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Does abiotic noise promote segregation of functional diversity in Neotropical anuran assemblages?

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The abiotic noise of streams can mask the acoustic signals of anurans with a large body size calling at low frequencies, but not the signals emitted by anurans with a small body size calling at high frequencies. As a consequence, the body size of species in assemblages alongside streams is, on average, lower and less variable than that of assemblages away from streams. Given that the body size in anurans is frequently related to life-history traits, it is expected that functional diversity (FD) will be lower in anuran assemblages alongside streams than in assemblages away from streams. We calculated and compared FD, based on six functional traits, for anuran species in seven localities in different biogeographical regions in the Neotropics. In five lowland localities, FD was lower in assemblages alongside streams than in assemblages away from streams. However, the reverse trend was found in two Andean localities. Noise from streams, acting as an environmental filter, could promote low FD because taxa whose phenotype differs from an optimal type (high call frequency, small body size and associated traits) are excluded from riparian places. However, such habitat filtering could be stronger and affect more anurans in lowland assemblages than in those at medium elevation.

ADDITIONAL KEYWORDS: amphibians – assemblage rules – bioacoustics – ecoacoustics – geophony – habitat filtering – noise on streams – sensory ecology.

INTRODUCTION

Functional traits are those morphological, physiological or behavioural characteristics of organisms that influence their performance or fitness (Weiher, 2011; Huby *et al.*, 2019). Functional diversity (FD) refers to the variability of functional traits among species in a community (Tilman, 2001; Petchey & Gaston, 2002, 2006; Laureto *et al.*, 2015). Hence, FD can be a proxy between species traits, dynamics of species assemblages and ecosystem processes (Chapin *et al.*, 2000; Díaz *et al.*, 2013). Given that differences among species trait values can result in a greater diversity of ecological functions, higher FD in assemblages is commonly related to higher productivity and the recycling of nutrients into ecosystems (Tilman & Downing, 1994; Tilman *et al.*, 2001; Cardinale, 2011). Moreover, assemblages with higher FD are expected to be more resilient to anthropogenic disturbances or environmental stresses; in other words, FD is a good predictor of ecosystem function and stability (Tilman, 1997; Cadotte *et al.*, 2011; Laureto *et al.*, 2015). Therefore, it is important to identify the environmental factors that promote changes in the structure of assemblages and their relationship to variations in FD (Laureto *et al.*, 2015).

The structure of assemblages is influenced by multiple factors acting at different scales (HilleRisLambers *et al.*, 2012; Mittelbach & Schemske, 2015), such as dispersion of species (MacArthur & Wilson, 1967; Mouquet & Loreau, 2003), interspecific competition (Connell, 1961; Tilman *et al.*, 1981), predation (Paine, 1974; Lubchenco, 1978), mutualism and facilitation (Stachowicz, 2001; Schmitt & Holbrook, 2003). Nevertheless, interspecific competition and habitat filtering are among the most studied factors (Webb *et al.*, 2002; Mayfield & Levine, 2010; Pausas & Verdú, 2010), and their

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importance in determining the FD of assemblages has been highlighted in several studies on plants (e.g. Hooper, 1998; Díaz, 2001; Garnier *et al.*, 2016) and animals (e.g. Villéger *et al.*, 2010; Francis *et al.*, 2012; González-Maya *et al.*, 2016). Interspecific competition promotes differentiation in functional traits (i.e. ecological dissimilarity) among co-occurring species (MaCarthur & Levins, 1967; Diamond, 1975), which in turn can be related to higher FD (Kluge & Kessler, 2011; but see Mayfield & Levine, 2010). In contrast, habitat filtering promotes low dissimilarity in functional traits among co-occurring species because taxa whose phenotype differs from an optimal value are excluded from the habitat (Kraft *et al.*, 2007; Kluge & Kessler, 2011; HilleRisLambers *et al.*, 2012). Therefore, habitat filtering is related to a reduction in FD (Kluge & Kessler, 2011).

Communication is essential in species recognition, mate choice, competition, predation and other ecological interactions between conspecifics and heterospecifics, directly affecting the fitness of individuals (Bradbury & Vehrencamp, 2011; Garey *et al.*, 2018). Natural abiotic noise (geophony) is one of the habitat characteristics that can prevent acoustic communication between individuals through a process of masking. Acoustic masking refers to the overlap of signals and background noise in features such as frequency, which impede the detection and decoding of information contained in signals by receivers (Brumm & Slabbekoorn, 2005; Blickley & Patricelli, 2012). Abiotic noise, either natural or anthropogenic, is characterized by higher intensities at lower frequencies (Fig. 1) and can mask the acoustic signals of species calling at low frequencies, but not the signals emitted by species calling at high frequencies (Brumm & Slabbekoorn, 2005). Therefore, the structure of assemblages of species using acoustic signals to communicate can vary between places exposed to different levels of abiotic noise (Francis *et al.*, 2011; Proppe *et al.*, 2013; Vargas-Salinas & Amézquita, 2014; Mullet *et al.*, 2017), and these changes might have consequences for the FD of assemblages (Francis *et al.*, 2009, 2011, 2012).

In anurans, the dominant frequency of the advertisement call is negatively correlated with the body size of males in most species (Gerhardt & Huber, 2002; Vargas-Salinas & Amézquita, 2014), albeit with some notable exceptions, which include species that vocalize in noisy streams (Feng *et al.*, 2006; Boeckle *et al.*, 2009; Vargas-Salinas & Amézquita, 2014; Tonini *et al.*, 2020). In addition to call frequency, male body size in anurans is also related to phylogeny and to the physiological, ecological and life-history functional traits of the species (Duellman & Trueb, 1994; Morrison & Hero, 2003; Wells, 2007). For instance, species whose males have a larger body size could have larger females (which, in turn, produce more eggs) and eat larger prey than species whose individuals are smaller; smaller species, on the contrary, could be more cryptic or occupy specific niches, such as small crevices in the ground (Wells, 2007; Zimkus *et al.*, 2012; Womack & Bell, 2020). Little is known about the evolution of body size in anurans (Amado *et al.*, 2019; Womack &

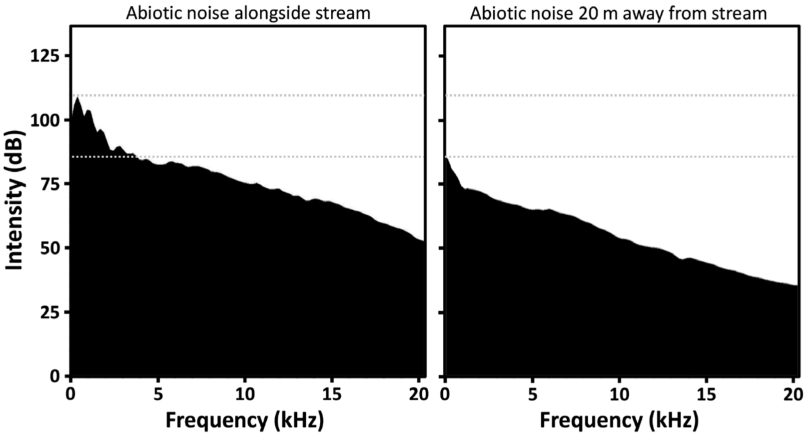

Figure 1. Power spectra showing that the intensity of the natural abiotic noise (geophony) on streams is higher at lower frequencies than at higher frequencies (intraplot comparison) and how this noise intensity decreases as the distance to the stream increases (interplot comparison). Both recordings were made with an omnidirectional microphone and equal technical specifications, in a small stream located in the western Andes of Colombia, South America (locality 'Dagua' in the study by Vargas-Salinas *et al.*, 2014). The horizontal dotted lines inside plots are for reference purposes only. It is expected that in larger streams the intensity of noise will be even higher than that recorded for this example, but the relationship between frequency and intensity will still be the same. A similar power spectrum is expected for anthropogenic noise in cities and alongside roads (Slabbekoorn *et al.*, 2018).

Bell, 2020), but diverse ecological factors are capable of promoting the present spatial segregation of the body size of species (Nevo, 1973; Duellman & Thomas, 1996; Morrison & Hero, 2003; Wells, 2007; Campos *et al.*, 2017), and one of these factors is the level of abiotic noise in the habitat (Goosem *et al.*, 2007; Vargas-Salinas *et al.*, 2014; Röhr *et al.*, 2016). In fact, anuran assemblages alongside streams tend to exhibit lower average values and less variability in male body size than anuran assemblages located away from streams (Preininger *et al.*, 2007; Boeckle *et al.*, 2009; Vargas-Salinas & Amézquita, 2014; Carvajal-Castro & Vargas-Salinas, 2016). Based on this, in addition to the relationship between body size and functional traits, FD is expected to be lower in anuran assemblages alongside streams than in anuran assemblages away from streams (Fig. 2), as a concomitant effect of a habitat filtering process imposed by abiotic noise (Francis *et al.*, 2009, 2011, 2012; Carvajal-Castro & Vargas-Salinas, 2016).

The aim of this study was to test the hypothesis that FD is lower in anuran assemblages alongside streams than in anuran assemblages away from streams. Testing this hypothesis would provide insights about the factors shaping the FD of anuran assemblages in different acoustic habitats (Mullet *et al.*, 2017). For this, we used personal observations and published data in the scientific literature about breeding sites and functional traits in anurans (Table 1). Given that acoustic signal masking would depend on the intensity of the natural abiotic noise produced on streams (hereafter, noise on streams) and that this noise intensity can vary among habitats, we mapped seven localities distributed at different elevations and in different biogeographical regions. By doing this, we also tested the generality of our hypothesis for anuran assemblages in the Neotropics.

MATERIAL AND METHODS

We obtained data for 265 anuran species (Supporting Information, Appendix S1, available at figshare 10.6084/m9.figshare.9779162) distributed in seven localities; five in lowlands (elevations < 1000 m a.s.l.) and two in the Andes in the north of South America (> 1000 m a.s.l.). Three localities were in the lowlands of Central America, two in the northern part of the South American Andes and two in the Amazon (Fig. 3). Inventories of the amphibian fauna in those localities were performed by different people, which might be a source of variability in the data; however, the amphibian fauna is very well known for each of these localities. Information on the habitat characteristics for each locality is summarized in Table 2. We followed the anuran taxonomic arrangement of Frost (2020).

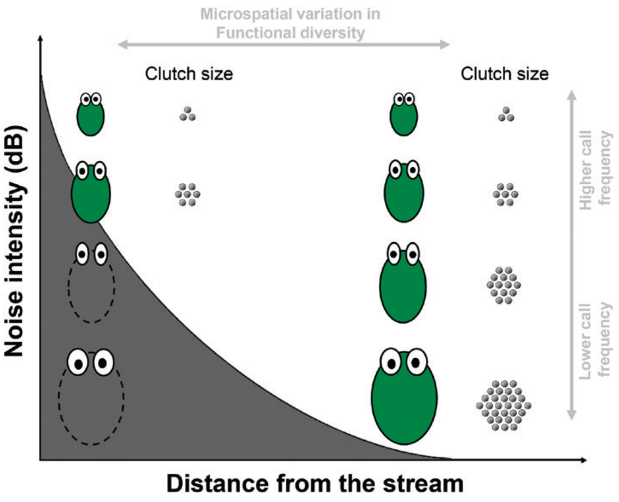

Figure 2. Diagram showing the expected spatial differences in functional diversity between anuran assemblages alongside streams and away from streams. Anuran species whose males have a larger body size produce acoustic signals at lower frequencies than those with a smaller body size (Gerhardt & Huber, 2002; Vargas-Salinas & Amézquita, 2014). Acoustic signals at lower frequencies are more susceptible to masking by abiotic noise than those at higher frequencies (Brumm & Slabbekoorn, 2005). If acoustic signals of species with large body size are masked in places alongside streams, the individuals and populations of these species will experience a reduction in fitness and in chance of becoming established in these sites (grey frog symbols). On the contrary, the acoustic signals of species with a small body size can be detectable by receivers despite background noise alongside streams (green frog symbols). In sites away from streams, the intensity of abiotic noise (grey area) decreases; therefore, acoustic signals produced by species with either large or small body size are not greatly masked. Given that body size is related to several functional traits in anurans (e.g. number of eggs per clutch), the differential masking of acoustic signals and the concomitant effect on body size variability between assemblages might be reflected in a lower functional diversity in anuran assemblages alongside streams than in anuran assemblages away from streams.

For each species, we defined the breeding habitat (the site where the male calls to attract a mate and where courtship and amplexus happens, if present) as 'alongside stream' and 'away from stream', according to Vargas-Salinas & Amézquita (2014). These authors categorized the breeding habitat according to the expected level of noise produced by flowing water (i.e. noisy alongside streams and less noisy or not noisy away from streams). There is variation in the intensity of abiotic noise among streams, and even in the same stream; however, the authors of the reviewed papers do not provide enough information to discriminate species according to this variation in abiotic noise. In fact,

Table 1. Summary of functional traits in anurans and their associated ecosystem functions

Functional trait	State of trait	Importance of the functional trait	Allometric relationship with body size
Morphometric			
Body size of males and females*	Numerical variable based on the snout–vent length of individuals	Trait related to the flow of energy through the trophic chains as a predator or prey. Given that body size is positively related to body mass (Santini *et al.*, 2018), this trait is associated with the capacity for nutrient transport by the animal (Toledo *et al.*, 2007; Oliveira *et al.*, 2017)	In most anuran species, the male is smaller than the female (Monnet & Cherry, 2002); when species are compared, the body size of females is positively related to the body size of males (Vargas-Salinas & Amézquita, 2014; Wells, 2007)
Natural history			
Activity period	Diurnal, nocturnal, diurnal–nocturnal	According to the activity period, anurans will be the prey or predator of different species	Diurnal species are smaller, on average, than nocturnal species; moreover, nocturnal species are more diverse in body size than diurnal species (Duellman & Trueb, 1994; Wells, 2007)
Habitat use	Terrestrial, aquatic, arboreal, terrestrial–aquatic, terrestrial–arboreal	Trait related to the flow of energy through the trophic chains as a predator or prey. The food items consumed by anurans and their predators reflect their habitat preferences (Vitt & Caldwell, 2014). In terrestrial habitats, anurans can reduce herbivory and influence plant growth rates; in addition, excrement and carcasses of anurans can also provide soluble nutrients that increase nutrient cycling (Beard *et al.*, 2002, 2003). Something similar can be expected in aquatic habitats (Hocking & Babbitt, 2014)	Arboreal and terrestrial species are, on average, smaller than aquatic species (Santini *et al.*, 2018; Womack & Bell, 2020)
Clutch size	Numerical variable based on the number of eggs per clutch	Feature related to the amount of matter and energy available to predators in aquatic and terrestrial habitats (Vitt & Caldwell, 2014)	Species with larger body size produce clutches with more eggs than species with smaller body size (Duellman & Trueb, 1994; Wells, 2007)
Reproductive mode*	Categorical variable with seven levels (for details, see the Material and Methods section)	Feature related to the contribution of matter and energy to both aquatic and terrestrial egg-eating predators. Free-swimming tadpoles consume mosquito larvae in ephemeral and permanent ponds; tadpoles also decrease algal abundance and reduce sediment accumulation (Ranvestel *et al.*, 2004). Eggs out of water and tiny froglets in species with direct development are prey of diverse organisms (Toledo, 2005; Vitt & Caldwell, 2014)	Species with reproductive modes that include oviposition out of water and direct development are smaller, on average, than species with reproductive modes that include a free-swimming larval phase (Wells, 2007; Womack & Bell, 2020)

*Trait states are modified from Cortés-Gómez *et al.* (2015; for details, see the Material and Methods section). Other functional traits (e.g. diet, foraging strategy) suggested by Cortés-Gómez *et al.* (2015) were not included owing to a lack of information for most of the species. For more detailed information about the importance of anuran functional traits in ecosystem functions and services, see Valencia-Aguilar *et al.* (2013) and Hocking & Babbitt (2014).

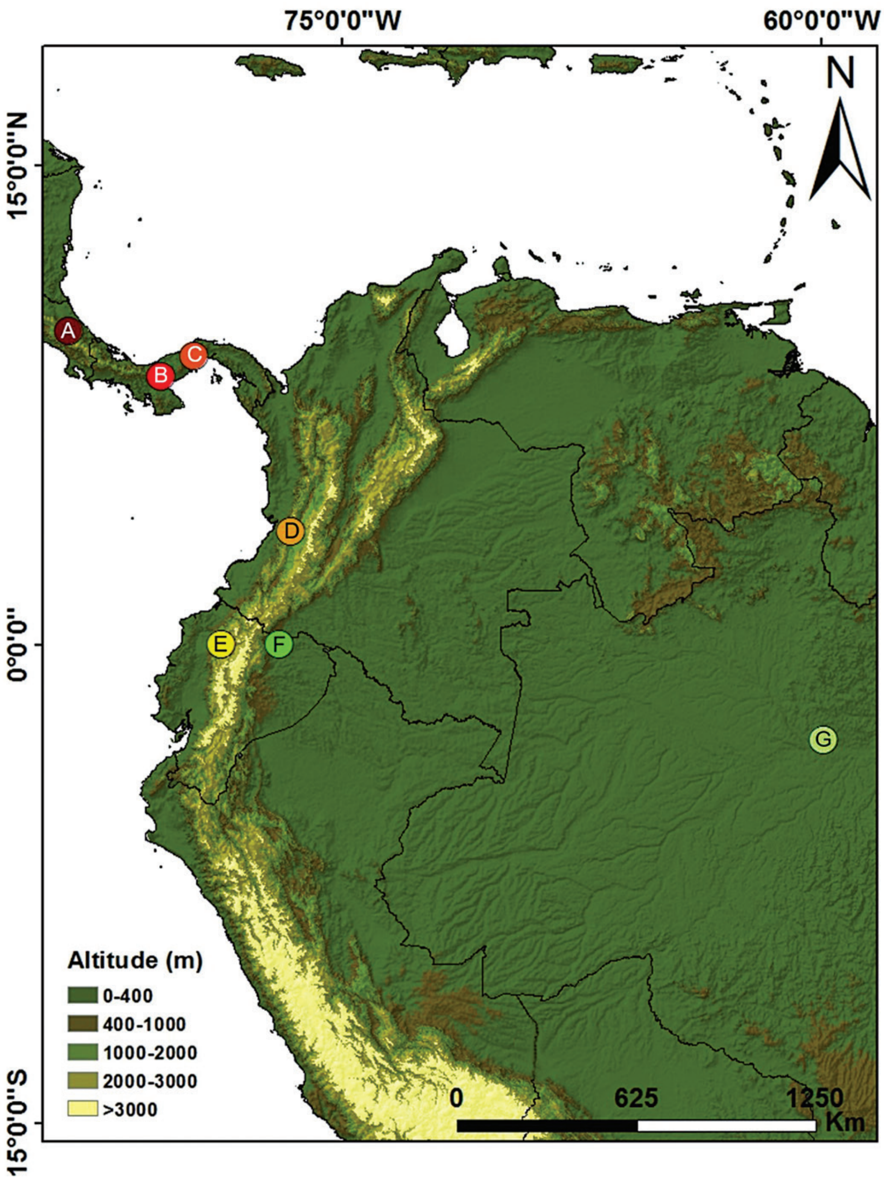

Figure 3. Geographical distribution of the seven localities of study: A, La Selva, Costa Rica; B, El Copé, Panamá; C, Parque Soberanía–Isla Barro Colorado, Panamá; D, Chicoral, Valle del Cauca, Colombia; E, Mindo, Ecuador; F, Santa Cecilia, Ecuador; and G, Reserva Adolpho Ducke, Brazil.

despite its importance for understanding habitat use in soniferous species, the noise level is rarely recorded and included in classic animal ecology (Goutte *et al.*, 2013). As a consequence, we handled breeding habitat as a categorical variable with two levels; in addition, we pooled streams, creeks and waterfalls in the same category (i.e. alongside streams).

Based on personal observations, published literature (scientific papers, books and field guides) and digital databases (e.g. AmphibiaWeb and AmphiBIO), we obtained information about the morphological and ecological functional traits of the species (Supporting Information, Appendix S1). The numbers and types of functional traits included in this study were selected according to Cortés-Gómez *et al.* (2015) and because they are related to the body size of species and can influence species responses to environmental changes and ecosystem processes, such as energy flow between trophic levels (Table 1). However, the inclusion of functional traits was restrained by the availability of information in the literature for most species (Oliveira *et al.*, 2017; Etard *et al.*, 2020). We included some modifications in the state of some traits suggested by Cortés-Gómez *et al.* (2015; see Table 1). For instance, the body size of

Table 2. Summary of species richness and habitat characteristics for each of the seven Neotropical localities included in this study

Locality	Species richness*	Elevation (m a.s.l.)	Habitat characteristics	Source
La Selva, Costa Rica	43 (41)	211	Tropical wet forest. Rainfall is about 4000 mm/year; the temperature is around 24ºC	McDade *et al.* (1994); Guyer & Donnelly (2005)
El Cope, Panamá	58 (53)	244	Tropical wet forest. Rainfall is ~2000–4000 mm/year; temperature is between 20 and 25 °C	Crawford *et al.* (2010)
Parque Soberanía–Isla Barro Colorado, Panamá	59 (58)	88	Tropical wet forest. Rainfall is ~1500–3000 mm/year; temperature is ~24 °C	Ibáñez *et al.* (1999)
Chicoral, Valle del Cauca, Colombia	26 (23)	1636	Cloud forest. Rainfall is ~2000 mm/year; temperature varies between 14 and 18 °C	Bolívar *et al.* (2010)
Mindo, Ecuador	53 (47)	2200	Lower-montane forests and cloud forests. Rainfall is ~2825 mm/year; temperature is ~21 °C	Arteaga *et al.* (2013)
Santa Cecilia, Ecuador	85 (77)	340	Tropical wet forest. Rainfall is ~4390 mm/year; temperature varies between 18 and 35 °C	Duellman (1978)
Reserva Adolpho Ducke, Brazil	49 (47)	111	Tropical wet forest. Rainfall varies between 1900 and 2300 mm/year; temperature is ~26 °C	Lima *et al.* (2006)

*Data in the 'Species richness' column indicate the number of anuran species in the locality, followed, in parentheses, by the number of species for which it was possible to find information about functional traits.

individuals (snout–vent length) was separated for males and females because in anurans a large sexual size dimorphism is common (Monnet & Cherry, 2002). Also, Cortés-Gómez *et al.* (2015) suggest six general states for the trait 'reproductive mode', but we use the following state categorization based on the table of reproductive modes in the book by Vitt & Caldwell (2014): (I) eggs and tadpoles in ponds or streams; (II) eggs out of water (terrestrial, arboreal or foam nest), with tadpoles in ponds, streams or small pools in ground cavities; (III) eggs out of water, with tadpoles in phytotelma; (IV) eggs and tadpoles in phytotelma; (V) eggs out of water that hatch into non-aquatic tadpoles or froglets by direct development; (VI) eggs carried by the adult, with tadpoles in ponds or streams; and (VII) eggs carried by the adult hatch into froglets by direct development.

There are some additional clarifications regarding the elaboration of the functional trait database in this study. First, given that intraspecific geographical variations in morphology and ecology have been recorded in anurans (Nevo, 1973; Wilczynski & Ryan, 1999; Morrison & Hero, 2003), as far as possible we used data of functional traits recorded for individuals from each of the seven localities included in this study. When this was not feasible, we used data originating from other localities in the same country or region. Second, we used the mean value for quantitative traits instead of the range values included in some published descriptions. Where the published descriptions included ranges rather than average values, we used the range midpoint value. Third, species whose taxonomic identity is undefined were excluded from the functional trait database (e.g. *Craugastor* aff. *longirostris* and *Diasporus* aff. *diastema* in El Cope, Panamá; Crawford *et al.*, 2010). Fourth, we excluded from FD calculations the species *Dendropsophus ebraccatus* because it can exhibit more than one reproductive mode in the same population; females can lay eggs directly in water or in arboreal substrates out of water (Touchon & Warkentin, 2008; Touchon & Worley, 2015). Fifth, data about specific functional traits are unavailable for some species, which could affect the accuracy of FD values (Májeková *et al.*, 2016); however, such missing data are scattered through assemblages and localities in our study; hence, the existence of a systematic bias promoting the pattern observed in our results is unlikely. The amount of missing data in our localities varies between 1.41 and 10.28%, mainly owing to the lack of availability of data about the trait 'number of eggs'. When we re-ran calculations without this trait for the localities of Mindo and Chicoral (where incompleteness of data was the highest), we obtained similar results, suggesting that our results are little skewed by this concern.

The FD was calculated using the index based on Hill numbers proposed by Chiu & Chao (2014) in the package hillR (Li, 2018) for the R platform (R Core Team, 2018). We only have presence–absence data; for this reason, we calculated FD only at the order of diversity $q = 0$ (Chiu & Chao, 2014). We carried out FD calculations, pooling both morphological and ecological functional traits per species for each assemblage/locality. To compare the FD between assemblages in the same locality, we calculated a FD ratio with the corresponding values for assemblages (i.e. FD away from streams/FD alongside streams). If the FD ratio was higher than one, this indicated that FD was higher in the assemblage away from streams, whereas a ratio lower than one implied the opposite, and a ratio equal to one suggested that the FD did not differ between assemblages.

The FD based on Hill numbers is a distance-based measurement and, like other FD indexes, it is correlated with species richness (Li, 2020); hence, is not possible to discriminate whether potential FD differences between assemblages are attributable to a disparity in the number of species or because of ecological factors acting over functional dimensions (Swenson, 2014). To corroborate the correlation for the assemblages alongside streams and away from streams included in this study, we performed two Spearman rank tests in the software SPSS v.21 (SPSS, 1999). Subsequently, we calculated a standardized effect size (SES; Webb *et al.*, 2002) for FD through a null model approach that removed the influence of species richness (Gotelli & Graves, 1996; Swenson, 2014). The null model was based on randomizations of the species and the corresponding functional traits for calculating simulated FD ratios between assemblages alongside and away from streams in the same locality; for this, we used 10 000 permutations under the model 'Independent Swap' (Gotelli & Entsminger, 2001) in the R software. We chose the 'Independent Swap' algorithm because it randomizes the matrix of assemblages, conserving the total sums of columns and rows across all randomizations, and it applies a constrained randomization, preventing type I error. In addition, it is used for the presence–absence matrix and does not randomize trait data (Gotelli & Entsminger, 2001; Swenson, 2014). Our criterion for establishing whether the FD ratio obtained between assemblages in a given locality was different from those FD ratios obtained by random processes for the same locality was $\alpha = 0.05$. In other words, a P-value < 0.05 means that possible differences in FD between anuran assemblages alongside and away from streams are attributable not to stochastic processes, but instead to a deterministic factor. In all the previous analyses, we

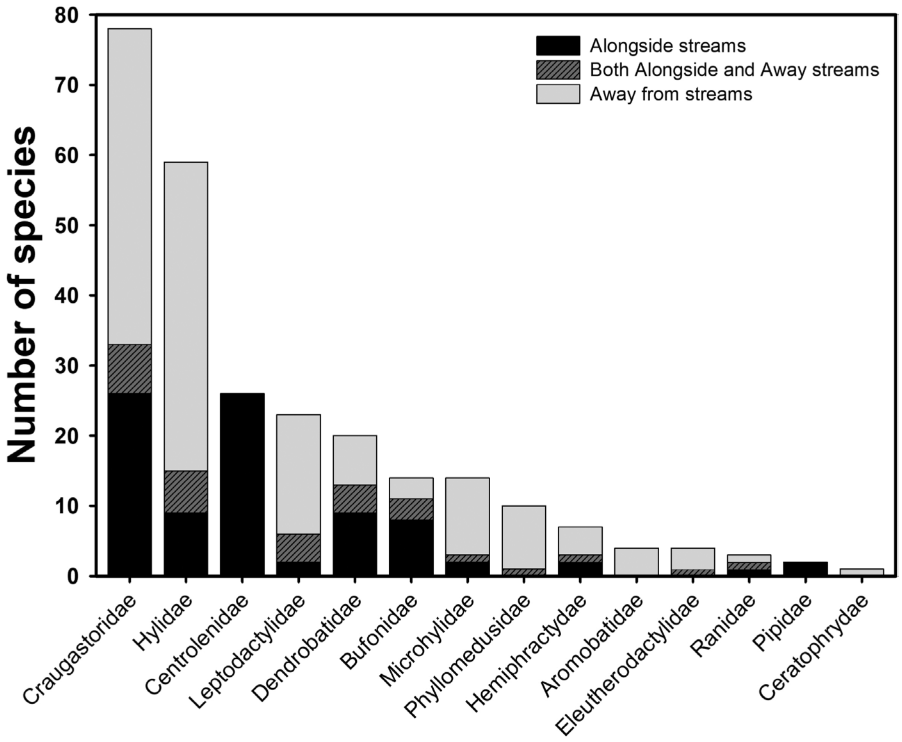

Figure 4. Summary of the 265 anuran species included in this study distinguished according to family and breeding site. The plot is based on data from the Supporting Information (Appendix S1, available at figshare 10.6084/m9.figshare.9779162). Species that call both alongside and away from streams in the same locality were not included in statistical analyses.

excluded 14 species (in addition to *D. ebraccatus*; see commentary above) that call and breed both alongside and away from streams in the same locality (see Supporting Information, Appendix S1).

RESULTS

The 265 anuran species (15 excluded from our statistical analysis) belong to 14 families; most of these families (except Aromobatidae, Centrolenidae, Ceratrophydae and Pipidae) have species both breeding alongside streams and away from streams (Fig. 4). There was a positive relationship between FD and species richness in assemblages alongside streams (Spearman coefficient [Sr] = 0.98, $P < 0.01$, $N = 7$) and assemblages away from streams (Sr = 0.99, $P < 0.01$, $N = 7$) (Fig. 5). In five of the seven localities, the value of the FD index was lower in the assemblage alongside streams than in the assemblage away from streams (i.e. FD ratio > 1); in only two localities there was an opposite tendency (i.e. FD ratio < 1; Table 3). However, the comparison using the null model approaches indicates, for all the localities, that the calculated FD ratio does not differ from that generated by simulation (Table 3).

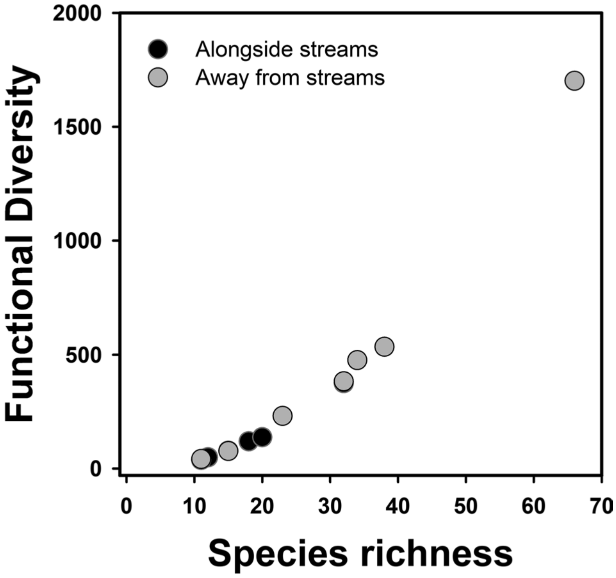

Figure 5. Relationship between number of species and functional diversity for anuran assemblages alongside streams and away from streams in seven Neotropical localities (see Fig. 3). Functional diversity was calculated with the index proposed by Chiu & Chao (2014); those calculations and this figure do not include the frog *Dendropsophus ebraccatus* (for details, see Material and Methods section) or the 14 species that call both alongside and away from streams in the same locality (indicated in the Supporting Information, Appendix S1, available at figshare 10.6084/m9.figshare.9779162). Note that some dots overlap.

DISCUSSION

The FD in anuran assemblages alongside streams was lower than the FD in anuran assemblages away from streams at five of the seven Neotropical localities included in this study. Assemblages in those five localities (all in lowlands) are clearly in agreement with our hypothesis and prediction (Fig. 2). A similar relationship between abiotic noise, acoustic signal masking and a reduction in ecological functional traits of species persisting in human-disturbed habitats has been found in birds (Francis *et al.*, 2009, 2011, 2012).

A positive relationship between species richness and FD (Halpern & Floeter, 2008; Kluge & Kessler, 2011) was corroborated for our data. In addition, the absence of differences between the calculated FD ratios and those expected under stochastic processes (null model) suggests that our results cannot be attributable to noise on streams acting over functional dimensions, but to a disparity in the number of species (see Fig. 2). In other words, the differences in FD in the five lowland localities is an indirect effect associated with differences in species richness between sites (stream and away from stream). Testing all the ecological and evolutionary processes underlying such disparity in the number of species is beyond the scope of the present study, but a process of habitat filtering promoted by abiotic noise seems to be important (Vargas-Salinas & Amézquita, 2014; Carvajal-Castro & Vargas-Salinas, 2016). Abiotic noise can impose restrictions on the establishment of species alongside streams, especially of species with a large body size, through the effect of acoustic signal masking (Vélez *et al.*, 2013; Vargas-Salinas & Amézquita, 2014).

Two apparently contradictory results arose in two localities, i.e. FD was higher in anuran assemblages alongside streams than in assemblages away from streams. These two localities, however, are situated at middle elevations of the Andes of Colombia and Ecuador. The average value and the variability of body size can change drastically between anurans in lowlands and anurans in Andean localities (Amado *et al.*, 2019; Vasconcelos *et al.*, 2019). In the lowlands, anuran assemblages include many species with medium to large body size (e.g. *Rhinella horribilis*, *Leptodactylus pentadactylus*, *Boana rosenbergi* and *Agalychnis spurrelli*), whereas other species have a small body size (e.g. species of the genus *Dendropsophus* and the family Centrolenidae) (Campbell 1999; Duellman, 1978, 2005; Lynch, 1979; Ibáñez *et al.*, 1999; Hilje & Aide, 2012). Contrary to the lowlands, anuran assemblages in the

Table 3. Comparison of functional diversity between anuran assemblages alongside streams and away from streams in seven Neotropical localities

Locality	Species richness		Functional diversity			
	Alongside streams	Away from streams	Alongside streams	Away from streams	FD ratio	*P*-value
La Selva, Costa Rica	18	23	119.59	231.34	1.93	0.84
El Cope, Panamá	20	33	137.87	476.14	3.45	0.97
Parque Soberanía–Isla Barro Colorado, Panamá	20	38	137.69	534.89	3.88	0.80
Chicoral, Valle del Cauca, Colombia	12	11	49.71	41.97	0.84	0.52
Mindo, Ecuador	32	15	375.24	76.69	0.20	0.44
Santa Cecilia, Ecuador	11	66	38.31	1701.21	44.40	0.25
Reserva Adolpho Ducke, Brazil	15	32	78.18	383.26	4.90	0.61

The functional diversity (FD) ratio = FD away from streams/FD alongside streams. The *P*-value is derived from comparisons of the calculated FD ratio vs. a distribution of probability of FD ratios generated with 10 000 randomizations at α = 0.05 (null model; see main text for details). Calculations of FD are based on the index proposed by Chiu & Chao (2014). The species richness refers to those species included in the calculations of FD.

Andean forests of Colombia and Ecuador are mainly composed of small species belonging to the families Centrolenidae and Craugastoridae (Lynch & Duellman, 1997; Bolívar *et al.*, 2010; Meza-Joya & Torres, 2016; Hutter *et al*., 2013, 2017; Amador *et al.*, 2018; Duarte-Marín *et al.*, 2018; Flórez *et al.*, 2018), and the family Dendrobatidae is represented by *Andinobates*, a genus composed of species with small body size (Brown *et al.*, 2011). Therefore, given the inverse relationship between body size and call frequency in anurans, and the acoustic properties of noise on streams (Fig. 1), the call of many species in lowlands would be highly susceptible to be masked in places alongside streams, whereas the frequency of the advertisement call of most anurans in Andean localities could be high enough not to be masked by noise on streams. Altogether, the process of habitat filtering attributable to noise on streams (Vargas-Salinas & Amézquita, 2014; Carvajal-Castro & Vargas-Salinas, 2016) could reduce the FD of anuran assemblages more in lowlands than in Andean localities at medium elevations, at least for those included in the present study.

Other factors aside from noise on streams can affect the distribution of species in a given locality and thus, the FD of assemblages. For instance, a reduction in humidity levels from habitats alongside streams to habitats away from streams might explain the differences in anuran body size between assemblages that we compared, and therefore, offer an alternative explanation to that about biased masking of acoustic signals by abiotic noise. Small species could predominate in assemblages alongside streams because the high humidity present there would reduce the evaporative water loss associated with the high surface-to-volume ratio in such species (Schmidt, 1965; Nevo, 1973). However, the presence of small species in assemblages away from streams does not support this alternative explanation. Moreover, such a gradient in humidity with respect to streams, and the related effect in the distribution of anurans, is expected to be stronger in xeric ecosystems than in humid forest (Duellman & Thomas, 1996; Vargas-Salinas *et al.*, 2014); all the lowlands localities in our study are tropical rain forest characterized by a high precipitation level.

We are aware of limitations in the present study. First, there are anuran species in which vocalizations are not traits crucial for obtaining mates, because apparently, they do not vocalize (e.g. *Pristimantis pardalis*; Savage, 2002) or they use other sensory modalities (e.g. visual displays; Hödl & Amézquita, 2001; Wells, 2007; Vitt & Caldwell, 2014; von May *et al.*, 2018); therefore, the effect of noise on streams might not be straightforward for them. However, to our knowledge most of the species included in the present study use acoustic signaling, and visual displays have been reported in species both alongside streams and away from streams. Second, we did not test the role of historical factors in the evolution of body size, reproductive mode and, ultimately, in species richness and FD. For instance, high species richness has been linked to climatic refuges during the Pleistocene and Antropocene (Carnaval *et al.*, 2009; Lourenço-de-Moraes *et al.*, 2019) and to the rise of the Andes (Rangel *et al.*, 2018). Also, the inclined topography in the Andes precludes the formation of many large lentic bodies of water, which has favoured the establishment of anuran species with reproduction associated with streams (Duellman, 1979, 1999; Ortiz von Halle, 1991). More species alongside streams in these assemblages means a higher value in FD and might therefore explain the opposite tendency in FD found in Andean assemblages. The potential explanatory role of these factors in our results warrants further studies.

In summary, our data support a proxy between acoustic habitat characteristics and sensory ecology with FD in Neotropical anuran assemblages. Functional diversity was consistently higher in anuran assemblages alongside streams than in assemblages away from streams in lowland localities. This tendency could be because of an effect of natural abiotic noise in restraining the establishment of species (especially the larger ones) alongside streams. This statement is in line with the study by Goutte *et al.* (2013), who confirmed the role of natural noise intensity as a strong predictor of calling site selection and species distribution in frogs. Certainly, this effect also depends on the attributes of streams that shape the intensity of the abiotic noise produced (e.g. inclination of terrain, presence of waterfalls and substrate). Further studies, with more quantitative functional traits (e.g. mouth width) and localities with different environmental characteristics, are necessary in order to draw more robust conclusions. Last but not least, FD is commonly related to community functioning and ecosystem processes (Naeem *et al.*, 1994; Hooper *et al.*, 2005; Flynn *et al.*, 2009; Cadotte *et al.*, 2011), and it will be important to determine whether this is the case in our study system.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Summary of morphological and ecological functional traits for 265 anuran species present in seven Neotropical localities. Species breeding away from streams and alongside streams are indicated as zero and one, respectively. Anurans that call and breed alongside streams and away from streams in the same locality (coded as 0,1) are included in this Appendix, but were excluded from statistical analyses of functional diversity (for details, see the main text). The body size of males and females was measured as the snout–vent length (SVL). For the variable 'reproductive mode', the categories used in this study were as follows: (I) eggs deposited in water, with tadpoles in ponds or streams; (II) eggs out of water (terrestrial, arboreal or foam nest), with tadpoles in ponds, streams or small pools in ground cavities; (III) eggs out of water, with tadpoles in phytothelmatas; (IV) eggs and tadpoles in phytothelmatas; (V) eggs out of water that hatch into non-aquatic tadpoles or froglets by direct development; (VI) eggs carried by the adult, with tadpoles in ponds or streams; and (VII) eggs carried by the adult, which hatch into froglets by direct development.

SHARED DATA

The data from this study (Supporting Information, Appendix S1) are also archived at figshare: https://doi.org/10.6084/m9.figshare.9779162.