

Changes on Anuran Tadpole Functional Diversity along an Environmental Gradient at the Southernmost Atlantic Rainforest Remnant

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Abstract For decades the ecologists are using the same methods in order to determine the environmental health of a community, however, the crescent need on defining how these processes act, triggered the development of new methods that could classify the organisms and their function at the habitats. Here we used the anuran larvae to understand the effects of an environmental gradient on the structure and organization of the anuran assemblages along it, and to access in a realistic form, the actual state of preservation of the largest remnant of Atlantic Rainforest on the Southernmost portion of Brazil. We found that despite the higher diversity of species and the conservation unit status of the place, the ecosystem itself is still in danger, given the low number of functional groups and thus a higher number of ecosystem services that can be lost.

Keywords Anuran, ecosystem function, conservation unities, tadpoles

1. Introduction

The emergence of the functional ecology as a discipline itself have made necessary the coinage of an expression that could classify the organisms, in order to define the functional diversity of a community and access the species effects on the ecosystems (Woodward and Cramer, 1996; Violle *et al.*, 2007). Thus, the functional traits of a given species were usually defined by characteristic that exerts effects on fitness of an organism, being it physiological, morphological behavioural or developmental (Geber and Griffen, 2003; Violle *et al.*, 2007). In this way, the very establishment and/or persistence of a given species on an environment, is somehow a response from the biological characteristics under a set of environmental variables (Southwood, 1977; Schmid-Hempel, 1991; McGill *et al.*, 2006; Tellería, 2016).

A common approach in community ecology is to investigate the usual associations of environmental characteristics with number of species and their taxonomic identity (Diamond, 1975; Rojas-Ahumada *et al.*, 2012; Prado and Rossa-Feres, 2014), but let aside the contributions of individual traits and their interactions as a response to the environmental characteristics (Elton, 1958; Southwood, 1977). In fact, even the species (species level) itself can be considered an assembly of individuals with different arrays of behaviour and phenotypic characteristics, which will determine when and where the species can exist and will also determine how they will interact with individuals from other species (McGill *et al.*, 2006b).

There is an emerging view that uses these eco-morphological measures which make possible understand the trait diversity on an assemblage, and by using these tools we can promote complementary conservation and/or restoration decisions

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(Cadotte *et al.*, 2011). In this context, studies aiming to measure the species traits variation as a variable to be modified by the shifts on the environmental conditions (and thus, inducing the species composition in a community), have raised a new tool to evaluate the mechanisms that determine the communities assembly either at modified landscapes and preserved ones (Petchey and Gaston, 2002a; Petchey, 2003; de Souza Queiroz *et al.*, 2015).

In our study, we worked with three main objectives: (1) to access the functional diversity of the anuran larvae along an environmental gradient, testing the hypothesis that (H1) the functional diversity of the anuran tadpoles would be higher at the borders of the environmental gradient following the premise that the ponds located close to the agricultural areas would provide both specialized traits and generalist traits, enhancing the values of functional diversity; (2) to test if the values of functional diversity obtained were related with the usual environmental descriptors sampled along the gradient, testing the hypothesis (H2) that the functional diversity would be enhanced following an gradient of complexity of the habitats, following the premise that the dynamism of the landscape provided by more complex environments (e.g. higher number of microhabitat, differences on hydroperiod) could trigger differences on individual responses from the species, which generates different number of functional traits (see Cadotte *et al.*, 2011); (3) to test if the richness values varies (significantly) along the gradient, and if so, would the functional diversity values be related with the richness values; by testing the hypothesis (H3) that richness would present minimal changes along this gradient, and the functional diversity would not be related to these values.

2. Materials and Methods

2.1. Data acquisition and study site The field surveys were carried out in two years, during the anuran breeding season (two springs and two summers) at the Turvo's State Park (TSP, Figure 1), a Conservation Unit inserted on a Mesophytic Semideciduous Forest (Prado, 2000). TSP comprises an area of 17 491 hm^2 , with about 90 km of perimeter, without a buffer zone to diminish the effects of the agropastoral activity. We gathered information on the species of anuran tadpoles in 19 ponds inserted in a gradient of distance that ranged from the border of the TSP (this ponds were close to an agricultural ecosystem) to its interior (a well preserved ecosystem), all with different physiognomic characteristics, where were recorded data on environmental descriptors such as: (i) water depth; (ii) distance from TSP's nearest border; (iii) the number of vegetation types in the interior of ponds (floating plants, emergent and underwater plants, trees and bushes); (iv) water temperature, and (v) canopy coverage (%).

Anuran tadpoles were collected with a dip net (mesh of 2 mm^2) by exploring the available microhabitats at each pond (e.g. floating vegetation, different profiles of emergent vegetation, clear water following McDiarmid and Altig (1999). Larvae were immediately euthanatized (Lidocaine 10%) and fixed in 10% formalin to posterior identification at laboratory. For each of the anuran species recorded, we compiled 13 functional traits (Table S1, S2), chosen to represent relationships with feeding, swimming, habitat use and/or life-history strategies of the anuran tadpoles ecology, as well as we measure 10 morphometric attributes (Altig and McDiarmid, 1999; Strauss *et al.*, 2010) from five tadpoles with stages ranging from 33 to 39 (*sensu* Gosner, 1960) (see de Souza Queiroz *et al.*, 2015).

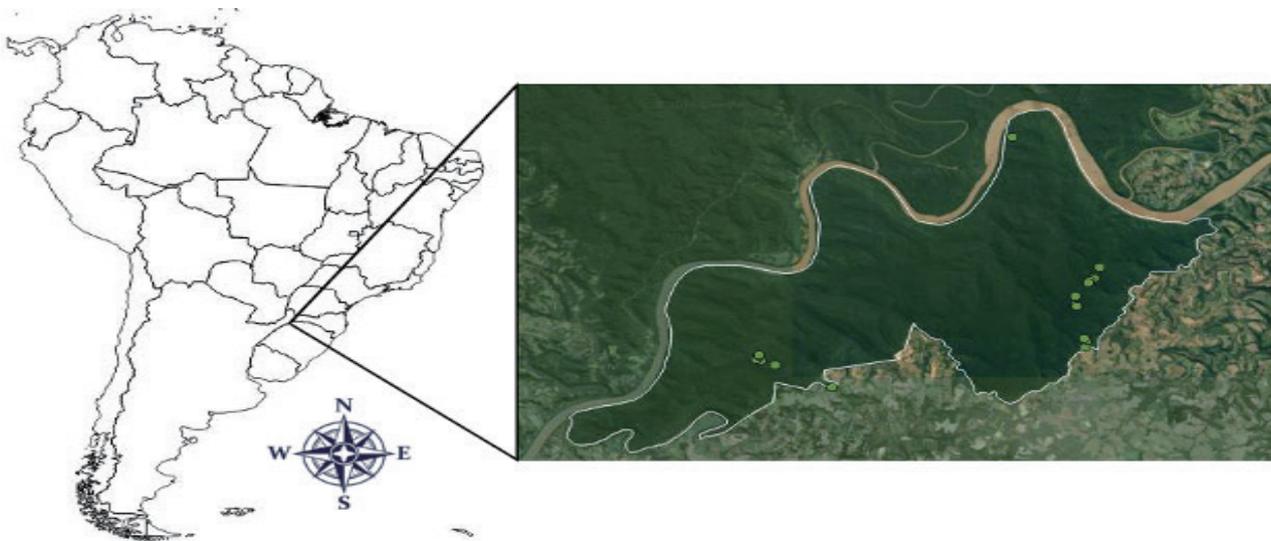


Figure 1 Map showing the location of TSP at South America. The green dots represent the location of 19 sampled ponds.

The collected tadpoles were identified, measured and deposited at the “Coleção Herpetologia da Universidade Federal de Santa Maria” (ZUFMS), Santa Maria, Rio Grande do Sul state, Brazil.

2.2. Data analysis To access the Functional Diversity (*FD*), the Functional Divergence (*Fdiv*) and the Functional Dispersion (*Fdis*) of the anuran community we obtained three data matrix: 1) a trait matrix of the species with the functional traits of the tadpoles; 2) a community composition matrix with presences and absences of the species at larval stages; 3) a matrix with environmental descriptors of the ponds, to test the association of it with the functional measures (see Supplementary Material S1 for tadpole traits and Supplementary Material S2 for environmental descriptors).

To perform the Functional analysis, we first reduced the dimensionality and correlations between our continuous data of morphometric traits (tadpole body forms) in two axes explaining ~80% of the variation by using a Principal Component Analysis (PCA). Then with the matrixes of morphometric traits (1) and the community composition (2), we used a flexible distance-based framework to compute multidimensional functional diversity (*FD*) indices for each sampled pond. We used the function, *dbFD* (Laliberté and Legendre 2010), this method can handle with any distance or dissimilarity measure, any number of traits (binary, continuous, nominal or ordinal) and have no strong influences of outliers. By using this function, we obtained the values of Functional Divergence (*Fdiv*), that varies from -1 to 1, and Functional Dispersion (*Fdis*) that have no upper limit and then, constructed a dendrogram, based on the functional groups (*FGR*) that represents the similarity/dissimilarity among species according to their ecological traits (Petchey and Gaston 2002a; Petchey et al. 2009).

We tested, by using a Moran's I index (R's *Moran's I function*), the spatial influence on our data and used a GLM (R's *glm function*) with the environmental matrix (3) to test the

existence of any relation of the obtained *FD* measures with the environmental variables. All analysis were performed using the software R (R Development Core Team 2011)

3. Results

Our sampling effort resulted in the record of larvae from 10 anuran species. The species recorded at the 19 sampled ponds throughout the environmental gradient corresponds to approximately 35% of the total number of species registered to Turvo's State Park, and belongs to five anuran families: Bufonidae, Hylidae, Leptodactylidae, Microhylidae, and Phyllomedusidae (Table 1).

Our first analysis showed that, as expected, there is a variation on *FD* measures among each sampled pond at the environmental gradient. The values of *FD* ranged from 0.19 to 0.31, the values of *Fdiv* ranged from 0.67 to 0.89, the *Fdis* values ranged from 2.0 to 4.6 and the *FGR* showed the number of functional groups per pond, which resulted in the clustering of seven functional groups based on the species traits (Figure 2). Furthermore, the Moran's *I* index showed the absence of spatial correlation among the ponds ($P > 0.05$), and the GLM showed a positive relation of the enhance of distance from TSP's border towards the interior on values of *FD* (Figure 3).

4. Discussion

Our main findings here show that the anuran larvae sampled in this environmental gradient, even been one-third of the total species richness (represented only by the pond breeders), belongs to communities probably structured by low competition on resource use and a high level of niche differentiation, explained by the elevated values on Functional Divergence. These findings are supported when we saw that the high values of Functional Diversity are also a signal or a characteristic of assemblages that act more efficiently on resource exploitation, thus competition

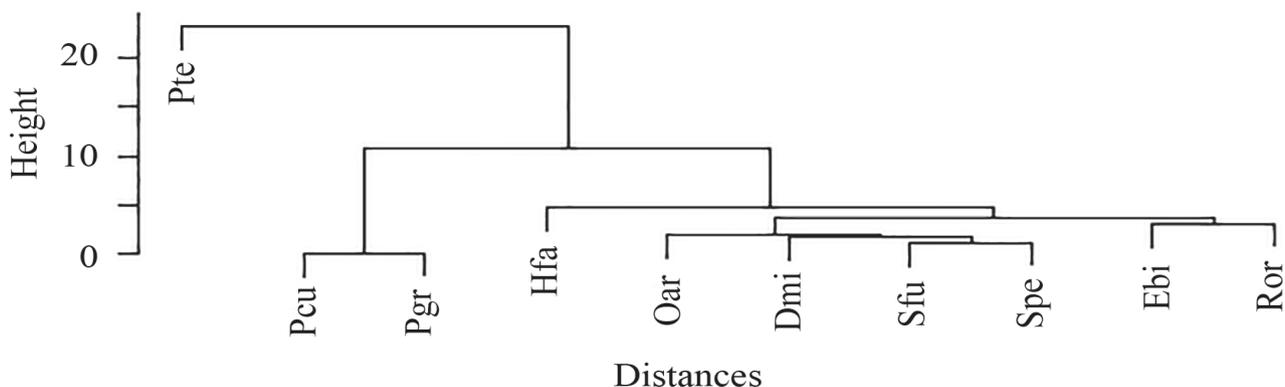


Figure 2 Functional Dendrogram (FGR) with the seven groups of species. *Pte = *Phyllomedusa tetraploidea*, Pcu = *Physalaemus cuvieri*, Pgr = *Physalaemus gracilis*, Hfa = *Boana faber*, Oar = *Oolygon aromothyella*, Dmi = *Dendropsophus minutus*, Sfu = *Scinax fuscovarius*, Spe = *Scinax perereca*, Ebi = *Elachistocleis bicolor* and Ror = *Rhinella ornata*.

Table 1 Anuran larvae species list, their respective reproductive modes* and the water column position.

Species	Reproductive mode	Behaviour
Bufonidae		
<i>Rhinella ornata</i>	1	Benthic-Neustonic
Hylidae		
<i>Dendropsophus minutus</i>	1	Nectonic
<i>Boana faber</i>	4	Benthic
<i>Oolygon aromothyella</i>	1	Nectonic
<i>Scinax fuscovarius</i>	1	Nectonic
<i>Scinax perereca</i>	1	Nectonic
Leptodactylidae		
<i>Physalaemus cuvieri</i>	11	Benthic
<i>Physalaemus aff gracilis</i>	11	Benthic
Microhylidae		
<i>Elachistocleis bicolor</i>	1	Nectonic
Phyllomedusidae		
<i>Phyllomedusa tetrapoidea</i>	24	Nectonic

*Reproductive modes following Haddad and Prado (2005).

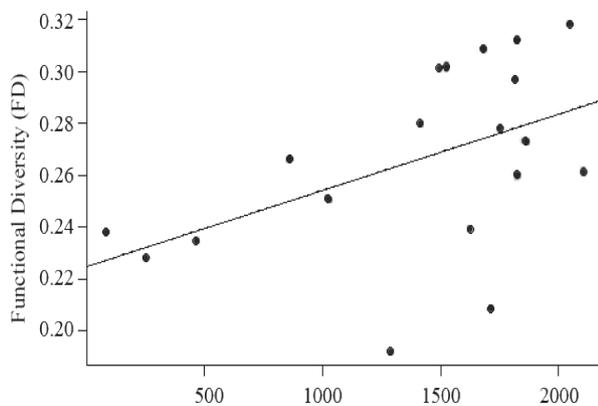


Figure 3 Graphical representation of the relation between the distance from the nearest border of the TSP and the Functional Diversity of anuran larvae.

is not an important force acting at these places. Furthermore, the seven functional groups clustered by the analysis have both biological and ecological sense when thinking on the morphological and behavioural characteristics of the species presented by each group.

The usual changes observed on the landscape structure along environmental gradients can alter many ecosystem functions, by enhancing or diminishing pressures like the biological filters and abiotic conditions, generating different responses by the community. In this way, these environmental modifications can alter, not only the species richness (a measure largely used to infer the environmental health), as found in many other studies with several other groups (Connell, 1978; Kirkman *et al.*, 2001; Werner *et al.*, 2007; Nord and Forslund, 2015; Barrett *et al.*, 2016), but can also exert important influence on the Functional

Diversity and other features that, in general, maintain the functionality of the communities.

It is known that the stress caused by these environmental changes, natural or not, do not affect all species equally (Tscharrntke *et al.*, 2012). As predicted, in natural ecosystems, all species may have the same probability of extinction, however, the ecological interactions may act in favour or prejudice the capacity of some species (Fonseca and Ganade, 2001). These ecological interactions, can be seen at species level as an interaction between evolutionary and ecological dynamics, a relation of trait-environment that shape the capacity of a given species in transpose a barrier and establish itself in a given place (Hutchinson, 1957). These kind of information is crucial to understand how communities assemblies and the tolerances of each individual or species to the growing modifications of habitat (Urban *et al.*, 2008).

In this way, our results showed crescent values of Functional Diversity towards the inner places of the TSP, and thus showed that the larval community organizes itself given the functional space occupied by those species, which leads to the formation of the functional groups (Tilman, 2001), supporting the theory of ecological guilds (Root, 1967). In our case of study, the seven functional groups may point to a factor of importance to environmental conservation, the functional redundancy of species. The low number of species present in each functional group with similar ecological functions is preoccupant, since the higher is the number of species present on each group (with similar functions) would ensure the ecosystem's higher power of resilience to perturbation (Walker, 1995; Rosenfeld, 2002).

Contrasting the assumptions of Charles S. Elton (1958) on the book “*The ecology of invasions by animals and plants*”, the complexity (higher or lower) of habitat is not leading higher or lower diversity in our environmental gradient. Since we sampled ponds with different hydrological periods, sizes and presence of predators along the gradient, so different levels of complexity. Although, the values found (FD) at the ponds closer to the borders were smaller than the values found at higher distances. In relation to the environment, the ponds closer to the disturbances (human activity, agriculture/ pasture) showed themselves more stable places, following the idea of the intermediate disturbance hypothesis proposed by Connell (1978). Furthermore, this absence of drastic processes of modification may enhance predation, intra and interspecific, an ecological factor that could limit the diversification of traits (Pearman, 1995; Wellborn *et al.*, 1996).

The constant changes, or “instability” of the ponds located at more distant places may act as an environmental pressure, triggering diversification morphological and ecological attributes enhancing FD on these places. This means that these communities are more efficient on resource exploitation that

may be the reason of the high values found to Functional Divergence. In this way, the presence of similar species would not be limited by competition given a higher differentiation on niche usage (Morin, 2011). For example, differences on time of spawning would produce tadpoles with different sizes, or different swimming behaviours, fins and tails could enhance the performance and consequently, the success in locomotion and avoiding predation at these places (Cronin and Travis, 1986; Nomura *et al.*, 2011; Johnson *et al.*, 2015; de Souza Queiroz *et al.*, 2015).

Since our sampled ponds do not respond to competitive pressures, we can expect that the environment also plays a restrictive role, following the Hutchinsonian Niche Theory (Hutchinson, 1957) where some species do not showed the necessary morphological characteristics to overcome the restrictions imposed by the habitat and could not stablish or have difficulty to do it in these places (Cornwell *et al.*, 2006). This is the case of species like *Phyllomedusa tetraploidea* which reproductive mode needs a waterbody below the leaves when the tadpoles hatch, or the larvae from the *Leptodactylus fuscus* group that needs a flood on their subterranean chambers to reach the waterbody and complete the life cycle (Haddad and Prado, 2005).

The constant anthropic pressures suffered by the conservation unities, the climatic changes and even some natural processes are putting in danger the health and the stability of the environments. These constant modifications or impoverishment of the natural areas do not affect only a restricted number of species, but the entire trophic web and so, the ecosystem functionality. As stated by Cianciaruso *et al.* (2009) emerging tools that can incorporate the phylogenetic, phylogeographic and functional information of the species tend to be better than those traditional measures (Díaz and Cabido, 2001; Petchey and Gaston, 2006). In addition to this, our results showed that the richness of species do not varies significantly along the gradient, and, according to Purvis *et al.* (2005) and Faith and Baker (2006) this pattern alone is not enough to predict threats on communities. Furthermore, the majority of species was abundant at the sampled ponds, with exception of species like *Boana faber* that occurred only at the ponds located closer to the border, probably given the plasticity of the species in habit both anthropized ponds and natural ones; and *Scinax fuscovarius* that occurred only at the ponds located far from the border, probably given the habit of vocalize perched on tree branches, that were more common in the inner portion of the gradient; and *Elachistocleis bicolor* that was poorly represented at the ponds located both at intermediary and longer distances.

Our results show that the TSP, despite of being a large conservation unit still must deal with the possibility of losses on ecosystemic functions and remarks the importance of the

correct application of the environmental laws. When analysing only the anuran larvae (that occurs in ponds) community we saw a low number of functional groups, and low number of species inserted in these groups, and thus to lose one species of this community means to put at risk functions that could be of paramount importance to the conservation of the biodiversity.

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Appendix

Table S1 Table showing the tadpole eco-morphological traits.

Trait type	Trait	Variable
Position on the water column	Benthic (live in the bottom of ponds, either in shallow or deep water),	Categorical
	Nektonic (live in open water of ponds, of ten moving through vegetation)	
	Neustonic (move from bottom to surface films of ponds to feed on organisms)	
Feeding behaviour	Scratcher (feeding by rasping substrate or taking in particulate matter),	Categorical
	Filter (feeding by filtering microscopic particles out of the water)	
	Microphagous (feeding on large food particles)	
Position of the eyes	Lateral or dorsal quantified by the angular orientation of the oral disc of anuran tadpoles	Categorical
Position of oral disc	relative to a defined longitudinal body axis: terminal (90° angle—extreme one), ventral (0° angle—extreme one) or antero-ventral (angles that fall between the two previous positions)	Categorical
Presence of flagella	Presence or absence	Binary
Body form	body length/total length	Continuous
Body form	body width/total length	Continuous
Body form	body height/total length	Continuous
Body form	width of the tail musculature/total length	Continuous
Body form	height of dorsal tail/width of the tail musculature	Continuous
Body form	height of ventral tail/width of the tail musculature	Continuous

Table S2 Table showing the environmental description of the ponds (P1 to P17). ANVP = information on vegetation profiles. HP = hidroperiod, being P a permanent pond, T a temporary pond and ST a semi-permanent pond.

Pond	Distance from Border (m)	Average Depth (m)	Average Temperature (°C)	Canopy Coverage (%)	ANVP	HP
PI1	85	0.17	20.70	0.01	5	P
PI2	255	0.12	22.80	0.01	5	P
PI3	465	0.02	6.20	0.02	4	P
PI8	863	0.19	15.20	0.01	4	SP
PI4	1022	0.04	22.00	0.03	3	P
PI9	1285	0.15	15.40	0.01	3	SP
PI10	1414	0.21	14.10	0.01	3	SP
PI11	1494	0.15	10.70	0.01	3	T
PI12	1522	0.20	8.20	0.01	3	T
PI14	1625	0.02	6.30	0.01	4	T
PI19	1680	0.20	13.90	0.01	3	T
PI5	1712	0.02	10.00	0.01	3	T
PI13	1754	0.23	14.00	0.01	4	SP
PI18	1814	0.25	8.10	0.01	5	T
PI15	1822	0.10	10.00	0.01	4	P
PI16	1824	0.02	6.10	0.01	3	P
PI6	1860	0.27	16.10	0	4	P
PI7	2049	0.12	14.40	0	4	P
PI17	2106	0.15	8.40	0.01	3	P