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Stream noise, habitat filtering, and the phenotypic and phylogenetic structure of Neotropical anuran assemblages

Juan David Carvajal-Castro[1] · Fernando Vargas-Salinas[1]

Abstract The structure of assemblages may be determined by interspecific interactions or environmental factors (e.g. competition and habitat filtering). Since communication between conspecific and heterospecific affects fitness of individuals, habitat characteristics that prevent communication could determine habitat use and co-occurrence of species. However, at present there are few studies, most with birds, testing the relationship between sensory ecology and community ecology. Abiotic noise on streams could impede the detection and decoding of auditory signals by receivers through a process named auditory masking. Therefore, we tested the role of abiotic noise on streams as a habitat characteristic influencing the phenotypic and phylogenetic structure of Neotropical anuran assemblages. We tested this hypothesis using data of male body size, call frequency, calling place (alongside and away from streams), and phylogenetic relationship of 110 and 38 anuran species at regional and local scale, respectively. After we found quantitative evidence suggesting that call frequency and body size are conserved phenotypic traits, we found that assemblages alongside streams exhibit both phenotypic and phylogenetic clustering, while assemblages away from streams exhibit both phenotypic and phylogenetic overdispersion. These results offer quantitative evidence suggesting a role of noise on streams promoting a process of habitat filtering and affecting the structure of anuran assemblages alongside streams both at Neotropical and local scale. This is the first study using modern phylogenetic comparative metrics for covering potential causes of phenotypic and phylogenetic structure of anuran assemblages, and one of the few testing a link between community ecology and the evolutionary biology of acoustic communication to understand the processes mediating species co-occurrence in vertebrates.

Keywords Community ecology · species co-occurrence · Acoustic communication Auditory masking · Advertisement calls

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Introduction

One of the most intriguing questions in evolutionary ecology is what process determines the structure and species composition of assemblages (Cornell and Lawton 1992; Ricklefs and Schluter 1994; Mittelbach 2012). Because phylogenetically related species tend to be similar in morphology, behavior and ecology (Kozak and Wiens 2006), traditionally it has been expected that recently diverged taxa do not co-occur unless they accomplish a minimum degree of dissimilarity (limiting similarity hypothesis; MacArthur and Levins 1967; Diamond and Cody 1975). Hence, competition has been considered the main driver of the ecological dissimilarity of co-occurring species (Darwin 1859; MacArthur 1958; Pain 1974; Schoener 1974; Lubchienco 1978). Another point of view claims that environmental factors can restrict the persistence of species that do not match a specific optimal phenotype; that is, environmental factors (i.e. filters) select species with particular traits from a species regional pool, but exclude those with traits which deviate from that optimal trait (habitat filtering hypothesis; Keddy 1992; Forrest 1994). Alternatively, stochastic forces also have been suggested to explain co-occurrence of species (Webb et al. 2002; Hubbell 2006).

A phenotypic trait can evolve in a conserved or convergent way, and this evolution pattern may influence the phylogenetic structure of the assemblages (Webb et al. 2002). Because interspecific competition limits the ecological similarity of co-occurring species, for phylogenetically conserved phenotypes an overdispersed phylogenetic pattern is expected; conversely, if there is habitat filtering, a phylogenetic clustering pattern would be expected. For converged phenotypes, it is expected a phylogenetic random pattern and a phenotypic overdispersed pattern if competition is the main process influencing the co-occurring species; on the contrary, if habitat filtering is the main process influencing co-occurrence of species, a phylogenetic overdispersion and a phenotypic clustered pattern would have arisen (see Vamosi et al. 2009; Emerson and Gillespie 2008; and Pausas and Verdú 2010 for reviews). Recent studies using modern theories and molecular phylogenetic methods for addressing the causes of assemblage structure of animals and plants have found support for both limiting similarity and habitat filtering hypotheses (Kraft et al. 2007; Riedinger et al. 2013; Gómez et al. 2010; Maire et al. 2012; Spasojevic and Suding 2012; Luza et al. 2015). Nevertheless, given the high diversity of phenotypic traits and natural history characteristics of species, and the possibility that interspecific competition produces a phenotypic and phylogenetic pattern similar to that expected by habitat filtering (Cahill et al. 2008; Mayfield and Levine 2010), more studies are necessary to really understand the relationship between ecology, evolutionary biology, and co-occurrence of species.

Communication between individuals affects life history, reproduction, and thereby fitness; therefore, habitat characteristics that prevent communication could determine habitat use, and hence, the phenotypic and phylogenetic structure of assemblages. Abiotic noise (e.g. noise on streams, traffic noise on roads) can impede the detection and decoding of auditory signals by receivers through a process named auditory masking (Brumm and Slabbekoorn 2005). The level of auditory masking is expected to be higher in areas near the noise source because intensity of sound reduces with distance (Brumm and Slabbekoorn 2005; Vargas-Salinas et al. 2014). Moreover, since most energy of abiotic noise is concentrated at relatively low frequencies (Dubois and Martens 1984; Cunnington and Fahrig 2010), noise produced by flowing water on streams and traffic on roads has been proposed multiple times as a selective force promoting the evolution of high frequency

calls in animals using auditory signals for communicating (Slabbekoorn and Peet 2003; Narins et al. 2004; Feng et al. 2006; Boeckle et al. 2009; Parris et al. 2009; Römer 2013; Vargas-Salinas and Amézquita 2013). If the species do not evolve an adaptation or exhibit a behavioural adjustment that increases signal-to-noise ratio of auditory signals they are filtered out from the noisy habitat (Francis et al. 2011).

Despite the fundamental role that animal communication can have in shaping the structure and composition of animal assemblages, little empirical work has tested this relationship (Amézquita et al. 2011; Cardoso 2014; Francis et al. 2011; Francis 2015). Further, most of these studies use birds as model system, but differences in natural history and communicating behavior (e.g. learning and plasticity in acoustic signals) between animal groups, restrict the extrapolation of accumulated evidence. Anurans offer an excellent opportunity for expanding our knowledge about the role of abiotic noise as a habitat factor influencing the structure of assemblages; they are relatively abundant, most species use auditory signals for communication, and many breed and call away from streams while others do so alongside streams (Duellman and Trueb 1994; Wells 2007). Moreover, there is evidence suggesting that in some species high frequency calls have evolved as an adaptation that allows acoustic communication alongside streams (Feng et al. 2006; Arch et al. 2008; Vargas-Salinas and Amézquita 2013), but this phenomenon might be highly constrained in most species due to strong pleiotropic connection between call frequency and body size (Gerhardt and Huber 2002; Wells 2007). Therefore, it is possible that the masking of auditory signals by abiotic noise could be filtering species in areas alongside streams instead of promoting the evolution of high call frequency in many anuran species, as reported for birds in habitat dominated by anthropogenic noise (Francis et al. 2011; Francis 2015).

Vargas-Salinas and Amézquita (2014) suggest that habitat filtering could explain why anuran species breeding alongside streams utter calls at higher frequencies and are smaller in body size compared to species breeding away from streams; however, these authors did not test this hypothesis. Here we used the framework by Webb et al. (2002) and modern phylogenetic comparative analysis (see Pearse et al. 2014) to quantify the importance of ambient sounds shaping the phenotypic and phylogenetic structure of anuran assemblages. In addition, since patterns arising from ecological studies are necessarily constrained by the spatial scale of the analyses (Wiens 1989; Swenson et al. 2006; Emerson and Gillespie 2008), we tested the habitat filtering hypothesis at two levels: at Neotropical and local scale. It is expected that at large scale the role of habitat filtering is more detectable than at local scale (Swenson et al. 2006; Emerson and Gillespie 2008). At former scales the high habitat heterogeneity can promote coexistence of species with similar phenotypes and environmental requirements across contrasting habitats while at the latter scales, the habitat homogeneity should promote strong interspecific competition that can limit the co-occurrence of phenotypically similar species (Weiher and Keddy 1995; Cavender-Bares et al. 2006; Swenson et al. 2007). Nevertheless, not all habitat characteristics change at the same spatial scale, which can explain mixed results in literature concerning the relative role of habitat filtering and competition (Gómez et al. 2010; Luza et al. 2015).

For conserved traits in which the habitat filtering hypothesis is right, we expect to find (1) a phylogenetic and phenotypic (e.g. body size, call frequency) clustering pattern in the assemblage of anuran species calling and breeding alongside streams, and (2) a phylogenetic and phenotypic overdispersion in anuran species calling and breeding away from streams (Fig. 1a; but see Mayfield and Levine 2010). If the structure of assemblage is influenced mainly by interspecific competition we expect to find a phylogenetic and phenotypic overdispersed pattern both in assemblages alongside streams and away from
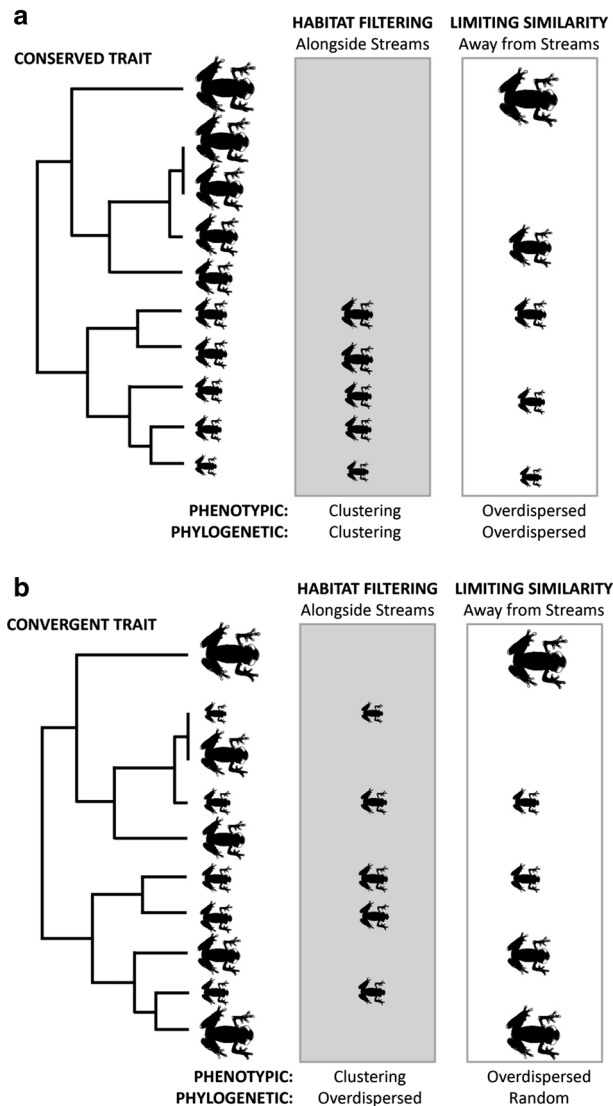
Fig. 1 Alternative hypothesis of the phenotypic and phylogenetic structure of anuran assemblage as a consequence of the dominant assembly process (habitat filtering versus limiting similarity) for a conserved (**a**) and a convergent (**b**) anuran phenotypic trait. Size of the frog silhouettes represent a quantitative trait (e.g. male body size) which is inversely correlated with dominant call frequency. *Gray boxes* represent noisy habitats characterized by intense abiotic noise at low frequencies (alongside streams); *white boxes* represent less noisy habitats (away from streams). Habitat filtering would allow the persistence of species whose individuals utter auditory signals at high frequency (and the concomitant small body size) alongside streams. For assemblages away from streams would be expected that limiting similarity processes prevent similar species in call frequency and body size co-occurring. Figure adapted from Pausas and Verdú (2010)

steams. Other phenotypic and phylogenetic patterns are expected for convergent traits (Fig. 1b). To test the previous predictions we first analyzed whether phenotypic traits exhibit phylogenetic signal, which would offer evidence about the trait evolution pattern

(conserved *vs* convergent). Later, we estimated metrics that allow us to contrast alternative phylogenetic and phenotypic pattern (i.e. clustering, overdispersion). In this study we make a link between sensory ecology and community ecology, two research disciplines that have traditionally developed apart from each other.

Materials and methods

To test our hypotheses at a Neotropical scale, we used the topology and database published by Vargas-Salinas and Amézquita (2014) which was based on Pyron and Wiens (2011) phylogenetic analysis and literature. To test our hypotheses at a smaller scale (hereafter "local scale") we used the genetic sequences used by Crawford et al. (2010) for an amphibian assemblage in the Natural Reserve El Copé, at Central Panamá. We used sequences of two mitochondrial genes, the ribosomal subunit 16S and the Cytochrome Oxidase I (16S, COI) corresponding to 58 anuran species from GeneBank (Table 1). The sequence alignment was performed with MUSCLE (Edgars 2004) in MEGA 6 (Tamura et al. 2013), and made a matrix of concatenated alienated genes. Like Crawford et al. (2010), for the 16S gene we excluded sites with gaps plus one additional base on either side of gaps with a length greater than 1 bp. Then, we ran a maximum likelihood (ML) analysis in the graphical interface of RAxML (Stamatakis 2006; Silvestro and Michalak 2012). The phylogenetic analysis was performed using four data partitions as suggested by Crawford et al. (2010) and the GTR + GAMMA (=GTR + Γ) model of nucleotide substitution used for all data partitions. We used 1000 bootstraps for searching the best topology. Both the tree at Neotropical and local scale were converted into an ultrametric tree using semi-parametric method based on penalized likelihood (Sanderson 2002) implemented in the package APE (Paradis et al. 2004) for R (R Development Core Team 2015).

Later, we reviewed the literature for the natural history information for each species. Specifically, we looked for male body size (SVL, Snout-to-vent length), dominant frequency of the advertisement call (hereafter "call frequency"), and breeding habitat (streams, away from streams). As possible, we used average data on male body size and call frequency calculated from several individuals. Where the published descriptions included ranges rather than average values, we used the range midpoint as an approximation to the mean. Breeding habitat was categorised in agreement to the expected level of natural abiotic noise: noisy (alongside streams) and less noisy (away from streams) habitats. To test whether our species assemblage at local scale exhibit similar patterns that those found at Neotropical scale by Vargas-Salinas and Amézquita (2014), we used similar analysis to those performed by them: a t-tests to compare call frequency and male body size between species that breed alongside streams and away from streams. We also tested for an inverse relationship between male body size and call frequency with a linear regression analysis. Species cannot be considered as independent statistical units because they share ancestry (Felsenstein 1985); therefore, we compared call frequency and male body size between habitats (streams, away streams) with a phylogenetic ANOVA (Garland et al. 1993). The relationship between male body size and call frequency after controlling for the phylogenetic relationship of species was tested using Phylogenetic Generalized Least Squares (Freckleton et al. 2002).

Phylogenetic signal is a common phenomenon in the phenotypic traits of animals (Blomberg et al. 2003; Hof et al. 2010) and is arguably present in phenotypic traits such as call frequency and body size in anurans (Erdtmann and Amézquita 2009). Nevertheless,

Table 1 Summary of phenotypic characters included in our analyses for 16 anuran species breeding alongside streams (with bold), and 22 species breeding away from streams at El Copé, Panamá (analysis at local scale; Crawford et al. 2010)

Taxa	Mean body size (mm)	Mean call frequency (kHz)	Number of males recorded	Information source	Genetic sequence 16S	COI
Bufonidae						
Atelopus zeteki	38.5	2.35	1	Cocroft et al. (1990)	FJ784541	FJ766577
Incilius coniferus	62.5	1	1	Porter (1966), Savage (2002)	FJ784379	FJ766768
Rhinella marina	115	0.715	≥1	Lee (1996), Savage (2002)	FJ784357	FJ766819
Dendrobatidae						
Allobates talamance	20.5	4.075	≥1	Savage (1968, 2002)	FJ784370	FJ766610
Dendrobates auratus	27.69	3.302	15	Erdtmann and Amézquita (2009)	FJ784317	FJ766698
Oophaga vicentei	20	5.525	>1	Lötters et al. (2007)	DQ502167	DQ502869
Andinobates minutus	14.5	5.9	>1	Myers and Daly (1976), Brown et al. (2011)	DQ502168	DQ502870
Silverstoneia flotator	15.6	5.85	10	Ibáñez and Smith (1995)	FJ784352	FJ766822
Silverstoneia nubicola	17.5	4.6	6	Ibáñez and Smith (1995)	FJ784563	FJ766824
Centrolenidae						
Cochranella euknemos	23	4.2	>1	Savage and Starrett (1967,2002)	FJ784458	FJ766601
Cochranella granulosa	25.75	4.25	≥1	Savage and Starrett (1967), Ibáñez et al. (1999)	FJ784455	FJ766604
Espadarana prosoblepon	26.5	5.758	10	Jacobson (1985)	FJ784362	FJ766593
Hyalinobatrachium colymbiphyllum	25	4.5	≥1	Savage (2002)	FJ784366	FJ766708
Hyalinobatrachium talamancae	23.5	4.6	≥1	Kubicki (2007)	FJ784480	FJ766718
Teratohyla spinosa	18.9	7	≥1	Ibáñez et al. (1999), Savage (2002)	FJ784348	FJ766607
Sachatamia albomaculata	26	6.6	≥1	Kubicki (2007)	FJ784392	FJ766599
Sachatamia ilex	28.5	6	≥1	Kubicki (2007)	FJ784582	FJ766585
Hylidae						
Agalychnis callidryas	45.9	2.097	25	Duellman (2001)	FJ784436	FJ766570
Cruziohyla calcarifer	66	0.8	1	Myers and Duellman (1982), Duellman (2001), Savage (2002)	FJ784368	FJ766571

Table 1 continued

Taxa	Mean body size (mm)	Mean call frequency (kHz)	Number of males recorded	Information source	Genetic sequence 16S	COI
Hylomantis lemur	35.5	2.25	2	Savage (2002), Duellman (2001)	FJ784355	FJ766721
Hyloscirtus colymba	34	3.6	3	Duellman (2001), Savage (2002)	FJ784381	FJ766731
Hyloscirtus palmeri	38.95	2.5	1	Ibáñez et al. (1999), Duellman (2001), Savage (2002)	FJ784457	FJ766738
Hypsiboas rufitelus	44	1.6	3	Duellman (2001)	FJ784372	FJ766740
Smilisca phaeota	53	0.415	10	Duellman (2001)	FJ784413	FJ766835
Smilisca sila	38	1.55	15	Duellman (2001)	FJ784578	FJ766837
Hemiphractydae						
Gastrotheca cornuta	73.5	0.8	1	Duellman (2001)	FJ784373	FJ766706
Craugastoridae						
Craugastor crassidigitus	25.5	2.95	1	Lynch and Myers (1983)	FJ784328	FJ766642
Craugastor fitzingeri	29	3	1	Lynch and Myers (1983)	FJ784337	FJ766648
Pristimantis caryophyllaceus	21.59	2.75	4	Batista et al. (2014)	FJ784421	FJ766774
Pristimantis cerasinus	22	3.55	≥1	Ibáñez et al. (1999), Savage (2002)	FJ784387	FJ766786
Pristimantis ridens	17.5	5.6	≥1	Savage (2002)	FJ784389	FJ766807
Strabomantis bufoniformis	55	0.85	≥1	Ibáñez et al. (1999)	FJ784410	FJ766635
Leptodactylidae						
Engystomops pustulosus	29.5	0.65	11	Rand and Ryan (1981), Savage (2002)	FJ784414	FJ766703
Leptodactylus fragilis	34.8	1.305	>1	de Sá et al. (2014)	FJ784331	FJ766745
Leptodactylus insularum	86.6	0.58	3	Heyer and de Sá (2011), de Sá et al. (2014)	FJ784467	FJ766746
Leptodactylus poecilochilus	41	0.45	1	Fouquette (1960), Straughan and Heyer (1976), Savage (2002)	FJ784321	FJ766747
Leptodactylus savagei	133.2	0.41	>1	Heyer et al. (2010), de Sá et al. (2014)	FJ784394	FJ766748
Ranidae						
Lithobates warszewitschii	44.5	1	5	Greding (1972), Savage (2002)	FJ784454	FJ766752

Database for analysis at neotropical scale is in Vargas-Salinas and Amézquita (2014). Genetic sequences codes from Crawford et al. (2010)

there is evidence suggesting that phylogenetic signal is not ubiquitous (Losos 2008). Therefore, in our study we evaluated whether male body size and call frequency exhibit phylogenetic signal, which would suggest a trait is conserved, using the statistic K (Blomberg et al. 2003) performed in the R package Picante (Kembel et al. 2010). For testing phylogenetic signal and phenotypic structure of assemblages (see below) we used transformed values (Ln) of male body size and call frequency according to suggestion by Gotelli and Graves (1996; cited by Gómez et al. 2010). K values vary continuously from zero to infinity. K values greater than 1 indicate a strong phylogenetic signal (i.e. conserved trait), K values equal to 1 indicate a Brownian motion process which implies some degree of phylogenetic signal and conservatism, K values less than 1 indicate that the evolution of the trait is labile, and K values equal to 0 indicate that trait evolution pattern is random or convergent (Blomberg et al. 2003; Gómez et al. 2010, Kraft et al. 2007; Revell et al. 2008).

To test for the phylogenetic assemblage structure we obtain the metric standardized effect size (SES) of mean pairwise phylogenetic distance (SES_{mpd}) in the R package Picante. The SES_{mpd} was calculated from a comparison between observed mean pairwise phylogenetic distance (MPD) and an expected pairwise phylogenetic distance. The latter was obtained from randomization of the anuran assemblage (Webb et al. 2002) using 1000 random assemblages under the null model of sample pool (Kembel et al. 2010; Hardy 2008). From this randomization process we obtain the p value ($\alpha = 0.05$) derived from SES_{mpd} calculations (for more details see Kembel et al. 2010). A negative value of SES_{mpd} indicates phylogenetic clustering, while a positive value indicates phylogenetic overdispersion; this index is similar to the NRI index proposed by Webb et al. (2002, 2008).

The phenotypic structure of assemblages was tested similarly to the phylogenetic assemblage (see above), but the phylogenetic distance matrix is replaced by a trait distance matrix for both call frequency and male body size (calculating the Euclidian distance). Then, we calculated the MPD and SES_{mpd} for each phenotypic trait, for each anuran assemblage, and for both scales of analysis. The null model (sample pool) was calculated using 1000 randomizations. Similar to the phylogenetic structure of assemblages, a negative value of SES_{mpd} indicates phenotypic clustering while a positive value indicates phenotypic overdispersion. The p value was derived from SES_{mpd} calculations (Kembel 2009; Kembel et al. 2010).

Results

The 110 anuran species used at Neotropical scale belong to five families (11 species in Bufonidae, 9 in Centrolenidae, 34 in Dendrobatidae, 51 in Hylidae, and 5 in Ranidae); see Vargas-Salinas and Amézquita (2013) for phenotypic data and comparative analyses of those species. The compiled data for the anuran assemblage at El Copé, Panama (local scale) about male body size and breeding habitat for 58 anurans is presented in Table 1. Call frequency information was available only for 38 taxa; in phylogenetic analyses we only used these latter species. Those 38 species belongs to Bufonidae (3 species), Centrolenidae (8), Craugastoridae (6), Dendrobatidae (6), Hemiphractidae (1), Hylidae (8), Leptodactylidae (5), and Ranidae (1); 16 of them breed alongside streams and 22 breed away from streams (Fig. 2). Call frequency was on average 2.16 kHz higher in streamside breeders than in other species (t = −3.73, df = 36, $p = 0.001$, Fig. 3a). Moreover, smaller anurans are less variable in body size than anurans that breed away from streams
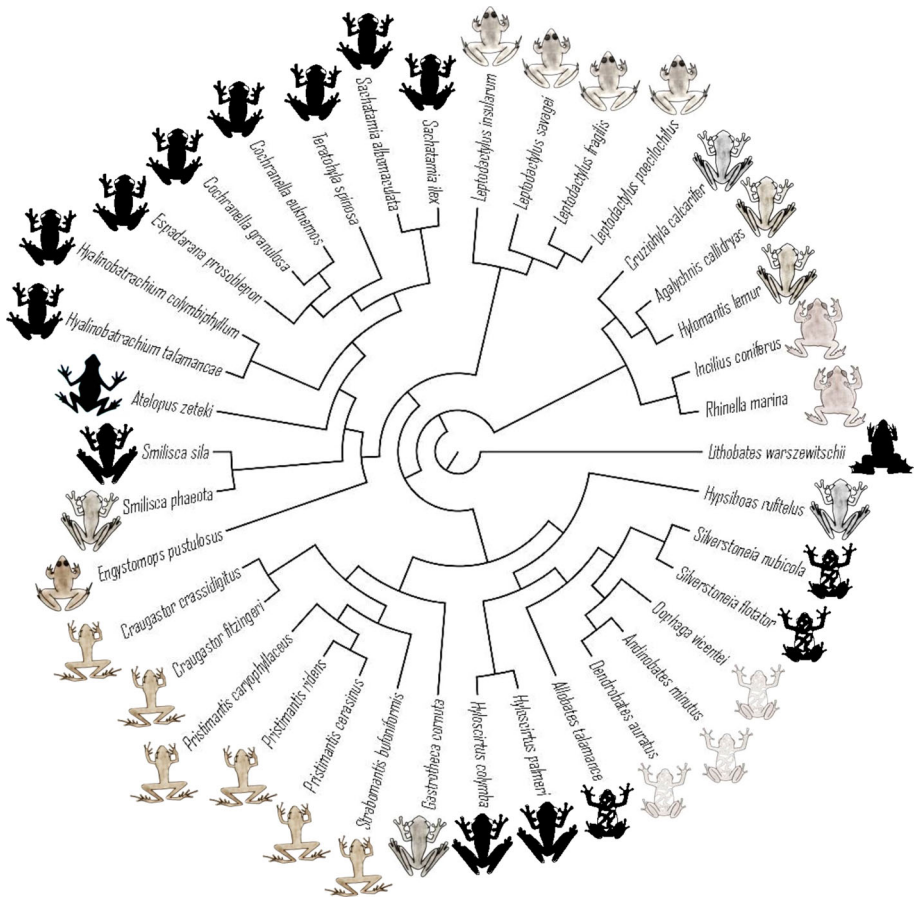
Fig. 2 Phylogenetic analysis of mitochondrial genes (16S, COI) showing relationships between 38 anuran species used for analysis at local scale (El Copé, Panamá). The topology shows the best tree of the maximum likelihood analysis of mtDNA for 16 anuran species breeding alongside streams and 22 species breeding away from streams. Sequences from GenBank (see Table 1 for accession numbers). Anuran silhouettes indicate calling habitat (*Black silhouettes*: noisy habitats alongside streams, *Gray silhouettes*: away from streams)

(Levene test for homogeneity of variances $= 10.995$, $p = 0.002$; $t = 2.855$, df $= 25.17$, $p = 0.018$; Fig. 3b). Species whose males are large in body size produce calls with lower dominant frequency than those species whose males have smaller body size ($R^2 = 0.42$, $\beta = -0.53$, $F = 18.96$, df $= 27$, $p > 0.001$; Fig. 3c). A similar tendency was obtained after controlling by the phylogenetic relationship between species (call frequency vs calling site: phylogenetic p value $= 0.0005$; male body size vs calling site: phylogenetic p value $= 0.018$; relationship male body size-call frequency: $R^2 = 0.55$, $F = 45.50$, df $= 36$, $p < 0.001$).

There was phylogenetic signal for body size and call frequency at both spatial scale analyses; however, the K values suggest that at Neotropical scale the evolution pattern of those traits is labile whist at local scale is highly conserved (Table 2). Consistent with our hypothesis, anuran assemblages alongside streams are more related phylogenetically than
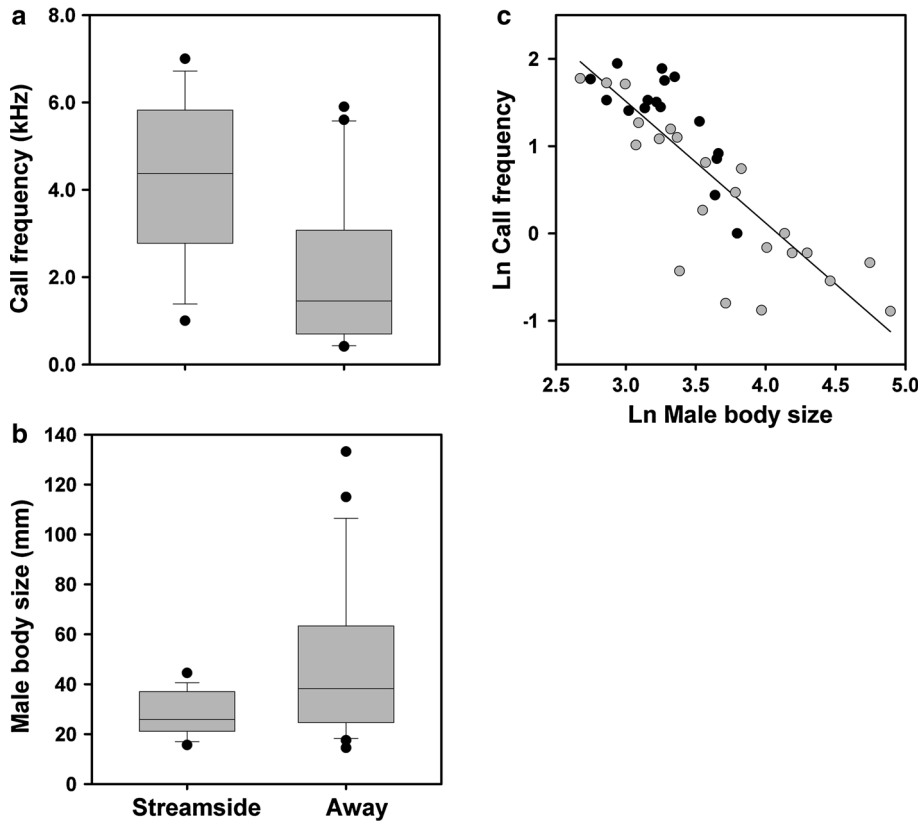
Fig. 3 Analyses for anuran assemblages at local scale comparing dominant call frequency (**a**) and body size (**b**) of males between 16 anuran species that breed alongside streams and 22 that breed away from streams (total = 38 species), and the relationship between body size and call frequency (**c**). Box plots (**a**, **b**) show 25th and 75th percentiles (*box*), median (*line* within *box*), and 5th and 95th percentiles (whiskers). *Gray* and *black filled dots* at **c** indicate species calling away and alongside from streams, respectively. Similar results are found after controlling by the phylogenetic relationship between species (see text)

Table 2 Test of phylogenetic signal for body size and call frequency for anuran assemblages at two scales of analysis (Neotropical and local)

Scale of analysis	Trait	K value	*p* value
Neotropical	Male body size	0.9283379	0.001*
	Call Frequency	0.7036232	0.001*
Local	Male body size	1.431717	0.001*
	Call Frequency	1.670593	0.001*

K-value according to Blomberg et al. (2003)

* Indicates a phylogenetic signal

expected by chance, while anuran assemblages at areas away from streams are less phylogenetically related than expected by chance. These two results were consistent for both Neotropical and local assemblages (Table 3). Likewise, at both scales, the male body size

Table 3 Phylogenetic diversity metrics for body size and call frequency for anuran assemblages at two scales of analysis (Neotropical and Local)

Scale	Assemblage	Phylogenetic structure		Phenotypic structure		
		SES_{MPD}	p value	Trait	SES_{MPD}	p value
Neotropical	Alongside streams	−1.7558150	0.04595404*	Call frequency	−3.5802971	0.000999001*
				Male body size	−4.3782086	0.000999001*
	Away from streams	0.65022719	0.70229770	Call frequency	0.7581765	0.756243756
				Male body size	0.9243831	0.829170829
Local	Alongside streams	−6.820764	0.000999001*	Call frequency	−3.8715889	0.000999001*
				Male body size	−2.623893	0.002997003*
	Away from streams	0.5295899	0.674325674	Call frequency	0.2397145	0.558441558
				Male body size	1.516330	0.944055944

Statistics according to Webb et al. (2002), and Kembel et al. (2010)

* Indicates a phylogenetic or phenotypic structure different than expected by chance

and the call frequency exhibit phenotypic clustering in assemblages breeding alongside streams, whilst they are overdispersed for assemblages away from streams (Table 3).

Discussion

We found evidence supporting the hypothesis that noise on streams promotes a process of habitat filtering upon species with low call frequencies and the concomitant larger body size (Fig. 3; Table 3). In this way, noise on streams could have major role in determining the phylogenetic and phenotypic structure of anuran assemblages (but see next paragraph). Abiotic noise on streams is characterized by a high intensity at low frequencies and a low intensity at higher frequencies (Dubois and Martens 1984; Schwartz and Bee 2013). Hence, acoustic communication of species whose individuals utter auditory signals at low frequencies is especially difficult because signal masking by noise (Hödl and Amézquita 2001; Brumm and Slabbekoorn 2005). As a consequence, the phenotype favored by the noisy conditions alongside streams may be high call frequencies and small body size (phenotypic clustered pattern). Furthermore, it is expected that the habitat filtering effect imposed by noise on streams reflects in multiple aspects of species' natural history because body size in anurans is related to size and type of diet, fecundity, physical strength and other traits related to fitness (Duellman and Trueb 1994; Wells 2007).

A labile evolution pattern for call frequency and body size at Neotropical scale (Table 2) does not discard conservatism of these traits; rather, K-values less than unity (i.e. deviation of simple Brownian motion) may be attributed to adaptations to a particular environment factor in some species but not others (Blomberg and Garland 2002; Blomberg et al. 2003). Indeed, there is empirical evidence suggesting that some species calling alongside streams have evolved high call frequencies (and usually small body size) as an adaptation to noise on streams (Feng et al. 2006; Arch et al. 2008; Grafe et al. 2012; Vargas-Salinas and Amézquita 2013; Vargas-Salinas et al. 2014). This adaptation however, may have been constrained in most species by the effects of body size and selection acting in diverse contexts (Gerhardt and Huber 2002; Wells 2007). On the other hand, our analyses at local scale suggest that call frequency and male body size are conserved phenotypic traits; similar conclusions have been reached by Gerhardt and Huber (2002), and Erdtmann and Amézquita (2009). The fact that possible adaptations promoted by abiotic noise on streams may be detected at one scale but not another could be attributable to differences in the number of species included in the analysis of phylogenetic signal (Krasnov et al. 2011; Losos 2008). We believe the difference in K values between Neotropical and local scales do not discard the major role of habitat filtering in structuring Neotropical anuran assemblages, but highlight the role of selective process acting in some species and the importance of studies at different scales in community ecology.

We showed a phylogenetic and phenotypic pattern expected under the hypothesis of habitat filtering for assemblages alongside streams both at Neotropical and local scale. Predictions regarding habitat filtering are often assumed to operate at larger scales, but over-dispersion may dominate at local scales due to competition (but see Gómez et al. 2010; Luza et al. 2015). Researches usually have tested broadly distributed environmental factors such as temperature, precipitation gradients, winds, or nutrients in soils (e.g. Maire et al. 2012; Lososová et al. 2015; Lanier et al. 2013; Graham et al. 2009) while we tested noise on streams, a habitat feature that rapidly decreases in intensity as it propagates from the source (Brumm and Slabbekoorn 2005; Vargas-Salinas et al. 2014). In other words, the

acoustic ambient can change drastically in just few meters and hence promote a turnover of species at small spatial scales as a consequence of differential signal masking levels. In fact, even along an individual stream can be a heterogeneous acoustic environment depending of landscape topography, waterfall presence, kind of substrates, or stream size (Vasudevan et al. 2006; Keller et al. 2009). It is possible that the variability of noise intensity along a stream influences the strength of habitat filtering process acting upon call frequency and anuran body size at micro-spatial scale, but this hypothesis deserves further analysis. Unfortunately, data about ambient sound level and other specific calling site attributes (e.g. height) are absent for most anuran species (Goutte et al. 2013).

We do not discard the importance of competition influencing the co-occurrence of species in our study system. In fact, there is abundant empirical evidence about intra and interspecific competition for communication channels in anurans (see review in Gerhardt and Huber 2002; Wells 2007) and other animals (Kirschel et al. 2009; Brumm 2006, 2013). We also agree that for conserved traits, competition could produce a phenotypic and phylogenetic pattern similar to that expected under the habitat filtering hypothesis (Mayfield and Levine 2010). However, we do not regard as plausible that our results for assemblages alongside streams can be the result of competition instead of habitat filtering because several reasons which are not mutually exclusive. First, contrary to the example (in plants) identified by Mayfield and Levine (2010) to support their arguments, an increase in call frequency implies an evolutionary change in body size for most anurans, and a potential reduction in mating success because signals at high frequency attenuate faster than signals at low frequencies (Gerhardt and Huber 2002). Second, in spite of the reduced band of frequency channels available for communicating because of abiotic noise, anuran species alongside streams can still coexist communicating if they partitioning the resource at finer frequency bands, using different calling perches, being active at different times, and using complementary sensory modalities (Amézquita et al. 2006; Schwartz and Bee 2013; Starnberger et al. 2014a, b). Third, our results are consistent at both scales of analysis. Summing up, the evidence suggest that competing species calling alongside streams are those that have previously overcome the filter effect of abiotic noise (i.e. high call frequency and small body size).

Several factors might restrict the comparability of information among the species included in our data matrix; for instance, differences in temperature at time of call recording, and among-sites differences in habitat vegetative physical structure (Vargas-Salinas and Amézquita 2013). However, those authors used published empirical evidence (e.g. Gerhardt 1978; Sullivan 1982; Zimmerman 1983; Bosh and De la Riva 2004) to argue that differences on call frequency and body size between assemblages alongside streams and away streams are real and not artefactual results caused by biased data. For our local scale analysis we used phenotypic trait information from populations other than the study site (El Copé, Panamá), and it is known that several anuran species exhibit geographic variation in body size and call frequency (e.g. Narins and Smith 1986; Ryan and Wilczynski 1991). Nevertheless, we consider it very unlikely that traits of species with geographic variation were recorded consistently in a way that produced the clustered phenotypic patterns we found at local scale. On the other hand, insect choruses produce a loud noise background that can mask auditory signals of vertebrates and hence, influence the frequency channels that birds and anurans use for communicating (Ryan and Brenowitz 1985; Wong et al. 2009). Given that insects produce sounds at relative high frequency (Ryan and Brenowitz 1985; Gerhardt and Huber 2002), similar patterns to those presented here could result if small-bodied and high frequency frogs are excluded from environments away from streams. We discard this possibility because a loud acoustic environment by

insects can be present both away and alongside streams, and because not necessarily the spectral features of the soundscape produced by insects must be equal in space and time (Lampe et al. 2012; Römer 2013).

Habitat filtering and its effect in the phylogenetic and/or phenotypic structure of community assemblages has been studied in plants (Maire et al. 2012; Spasojevic and Suding 2012; Lososová et al. 2015) and attributed to habitat characteristics such as disturbance regimens, winds, temperature and nutrients availability. The effect of habitat characteristics such as vegetation structure, climate, and anthropogenic disturbance in animal assemblages has been tested from similar approaches with lizards (Lanier et al. 2013), birds (Graham et al. 2009; Gómez et al. 2010), small mammals (Riedinger et al. 2013; Luza et al. 2015), fishes (Blanchet et al. 2014; Starnberger et al. 2014a, b), but ours is the first study of phenotypic and phylogenetic structure of anuran assemblages. With respect to abiotic noise, there is evidence suggesting that this kind of noise is an important habitat characteristic filtering some birds and frogs species but not others (Francis et al. 2011; Proppe et al. 2013; Vargas-Salinas and Amézquita 2013). However, those studies about the effect of abiotic noise did not test the effect on the phylogenetic structure of assemblages using modern phylogenetic metrics. Hence, our results point out a link between community ecology and the evolutionary biology of acoustic communication to understand the processes mediating species coexistence in Neotropical anuran assemblages. Further studies in phylogenetic assemblage structure should test the potential effects of metacommunity dynamics, speciation, extinction, adaptation, dispersion and even neutral processes (Emerson and Gillespie 2008; Mittelbach and Schemske 2015).

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