

Classification and sensitivity of taxonomic and functional diversity indices of anurans in the Andean coffee cultural landscape

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ABSTRACT

Taxonomical and functional facets of diversity are crucial to understanding the effects of landscape transformation on species assemblages, although there is a lack of consensus on the degree of congruence between diversity indices across land-uses. We evaluated the effect of natural and anthropogenic land cover types on anurans in the Andean region of Colombia. Changes between land cover types were detected but no effect of climatic season on the structure of anuran assemblages. Species with larger body sizes showed a greater affinity for anthropogenic land cover types. We analyzed the functional facet of diversity (based on diet and morphological traits) and discovered that the degree of congruence with taxonomic diversity metrics changed when comparing different land cover types. We evidenced a strong effect of the type of vegetation cover on the Hill numbers (from zero to third orders) for functional diversity but not for the other taxonomic diversity indices. Of all the diversity metrics evaluated, we found that Rao's quadratic entropy, functional dispersion, and average functional diversity were the most sensitive indices to land-use change. Surprisingly, the surrounding of houses, the land cover type with the greater degree of anthropogenic intervention had the higher values of functional diversity, suggesting broader types of species resource acquisition. These results suggest the importance of landscape mosaics in the conservation of different facets of anuran diversity. We also emphasize the importance of measuring anuran functional traits to understand more comprehensively the effects of landscape transformation at the assemblage level and to appropriately direct conservation and management actions.

1. Introduction

Changes in land use and cover have become one of the major environmental filters guiding the structuring of assemblages in transformed landscapes (Sala et al., 2000; Zebisch et al., 2004; Echeverría-Londoño et al., 2016; Nowakowski et al., 2018). Traditional approaches to studying the effect of landscape transformation on assemblages are based on the measurement of species richness, composition, and their relative abundances (Pavoine et al., 2016). However, this facet of diversity ignores the identity of the species, their contribution to the functioning of ecosystems (Hooper et al., 2005; Díaz et al., 2013), or their response to spatiotemporal gradients (Álvarez-Grzybowska et al., 2020; Jiménez-Vargas et al., 2021). In that sense, it is possible to

understand the different ways in which the species of the assemblage respond to landscape transformation by measuring their morphological, physiological, and life-history functional traits (Díaz & Cabido, 2001; Petchey & Gaston, 2006; Violle et al., 2007; Díaz et al., 2013; Thompson et al., 2015).

Although the study of the facets of taxonomic and functional diversity in transformed landscapes has increased (Morelli et al., 2018; Rincón-Aranguri et al., 2019; Ramírez-Mejía et al., 2020), our knowledge is still very limited regarding the degree of spatial congruence between their metrics (Devictor et al., 2010; Baraloto et al., 2012). We also are far of consensus about the sensitivity degree of diversity indices to anthropogenic environmental filters and their redundancy in terms of the information they provide (Hooper et al., 2005; Devictor et al., 2010;

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Mouchet et al., 2010; Luck et al., 2012; Cadotte & Tucker, 2018). Therefore, it is crucial to determine how the congruence between taxonomic and functional diversity varies between natural and anthropogenic land cover types, to guide the studies on functional traits towards the management and conservation of transformed landscapes (Morelli et al., 2018).

Amphibians are sensitive to the anthropogenic transformation of their habitats due to some functional traits (Cortés-Gómez et al., 2016) such as highly permeable skin that makes them susceptible to dehydration and highly dependent on ambient temperature to carry out their vital processes (Semlitsch, 2003). In addition, amphibians have a wide variety of reproductive modes that associate them with specific vegetation structures and water bodies that give them adequate resources for the development of their different stages (Wake & Vredenburg, 2008; Almeida-Gomes & Rocha, 2015). Likewise, they participate in different processes at the ecosystem level (Galindo-Urbe & Hoyos-Hoyos, 2007; Cortés-Gómez et al., 2015), within which their role as predators and potential controllers of insect populations represents other potential benefits for humans (Stebbins & Cohen, 1995; Whiles et al., 2006; Hoyos-Hoyos et al., 2012). Therefore, the loss of amphibian diversity might represent a change in the functionality of ecosystems (Whiles et al., 2006; Whiles et al., 2013) and in the ecosystem services they provide (Hocking & Babbitt, 2014). However, very few studies of functional ecology of amphibians have been carried out in transformed ecosystems (Trimble & van Aarde, 2014; Díaz-García et al., 2017; Ribeiro et al., 2017; Riemann et al., 2017; Hernández-Ordóñez et al., 2019; Dehling & Dehling, 2021).

Globally, amphibians are the most endangered group of vertebrates, and the main cause is the transformation of natural covers to anthropogenic matrices (IUCN, 2021). The tropical Andes is one of the regions with the greatest impact of agricultural intensification (Etter et al., 2006) and the highest number of threatened amphibian species without representation in protected natural area systems (Nori et al., 2015). However, beyond the relationships between richness and climate, the diversity of amphibians inhabiting tropical montane forests has not been explained from a functional trait-based perspective (Tobar-Suárez et al., 2021). As the agricultural frontier advances in Andean landscapes, the risk of extinction of endemic amphibians increases (Agudelo-Hz et al., 2019). The coffee region is one of the areas with the highest rate of transformation and habitat loss in Colombia, conserving only 30% of its original natural forests (Ecoandina & WWF-Colombia, 2004). This loss of native forest was due in part to the arrival of coffee crops in the late 1800s (Monsalve, 1927; Palacios 2002) and the increase in the extension of pastures for livestock around 1960 (Van Ausdal, 2009). Currently, the coffee cultural landscape (UNESCO, 2011) represents a mosaic of areas for livestock and agriculture with patches of bamboo (*Guadua angustifolia*) and Andean Forest which have been conserved to preserve water supplies and provide habitat for biodiversity (IGAC, 1996).

To measure the effect of natural and anthropogenic land cover types over anuran taxonomic and functional diversity on the Andean coffee region of Colombia we set five objectives: (a) to identify changes in the assemblage structure of anurans found in different types of land cover; (b) to determine changes in functional traits between land cover types and climatic season; (c) to classify taxonomic and functional diversity indices according to changes in their values across different land cover types; (d) to identify those indices that, due to their sensitivity, show changes to the different types of land cover; (e) to explore changes in the congruence between indices of taxonomic and functional diversity across land cover types. Our goals contribute to the controversy that points to the potential redundancy between the different diversity indices (Mouchet et al., 2010), but also highlights their importance in the complementarity of the information they provide (Legras et al., 2018). We expect to have similar species richness but a high turnover of species among anuran assemblages inhabiting natural and anthropogenic land covers due to the different degrees of tolerance of the species in each land cover type (Roach et al., 2020), and we expect the

assemblage structure to vary depending on the climatic season (Álvarez-Grzybowska et al., 2020). We expect to find that the different facets of diversity differ in the information they provide, as well as in their level of sensitivity, or ability to evidence the changes in the assemblages, due to the different ecological processes occurring within them (Baraloto et al., 2012; Morelli et al., 2018). We expect greater functional richness (Fric) in natural covers because anurans are encompassing a larger functional space compared to species inhabiting anthropogenic land cover types, where greater homogenization of assemblages is expected (Mouchet et al., 2010). In contrast, greater functional equity (Feve) would be expected in anthropogenic cover given the high abundances of a few species in the assemblages which may have an equitable distribution of abundance in the value of their traits (Mason et al., 2005). In this study, we use the indices of Hill numbers of taxonomic and functional diversity from the proposal of Chiu and Chao (2014), due to their principle of replicability between facets considering differences in the degree of species evenness in the assemblages, from their parameter q . Therefore, we expect to find an increase in the Hill numbers of taxonomic and functional diversity that give greater weight to the most abundant species, in the anthropogenic land cover types with a higher degree of intervention.

2. Methods

2.1. Study area

The coffee region of Colombia was declared a World Heritage Site by UNESCO (2011), an area of the country distributed in the departments of Caldas, Quindío, Risaralda, and Valle del Cauca. This region is influenced by mountainous relief that conditions humidity in the central mountain range and the Cauca River canyon. It has an average temperature between 18 °C and 21 °C (IGAC, 1996) and a bimodal precipitation regime with a range of average annual precipitation of 1800 mm with rainy periods from March to May, and September to November and a dry season during the months of January to February and from June to August.

2.2. Sampling

Sampling of the anurans was carried out during field trips between June 2006 and April 2008, in six farms located in the Departments of Quindío and Valle del Cauca at an altitude between 1200 and 1650 masl (Isaacs-Cubides & Hoyos-Hoyos, 2010; Hoyos-Hoyos et al., 2012; Moreno-Barbosa & Hoyos-Hoyos, 2014; Fig. 1). Fieldwork was carried out daily in the morning at 0900–1200 hrs, afternoon at 1500–1800 hrs, and night at 1900–2400 hrs. We searched for visual encounters (Heyer et al., 1994) of anuran individuals, post-metamorphic adults, and juveniles in six natural and anthropogenic land cover types (forest, forest-bamboo ecotone, bamboo, crops, pastures, and around houses), with a total effort of 210 man-hours. The specimens and their stomach contents were collected and deposited in the Natural History Museum of the Pontificia Universidad Javeriana (Isaacs-Cubides & Hoyos-Hoyos, 2010; Hoyos-Hoyos et al., 2012; Moreno-Barbosa & Hoyos-Hoyos, 2014).

2.3. Data analysis

2.3.1. Changes in the assemblage structure of anurans between land cover types and climatic season

A prediction of the total number of anuran species was made as a function of species accumulation, determined by non-parametric Chao 2, Jackknife 1, and Bootstrap estimators with 9999 permutations (Ugland et al., 2003) in the PRIMER program v. 7.0.13 (Clarke & Gorley, 2015). To determine the sampling completeness, for each land cover type, we calculated the percentage that the observed number of species represented of each of the species richness estimators (Chao & Chiu, 2014). We test for spatial autocorrelation between farms using a Moran's Index

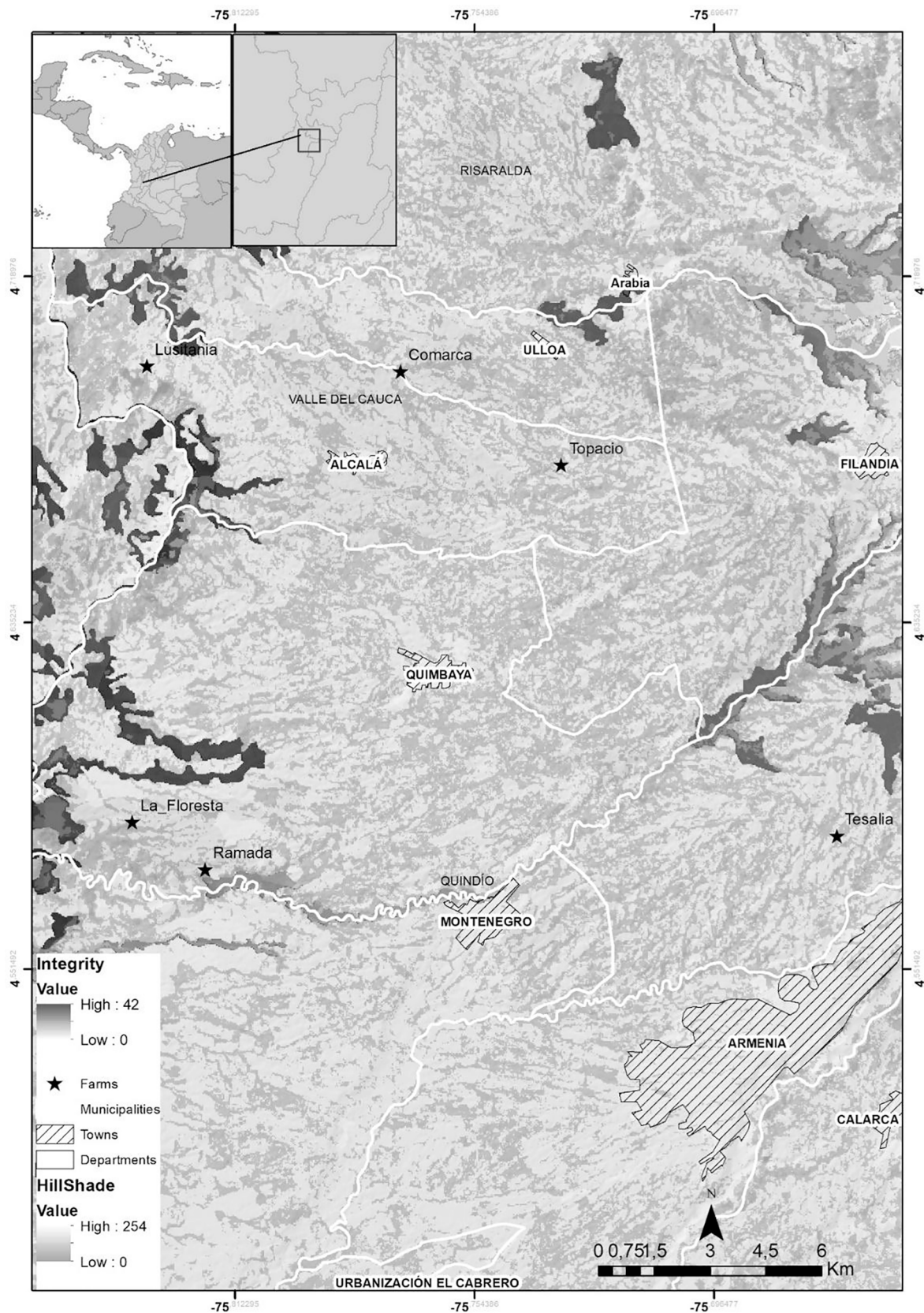


Fig. 1. Study area. Sampled farms (represented by a black star) between the Departments of Quindío and Valle del Cauca in the Coffee Region in the Andes of Colombia. The darker areas correspond to zones that present the more preserved covers related to landscape composition, the size and shape of patches, the distance between patches, and the structure of the vegetation (Hansen, et al., 2019; Isaacs-Cubides et al., 2021).

in Arcgis program v. 10.7 (ESRI, 2021).

The differences in the structure of the anuran assemblage between land cover types were evaluated using a two-way multivariate analysis of variance based on permutations (PERMANOVA), from the Bray - Curtis similarity matrix of square root transformed values, the sequential sum of the squares type I, and 9,999 permutations of the residuals under a reduced model. The sequential sum of squares is appropriate for designs that include covariates, in which each factor is fitted after considering all previous terms in the model (Anderson et al., 2008). The experimental design had two factors: season (fixed with two levels: dry and rainy seasons) and land cover type (fixed with six levels: Pasture, Bamboo, Forest, Forest-Bamboo, Crop, and House); and farms (six levels) were included into the model as a covariate without interactions with the two fixed factors. In the PERMANOVA the effect size is evaluated from the estimated component of variation of each factor and their interactions (Anderson, 2014). When an effect was detected on one of the factors, we compared within levels using a posteriori pair-wise t-statistic test with 9,999 permutations of residuals under a reduced model (Anderson et al., 2008).

We explored changes in anuran assemblage structure with Whitaker's (1952) association index across land cover types through a shade plot (Sommerfield & Clarke, 2013). This classification technique represented the association of the species by farm-land cover type based on a color palette that varied from black (showing the highest level of association of a species for a specific land cover type) to pale grey when there was a low level of association (Clarke et al., 2014). We inspected for significant multivariate structure on the classifications between species and farm-land cover types, allowing us to detect the degree of deviation of the observed profile relative to the null distribution of the permuted profiles (Clarke et al., 2008). These analyses were performed in the PRIMER v. 7.0.13 and PERMANOVA add on software (Anderson et al., 2008; Clarke & Gorley, 2015).

2.3.2. Changes in functional traits between species, land cover types and climatic season

We measured morphometric and dietary traits, for a total of 299 individuals in nine anuran species that consume 21 dietary items. For morphometric traits, seven parameters were selected from the protocols for measuring functional traits by Cortés-Gómez et al. (2016), Hernández-Ordóñez et al. (2019), and Mendoza-Henao et al. (2019): snout-vent length (SVL), mouth width (ABC), forelimb humerus length (AIAC), forelimb radius length (AIBC), posterior limb femur length (PIAC), and length of the tibia of the hind limb (PIBC). For the dietary traits, the percentages of occupation of dietary items in the stomachs per individual were used, based on the studies carried out by Hoyos-Hoyos et al. (2012), Isaacs-Cubides and Hoyos-Hoyos (2010), and Moreno-Barbosa and Hoyos-Hoyos (2014). From these percentages, the Hill numbers of taxonomic diversity were calculated as a measure of the diversity of the dietary items per species. Hill numbers correspond to diversity indices that incorporate the relative richness and abundance of the species; but they differ in the parameter q , which determines their sensitivity to the relative abundance of species (Chao, 1984; Chao & Jost, 2012). The numbers include species richness ($q = 0$ Diet), Shannon diversity ($q = 1$ Diet; the exponential of entropy), and Simpson diversity ($q = 2$ Diet; the inverse of Simpson's index) (Chao et al., 2014; Chiu & Chao, 2014).

To establish the degree of correlation between the morphometric variables and the Hill numbers of the diet, bivariate Pearson correlations were performed. The Hill numbers ($q = 0$ Diet, $q = 1$ Diet, and $q = 2$ Diet), obtained for the 21 items of the diet of the individuals present in the different land covers were highly correlated with each other. From the bivariate correlations between the morphometric traits considered, a high correlation coefficient was observed between all the traits with snout-vent length (SVL). The $q = 1$ Diet Hill number was the one that showed the highest correlation coefficient with $q = 0$ Diet and $q = 2$ Diet (Appendix 1). Based on these exploratory analyses, for the $q = 1$ Diet and SVL, we conducted a three-way PERMANOVA (Anderson et al., 2008)

analysis with land cover type, climatic season, and species as fixed factors, and farms as a covariate. The configuration of these analyses was the same as those performed for the structure of the anuran assemblage.

2.3.3. Classification of taxonomic and functional diversity indices across land cover types

For each land cover type per farm and season, the facets of taxonomic and functional diversity were characterized on the measurement of 23 indices. This was done by obtaining the Hill numbers according to Chao et al. (2014) and Chiu and Chao (2014), by using the hillR (Li, 2018) package in the R environment (R Core Team, 2019). For taxonomic diversity, understood as the effective number of taxonomic entities, Hill numbers of order $q = 0$, $q = 1$, and $q = 2$ were obtained, which corresponded to species richness, Shannon and Simpson, respectively. Functional diversity, through Hill numbers, measured the effective number of pairs of functionally equally species (from the values in the two measured functional traits: SVL and Hill number $q = 1$ of the Diet), corresponding to the Hill numbers of order $q = 0$, $q = 1$, $q = 2$ and $q = 3$ for the following metrics (see Appendix 2 for more information): Rao's quadratic entropy (Q); the functional Hill numbers (D(Q)); the mean functional diversity (MD(Q)); and total functional diversity (FD(Q)). A functional dispersion metric (FDis) was also calculated (Laliberté & Legendre, 2010).

We classify the taxonomic and functional diversity indices based on cluster analysis and using a similarity profile permutation test (SIMPROF with 9,999 permutations) to inspect for significant multivariate structure allowing us to detect the degree of deviation of the observed profile relative to the null distribution of the permuted profiles (Clarke et al., 2008).

2.3.4. Identifying indices sensitive to land cover types and their congruency

A Euclidean distance matrix was calculated for all the taxonomic diversity indices (the facet of taxonomic diversity), and for all the functional diversity indices (the facet of functional diversity), to evaluate these facets holistically. For each of the diversity indices, and the facets of taxonomic and functional diversities we conducted a two-way PERMANOVA (Anderson et al., 2008) analysis with land cover type and climatic season as fixed factors, and farms as a covariate. The configuration of these analyses was the same as those performed for the structure of the anuran assemblage. The size effect of the factors was calculated from the sum of the estimated components of variation of each factor and its explained percentage of variation. This calculation was made for each index of taxonomic or functional diversity that had a significant effect as a response variable (Anderson, 2014). Finally, to quantify the congruence between the facets of taxonomic diversity and functional diversity, bivariate Pearson correlations were performed between the different indices in the R environment (R Core Team, 2019).

3. Results

3.1. Changes in the assemblage structure of anurans between land cover types and climatic season

We found that there is no spatial autocorrelation between farms (Moran index (I) $z = -2.17$ p -value = 0.029). The mean completeness of anuran inventory was 91.4% for all the study areas and ranged between 82 and 100% for each land cover type (Appendix 3). The structure of the anuran assemblages was different between land cover types ($p(\text{perm}) < 0.0001$; Appendix 4); with 28.36% estimated component of variation this factor had the highest effect size between all the evaluated factors. The shade plot differentiated two groups of species according to their association by land cover types: species with high affinity for anthropogenic land cover types such as pastures and surroundings of houses and species with high affinity for non-anthropogenic cover types such as forest and bamboo (Fig. 2).

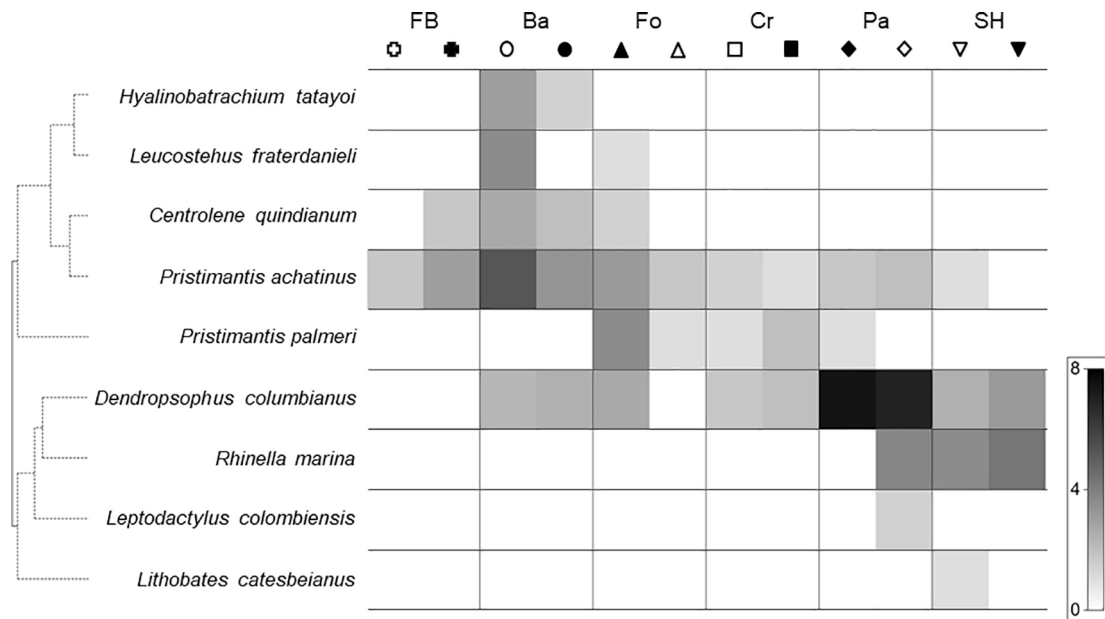


Fig. 2. Shadeplot of anuran assemblages associated with farms and land cover types at the coffee region in the Andes of Colombia. Land cover types correspond to forest-bamboo ecotone (FB), bamboo (Ba), forest (Fo), crops (Cr), pastures (Pa), and surroundings of houses (SH). Filled symbols correspond to the rainy season and empty symbols to the dry season. For each species, their degree of association with land cover types is represented with a color palette that goes from black (representing the highest level of association of a species for a specific land cover type), light grey when there is a weak association, and white when there is no association. Species were classified into tow groups that show a different multivariate structure.

3.2. Changes in functional traits between land cover types and climatic season

No significant differences were observed in the Hill number of Diet $q = 1$ per farm ($p(\text{perm}) = 0.242$), land cover type ($p(\text{perm}) = 0.868$), climatic season ($p(\text{perm}) = 0.996$), but significant differences were seen in the SVL ($p(\text{perm}) < 0.001$) per land cover type ($p(\text{perm}) < 0.001$) and species ($p(\text{perm}) < 0.001$), with a factor effect size of 30% and

58%, respectively (Appendix 5). The largest species occurred in pastures and surroundings of houses (Fig. 3).

3.3. Classification of taxonomic and functional diversity indices across land cover types

From the similarity profile routine, it was possible to classify the 23 diversity indices into 13 distinguishable groups, according to the change

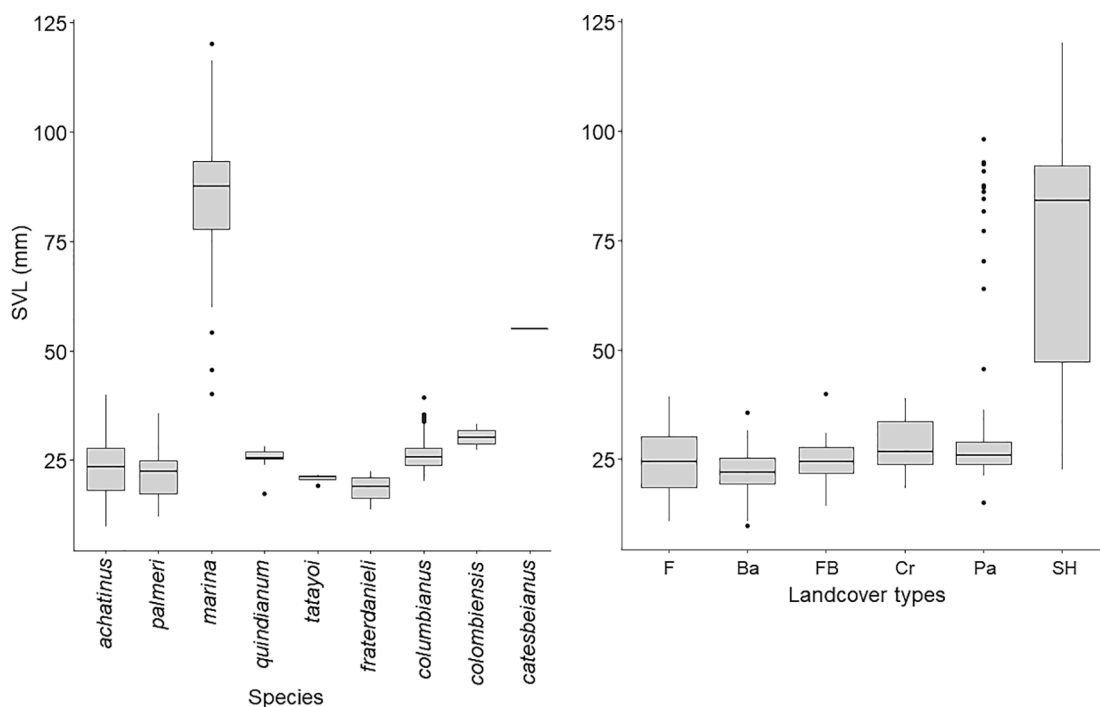


Fig. 3. Median and upper and lower quartiles of snout-vent length (SVL) per anuran species (left) and by land cover type (right): forest (Fo), forest-bamboo ecotone (FB), bamboo (Ba), crops (Cr), pastures (Pa), and surroundings of houses (SH). The complete name of the species is shown in Fig. 2.

in their values between land cover types and climatic season (Fig. 4).

3.4. Identifying indices sensitive to land cover types and their congruency

The Rao's quadratic entropy (Q), the functional dispersion (FDis) of orders $q = 0$ and $q > 0$, and the mean functional diversity (MD(Q)) of order $q > 1$, showed significant differences between land cover types, but none of the indices varied between climatic seasons or farms (Appendix 4, Fig. 5). Neither climatic season, nor farms, nor their interactions with land cover types affected on the q orders of taxonomic diversity (Appendix 4). The effect size of land cover type as a factor, for Hill's numbers of functional diversity as a response variable, ranged from 18.3 to 26.7%, with an average of 23.6%. The land cover type with the highest degree of anthropic intervention, that is surroundings of houses (SH), was the one with the highest values of functional diversity and differed from forest, bamboo, and crops. Surrounding of houses differed from bamboo (Ba) and forest (Fo) in Rao's quadratic entropy and functional dispersion of $q = 0$ and $q > 0$. The surrounding of houses also differed from the forest in the average functional diversity of $q > 0$ (Fig. 5, Appendix 6). The correlation coefficients between the indexes sensitive to changes in land cover types were > 0.9 for all coverage and showed a positive trend (Appendix 7).

4. Discussion

The conservation of biodiversity ensures the provision of ecosystem services through the ecological processes it offers and the resilience it gives to ecosystems after disturbances such as agriculture (Tilman et al., 1997; Díaz et al., 2013; Mason et al., 2005). Therefore, understanding the factors that put the integrity of biodiversity at risk due to the transformation of ecosystems is a priority for ecologists and conservationists (Cadotte et al., 2011; Díaz et al., 2013; Chao et al., 2014). The historical dynamics of transformation that faces the region of study, has left a mosaic of land cover that surrounds small remnant patches of native forest. According with the data from integrity of the land covers (Isaacs Cubides et al., 2020), the study farms are located in an area with medium to high levels of intervention that are highly fragmented and historically differ from the original composition of the forests (see

Fig. 1).

4.1. Changes in the assemblage structure and functional traits of anurans between land cover types and climatic season

We detected variation in the structure and composition of the anuran assemblages that inhabit the different natural and anthropogenic land cover types (Appendix 1, Fig. 2). Our results are in line with the patterns reported by other studies in which demonstrate how gradients of anthropogenic intervention generate an environmental filter that shapes amphibian assemblages. (Cáceres-Andrade and Urbina-Cardona, 2009; Cortés-Gómez et al., 2013; Hernández-Ordóñez et al., 2019). These changes in composition represent the replacement of specialist species mainly associated with native forest cover by generalist species associated with cover such as grasslands (Díaz-García et al., 2017). In our study region, *Hyalinobatrachium tatayoi* had an exclusive association with bamboo land cover, while *Centrolene quindianum* and *Leucostehus fraterdanieli* exhibited a preference for natural land cover types with a slight tolerance to anthropogenic disturbance, as previously observed (Guevara-Molina et al., 2017; Rios-Soto et al., 2017). Species of the genus *Pristimantis* and *Dendropsophus columbianus* appeared in both anthropic and natural land covers as in previous studies (Vargas-Salinas & Bolaños, 1999; Isaacs-Cubides & Urbina-Cardona, 2011; Cortés-Gómez et al., 2013), while the toad *Rhinella marina* was only present in pastures and near the houses, contrasting other studies in which it has been associated with different land cover types (Vargas-Salinas & Bolaños, 1999; Cortés-Gómez et al., 2013). Other species were associated only with high degrees of anthropic intervention, including *Leptodactylus colombiensesis* and *Lithobates catesbeianus* an exotic invasive species in Colombia (see Urbina-Cardona et al., 2012).

Some of the generalist species that occur throughout different land cover types, including the most transformed and least habitat-quality coverages, have larger body sizes (Fig. 3, Appendix 5). Large body size may confer greater dispersal capacity (Cushman et al., 1993; Faggioni et al., 2020) and may also reduce water loss, providing greater tolerance to desiccation (Nevo, 1973; Thorson & Svihla, 1943; Schmid, 1965). Within the Andean ecosystems of the same central mountain range, Zabala-Forero & Urbina-Cardona (2021) found that crop-dwelling

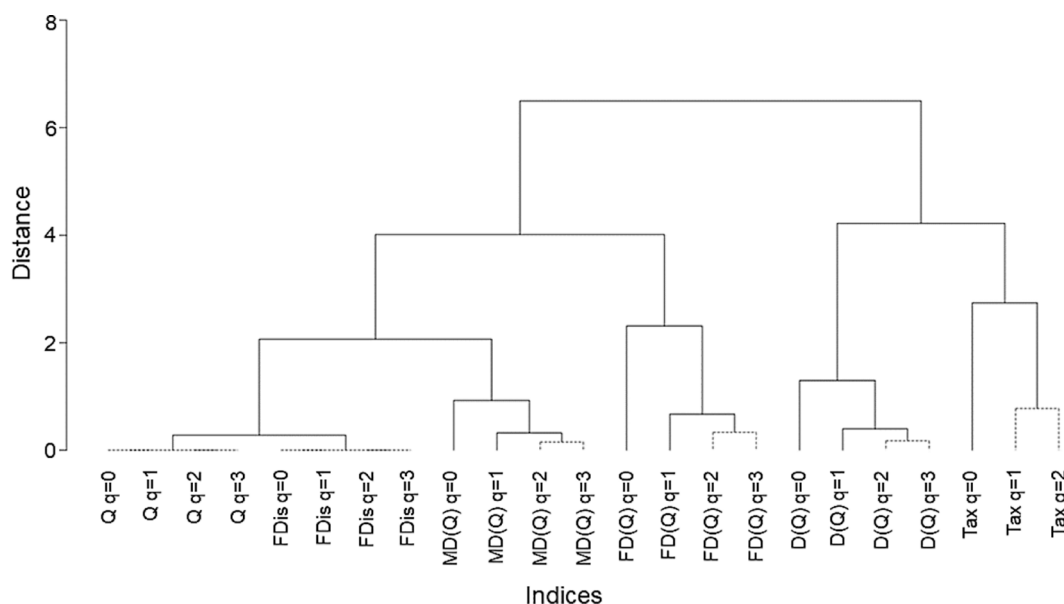


Fig. 4. Cluster analysis of taxonomic and functional diversity indices based on a similarity profile permutation test (SIMPROF). Continuous lines indicate significant multivariate structure relative to the null distribution of the permuted profiles (Clarke et al., 2008). The functional diversity indices correspond to Rao's quadratic entropy (Q), functional dispersion (FDis), the mean functional diversity (MD(Q)), the functional Hill number (D(Q)), the total functional diversity (FD(Q)). Hill numbers of order $q = 0$ correspond to species richness, $q = 1$ to Shannon's exponential, of order $q = 2$ to Simpson's inverse, and $q = 3$ increases sensitivity to dominant species. The taxonomic diversity indices (Tax) correspond to species richness, Shannon and Simpson diversity.

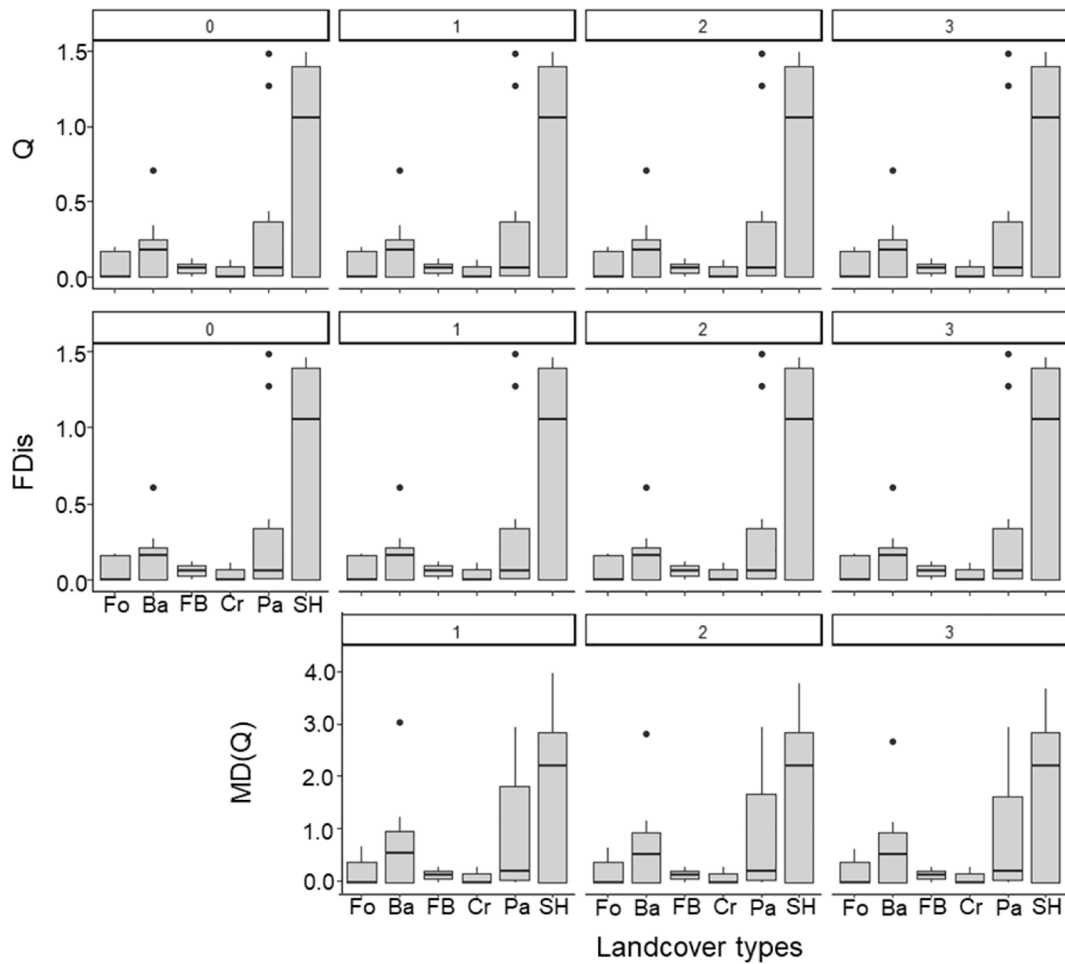


Fig. 5. Median values of Rao's quadratic entropy (Q), functional dispersion (FDis), and average functional diversity (MD(Q)), as indices of functional diversity sensitive to changes in landscape cover types. Values from 0 to 3 correspond to the values of the q parameter of the Hill numbers. $q = 0$ corresponds to species richness. $q > 0$ considers changes in species abundance, in which higher values confer greater relevance to more dominant species. Land cover types are forest (Fo), forest-bamboo ecotone (FB), bamboo (Ba), crops (Cr), pastures (Pa), and surroundings of houses (SH).

anuran species have a greater body mass than those of the native forest. Therefore, large body size may reduce the sensitivity to overheating and desiccation of amphibians in anthropogenic matrices (Watling & Braga, 2015; Pfeifer et al., 2017).

Our results suggest that landscape heterogeneity contributes to the coexistence of species with differential affinities for natural and anthropogenic vegetation types, which is given by the values in their functional traits. The assemblage structure and their dominant traits in these systems are the results of environmental filters that act at different spatial scales (Dunning et al., 1992; Fahrig et al., 2011; Tscharrntke et al., 2012). The agricultural mosaics, like those present in the study area, represent a gradient of the intensity of anthropic use with different levels of landscape heterogeneity and with different quality of habitat and resource availability (Watling et al., 2011; Driscoll et al., 2013). Therefore, the heterogeneity of land cover types positively affects the diversity of species at the landscape level and counteracts the negative effects of the low quality of habitat in vegetation with high intensity of anthropic use (Santana et al., 2017; Lee & Martin, 2017). An increase in the landscape heterogeneity in terms of vegetation structure represents a greater complementarity and supplement of niches or resources favoring the presence of species with different ecological requirements and degrees of specialization (Driscoll et al., 2013). Landscape heterogeneity also increases anuran coexistence through the colonization of species with greater dispersal abilities through more intervened covers in a context of metapopulations (Duelli, 1997; Fahrig et al., 2011; Watling et al., 2011; Parsley et al., 2020). In this sense, we emphasize the

importance of assess changes in assemblage structure and functional traits to understand the metacommunity dynamics of amphibians living in transformed high mountain landscapes.

4.2. Classification of taxonomic and functional diversity indices across land cover types

The classification of taxonomic and functional diversity indices allowed us to group them according to their response to land cover types, identifying both complementarity and redundancy in the information they provide, as previously documented by Mouchet et al. (2010) and Legras et al. (2018). The 13 distinguishable groups of indices represent the response of different facets of amphibian diversity to anthropogenic disturbance (Fig. 4) and therefore, the complementarity in the information provided by the different facets of diversity used in this study.

In relation to the parameter q in Hill's numbers, the indices behaved differentially within the facets considered with some showing redundancy relative to their q value. The Hill numbers corresponding to Rao's quadratic entropy Q and functional dispersion FDis of order $q = 0$ (species richness) and order $q > 0$ (from 1 to 3 as an increase in their sensitivity to abundant species) were grouped, and therefore appear to be redundant with each other as they do not respond differentially to the abundance or the most dominant species or the degree of evenness.

Hill numbers of mean functional diversity MD(Q), the total functional diversity FD(Q) and the functional Hill number D(Q), of order $q =$

0, exhibited a source of information other than $q = 1$ and $q > 2$ of greatest susceptibility to species dominance. These results suggest that these indices do vary according to changes in evenness in the assemblages and represent nonredundant facets of functional diversity.

Due to the complementarity observed between the different facets of functional diversity in Hill numbers, these may be appropriate to evidence changes in amphibian functional diversity between natural and anthropogenic cover types. The present study demonstrates that amphibian structure varies among vegetation cover types due to the change not only in assemblage composition but also in species abundances between sites (Appendix 4). Therefore, it is very important, to consider functional diversity indices that incorporate in their calculation changes in abundances, such as those based on Rao's quadratic entropy (Q). Due to their complementarity and the lack of redundancy, we specifically recommend the use of the functional Hill number $D(Q)$, the mean functional diversity $MD(Q)$, and the total functional diversity $FD(Q)$ metrics (Chiu & Chao, 2014) to study the effect of landscape transformation on the functional diversity of amphibians in high mountains.

4.3. Identifying indices sensitive to land cover types and their congruency

In our study, we show that the functional facet of diversity is more sensitive to land-use change than the taxonomic facet of amphibian assemblages. The Rao's quadratic entropy Q, functional dispersion $FDis$, and average functional diversity $MD(Q)$ were the sensitive indices; the latter, only when considering the relative abundances of the species. These results are consistent with Mouchet et al. (2010), Baraloto et al. (2012), suggesting that functional diversity is more sensitive to gradients of anthropogenic intervention compared to taxonomic diversity. Rao's quadratic entropy has been proposed as an index sensitive to changes in bee communities along burn succession gradients by Ricotta & Moretti (2011). But it has also been proposed as a useful index to identify patterns of convergence or divergence in functional traits (Ricotta & Moretti, 2011). Our results also contrast with the findings of Pardo et al. (2020), who found that Shannon's Hill number ($q = 1$) was sensitive to changes in pollinator assemblages present in the apple agroecosystems. Also, in contrast with the findings of Díaz-García et al. (2017) in amphibian assemblages associated with tropical montane forest with different degrees of restoration, who did not find changes in functional richness or divergence. Despite the low sensitivity of anuran functional diversity indices to changes in land use and land cover, in the Andean ecosystems, Zabala-Forero & Urbina-Cardona (2021) found that the functional richness index weighted by abundance at the community level ($FDwcomm$) did vary between natural vegetation cover and crops, highlighting its importance in evidencing anthropogenic changes in neotropical mountain anuran assemblages. Additionally, Jiménez-Vargas et al. (2021) found that functional Hill numbers of order $q = 0$ were good descriptors of the environmental filtering that occurs due to the proximity to streams within the native forest.

We found that the diversity indices that varied between land cover types were redundant with each other in the information they provide. Those indices were also redundant in relation to the parameter q , which refers to the incorporation of the abundances of the most dominant species. Our results differ in part from the patterns found by Chiu & Chao (2014) because, based on their simulations of data obtained in assemblages that inhabit dune ecosystems, they conclude that their indices do not differ in their response in relation to the facet they represent but do differ in relation to the different q parameters.

In general, a decrease in taxonomic and functional diversity is expected in land cover types with a higher degree of anthropic intervention, although contradictory patterns have also been found (Flynn et al., 2009). We found that the most degraded land cover types as pastures and surrounding of houses in general exhibit more functional dispersion and functional diversity. Our results contradict Strauß et al. (2010), and Hernández-Ordóñez et al. (2019), who found that the diversity,

functional richness, and functional dispersion of amphibian communities increase in old-growth forest patches in successional gradients. Also contradicting Ernst, Linsenmair & Rödel (2006), who found that functional diversity in amphibian's communities from West Africa and South America increase in primary forest. Greater differences between species' trait values represent greater trait complementarity and larger functional diversity (Petchey & Gaston, 2002). The presence of species with a greater variation in body size in the surroundings of house cover (Fig. 3), as well as a greater ontogenetic variation in body size (see Moreno-Barbosa & Hoyos-Hoyos, 2014), may explain the increase in functional diversity observed at the level of the anthropogenic land cover types; such is the case of *R. marina* (Mendoza-Henao et al., 2019).

This scenario also agrees with a process of functional homogenization and greater functional redundancy (Olden & Rooney, 2006) for all the land cover types other than the surroundings of houses, but this was not due to the disappearance of rare or more specialist's species. These coverages have less functional diversity, possibly due to the exclusion of species that are exclusive to the surrounding of houses since they are invasive (*L. catesbeianus*) and tolerant of disturbances (*R. marina* and *Leptodactylus colombiensis*). Our results agree with preliminary studies in birds, where functional homogenization occurs in less intervened land cover types (Clavero & Brotons, 2010), contradicting other studies, in which a greater functional homogenization has been identified in more human-intervened covers, due to the presence of more generalist species (Devictor et al., 2010).

Our results also suggest the relaxation of environmental filters that promote the arrival of exotic species, such as more general and invasive species that might possess new attributes in the functional traits, increasing functional diversity values (Farias & Jaksic, 2009) but increasing the probability of loss of native species due competition with invasive species (Manchester & Bullock, 2000). As assemblages become more homogenized due to the loss of native species, more functional space will be available, allowing some invasive species to become established (Mason, et al. 2013; Zhang, et al. 2017). Therefore, in the surroundings of houses, there could be a greater functional complementarity or dissimilarity, compared to coverages with less functional diversity, such as the forest, where there could be limiting similarity. This contrasts with what has been observed in other studies where the intensity of environmental filters increases and functional diversity decreases with increasing the intensity of land use (Lee & Martin, 2017; Morelli et al., 2018). These possible scenarios could be tested by measuring the degree of specialization of the species, as well as analytically testing the role of environmental filters (Mouchet et al., 2010; Mason et al., 2013). During the process of biological invasion, exotic amphibians that manage to establish their populations and colonize new areas exhibit rapid life history traits such as high fecundity and frequency of reproduction, early age of sexual maturity, and large clutches (Allen et al., 2017). In anthropogenic landscapes with such a high human footprint as the coffee-growing region in Colombia (Correa-Ayram et al., 2020), it is urgent to undertake ecological restoration actions that increases the composition, the heterogeneity of the structure, the size and the quality of the patches and monitor amphibian assemblages from their taxonomic and functional diversity facets (*sensu* Díaz-García et al., 2017), because of their possible vulnerability to invasion by bullfrogs (Urbina-Cardona et al., 2011).

In this sense, functional richness metrics can be a good indicator of ecosystem resilience to changes in environmental disturbance regimes and resistance to invasion (Suding et al., 2008; Pavoine & Bonsall, 2011). As the volume of the functional space occupied by an assemblage is contracted, the value of functional richness is reduced indicating a lower resilience capacity (Hooper et al., 2005). In other words, a low value of functional richness implicitly shows that there are empty functional spaces in the assemblage that can be invaded by species that can use the available resources (Mason et al., 2005). In our study area, the forest and bamboo vegetation covers are the ones with less functional richness compared to the surroundings of the houses in which the

presence of bullfrog was evidenced. In these vegetation covers, the reduction in the functional richness indexes of the order $q = 0$ indicates not only the loss of species but also of the attributes of their traits, the functions they performed in the ecosystem, and the decline in ecosystem functionality (Mason et al., 2013; Riemann et al., 2017).

Although the design and implementation of conservation and management actions have usually been informed with traditional taxonomic measures of diversity, special recognition has aroused the importance of including functional diversity metrics, to direct the local interventions (Miatta et al., 2020; Freitas & Mantovani, 2017). In this sense, the classification and evaluation of the sensitivity of taxonomic and functional diversity metrics is essential to be able to adequately target interventions (Cadotte and Tucker, 2018). In the Andean ecosystems, it has been proposed that to improve the quality of habitat for crop-dwelling amphibians it should be included the increase of tree and shrub vegetation structure and composition for shade generation, the accumulation of leaf litter (with different qualities and decomposition speed) on the soil, and the low use of agrochemicals, increasing the dispersal of anurans across fragmented landscapes (Zabala-Forero & Urbina-Cardona, 2021). At a landscape level, it is necessary to increase the size of the patches, remove limitants outside of the natural areas and increase the connectivity. However, these local management actions should be monitored to assess the spatio-temporal dynamics in taxonomic and functional diversity metrics to ensure the effectiveness of the interventions (Smith et al., 2020).

Based on the literature and the results obtained, we propose some management and conservation actions for the survival of amphibians in Andean production systems. However, the survival of many specialist amphibian species of neotropical native forest interior habitats depends on the management of edge effects (Schneider-Maunoury et al., 2016). It is essential to amortize the edge effects on native vegetation with productive systems such as agroforestry, forestry and non-forestry products to improve habitat quality for Andean amphibians and generate heterogeneous ecotones (Santos-Barrera & Urbina-Cardona, 2011; Roach et al., 2020), as the pressures of the transformed matrix could be affecting the integrity of those natural covers (Häkkinen et al., 2017). It should be emphasized that the interior of the Andean forests maintains the greatest taxonomic and functional richness for amphibians (Zabala-Forero & Urbina-Cardona, 2021) indicating that in this habitat the species of the assemblage cover a broader functional space with better potential to explore the resources they need for their survival (Mason et al., 2005).

The study of functional traits of amphibians at the assemblage level allows us to understand their contribution to ecosystem processes and to guide effective conservation actions (Becker et al., 2010; Ribeiro et al., 2016; Bolochio et al., 2020). In this sense, with the appropriate selection of functional traits and functional diversity indices and their monitoring, it is possible to warn about the loss of assemblage traits and ecosystem functions that may jeopardize ecosystem resilience under scenarios of land use and land cover. However, it is urgent to conduct functional redundancy studies in order to understand the degradation of ecosystem processes caused by the loss of species (Loreau, 2004).

In our study we found that only a few of the Hill number indices responded significantly to land use change and some exhibited high collinearity with each other (Appendix 7). This suggests additional redundancy in the information provided by the indices, and it draws attention to the usefulness of Hill's numbers as a generalizing and unifying framework that facilitates the interpretation of the behavior of the indices in land use gradients (Chao et al., 2010). In our study, we highlight the importance of identifying those indices that, in the framework of Hill numbers, are informative for alerting about the effect of landscape transformation on biotic communities. However, Hill numbers have yet been little studied in relation to their ability to be applied to facets of taxonomic and functional diversity. Therefore, we emphasize the relevance of continuing with this type of studies that contribute to understanding the behavior of these indices, keeping in

mind the objective of the studies, since according to this the selection of the indices may vary (Daly et al., 2018).

5. Conclusions

Our study highlights the importance of deepening the relationship between species diversity and assemblage structure, from a functional diversity perspective, for which it is crucial to select functional traits that have a clear relationship with the environmental filter under study. The performance of the functional diversity indices calculated in our study is ultimately the result of the type and value of functional traits selected by the researchers and of the changes in abundance and species composition in the study assemblages. Our results show redundancy in the taxonomic and functional diversity metrics in relation to the facets they represent, but also in relation to q values, which assign different weight to species abundances, mainly within the most used Q and $FDIs$ metrics. The functional diversity measures proposed by Chiu and Chao (2014) provide different and complementary facets when considering and disregarding the value of the relative abundances of the species. Functional diversity, but not taxonomic diversity, was sensitive to land cover types in our study area. The Hill numbers Q , $FDIs$ and $MD(Q)$ were sensitive and the congruence in their response, but they are redundant when considering their sensitivity to changes in natural and anthropogenic vegetation cover types. We discuss the relevance of diversity indices of order $q = 0$ as a good alternative to compare congruently between facets of taxonomic and functional diversity. We also suggest the advantages of using Hill numbers as an approach that increases the comparability and interpretability contributing to the identification of additional redundancy in functional indices. Therefore, it represents an option in view of the need for unification of analysis methods for the proposal of adequate management guidelines.

We therefore support the need to incorporate facets of taxonomic and functional diversity, to evidence the complexity of changes in biotic communities in response to anthropogenic disturbances (Ernst et al., 2006). So far, it is well known that the values of functional diversity vary according to the susceptibility of these measurements to the functional traits used (Tsianou & Kallimanis, 2019; Legras et al., 2020), the intensity of the disturbances (Baraloto et al., 2012), the pool of species present in the landscape (Devictor et al., 2008), and the ecological processes that occur in them (Morelli et al., 2018). Zabala-Forero & Urbina-Cardona (2021) draw attention to the lack of studies on functional diversity in Andean anurans and the importance of including functional traits from the diet of the species. In this regard, it is necessary to evaluate the performance of metrics that represent the functional and taxonomic facets of diversity based on different pools of functional traits, in other biotic groups and ecosystems to evidence general patterns.

We stress the relevance of landscape heterogeneity for the conservation of anuran assemblages composed of species with different degrees of association to anthropogenic disturbance, which may also differ in their functional traits and therefore in their contribution to ecosystem processes. We also highlight the relevance of studying areas with anthropogenic disturbances to understand the dynamic of the anuran diversity in areas with different land cover types, most of which are clearly degraded (Correa-Ayram et al., 2020; Isaacs-Cubides et al., 2021).

CRedit authorship contribution statement

Diana María Galindo-Urbe: Conceptualization, Investigation, Methodology, Data curation, Formal analysis, Writing – original draft. **Julio Mario Hoyos-Hoyos:** Conceptualization, Investigation, Methodology, Writing – review & editing. **Paola Isaacs-Cubides:** Data curation, Writing – review & editing. **Nicolás Corral-Gómez:** Data curation, Writing – review & editing. **Nicolás Urbina-Cardona:** Conceptualization, Investigation, Methodology, Formal analysis, Writing – original

draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

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