).

Each vegetation coverage and use had at least one permanent body of water. Eight permanent transects of 250 m x 2 m were identified in each type of vegetation coverage, one of which was always situated parallel to a permanent stream. The minimum distance between transects was 150 m to guarantee the independence of each sample; the transects were located in an altitudinal range that was between 300 and 530 m asl.

### *Sampling of the amphibian species and their habitats*

Six trips to the field were made between the months of April, June, and July of 2009 and January, March, and April of 2010. A total of three hours of sampling was performed in each transect at a maximum height of 2 m so that this study would only focus on species in the understory of the forest (*sensu* Urbina-Cardona & Reynoso [19]). The sampling was randomized daily between transects. The sampling was performed by two people at night (between 18h and 24h), for a total capture effort of 432 man-hours.

Eight environmental and vegetation structure variables were evaluated in the amphibian microhabitats at individual and transect level. For each individual found in its first observed location, measurements were taken according to the protocol proposed by Urbina-Cardona and collaborators [12]: the temperature and relative humidity were measured using a thermo-hygrometer; the depth of the leaf litter was measured using a graduated metal ruler; the percentage of herbaceous cover was measured using a 0.50 x 0.50 m wooden frame that was divided into four quadrants with a nylon cord, estimating the percentage of spaces covered by vegetation.

For each transect (n = 12), a prefixed transect line was followed (250 m) and at 1 m to each side, the basal area and DBH for each individual was measured [24]. Density of trees with a DBH above 3 cm were also measured. The canopy cover was estimated using a densitometer at ten random points where the shaded squares were counted. Linear distance from bodies of water were measured using a GPS.

### *Data analysis*

The specific species richness of the amphibians in each type of cover was determined as the sum of the number of species found in each of the eight transects. The representativeness of the species richness obtained in the field was evaluated by comparing it with different estimators of richness, using the EstimateS version 7 software [25]. To estimate the total richness in the studied landscape, the Jack 1 and Jack 2 methods were applied. To estimate the richness per cover type, the Chao 1, Chao 2, and bootstrap methods were used.

The composition and hierarchization of species in the ensembles were compared for each cover type using rank abundance curves [26]. Differences in the amphibian species composition and their relative abundance, as measured by the Bray–Curtis distances, among the three vegetation cover types was evaluated using a permutation multivariate analysis of variance (PERMANOVA). This analysis was based on a zero-adjusted Bray-Curtis similarity matrix, type III partial sums of squares, and 9,999 random permutations of the residuals under the reduced model. This routine was performed using the PRIMER v6.1.14 & PERMANOVA *add on* v1.0.4 software [27, 28].

Pearson correlation coefficients were used to determine correlations among microhabitat variables and to identify non-correlated variables (less than 70%; [5, 29]). Kruskal-Wallis tests were used to compare the three vegetation cover types on different environmental and structural variables. Both of these analyses were performed using the Statistica 6.0 software [30].

The best adjusted candidate model, that related amphibian ensembles and gradients in environmental variables, was identified and generated via a distance-based linear model (DistLM subroutine), using the Akaike Information Criterion for small samples and second order correction (AICc). Subsequently, ordination and visualization of the best adjusted model were done with the distance based redundancy analysis (dbRDA subroutine). A regression and classification tree (LINKTREE) was created to link the composition of amphibian ensembles in transects with the best adjusted environmental variables (identified through the DistLM subroutine). Critical threshold values were detected for each of these variables, in which the binary divisions were defined in groupings of amphibian´ composition. All of these analyses were performed by the PRIMER v6.1.14 & PERMANOVA *add on* v1.0.4 program [27, 28].

## Results

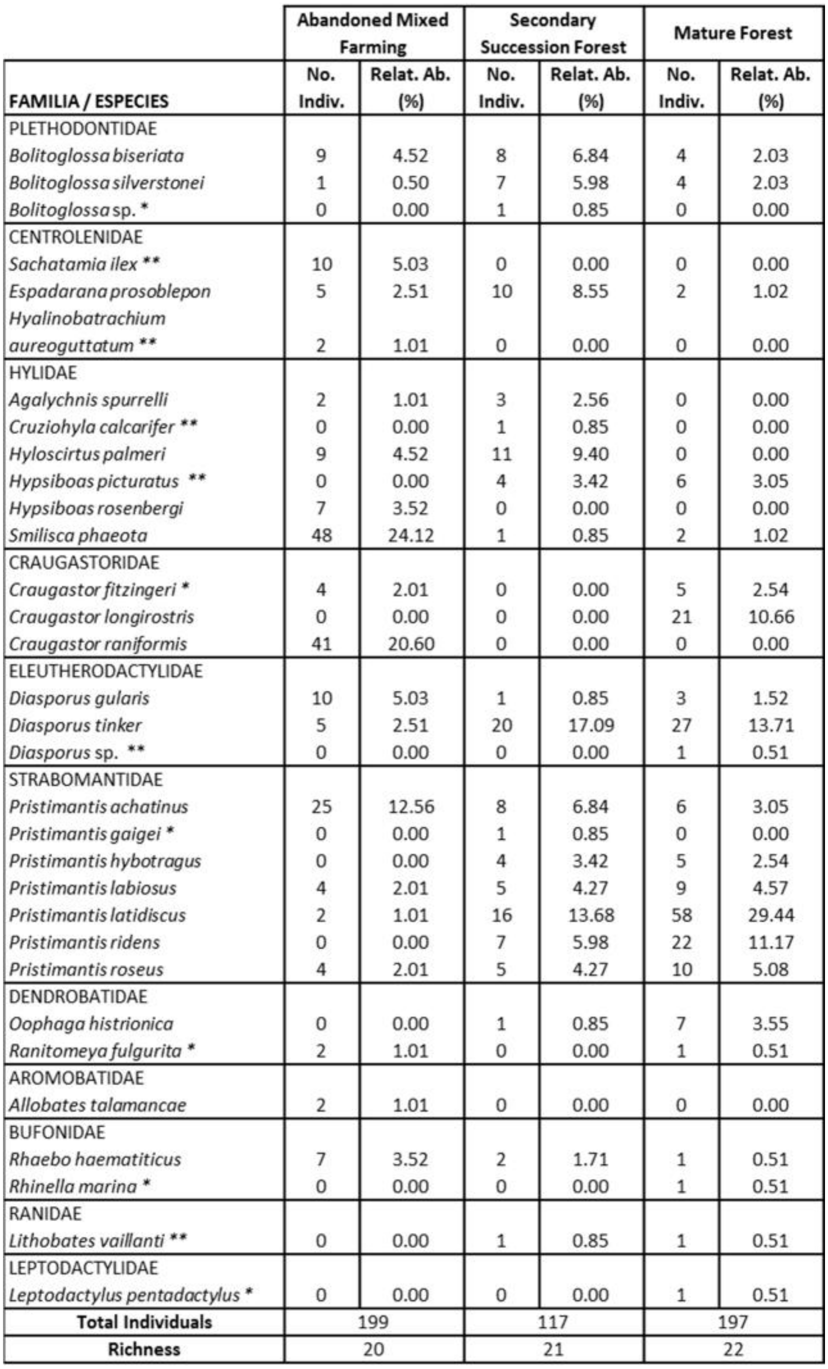
**Amphibian ensembles in the Colombian Pacific Coast study area:** After a total capture effort of 432 man-hours, 513 individual amphibians belonging to 32 species, 11 families, and 2 orders were registered. For the study area, the greatest percentage of relative abundance was held by the *Pristimantis latidiscus* species (14.81%), represented by 76 individuals in the studied vegetation cover types (Table 1). The species accumulation curves tended to be asymptotic, although the Jack 1 and Jack 2 estimators demonstrated that between five and six additional species were expected in the inventory. Thus, the present study is based upon a completeness of inventory between 84.2% and 86.4% of the estimated species richness. Singleton and doubleton species represented 25% of the species in the study area (Table 2, Appendix 1).

The reproductive modes found for these species were frogs with terrestrial eggs (genera *Allobates, Bolitoglossa, Craugastor, Diasporus, Oophaga, Pristimantis*, and *Ranitomeya*), which accounted for 59.3% of the total species richness, followed by species with arboreal eggs and aquatic larva (21.8%) and by species with aquatic eggs and larva (18.7%).

**Amphibian ensembles composition in vegetation cover types:** The species richness was similar in the mature forest, the secondary forest, and the abandoned mixed farming areas, with each having 22, 21, and 20 species, respectively (Table 1). In the abandoned mixed farming areas, the completeness of inventory was between 95.2% and 100%, which led to the expectation of finding just one additional species in the inventory (Table 2, Appendix 2A). In the forest covers, the curves did not stabilize (Appendix 2B-C) and determined a completeness between 66% and 67% for the secondary forest (3 - 10 species in addition to the inventory) and between 81% and 86% for the mature forest (3-5 species in addition to the inventory) (Table 2).

When analyzed separately, transects parallel to streams and terrestrial transects have different patterns in amphibian ensemble. At terrestrial transects 376 individuals (73% of total abundance) were registered in 26 species (81% of all species). Sixty-six percent of the abundance in streams was composed of seven species (*Pristimantis latidiscus, Diasporus tinker, Pristimantis achatinus, Smilisca phaeota, Pristimantis ridens, Craugastor raniformis, Bolitoglossa biseriata*). Species richness is similar between vegetation cover types but species composition is different, as number of exclusive species, between them: Abandoned mixed farming has the greatest number of species (19) and exhibit three exclusive species (*Craugastor raniformis, Hypsiboas rosenbergi, Allobates talamancae*); mature forest has 18 species and two exclusive species (*Leptodactylus pentadactylus, Rhinella marina*); and secondary forest has 17 species with two exclusive species (*Bolitoglossa sp., Prisitmantis gaigeae*).

**Table 1**. Composition, richness, and relative abundance of the amphibian species found in three vegetation cover types in the Colombian Pacific coast rainforest.



| | Abandoned Mixed Farming | | Secondary Succession Forest | | Mature Forest | |
|---|---|---|---|---|---|---|
| **FAMILIA / ESPECIES** | **No. Indiv.** | **Relat. Ab. (%)** | **No. Indiv.** | **Relat. Ab. (%)** | **No. Indiv.** | **Relat. Ab. (%)** |
| PLETHODONTIDAE | | | | | | |
| *Bolitoglossa biseriata* | 9 | 4.52 | 8 | 6.84 | 4 | 2.03 |
| *Bolitoglossa silverstonei* | 1 | 0.50 | 7 | 5.98 | 4 | 2.03 |
| *Bolitoglossa* sp. * | 0 | 0.00 | 1 | 0.85 | 0 | 0.00 |
| CENTROLENIDAE | | | | | | |
| *Sachatamia ilex* ** | 10 | 5.03 | 0 | 0.00 | 0 | 0.00 |
| *Espadarana prosoblepon* | 5 | 2.51 | 10 | 8.55 | 2 | 1.02 |
| *Hyalinobatrachium aureoguttatum* ** | 2 | 1.01 | 0 | 0.00 | 0 | 0.00 |
| HYLIDAE | | | | | | |
| *Agalychnis spurrelli* | 2 | 1.01 | 3 | 2.56 | 0 | 0.00 |
| *Cruziohyla calcarifer* ** | 0 | 0.00 | 1 | 0.85 | 0 | 0.00 |
| *Hyloscirtus palmeri* | 9 | 4.52 | 11 | 9.40 | 0 | 0.00 |
| *Hypsiboas picturatus* ** | 0 | 0.00 | 4 | 3.42 | 6 | 3.05 |
| *Hypsiboas rosenbergi* | 7 | 3.52 | 0 | 0.00 | 0 | 0.00 |
| *Smilisca phaeota* | 48 | 24.12 | 1 | 0.85 | 2 | 1.02 |
| CRAUGASTORIDAE | | | | | | |
| *Craugastor fitzingeri* * | 4 | 2.01 | 0 | 0.00 | 5 | 2.54 |
| *Craugastor longirostris* | 0 | 0.00 | 0 | 0.00 | 21 | 10.66 |
| *Craugastor raniformis* | 41 | 20.60 | 0 | 0.00 | 0 | 0.00 |
| ELEUTHERODACTYLIDAE | | | | | | |
| *Diasporus gularis* | 10 | 5.03 | 1 | 0.85 | 3 | 1.52 |
| *Diasporus tinker* | 5 | 2.51 | 20 | 17.09 | 27 | 13.71 |
| *Diasporus* sp. ** | 0 | 0.00 | 0 | 0.00 | 1 | 0.51 |
| STRABOMANTIDAE | | | | | | |
| *Pristimantis achatinus* | 25 | 12.56 | 8 | 6.84 | 6 | 3.05 |
| *Pristimantis gaigei* * | 0 | 0.00 | 1 | 0.85 | 0 | 0.00 |
| *Pristimantis hybotragus* | 0 | 0.00 | 4 | 3.42 | 5 | 2.54 |
| *Pristimantis labiosus* | 4 | 2.01 | 5 | 4.27 | 9 | 4.57 |
| *Pristimantis latidiscus* | 2 | 1.01 | 16 | 13.68 | 58 | 29.44 |
| *Pristimantis ridens* | 0 | 0.00 | 7 | 5.98 | 22 | 11.17 |
| *Pristimantis roseus* | 4 | 2.01 | 5 | 4.27 | 10 | 5.08 |
| DENDROBATIDAE | | | | | | |
| *Oophaga histrionica* | 0 | 0.00 | 1 | 0.85 | 7 | 3.55 |
| *Ranitomeya fulgurita* * | 2 | 1.01 | 0 | 0.00 | 1 | 0.51 |
| AROMOBATIDAE | | | | | | |
| *Allobates talamancae* | 2 | 1.01 | 0 | 0.00 | 0 | 0.00 |
| BUFONIDAE | | | | | | |
| *Rhaebo haematiticus* | 7 | 3.52 | 2 | 1.71 | 1 | 0.51 |
| *Rhinella marina* * | 0 | 0.00 | 0 | 0.00 | 1 | 0.51 |
| RANIDAE | | | | | | |
| *Lithobates vaillanti* ** | 0 | 0.00 | 1 | 0.85 | 1 | 0.51 |
| LEPTODACTYLIDAE | | | | | | |
| *Leptodactylus pentadactylus* * | 0 | 0.00 | 0 | 0.00 | 1 | 0.51 |
| **Total Individuals** | 199 | | 117 | | 197 | |
| **Richness** | 20 | | 21 | | 22 | |

Species encountered exclusively at: * terrestrial transects, ** transects on streams

When analyzing exclusively transects parallel to streams (one on each vegetation type) 138 individuals (27% of total abundance) were registered in 26 species (81% of all species). Sixty-five percent of the abundance in streams was given by seven species (*Smilisca phaeota, Craugastor raniformis, Hyloscirtus palmeri, Centrolene prosoblepon, Pristimantis latidiscus, Sachatamia ilex, Hypsiboas picturatus*). There is a slight reduction in species richness for each vegetation type, but the number of exclusive species increased: Abandoned mixed farming has 17 species with six exclusive species (*Craugastor raniformis, Rhaebo haematiticus, Pristimantis labiosus, Bolitoglossa biseriata, Allobates talamancae, Hypsiboas rosenbergi*); secondary forest has 13 species with two exclusive species (*Bolitoglossa biseriata, Prisitmantis hybotragus*); and mature forest has 12 species and four exclusive species (*Craugastor longirostris, Pristimantis ridens, Bolitoglossa silverstonei, Oophaga histrionica;* Appendix 3).

**Table 2.** The observed and estimated species richness of the amphibians in three vegetation cover types on the Colombian Pacific coast.

| | **Vegetation cover types** | | | **All landscape** |
|---|---|---|---|---|
| | **Abandoned Mixed Farming** | **Secondary Succession Forest** | **Mature Forest** | |
| Number of Species Observed (Sobs) | 20 | 21 | 22 | 32 |
| Sobs SD (Mao Tau)* | ±0,31 | ±3,33 | ±2,14 | ±1,68 |
| Number of Individuals | 199 | 117 | 197 | 513 |
| Chao 1 | 20 | 31 | 27 | — |
| Chao 2 | 20 | 31 | 26 | — |
| Boopstrap | 21 | 24 | 25 | — |
| Jack 1 | — | — | — | 37 |
| Jack 2 | — | — | — | 38 |
| Singletons | 1 | 7 | 6 | 5 |
| Doubletons | 5 | 1 | 2 | 4 |

* Standard deviation of the expected Mao Tau richness.

The slopes of the rank abundance curves between the different types of cover were similar, and the abundance pattern and hierarchical order of the species exhibited a logarithmic series distribution, with a few dominant species and between six and seven less abundant species (Fig. 1). Seven species related to the abandoned mixed farming areas were found (*Smilisca phaeota*, *Sachatamia ilex*, *Hypsiboas rosenbergi, Smilisca phaeota, Craugastor raniformis, Diasporus gularis, Pristimantis achatinus,* and *Rhaebo haematiticus*), of which *Smilisca phaeota* had the greatest relative abundance (24.12%), followed by *Craugastor raniformis* (20.60%). In the secondary forest, the species *Diasporus tinker* was the most abundant (17.09% relative abundance), and other species (*Cruziohyla calcarifer, Bolitoglossa* sp*.,* and *Pristimantis gaigei*) were related to this cover type. For the mature forest, the greatest abundance percentage was obtained by *Pristimantis latidiscus* (29.44%), and other species (*Craugastor longirostris, Diasporus tinker, Pristimantis ridens*) were also highly abundant in this cover type (Table 1).

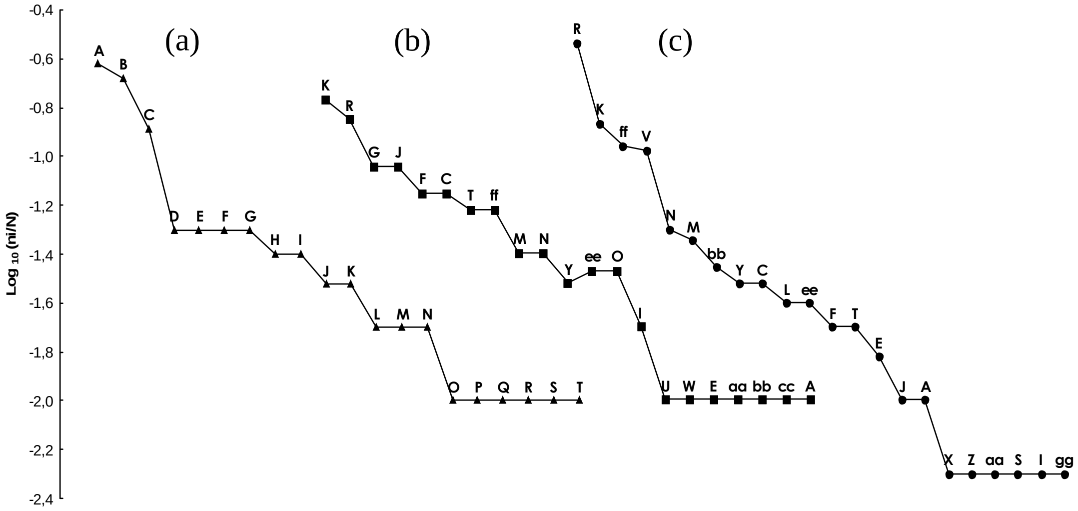


**Fig. 1. Range abundance curves of the amphibian species ensembles that were present in three vegetation cover types in the Colombian Pacific forests. (a) Abandoned mixed farming areas, (b) secondary forests, and (c) mature forests. A. *Smilisca phaeota,* B. *Craugastor raniformis,* C. *Pristimantis achatinus,* D. *Sachatamia ilex,* E. *Diasporus gularis,* F. *Bolitoglossa biseriata,* G. *Hyloscirtus palmeri,* H. *Hypsiboas rosenbergi,* I. *Rhaebo haematiticus,* J. *Espadarana prosoblepon,* K. *Diasporus tinker,* L. *Craugastor fitzingeri,* M. *Pristimantis labiosus,* N. *Pristimantis roseus,* O. *Agalychnis spurrelli,* P. *Allobates talamancae,* Q. *Hyalinobatrachium aureoguttatum,* R. *Pristimantis latidiscus,* S. *Ranitomeya fulgurita,* T. *Bolitoglossa silverstonei,* U. *Bolitoglossa sp,* V. *Craugastor longirostris,* W. *Cruziohyla calcarifer,* X *Diasporus sp.* Y. *Hypsiboas picturatus,* Z. *Leptodactylus pentadactylus,* aa. *Leptodactylus pentadactylus,* bb. *Oophaga histrionica,* cc. *Pristimantis gaigei,* ee. *Pristimantis hybotragus,* ff. *Pristimantis ridens,* and gg. *Rhinella marina*.**

There were no significant differences in the composition of the amphibian ensembles between the seasons (pseudo-F = 1.02; p-perm = 0.43) nor were significant differences observed between seasons and their interaction with the vegetation cover types (pseudo-F = 0.99; p-perm = 0.48). Significant differences were found between vegetation cover types (pseudo-F = 10.2; p-perm = 0.0001) All of the cover types exhibited differences in the composition of the amphibian ensembles: the secondary forest was different from the mature forest (t = 2.16; p-perm = 0.005; similarity percentage between transects= 35.63) and the abandoned mixed farming areas (t = 3.6; p-perm = 0.001; similarity percentage between transects= 26.157). The latter was also different from the mature forest (t = 3.5; p-perm = 0.001; similarity percentage between transects= 23.17).

When analyzing the terrestrial transects (excluding transects parallel to streams), there were no significant differences in the composition of the amphibian ensembles between the seasons (pseudo-F = 1.05; p-perm = 0.43) nor were significant differences observed between seasons and their interaction with the vegetation cover types (pseudo-F = 1.3; p-perm = 0.27). Significant differences were found between vegetation cover types (pseudo-F = 7.7; p-perm = 0.0001). The mature forest was different from the abandoned mixed farming (t = 3.5; p-perm = 0.003; similarity percentage between transects=23, 4; number of shared species=14). The latter was also different from the secondary forest (t = 2.75; p-perm = 0.0002; similarity percentage between transects=28, 2; number of shared species=12). Secondary and mature forest were different (t = 1.75; p-perm = 0.031; similarity percentage between transects=39, 6, 2; number of shared species=13).

When analyzing only the transects parallel to streams (one transect per vegetation cover type), there were no significant differences in the composition of the amphibian ensembles between field trips nested in seasons (pseudo-F = 0.83; p-perm = 0.7) nor were there significant differences between seasons and their interaction with vegetation cover types (pseudo-F = 0.44; p-perm = 0.92).

Significant differences were found between vegetation cover types (pseudo-F = 4.39; p-perm = 0.0009): There were no differences between the mature and secondary forest (t = 1.58; p-perm = 0.11; similarity percentage between transects=32, 44; number of shared species = 7). The abandoned mixed farming areas were different from secondary forest (t = 1.95; p-perm = 0.04; similarity percentage between transects= 27, 52; number of shared species = 9) and from mature forest (t = 2.72; p-perm = 0.012; similarity percentage between transects= 19,6; number of shared species = 4).

**Table 3**. Structural and environmental characterization of the types of vegetation cover.

| | **Abandoned Mixed Farming** | | **Secondary Succession Forest** | | **Mature Forest** | | **Kruskal-Wallis Analysis** |
|---|---|---|---|---|---|---|---|
| **Variables** | **Median (range)** | **SD** | **Median (range)** | **SD** | **Median (range)** | **SD** | |
| Temperature (°C) | 24.63 (21-28)* | 1 | 23.70 (21.5-26.9) | 1.1 | 23.4 (21-26) | 1.2 | H (2, N12)=8.76; p=0.01 |
| Relative Humidity (%) | 91.38 (75-98) | 5.8 | 91.8 (73-97) | 5.3 | 93.6 (73-98) | 4.8 | H (2, N12)=4.15; p=0.12 |
| Leaf litter depth (cm) | 1.79 (0-15)* | 3.0 | 3.1 (0-22) | 22.0 | 3.2 (0-60) | 6.0 | H (2, N12)=6.26; p=0.04 |
| Herbaceous cover (%) | 58.29 (0-100)* | 36.7 | 37.3 (0-100) | 30.8 | 31.5 (0-100) | 26-4 | H (2, N12)=6.73; p=0.03 |
| Canopy cover (%) | 65.22(50-92) | 8.6 | 75 (58-88) | 11-0 | 85.9 (80-92)* | 4.6 | H (2, N12)=6.52; p=0.03 |
| Woody plants (#) | 103.4 (75-305)* | 23.8 | 273.6 (176-388) | 73.1 | 300 (231-325) | 31.5 | H (2, N12)=7.42; p=0.02 |
| Basal area (cm$^2$) | 13,40 (50-13,8) | 13,8 | 35 (9-58,4) | 20,7 | 52.5 (41.8-61.1) | 7.5 | H (2, N12)=3.50; p=0.17 |

* Values are significantly different from the other two vegetation cover types. Refer to the text, in the results section, to consult *p* values between vegetation cover types.

### *Amphibian distribution along environmental and vegetation structure gradients*

From the eight environmental and vegetation structure variables that were measured, only the relationship between basal area and DBH exhibited collinearity ($r^2$ 98%; Appendix 4). DBH were negatively correlated with herbaceous cover (-42%); and positively with canopy cover (56%) and density of woody plants (60%). The density of woody plants was negatively correlated with temperature (-57%) and herbaceous cover (-60%); and positively correlated with basal area (59%) and canopy cover (60%, Appendix 4). Canopy cover was negatively correlated with temperature (-51%); and positively correlated with basal area (62%; Appendix 4).

Four out of seven of the environmental and structural characteristics changed among the cover types. The abandoned mixed farming areas showed the highest values in the average temperature, 24.6°C, and the percentage of herbaceous cover was 58.2%, while in forest habitats the average temperature was 23.7°C in Secondary Forest and 23.4°C in Mature Forest. There were statistical differences between the temperature in abandoned mixed Farming and forest (secondary and mature; H=8.76; p=0.012). Also the abandoned mixed farming showed lower values in the canopy cover 65.2%, density of woody plants 103.4, and depth of the leaf litter layer on the soil 1.79 cm, compared with the secondary forest (canopy cover: 75%; density of woody plants: 273.6; depth of the leaf litter: 3.1 cm) and mature forest cover (canopy cover: 85.9%; density of woody plants: 300; depth of the leaf litter: 3.2 cm). There were statistical differences between these variables in abandoned mixed forest and forest cover (secondary and mature ). The mature forest presented a greater average canopy cover 85.9% (min: 80%; max: 92%) than did the secondary forest and mixed farming areas (H=6.52; p= 0.038) (Table 3).

The variable that best explained the variation in amphibian composition was the density of woody plants (adjusted $R^2$=26%); followed by the interaction between density of woody plants and canopy cover (adjusted $R^2$=34%); and by the interaction among density of woody plants, canopy cover and leaf litter depth (adjusted $R^2$=36%; Table 4).

**Table 4.** Best fitted models, ranked by number of variables, explaining amphibian composition in three vegetation cover types on the Colombian Pacific coast.

| AICc | Adjusted R2 | Residual sum of squared deviations | Number of variables | Selected variable* |
|---|---|---|---|---|
| 182.57 | 0.26156 | 39919 | 1 | 8 |
| 181.45 | 0.33833 | 34143 | 2 | 7,8 |
| 182.5 | 0.35672 | 31613 | 3 | 3,7,8 |
| 183.66 | 0.37887 | 28999 | 4 | 3,7-9 |
| 184.88 | 0.4065 | 26251 | 5 | 2,3,7-9 |
| 187.05 | 0.41902 | 24269 | 6 | 1-3,7-9 |
| 199.62 | 0.38666 | 21099 | 9 | All (9) |

* 1=Temperature; 2= Relative humidity; 3= Leaf litter depth; 4= herbaceous cover; 5= DBH; 6= Basal area; 7= Canopy cover; 8= Density of woody plants; 9= Distance to bodies of water.

Based on the best-adjusted model (using the subroutine DistLM), the first two axes explained the 91.04% variation in the amphibian ensemble (AICc = 182.5; Table 4). Of the eight measured environmental and vegetation structure variables, just three were significant in the best fitted model: the canopy (pseudo-F = 9.04; p = 0.002), the density of woody plants (pseudo-F = 9.14; p = 0.001), and the depth of the leaf litter (pseudo-F = 1.31; p = 0.017). Those variables had a similar explanatory value (i.e., the longitude of each variable) in the changes in the amphibian ensemble compositions among the abandoned mixed farming areas, the secondary forest, and the mature forest (Fig. 2). The canopy cover explained 93% of the changes in the amphibian ensemble composition in the forests (secondary and mature) and in the mixed farming areas. This binary division in the amphibian composition across transects was revealed by the canopy-cover values, which exceeded 76% in the forest and were less than 74% in the mixed farming areas (Fig. 3). The density of woody plants and the depth of the leaf litter explained the 87% change in the amphibian ensemble in two secondary forest transects and in the mixed farming areas (Fig. 3).

## Discussion

In Colombia, the Strabomantidae family accounts for over one-third of the frog species in the country [31], followed by the Hylidae family. This pattern was retained in the composition of amphibian ensembles in the vegetation covers that were studied. Therefore, the species that belong to these three reproductive modes are an important component in the Pacific lowlands (≤1,000 m; [30]), and a high level of species richness has been demonstrated by various authors [6, 33, 34].

The Valle del Cauca Department, the Western mountain range, and the Pacific region possess the largest amphibian species diversity of Colombia. According to Castro-Herrera and Vargas-Salinas [33], the Pacific ecoregion hosts 73 amphibian species and is the region with the second biggest diversity of this group in the Valle del Cauca department. In comparison, our study had a representativeness that was relatively high (43%) of the total historic amphibian species inventory of this entire region, despite the fact that we had a relatively small area.

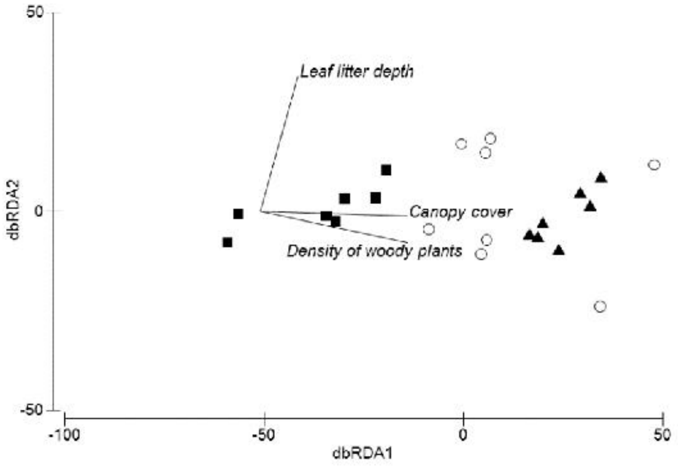


**Fig. 2. Redundancy analysis based on the distances (dbRDA) of the composition of the amphibian ensemble in the abandoned mixed farming areas (■ ), the secondary forests (○ ), and the mature forests ( ▲ ). The first two axes account for 82% and 9% of the variation in the model, respectively. The association, direction, and robustness between the structural variables and the ordering axes are represented by the direction and length of the arrows.**

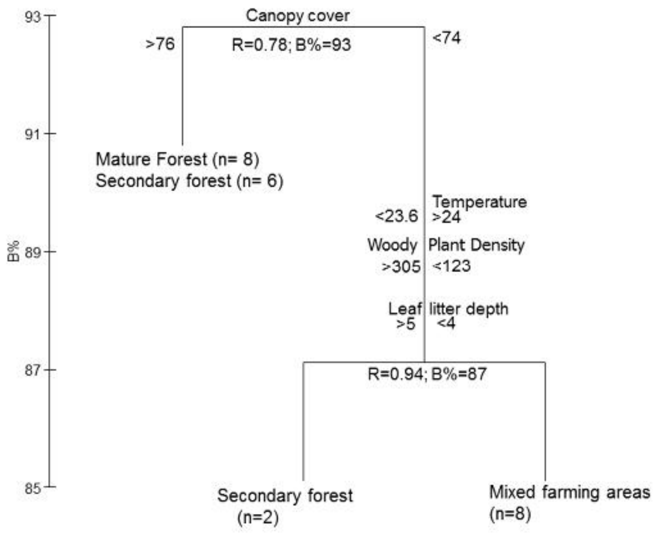


**Fig. 3. Regression/classification tree for the amphibian ensemble composition along the length of transects in three types of plant covers at different successional stages in the Colombian Pacific forests. R= non parametric measure of multivariate difference (or degree of separation) between transects; B% = absolute measure of group difference that is calculated by the average of the between-group ranks as a % of the largest rank in the original resemblance (Bray-Curtis distance) matrix.**

### *Amphibian ensembles along rainforest vegetation gradient*

In the current study, differences in the amphibian species richness were not found among the three forest cover types with different successional stages. Additionally, other studies have not demonstrated differences in the species richness and diversity (using the Shannon-Wiener index) along gradients of anthropogenic disturbance in rainforests [35] or when comparing productive systems and remnant forests [34]. Similar results were reported by Herrera-Montes & Brokaw [37], who found no significant changes in the amphibian and reptile species or in the total abundance among sites with different successional stages. However, they did observe differences in the relative abundance or dominance of the species, which indicates a changing contribution of the various species during forest regeneration. These findings suggest that species richness is not an adequate response variable for observing amphibian ensemble changes over the length of spatio-temporal gradients. This is because in transformed and fragmented landscapes, certain species arise from anthropogenic landscapes, which reach the edges of forests (ecotones) and increase the species richness in some habitats.

Although some unique species reported for the Primary forest are in fact commonly associated with the forest edge or a perturbed forest, they are also associated with riverine forest. This is the case of *Rhinella marina,* which has been reported to be associated with disturbed habitats. However, our study found this species in forest coverage, which also has been reported in other studies (5, 38, 39, 40, 41). On the other hand, glass frog species could be considered as typical species of secondary or primary forests, but they have also been found in gallery forest remnants that are immersed in a transformed matrix [42, 43].

When ensemble composition was analyzed based on the hierarchical positions of the species in the range abundance curve (Fig. 1) and when analyzing separately the transects parallel to streams and terrestrial transects per each vegetation cover type, some patterns appear: (a) there are slightly more species in terrestrial transects than in stream transects on each vegetation cover type; (b) there were more exclusive species at stream transects per vegetation cover type; and (c) secondary forest has fewer exclusive species, maybe due to being an ecotone that shares species with mature forest and mixed abandoned farming. In this regard, mixed abandoned farming has more exclusive species (9) than mature forest (6) and secondary forest (4). Thus, in the abandoned mixed farming areas, it was found that the ensemble was mainly composed of species of the Hylidae family and the dominant species *Smilisca phaeota* and *Craugastor raniformis*. According to Lynch & Arroyo [44], many of the species of this family display low fidelity to forests and a considerable attraction to open areas (whether produced naturally or via habitat modification), especially during their reproductive period, during which they seek stagnant water sources.

Secondary forests act as ecotones in the forest landscape, thereby hosting a high proportion of ensemble species, as well as sharing species from highly intervened areas and from mature forests [6, 45]. However, mature forests exhibit a low level of species richness, and ensembles with a high number of less abundant species that prefer the forest interior are affected by edge effects, and require a higher habitat quality to survive [12, 46]. The above-mentioned phenomenon suggests that the amphibian composition would be different in the three evaluated vegetation cover types, whereas the percentage of similarity between the ensembles would be greater between the secondary and mature forests (36.7%) and lower between the latter and abandoned farming areas (17.6%).

Confirming the results obtained by Vargas-S & Bolaños-L [34] in forests of the Cauca Valley Pacific Coast region and by Urbina-Cardona & Londoño-M [6] on Gorgona Island (Colombian Pacific), the secondary and mature forests appeared to be similar in terms of the composition of their herpeto-faunal ensembles. These findings indicate that the natural secondary forest succession hosts a subgroup of mature forest amphibians, and these forests might contribute to forest conservation in abandoned or degraded areas (*sensu* Gardner *et al.* [47], Pawar *et al*. [48). Nevertheless, to assure the conservation and persistence of amphibian diversity and the general native biodiversity of the region, an adequate recovery of disturbed areas must be achieved. The mosaic pattern of large forest fragments (altitudinal and horizontal) must be maintained in proximity to mixed farming systems that possess a complex vegetation structure and an infrequent and reduced disturbance regime [16].

Thus, while the composition of mature and secondary forests is very similar, the abundance patterns in each ensemble change for each cover type. The present study demonstrates that slight changes in the vegetation structure of the tree canopy cover (threshold of 76% to 74%) and in the leaf litter depth (threshold between 5 cm and 4 cm) cause very significant changes in the composition of the amphibian ensembles between the mixing farming areas and the forests (secondary and mature). In contrast, the relative humidity and temperature were not determining factors in the amphibian ensemble composition along the rainforest vegetation gradients. These findings disagree with the results of Urbina-Cardona and Londoño [6], who suggested that for the amphibian species distribution in coconut fields and abandoned prison areas that have been recolonized by the rainforest vegetation, microhabitat temperature gradients have a greater effect than the vegetation structure [6]. According to Cortés and collaborators [49], the canopy cover may be an important forest component that contributes to the necessary and appropriate environmental conditions for the establishment and persistence of frog species. In the present study, we observed that the cover was also an important component for amphibians inhabiting areas (in this case, the abandoned mixed farming areas) that have undergone interventions and recovery processes for a considerable amount of time. Here, small changes (2%) in the tree canopy provided specific environmental conditions for an ensemble composition that was markedly different from the other two forest cover types and that included species tolerant of certain environmental conditions.

In the rainforests in the area under study, maintaining a canopy cover greater than 76% provides the appropriate environmental conditions for maintaining an amphibian composition that is more similar to a forest than to an intervened area. However, for this amphibian ensemble composition to preserve species belonging to the mature forest, it is also necessary to maintain a high density of woody plants (> 231 individuals per 500 $m^2$) and a habitat with a thick leaf litter layer on the floor (> 23 cm) to provide adequate conditions that would allow for a change from the secondary forest amphibian species to a composition more in line with a mature forest (Table 3). Thus, it is necessary for other vegetation succession events that tend toward a mature forest to occur, including the buffering of edge effects, which allow the re-colonization of groups functioning in a variety of cover types (*sensu* Laurance *et al.* [50]).

However, it is noteworthy that at the forest edge there is a highly dynamic pattern of species flux, from the different matrix to the edge that extends into the forest. At the forest edge there are changes in microclimate and an increase in tree mortality caused by wind turbulence [51]. The constant canopy openings caused by tree mortality promote the movement of light-loving species into the forest interior [52]. Urbina-Cardona et al. [12], found the pasture species, the rainbow lizard *Ameiva undulata* and *Sceloporus variabilis*, in forest interior gaps at 200 m from the edge, and concluded that the intrusion of alien species into the forest interior can modify amphibian and reptile interactions (e.g., competition and predation) as an indirect effect of the creation of gaps in the canopy.

Caceres-Andrade and Urbina-Cardona [36] found that the presence of *Rhinella marina* is directly related to the distance to water bodies and inversely with leaf litter depth. In this study, the unique individual of *R. marina* was found in a canopy gap without leaf litter on the floor at the mature forest. In this regard, it is possible that *R. marina* uses the canopy openings as “stepping stones” to invade the forest interior.

## Implications for conservation

If the animal succession in tropical forests is clarified, then the elements mosaic may be appropriately managed in fragmented landscapes, with the resultant tendency to increase the structural and species functional connectivity in the landscape. As such, it is crucial that information be generated about the amphibian ensemble composition in the Cauca Valley Pacific region, as is recommended in the Action Plan for Amphibian Conservation in the Cauca Valley [53]. Because of the fundamental role played by secondary forests in the conservation of amphibians in the Valle del Cauca Pacific Coast region, it is also crucial that Government and local environmental authorities adopt measures that would help to stop the expansion of coca (*Erythroxylum coca*) fields in the region [54]. Concurrently, the establishment of natural protected areas with proper management and control plans, and with well-defined buffer zones [53] is an indispensable strategy for controlling the deforestation. Currently the recent increase in the population density in the region and the displacement of the protected area staff and conservationists due to the armed conflict [3] create new challenges for biodiversity conservation in the region. In this sense, the role of land conservation through social initiatives becomes increasingly crucial to the conservation of amphibians [55].

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## References

[1] Hartshorn, G. S. 2002. Biogeografía de los bosques neotropicales. In*: Ecología y Conservación de Bosques Neotropicales*. Guariguata, M. R. & Kattan, G. H. (eds), pp. 59-82. Libro Universitario Regional (EULAC-GTZ). Costa Rica.

[2] Etter, A., Mcalpine, C. and Possingham, H. 2008. A historical analysis of the spatial and temporal drivers of landscape change in Colombia since 1500. *Annals of the American Association of Geographers* 98: 2-23.

[3] Armenteras-Pascual, D., Renata-Alumbreros J., Molowny-Horas R., Romana-Cuestas R.M., Gonzales-Alonso F. and Morales-Rivas, M. 2011. Characterising fire spatial pattern interactions with climate and vegetation in Colombia. *Agricultural and Forest Meteorology* 151:279-289.

[4] Etter, A., Mcalpine, C., Phinn, S., Wilson, K. and Possingham, H. 2006. Regional patterns of agricultural land use and deforestation in Colombia. *Agriculture, Ecosystems and Environment* 114: 369-386.

[5] Isaacs, P. and Urbina-Cardona, J. N. 2011. Anthropogenic disturbance and edge effects on anuran ensembles inhabiting Cloud Forest fragments in Colombia. *Natureza e Conservação: Brazilian Journal of Nature Conservation* 9: 39-46.

[6] Urbina-Cardona J. N. and Londoño-M, M. C. 2003. Distribución de la comunidad de herpetofauna asociada a cuatro áreas con diferente grado de perturbación en la Isla Gorgona, Pacífico colombiano. *Revista de la Academia Colombiana de Ciencias* 27:105-113.

[7] Deichmann, J.L., Toft, C. A., Deichmann, P. M., Lima, A. P. and Williamson, G. B. 2012. Neotropical primary productivity affects biomass of the leaf-litter herpetofaunal assemblage. *Journal of Tropical Ecology* 28:427-435.

[8] Urbina-Cardona, J. N. and Reynoso, V. H. 2009. Uso del microhábitat por hembras grávidas de la rana de hojarasca *Craugastor loki* (shannon y werler, 1955) en la Selva Alta Perennifolia de Los Tuxtlas, Veracruz - México. *Revista Mexicana de Biodiversidad* 80:571-573.

[9] Santos-Barrera, G. and Urbina-Cardona, J. N. 2011. The role of the matrix-edge dynamics of amphibian conservation in tropical montane fragmented landscapes. *Revista Mexicana de Biodiversidad* 82:679-687.

[10] Dunn, R. R. 2004. Recovery of Faunal Communities During Tropical Forest regeneration. *Conservation Biology* 18: 302-309.

[11]Saunders, D. A., Hobbs, R. J. and Margules, C. R. 1991. Biological Consequences of Ecosystem Fragmentation: A Review. *Conservation Biology* 5:18-32.

[12]Urbina-Cardona, J. N., Olivares-Pérez, M. and Reynoso, V.H. 2006. Herpetofauna diversity and microenvironment correlates across a pasture-edge-interior ecotone in tropical rainforest fragments in the Los Tuxtlas Biosphere Reserve of Veracruz, Mexico. *Biological Conservation* 132: 61-75.

[13]Lips, K.R. 1998. Decline of a tropical montane amphibian fauna. *Conservation Biology* 12:106-117.

[14]Semlitch, R. 2003. *Amphibian Conservation*. Smithsonian Institution. United States of America.

[15]Wake, D. B. 1991. Declining Amphibian Populations. *Science*. 253:860- 873.

[16]Haddad, C. F. B. & Prado, C. P. A. 2005. Reproductive modes in frogs and their unexpected diversity in the Atlantic Forest of Brasil. *BioScience* 55:207-217.

[17]Crump, M. L. 1974. Reproductive Strategies in a Tropical Anuran Community. *University of Kansas* 61: 1-66.

[18]Pineda, E. and Halffter, G. 2004. Species diversity and habitat fragmentation: frog in a tropical montane landscape in México. *Biological Conservation* 117:499-508.

[19]Urbina-Cardona, J. N. and Reynoso, V. H. 2005. Recambio de anfibios y reptiles en el gradiente potrero-borde-interior en la Reserva de Los Tuxtlas, Veracruz, México. In: Sobre Diversidad Biológica: El significado de las Diversidades Alfa, Beta y Gamma. Halffter, G., Soberón, J., Koleff, P. & Melic, A. (Eds.), pp.191-207. CONABIO, SEA, DIVERSITAS & CONACyT. Volumen 4. Editorial Monografías Tercer Milenio, Zaragoza, España.

[20]Anderson, M. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26:32-46.

[21]Fauth, J. E., Bernardo, J., Camara, M., Resetarits, J R. W. J., Van Buskirk, J. and McCollum, S. A. 1996. Simplifying the jargón of community ecology: a conceptual approach. *The American Naturalist* 147 (2): 282-286.

[22]Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A. B. and Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853-845.

[23]GOOGLE Inc. 2009. Google Earth (versión 6) [Software]. Disponible en www.google.es/intl/es/earth/index.html

[24]Villarreal, H., Álvarez, M., Córdoba, S., Escobar, F., Fagua, G., Gast, F., Mendoza, H., Ospina, M. and Umaña, A. M. 2006. *Manual de métodos para el desarrollo de inventarios de biodiversidad. Programa de Inventarios de Biodiversidad*. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt. Bogotá, Colombia.

[25]Colwell, R. K. 2009. *EstimateS: Statistical estimation of species richness and shared species from samples*. Version 8.2. User's Guide and application published at: http://purl.oclc.org/estimates.

[26]Feinsinger, P., 2001. *Designing Field Studies for Biodiversity Conservation*. Island Press, Washington, DC.

[27]Clarke, K. R and Gorley, R. N. 2006. *PRIMER v6*: User Manual/Tutorial. PRIMER-E, Plymouth.

[28]Anderson, M. J., Gorley, R. N. and Clarke, K. R. 2008. *PERMANOVA + for PRIMER: Guide to Software and Statistical Methods*. PRIMER-E: Plymouth, UK.

[29]Bray, J. R. and Curtis J. T. 1957. An ordination of upland forest communities of southern Wisconsin. *Ecological Monographs* 27:325-349.

[30]STATSOFT. 2001. *STATISTICA: Data Analysis Software System*, Version 6.0. StatSoft, Oklahoma.

[31]Frost, D.R. 2011. *Amphibian Species of the World: an Online Reference*. Version 5.4 (visitado 10 February, 2011). Electronic Database accessible at

http://research.amnh.org/vz/herpetology/amphibia/ American Museum of Natural History, New York, USA.

[32]Lynch, J. D. 1999. Ranas pequeñas, la geometría de evolución, y la especiación en los Andes colombianos. *Revista de la Academia Colombiana de Ciencias* 23:143-159.

[33]Castro-Herrera, F. and Vargas-Salina, S. F. 2008. Anfibios y reptiles en el departamento del Valle del Cauca Colombia. *Biota Colombiana* 9: 251-277.

[34]Vargas-S, F. and Bolaños-L, M. E. 1999. Anfibios y Reptiles presentes en hábitats perturbados de selva lluviosa tropical en el Bajo Anchicayá, Pacífico colombiano. *Revista de la Academia Colombiana de Ciencias* 23 (Special issue): 499-511.

[35]Pearman, P.B. 1997. Correlates of amphibian diversity in an altered landscape of Amazonian Ecuador. *Conservation Biology* 11:1211-1225.

[36]Cáceres-Andrade, S. and Urbina-Cardona, J. N. 2009. Ensamblajes de anuros de sistemas productivos y bosques en el piedemonte llanero, Departamento del Meta, Colombia. *Caldasia* 31:175-194.

[37]Herrera-Montes, A. and Brokaw, N. 2010. Conservation value of tropical secondary forest: A herpetofaunal perspective. *Biological Conservation* 143: 1414-1422.

[38]Cogger, H. 1983.*Reptiles and Amphibians of Australia*. Sanibel, Florida: Ralph Curtis Press.

[39]Krakauer, T. 1968. The Ecology of the Neotropical Toad, *Bufo marinus* in southern Florida. *Herpetologica*, 24(3): 214-221.

[40]Ibáñez, R., Solís, F., Jaramillo, C. and Rand, A. S. 2000. An overview of the herpetology of Panama. In: Johnson, J. D, Webb, R. G. and Flores-Villela, O.A. Eds. Mesoamerican Herpetology: Systematics, Zoogeography and Conservation, pp. 159-170. The University of Texas at El Paso, El Paso, Texas.

[41]Savage, JM. 2002. The Amphibians and Reptiles of Costa Rica: A Herpetofauna between two Continents, between two Seas. University of Chicago Press, Chicago.

[42]Valencia-Aguilar, A., Castro-Herrera, F. and Ramirez-Pinilla, M.P. 2012. Microhabitats for oviposition and male clutch attendance in *Hyalinobatrachium aureoguttatum* (Anura: Centrolenidae). Copeia 2012(4):722-731.

[43]Cabazo-Olarte L.C., Ramirez-Pinilla M.P. & Serrano-Cardozo V.H. 2013. Oviposition, Site preference, and evaluation of male clutch attendance in *Espadarana andina* (Anura: Centrolenidae). Journal of Herpetology, Vol.47(2): 314-320.

[44]Lynch, J. D. and Arroyo S. B. 2009. Risks to Colombian Amphibian Fauna from Cultivation of Coca (Erythroxylum coca): A Geographical Analysis. *Journal of toxicology and Environmental* Health, Part A, 72: 974-985.

[45]Rios-López, N. and Aide, T. M. 2007. Herpetofauna dynamics during secondary succession. *Herpetologica* 63: 35-50.

[46]Heinen, J. T. 1992. Comparisons of the leaf litter herpetofauna in abandoned cacao plantations and primary rain forest in Costa Rica: Some implications for faunal restoration. *Biotropica* 24: 431-439.

[47]Gardner, T. A., Ribeiro-Júnior, M. A., Barlow, J., Sauer Ávila-Pires, T. C., Hoogmoed, M. S. and Peres, C. A. 2007. The Value of Primary, Secondary, and Plantation Forests for a Neotropical Herpetofauna. *Conservation Biology* 21: 775-787.

[48]Pawar, S. S., Rawat, G. S. and Choudhury, B. C. 2004. Recovery of frog and lizard communities following primary habitat alteration in Mizoram, Northeast India. *BMC Ecology* 4: 1-18.

[49]Cortés, A. M., Ramirez-Pinilla, M. P., Suarez, H. A. and Tovar, E. 2008. Edge effects on richness, abundance and diversity of frogs in andean cloud forest fragments. *South American Journal of Herpetology* 3: 213-222.

[50]Laurance, W. F., Camargo, J. L. C., Luizao, R. C. C., Laurance, S. G., Pimm, S. L., Bruna, E. M., Stouffer, P. C., Williamson, G. B., Benitez-Malvido, J., Vasconcelos, H. L., Van Houtan, K. S., Zartman, C. E., Boyle, S. A., Didham, R. K., Andrade, A. and Lovejoy T. E. 2011. The

fate of Amazonian forest fragments: A 32-year investigation. *Biological Conservation* 144:56-67.

[51]Laurance, W.F., Lovejoy, T. E., Vasconcelos, H. L., Bruna, E. M., Didham, R. K., Stouffer, P. C., Gascon, C., Bierregaard, R. O., Laurance, S. G. and Sampaio, E. 2002. Ecosystem Decay of Amazonian Forest Fragments: a 22-Year investigation. *Conservation Biology* 16(3):605-618.

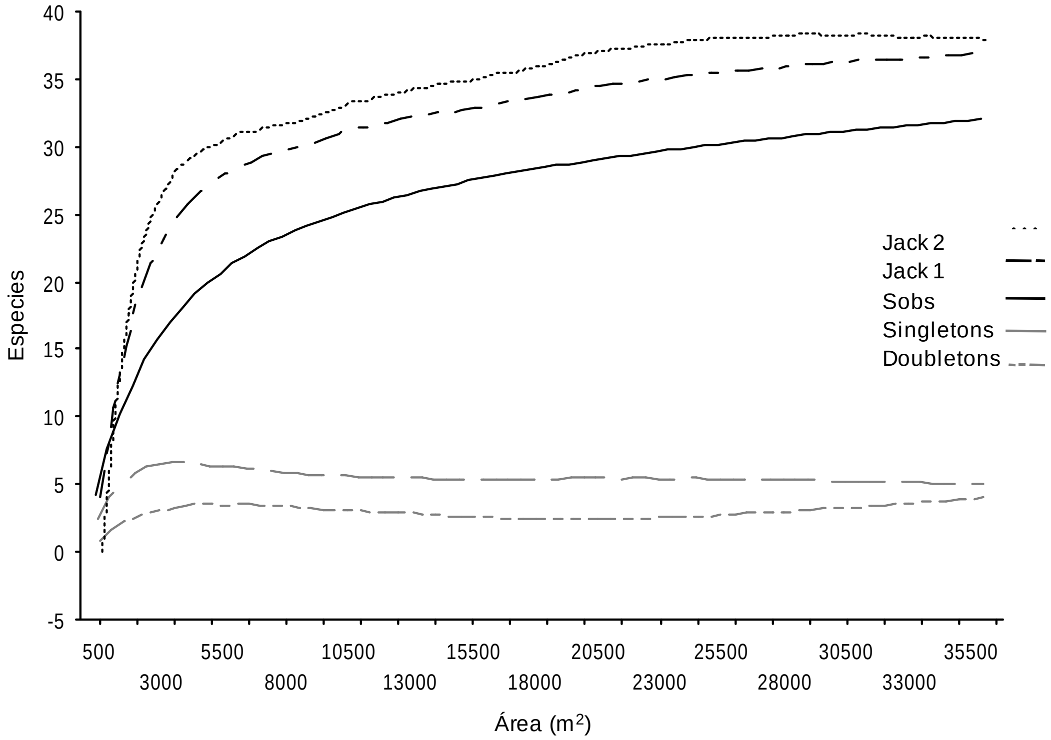
[52]Sartorius, S. S., Vitt, L. and Colli, G. R. 1999. Use of naturally and anthropogenic disturbed habitats in Amazonian rainforest by the teiid lizard *Ameiva ameiva*. *Biological Conservation* 90:91–101.

[53]Corredor-Londoño, G., Velásquez-Escobar, B., Velasco-Vinasco, J. A., Castro-Herrera, F., Bolívar-García, W. and Salazar-Valencia, M. L. 2010. *Plan de Acción para la conservación de los anfibios del departamento del Valle del Cauca.* Corporación Autónoma del Valle del Cauca-CVC, Fundación Zoológica de Cali y Universidad del Valle- Laboratorio de Herpetología.

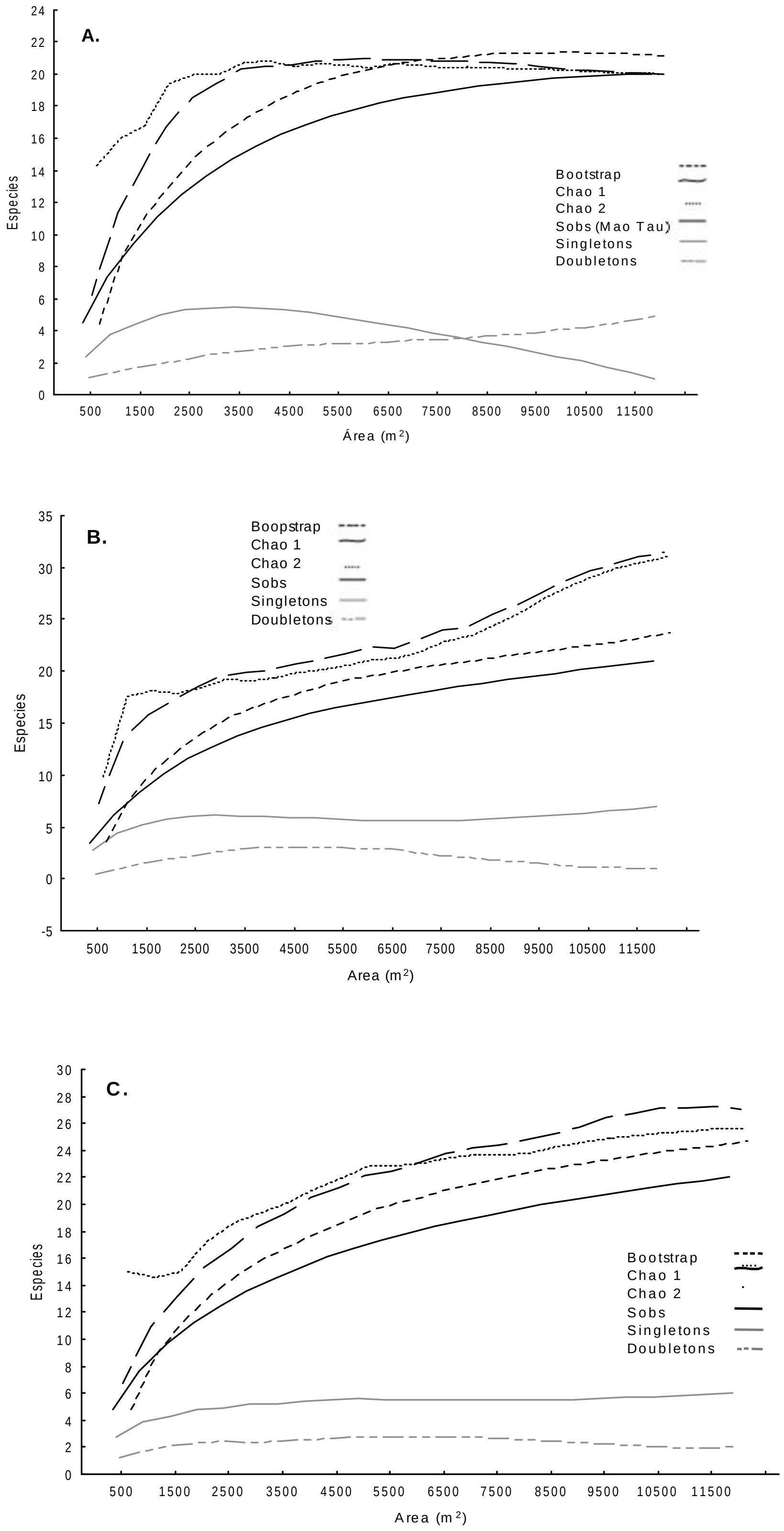
[54]Davalos, L. M., Bejarano, A. C., Hall, M. A., Correa, H. L., Corthals, A. and Espejo, O. J. 2011. Forests and Drugs: Coca-Driven Deforestation in Tropical Biodiversity Hotspots. *Environmental Science Technology* 45:1219–1227.

[55]Ochoa-Ochoa, L., Urbina-Cardona, J. N., Vázquez, L. B, Flores-Villela, O., and Bezaury-Creel, J. 2009. The Effects of Governmental Protected Areas and Social Initiatives for Land Protection on the Conservation of Mexican Amphibians. *PLoS ONE*: 4: e6878.

**Appendix 1.** Accumulation curves for the species in all of the forest types with different successional stages that were sampled on the Colombian Pacific coast.



**Appendix 2**. Accumulation curves for the species in each successional stage. (**A**) Abandoned mixed farming areas, (**B**) secondary forests, and (**C**) mature forests.



**Appendix 3**. Composition, richness, and relative abundance of the amphibian species found in streams at three vegetation cover types in the Colombian Pacific coast rainforest.

| **Species name** | **Abandoned Mixed Farming** | **Secondary Succession Forest** | **Mature Forest** |
|---|---|---|---|
| *Agalychnis spurrelli* | 1 | 2 | |
| *Allobates talamancae* | 1 | | |
| *Bolitoglossa biseriata* | 2 | 1 | |
| *Bolitoglossa silverstonei* | | | 1 |
| *Sachatamia ilex** | 10 | | |
| *Centrolene prosoblepon* | 4 | 8 | |
| *Craugastor longirostris* | | | 5 |
| *Craugastor raniformis* | 15 | | |
| *Cruziohyla calcarifer** | | 1 | |
| *Diasporus gularis* | 1 | | 1 |
| *Diasporus sp.** | | | 1 |
| *Diasporus tinker* | 3 | 2 | 2 |
| *Hyalinobatrachium aeroguttatum** | 2 | | |
| *Hyloscirtus palmeri* | 7 | 8 | |
| *Hypsiboas picturatus** | | 4 | 6 |
| *Hypsiboas rosenbergi* | 1 | | |
| *Lithobates vaillanti** | | 1 | 1 |
| *Oophaga histrionica* | | | 1 |
| *Prisitmantis hybotragus* | | 1 | |
| *Pristimantis achatinus* | 3 | 1 | |
| *Pristimantis labiosus* | 3 | | |
| *Pristimantis latidiscus* | 1 | 1 | 10 |
| *Pristimantis ridens* | | | 2 |
| *Pristimantis roseus* | 1 | 1 | 1 |
| *Rhaebo haematiticus* | 5 | | |
| *Smilisca phaeota* | 14 | 1 | 1 |
| Total abundance | 74 | 32 | 32 |
| Species richness | 17 | 13 | 12 |

*species encountered exclusively at transects on streams

**Appendix 4.** Pearson correlation coefficient between the environmental and structural variables that were measured in the Colombian Pacific coast vegetation cover types.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|---|---|---|---|---|---|---|---|---|---|
| Temperature (1) | 1.00 | | | | | | | | |
| %Relative Humidity (2) | 0.29 | 1.00 | | | | | | | |
| Leaf Litter Depth (3) | -0.17 | -0.16 | 1.00 | | | | | | |
| %Herbaceus cover (4) | 0.31 | 0.17 | -0.43[a] | 1.00 | | | | | |
| DBH (5) | -0.31 | -0.24 | -0.14 | **-0.42[a]** | 1.00 | | | | |
| Basal Area (6) | -0.36 | -0.31 | -0.22 | -0.37 | **0.98[c]** | 1.00 | | | |
| %Canopy cover (7) | **-0.51[b]** | -0.32 | -0.07 | **-0.52[b]** | **0.56[b]** | **0.62[c]** | 1.00 | | |
| Density of woody plants (8) | **-0.57[c]** | -0.27 | 0.27 | **-0.60[b]** | **0.60[b]** | **0.59[c]** | **0.60[c]** | 1.00 | |
| Distance to bodies of water (9) | 0.06 | -0.10 | -0.06 | 0.25 | 0.13 | 0.20 | -0.25 | -0.17 | 1.00 |

*p* values [a] ≤ 0.05, [b] ≤ 0.01, [c] ≤ 0.001.