Disentangling the multiple components of anuran diversity associated to different land-uses in Yungas forests, Argentina

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Abstract

Natural habitats have drastically regressed due to rapid changes in land-use during recent decades, generating a decrease in species diversity. In light of natural habitat destruction worldwide, there is a need to adopt an integrative approach to the study of biodiversity in order to better assess the magnitude of diversity loss in landscapes affected by human intervention. The aim of this study was to assess and compare anuran assemblages under different land-uses in a subtropical forest of NW Argentina using an integrative view of diversity through different measures. We assessed alpha and beta diversity components for three complementary diversity measures: species richness, functional diversity and phylogenetic diversity in three land-uses: forest, tobacco and suburban. We carried out generalized linear mixed models with an autocorrelation structure to compare the three diversity measures across the different land-uses. We also used a beta diversity partitioning method to determine nestedness and turnover processes in taxonomic, functional and phylogenetic dissimilarity. Our results suggest a filtering effect of the land-uses on the diversity of anuran assemblages in the surveyed area, with an increased loss of anuran diversity in areas with intensified land-use, such as tobacco monoculture. This study contributes to understand amphibian communities associated to modified habitats in the Southern Andean Yungas forests from Argentina. Our findings highlight the importance of disentangling each diversity component separately to detect more accurately the diversity patterns associated to land-use change.

Introduction

Diversity changes have classically been expressed through indices based on the number of species [species richness (SR)] and the evenness of abundance distribution among species (e.g. Shannon, 1948; Simpson, 1949). These approaches assume that all detected species are of similar importance and, therefore, comparable entities. However, since diversity is a complex multifaceted concept (Purvis & Hector, 2000; Pavoine & Bonsall, 2011), it is necessary to consider the biological identity and role of each species in the ecosystem to improve the assessment of biodiversity. In recent years, diversity studies have begun to include other dimensions, such as functional and phylogenetic diversities. Functional diversity (FD) quantifies the values and ranges of functional traits of the species in a community, which influence their performance and consequently ecosystem functioning (Díaz & Cabido, 2001; Pla, Casanoves & Di-Rienzo, 2012). Phylogenetic diversity (PD) reflects the evolutionary history of the species in the community, and can provide insight into how evolutionary processes may have shaped contemporary patterns of SR

within a landscape (Fritz & Rahbek, 2012). Both diversity dimensions can be strongly correlated with each other if traits evolve along the branches of phylogeny (Fritz & Purvis, 2010). In this case, PD can be used as an indirect measure of phenotypic diversity as suggested by some studies (Flynn et al., 2011). However, several studies have also shown that phylogenetic and functional diversities of a community may not be linked directly to each other, and therefore are not necessarily interchangeable (Prinzing et al., 2008; Fritz & Purvis, 2010; Strauß et al., 2016).

Beta diversity, considered as the variation in species composition between sites, can be decomposed into two components: species turnover and nestedness (Baselga, 2010). Species turnover refers to the replacement of species at a site by different ones at another site, leading to less frequent or even segregated species occurrence, with many species never co-occurring (Ulrich & Gotelli, 2007). Nestedness, on the other side, refers to the overlap of species occurrence among sites, indicating that the extent of the species composition of a given assemblage is a subset of the species composition of a larger assemblage (Ulrich & Gotelli, 2007).

Natural habitats have drastically regressed due to rapid changes in land-use during recent decades, transforming natural areas into agricultural and urbanized landscapes (Le Viol et al., 2012). Such landscape alteration can affect biological diversity through loss of suitable habitat, degradation of habitat quality, progressive habitat fragmentation, or isolation among remaining habitat patches (Hamer & Parris, 2011). Most pond-breeding amphibians can be quite sensitive to these human-induced disturbances, mainly due to their complex life cycles, their permeable skin, limited dispersal capabilities, and small home ranges (Guerry & Hunter, 2002; Pineda et al., 2005; Becker et al., 2009).

The Andean Yungas forests in north-western Argentina extend as a narrow strip of montane forest, corresponding to the southernmost extension of Neotropical cloud forests (Kappelle & Brown, 2001). Although it can be defined as mesodiverse when compared to other neighboring regions, this ecoregion is one of the most biodiverse ecosystems of Argentina (Brown et al., 2006), with 41 amphibian species registered, eight of which are endemic (actualized from Lavilla & Heatwole, 2010). The Yungas forests are included among the four ecoregions significantly over-threatened in the country (Vaira et al., 2017). Among the main threats identified to the amphibian diversity of Yungas forests are clear-cutting for sugarcane and tobacco monocultures, and the accelerated expansion of urbanization (Brown et al., 2006; Lavilla & Heatwole, 2010). These activities have produced alarming reductions in the forest range and transformed large areas into a mosaic of habitats with different land-uses, showing consequences on the composition, structure and function of ecological communities of this ecosystem (Izquierdo & Grau, 2009; Volante et al., 2012).

In light of habitat destruction worldwide, there is a need to adopt an integrative approach to the study of biodiversity to better assess the magnitude of diversity loss in landscapes with human intervention. Since diversity loss encompass not only species loss per se (Carvalho et al., 2010), associating these complementary diversity indices has become crucial to understand and predict the consequences of landscape modifications on ecosystem processes and to preserve long-term viability of biodiversity. The aim of this study was to assess anuran diversity among different land-uses in a subtropical montane forest of NW Argentina. Using an integrative approach, we compare anuran SR, FD and PD between forests remnant, suburban patches and tobacco fields. We also analyze differences in species composition among the three land-uses through taxonomic, functional and phylogenetic beta diversity measures.

Materials and methods

Study area

The study was conducted in two regions of 140 km^2 approximately, located in the Andean Yungas ecoregion in Jujuy province, Argentina: La Almona (24°15′4.41″S, 65°22′44.74″W) and Zapla (24°14′3.96″S, 65°10′7.51″W). Both regions are separated from each other by 20 km (Fig. 1). Human intervention has transformed both regions into mosaics of patches characterized by tobacco crops, rural patches, secondary growth forests and native forest fragments, which represent a disturbance gradient. Within each region, we selected a habitat patch of c. 3 km^2 in size representing each of these three dominant land-uses: (1) Tobacco: monocultures separated by hedgerows. Since the activity of planting and harvesting lasts the entire rainy season in coincidence with the reproductive activity of anurans, we consider that the reproductive sites located in this monoculture are highly and continuously disturbed. (2) Suburban: patches in a rural/suburban transition, with low levels of urbanization and unpaved roads. Landscaped areas and non-native trees replaced the native forest, maintaining patches of secondary growth forest. The disturbance of this land-use can be considered as moderate and occasional for anurans. (3) Forests fragments: patches that have suffered low levels of selective logging, but have not been exploited for over 15 years. These patches have well-preserved primary and secondary native forest, so they can be considered without disturbance for anuran's reproductive sites.

Frog sampling

We conducted visual and acoustic encounter surveys (Crump & Scott, 1994) at each water body between 2011 and 2013, starting early December until the end of March in each year (Vaira, 2002). Using a time-constrained technique (Scott & Woodward, 1994), we surveyed ponds and the surrounding 3 m perimeter during 15 min. Many species found in our study sites were not easy to detect visually as they exhibit a fossorial life habit or are cryptic species. Therefore, we choose to use the presence/absence data, as it can be more accurate in this case than the abundance surveys. We visited each pond five times throughout the study to ensure detection of rare species.

Diversity measures

We obtained three complementary diversity measures: taxonomic diversity, measured as SR, FD and PD.

Functional diversity is expressed as the variation on the roles performed by the species in the community, based on their functional traits, and related to ecosystem functioning (Weiher, 2011). FD was calculated following Petchey & Gaston (2006). This method measures the extent of species complementarity based on a dendrogram computed by hierarchical clustering; FD represents the functional richness (Petchey & Gaston, 2006). We selected functional traits related to relevant life history parameters within the anuran life cycle. Traits for each species were obtained from the literature and corroborated during field sampling. The traits selected were: reproductive mode (following Hadad & Prado, 2005), maximum male size (in mm), ecomorphological guild of tadpoles (following Altig & Johnston, 1989), general habitat use of adult frogs and reproductive activity patterns as described by Vaira (2002) (Table 1). We obtained the FD index with the FDiversity software (Casanoves et al., 2010).
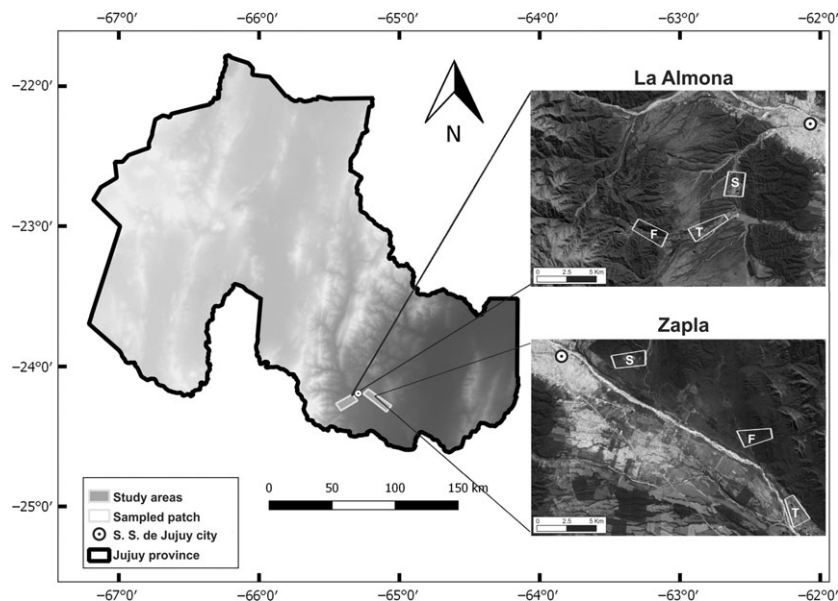
Figure 1 Map showing the study area and the spatial distribution of surveyed patches within two areas of Jujuy province, Argentina. F, forest remnants; S, suburban patches; T, tobacco fields.

Phylogenetic diversity is an approach to assess the evolutionary relatedness of species in a community (Thompson, Davies & Gonzalez, 2015). We used PD index proposed by Faith (1992), defined as the sum of the phylogenetic branch lengths represented by a set of co-occurring species. We thus built a phylogenetic tree for the species registered in the study following Pyron & Wiens (2011) for the family backbone. Genus relationships within Hylidae and Leptodactylidae families followed Duellman, Marion & Hedges (2016) and de Sá *et al.* (2014), respectively. Species nomenclature is in accordance to Frost (2017). This analysis was obtained with the *picante* package (Kembel *et al.*, 2010) in R (R Core Team, 2016).

Statistical analysis

To evaluate if the sampling effort was appropriate, we calculated the sample coverage for each land-use (Chao & Jost, 2012). This was computed in the package iNEXT in R (version 2.0.5, Chao, Ma & Hsieh, 2016).

Spatial autocorrelation (SAC) of three diversity measures at pond level was assessed using Moran's I statistic. Significance was assessed using 1000 permutations. Analyses were made using the *ape* package in R (Paradis, Claude & Strimmer, 2004).

In order to determine significant differences in SR, FD and PD values among land-uses we performed generalized linear mixed models with a Gaussian distribution of errors and a defined correlation structure. Diversity values were set as the dependent variable, land-uses as fixed effects, and regions (Almona, Zapla) as random effect to take into account the possible non-independence of sites within the same region. SR, FD, and PD presented a positive SAC (Moran's $I = 0.42$, $P < 0.05$, Moran's $I = 0.35$, $P < 0.05$, and Moran's $I = 0.42$, $P < 0.05$, respectively). To account for spatial structure, we tested different mixed-effects models with and without SAC structures (lineal, exponential, Gaussian, rational quadratic and spherical). We choose the one that produced the lower Akaike information criterion value. The optimal model for SR, FD and PD presented an exponential autocorrelation structure. For this analysis, we used *nlme* package in R (Pinheiro *et al.*, 2017).

We performed an additive partitioning of beta diversity following the framework proposed by Baselga (2010), and the analogous partitions for functional beta diversity developed by Villéger, Grenouillet & Brosse (2013), and for PD the one proposed by Leprieur *et al.* (2012). Using the Jaccard dissimilarity index, we assessed the anuran species dissimilarity between land-uses considering the total beta diversity (β_{JAC}), as well as the spatial turnover (β_{TU}) and nestedness (β_{NES}) components. These analyses were performed with the *betapart* package for R (Baselga & Orme, 2012).

Results

We recorded 22 anuran species belonging to seven families, representing 55% of the anuran species registered for the Yungas forests (Lavilla & Heatwole, 2010). The sample coverage obtained for the three land-uses were above 90%, indicating adequate sampling effort. We registered a cumulative richness of 19, 15 and 16 species in forest, tobacco and suburban land-uses, respectively (Fig. 2). Two species, *Melanophryniscus rubriventris* and *Oreobates berdemenos*, were only recorded in the forest remnants. *Elachistocleis haroi* was only registered in the suburban patches, and two species – *Pleurodema tucumanum* and *Leptodactylus elenae* – were registered only in the tobacco fields.

Table 1 List of anuran functional traits used to assess functional diversity

| Species | Functional traits | | | | |
	Reproductive mode	Larvae type	Max male size (mm)	Adult habitat use	Reproductive activity pattern
Bufonidae					
Melanophryniscus rubriventris	2	Benthic	45	Terrestrial	O, w
Rhinella arenarum	1	Benthic	108	Terrestrial	P, dw
R. schneideri	1	Benthic	210	Terrestrial	P, w
Hylidae					
Dendropsophus nanus	1	Nektonic	22	Arboreal	P, w
Boana riojana	2	Benthic	60	Arboreal	P, dw
Scinax fuscovarius	1	Nektonic	44	Arboreal	P, w
S. nasicus	1	Nektonic	35	Arboreal	P, w
Trachycephalus typhonius	1	Nektonic	100	Arboreal	O, w
Phyllomedusidae					
Phyllomedusa sauvagii	24	Suspension-rasper	70	Arboreal	P, w
Microhylidae					
Elachistocleis haroi	1	Suspensor	45	Fosorial	O, w
Leptodactylidae					
Leptodactylus fuscus	30	Benthic	55	Terrestrial	P, w
L. latinasus	30	Benthic	40	Terrestrial	P, w
L. mystacinus	30	Benthic	60	Terrestrial	P, w
L. elenae	30	Benthic	50	Terrestrial	P, w
L. gracilis	30	Benthic	50	Terrestrial	P, w
L. chaquensis	11	Benthic	85	Terrestrial	P, w
Physalaemus biligonigerus	11	Benthic	45	Terrestrial	P, w
P. cuqui	11	Benthic	32	Terrestrial	P, w
Pleurodema tucumanum	11	Benthic	45	Terrestrial	P, w
Pleurodema borellii	11	Benthic	55	Terrestrial	P, w
Odontophrynidae					
Odontophrynus americanus	1	Benthic	90	Terrestrial	O, w
Craugastoridae					
Oreobates berdemenos	23	Egg	32	Terrestrial	P, w

Reproductive modes (1) Eggs and exotrophic tadpoles in lentic water. (2) Eggs and exotrophic tadpoles in lotic water. (11) Foam nest floating on ponds; exotrophic tadpoles in ponds. (23) Direct development of terrestrial eggs. (24) Eggs hatching into exotrophic tadpoles that drop in lentic water. (30) Foam nest with eggs and early larval stages in subterranean constructed nests; subsequent to flooding, exotrophic tadpoles in ponds.

O, opportunistic; P, prolonged during dry (d) or wet (w) season.

We found significant differences in mean SR, with the highest mean value registered in the suburban patches (Fig. 3). Both FD and PD mean values were also significantly higher in suburban patches (Fig. 3). Results of the mixed models are presented in Supporting Information Appendices S1 and S2.

Anuran species composition did not differ greatly among the three land-uses, as total taxonomic beta values were <0.25 (Fig. 4). Functional beta diversity values between pairs of land-uses were higher than 0.7, with the highest differentiation in functional composition found between tobacco fields and both forest remnants and suburban patches. These differences were given entirely by a nestedness process, highlighting that although species composition between land-uses was not high, there is a loss in anuran functional traits in tobacco crops. Functional beta diversity between suburban and forest land-uses was due mainly to species turnover. Finally, phylogenetic beta diversity values were lower than 0.3, with phylogenetic differentiation between suburban and forest land-uses mainly given by species turnover, while phylogenetic differentiation between tobacco fields and both suburban and forest land-uses were mainly given by a nestedness process (Fig. 4).

Discussion

Our study represents a relevant contribution to the knowledge of the effect of land-use changes on amphibian diversity, being the first study of this type carried out in the Andean Yungas forests of Argentina. To date, global evaluations and predictions of the consequences of land-use changes for species diversity suggest a strong reduction in terrestrial biodiversity (Newbold *et al.*, 2015). Our findings were no different, as we observed a filtering effect of the land-uses on the diversity of anuran assemblages in the surveyed area, with an increased loss of anuran diversity in areas with intensified land-use, such as tobacco monoculture. This pattern of diversity erosion resulted more
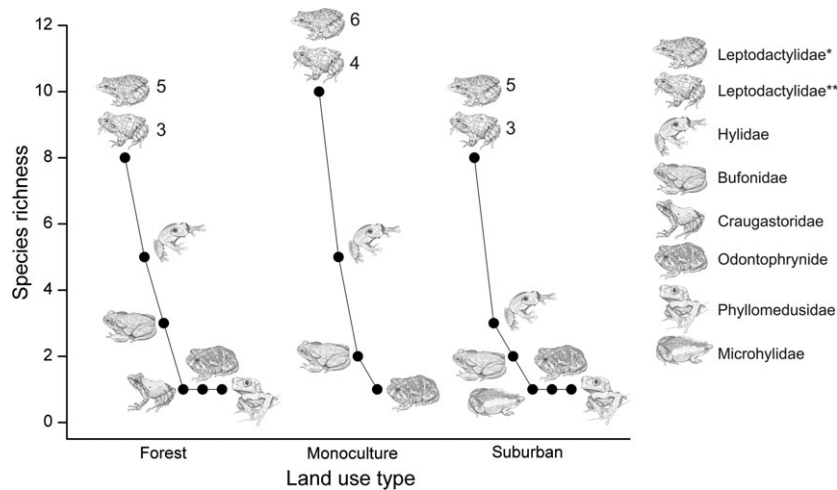
Figure 2 Rank-abundance curves of the number of species belonging to the seven anuran families registered in the three land-uses within the study area. Asterisks represents subfamilies within the family Leptodactyilidae: *Subfamily Leptodactylinae; ** Subfamily Leiuperinae.
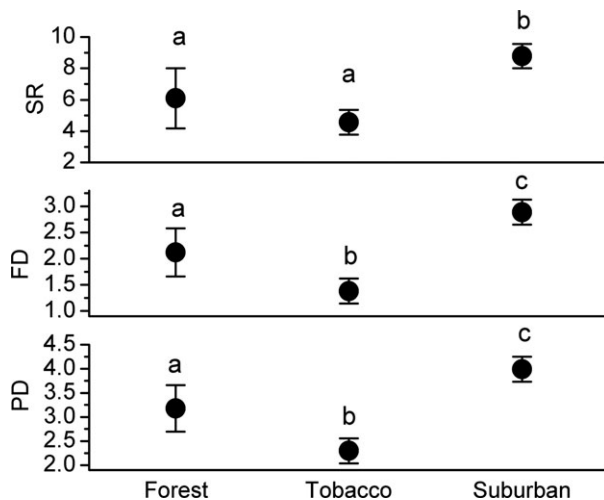

Figure 3 Results of the *post hoc* pairwise Tukey contrasts from the generalized linear mixed model, comparing the means of the three diversity measures among the different land-uses. Error bars are standard errors. Different letters above indicate significant statistical differences.

comprehensive when using the complementary functional and PD measures, highlighting that each diversity dimension could reveal more accurately the changes in diversity patterns than the conventional focus based exclusively on SR. In the last years, it has become more common to use these complementary diversity measures to assess diversity patterns under different scenarios (e.g. Devictor *et al.*, 2010; Strauß *et al.*, 2010; Flynn *et al.*, 2011; Fournier *et al.*, 2017).

When analyzing mean alpha diversities, we found congruence in the three diversity dimensions (SR, FD and PD), with the suburban patches as the most diverse. The vegetation structure found in this land-use comprised small remnants of secondary native forest, and recreational open areas such as a polo field and a golf course. This habitat

heterogeneity could potentially provide a high number of available resources and niches for the different anuran species, as well as provide shelter for species that generally avoid high-density urbanized areas, or are under threat from agricultural intensification (Tratalos *et al.*, 2007). Furthermore, these recreational suburban greens and semi-natural places can act as 'stepping stones', increasing the connectivity of the landscape (Dearborn & Kark, 2010; Graham, Haines-Young & Field, 2017). Some authors suggest that these areas can play a key role in species conservation if they are appropriately designed and managed (e.g. Hodgkison, Hero & Warnken, 2007; Puglis & Boone, 2012).

Surprisingly, tobacco and forest did not present a strong difference in SR mean values. Agricultural areas are sometimes dominated by generalist species, such as leptodactylid frogs (Baldi *et al.*, 2015), increasing the number of anuran species in those habitats. Therefore, the SR in tobacco may be increased by the income of these generalist species by habitat facilitation when the native forest was cut down, thus masking the negative effect of land-use changes on the anuran richness by a compensatory dynamics mechanism (Russildi *et al.*, 2016). However, from the 19 species found in the forest, only 13 were registered in the tobacco, and two leptodactylid species (*L. elenae* and *Pleurodema tucumanum*) were found to be exclusive of this land-use.

When applying the complementary diversity measures, an erosion effect of functional and PD in the tobacco monocultures compared to the other land-uses becomes evident. That is, if we consider the species as comparable entities we can conclude that the loss of a few anuran species between the forest and the tobacco is negligible. However, taking into account their phylogenetic and functional identity, we observe that the magnitude of the loss is highly noticeable. In this study we only address one aspect of taxonomic, functional, and phylogenetic alpha diversity: the richness dimension, which accounts for how much diversity is in each land-use. Furthermore research may include the other two
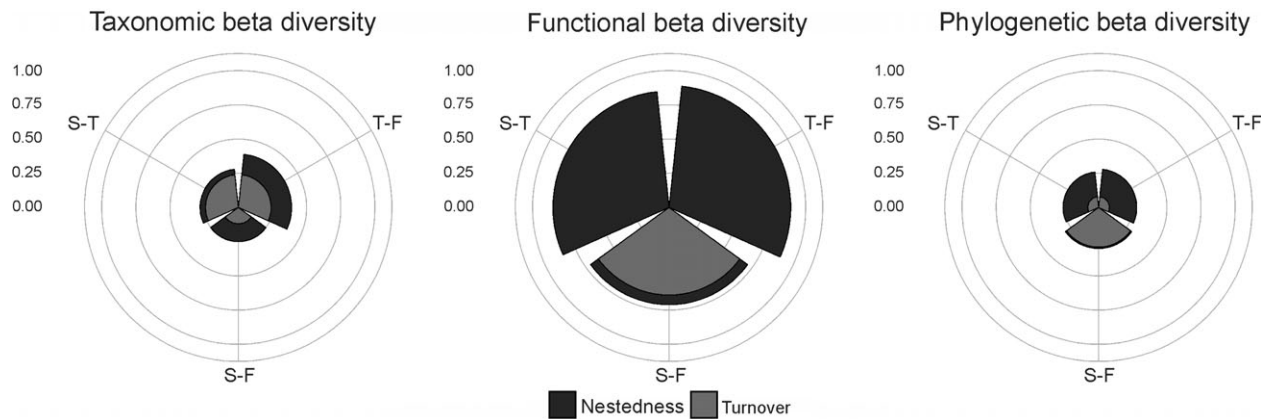
Figure 4 Additive partition of the beta diversity components for the three land-uses based on Jaccard's dissimilarity index. Bars correspond to total Jaccard beta diversity. F, forest remnants; T, tobacco fields; S, suburban patches.

aspects: evenness and divergence, that address how different and how regular is biodiversity in terms of functional (Villéger, Mason & Mouillot, 2008) and phylogenetic (Tucker *et al.*, 2017) measures. The richness, evenness and divergence dimensions of anuran FD have been applied, for example, to assess the recovery of frog communities after a habitat restoration program (Díaz-García *et al.*, 2017).

The anuran assemblage of the study area was dominated by the families Leptodactylidae, Hylidae and Bufonidae, with most of their species being generalist and occupying the three land-uses. Thus, the high phylogenetic relatedness of the species of the study area, together with the relatively mesodiverse anuran assemblage compared to neighboring countries, probably resulted in the low taxonomic and phylogenetic beta diversity observed among the studied land-uses. Nevertheless, the lack of registries of endemic species of the Yungas forests as *Oreobates berdemenos* and *M. rubriventris* in most human-intervened habitats (as tobacco crops and suburban patches) represent the loss of a phylogenetically distinctive Andean lineage as the Craugastoridae family and a basal bufonid clade, respectively (Gonzalez-Voyer *et al.*, 2011; Pyron & Wiens, 2011). In tobacco crops, we also observed a turnover from hylid species with certain habitat structure requirements (i.e. the arboreal *Trachycephalus typhonius* and *Scinax nasicus*) to a more habitat generalist species of the Leptodactylidae family. Similarly, we found a typical species of open grasslands, the microhylid *E. haroi*, exclusively in suburban patches (Pereyra *et al.*, 2013).

Although the taxonomic and phylogenetic beta diversity between land-uses were low, the functional beta diversity between them was high. This incongruence in phylogenetic and functional beta diversity values has been reported in other studies (Devictor *et al.*, 2010; Strauß *et al.*, 2010). In our study, both functional and phylogenetic diversities varied similarly, but differed in the magnitude of compositional differences. Functional beta diversity turned out to be the most sensitive measure to assess the effect of land-uses on local anuran diversity. Phylogenetic diversity covers additional traits than the defined number of traits used to estimate FD. Differences in beta values of FD and PD found in our study

could be given by ecologically non-relevant traits covered by PD that are masking the information of the relevant traits (Strauß *et al.*, 2010). Other possible explanation is the presence of species with unique traits in our assemblage, thus the loss of these functionally unique species may result in high beta diversity values. The total functional beta diversity registered between tobacco and both forest and suburban land-uses were caused solely by a nestedness process, evidencing the loss of certain functional traits in the anuran assemblage in tobacco crops, and thus highlighting the negative impact caused by intensive land-use. The structural simplification and degree of homogenization suffered in tobacco monocultures, along with high and continuous human disturbances, can act as a strong environmental filter limiting the occurrence of some anuran species with complex habitats requirements, and enabling the presence of more generalist species that can exploit highly modified environments. Thus, tobacco monocultures become dominated by species of the Leptodactylidae family, representing a redundancy on reproductive modes adapted to ephemeral habitats, like burrowing species of the *L. fuscus* species group, and foam nest builders like Leiuperinae frogs and *L. chaquensis* (Heyer, 1969; Ferraro *et al.*, 2016). We also registered the absence of a direct developing frog, *O. berdemenos* (a reproductive mode scarcely represented in the Yungas forests; Vaira, 2002). Coincidently, *T. typhonius*, the biggest arboreal frog with opportunistic reproduction during the wet season was absent in tobacco crops. We can therefore state that land-use intensification is diminishing FD in our study area by a simplification of the functional composition of the anuran assemblages, which can affect negatively the ecosystem functioning. The differences in functional composition found between suburban patches and forest remnants was mainly given by a functional turnover process, possibly because of the presence of environmental gradients and changes in structural habitat conditions that limited the presence of both arboreal and forest anurans specialists in the suburban patches. The high values of beta FD among the three land-uses could be revealing the functional uniqueness of these species within the region (Devictor *et al.*, 2010).

Other studies have shown that measures of FD and PD have similar abilities to predict biodiversity changes, suggesting that PD can be used as a good proxy for accurate measures of FD (e.g. Flynn *et al.*, 2011). This could be a useful surrogate since in many cases the traits used to assess FD in a great number of Neotropical amphibian assemblages are poorly known or even unknown, and there is no evidence on the actual effect of these traits on ecosystems functioning. Nevertheless, the difference in the values of both beta diversity measures could suggests that FD is more sensitive to contemporary selective pressures such as land-use changes than PD, and therefore can result more useful in these particular studies. In our case, the use of PD as a proxy measure may be underestimating differences in anuran diversity between different land uses, and even neglecting their negative effects on diversity. Based in our results, we considered preferable the use of FD rather than PD when studying diversity patterns on mesodiverse anuran assemblages at the landscape spatial scale.

Conclusion

The erosion of anuran diversity as a result of the land-use change is evident, and our results provide new insights by emphasizing the importance of employing complementary diversity measures, as the loss of a single species may represent a great loss in ecological functions, or even the loss of a complete phylogenetic lineage.

In countries with limited financial resources for conservation, an increased understanding of the effect of land-use changes on biodiversity will allow to make better predictions about the ecological consequences of anthropogenic disturbances, and thus optimize the prioritization of conservation efforts. Furthermore, we could delineate clear and achievable conservation goals on what species assemblages or ecosystem functions are more urgent to protect. In our particular case, the conservation of the Andean Yungas forests in Argentina is of paramount importance, as we are potentially loosing unique anuran species, lineages and/or functions. In addition, given the importance of suburban patches as refuge for particular species, a correct management of urbanization plans (e.g. considering the size and design of green spaces) should be taken into consideration. Lastly, there is a need to advance in the knowledge of the functional role of amphibians through studies of the relationships and effects of adults and larvae traits on the functioning of ecosystems.

Acknowledgments

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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. Results of the generalized lineal mixed models comparing species richness (SR), functional diversity (FD), and phylogenetic diversity (PD) values among the three land uses (forest, suburban and tobacco).

Appendix S2. ANOVA results for the mixed-effect models for the response variables species richness (SR), functional diversity (FD), and phylogenetic diversity (PD).