

Functional traits drive tadpole responses to land use in coastal areas

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Abstract

1. Land use changes are considered a significant cause of amphibian declines worldwide. However, little is known regarding which land uses have more pervasive impacts and which help to supplement the biodiversity conserved in protected areas. In addition, amphibian species respond to a broad array of geographical constraints, which may blur responses to disturbance, depending on the species' natural history.
2. Here, we explored whether functional diversity patterns of amphibian assemblages are linked to human land use while considering spatial autocorrelation and phylogenetic relatedness among species. We surveyed tadpoles along 500 km in coastal wetlands in southern Brazil and quantified four traits related to tadpole habitat use and predator avoidance.
3. Spatial components influenced functional richness to a greater extent than land use. Functional evenness was higher in ponds surrounded by more exotic reforestation, and to a lesser extent an effect of crop area. Functional divergence was also associated with reforestation areas.
4. Our results showed that some land uses (reforestation with exotic species and temporary crops) have more pervasive impacts on tadpole communities. Such changes in amphibian communities occurred even at low levels of landscape change. Our findings highlight that conversion to human land use requires complementary approaches (i.e., tadpole and adult responses) to provide early warning signals about habitat modification effects.

KEYWORDS

Atlantic Forest, exotic reforestation, functional diversity, Pampa, spatial patterns

1 | INTRODUCTION

Scientists have long known that habitat modification constrains biodiversity and ecosystem services (Nowakowski et al., 2018; Tscharnkte et al., 2005; Williams-Guillén & Perfecto, 2010). For freshwater environments, a recurrent pattern seems to be the positive relationship between functional diversity and environmental heterogeneity at different scales (Díaz-García et al., 2017; Queiroz

et al., 2015; Schmera et al., 2017). In this sense, species traits related to environmental heterogeneity might be a promising avenue for understanding the ecosystem effects of human land use (Colón-Gaud et al., 2010; Díaz-García et al., 2017).

An organism's traits affect its fitness (both directly and indirectly), making functional traits a proxy for understanding the habitat requirements and responses to disturbances (Mouillot et al., 2013). Therefore far, functional traits have encompassed any

feature that describes the effects of biodiversity on ecosystem functioning (effect traits) or the biodiversity response to environmental changes (response traits, Violle et al., 2007). However, many challenges remain to separate response from effect traits in the case of freshwater organisms (Hébert et al., 2017; Schmera et al., 2017). For example, tadpole feeding traits are linked to the aquatic environment type (response) and affect nutrient cycling (effect) (Montaña et al., 2019).

In addition, taxa that share a common ancestor show some phylogenetic signal in functional traits. Ignoring such phylogenetic relationships might distort inferences of assembly mechanisms because of biological and methodological reasons (Cadotte et al., 2017). For example, functional evenness (FEve) decreases with water depth, but such association seems to be a statistical artefact generated by phylogenetic non-independency among tadpole species (Moreira et al., 2020). As such, combining functional and phylogenetic metrics enables insights into evolutionary and ecological dynamics (Lipinski et al., 2020; Ribeiro et al., 2017).

For amphibians, traits associated with habitat use, reproductive modes, and food acquisition are valuable tools to assess the effects of habitat split and other common issues related to human land use. Environments modified by human land use often show fewer functional groups, yet not all human land uses affect amphibian functional richness (FRic) (Díaz-García et al., 2017; Riemann et al., 2017). Frequently, FRic shows a late response to disturbances because of the need for local extinctions of species with extreme traits (Mouillot et al., 2013). In places where human land use substitutes the native forests, larger amphibian species seem better adapted to high temperatures and low humidity than small arboreal species (Lourenço-de-Moraes et al., 2020). Meanwhile, metrics based on traits and abundances (e.g., FEve and functional divergence [FDiv]) may decline even under moderate levels of disturbance (Mouillot et al., 2013; Villéger et al., 2010). However, most of the research on functional diversity is related to the amphibian adult phase. Because of their complex life history, adults and tadpoles live in different ecological contexts, and land use may have distinct effects for each stage.

Several studies have demonstrated that spatially structured environmental variation and spatial processes' importance increase with spatial extent, the former being more critical for taxa with restricted dispersal ability (Dalmolin et al., 2019; Garey et al., 2023; Knauth et al., 2019). Such association is likely because the spatial distribution of amphibians depends on processes that differentially affect larval (tadpoles) and adult stages. At broader scales, climate-related dispersal limitation might result in spatial patterns of amphibian diversity (Garey et al., 2023). Landscape structure (i.e., land use and land cover types) can affect the importance of spatial and niche-based processes to anuran composition. Studies conducted in forested environments indicated that spatial rather than niche-based processes were better predictors of anuran β diversity in dense vegetation types (Prado & Rossa-Feres, 2014; Provete et al., 2014). In addition, human land uses affect habitat suitability for amphibian species and eventually affect tadpole morphology, depending

on adult reproductive mode and tadpole plasticity. Evidence from southern Brazil has shown that crop areas (Moreira et al., 2020; Saccol et al., 2022) and exotic reforestation (Machado et al., 2012; Saccol et al., 2017) promote amphibian biodiversity erosion in its different dimensions (e.g., taxonomic, functional, and phylogenetic).

The Brazilian coast encompasses different forest and non-forest ecoregions, which reflect patterns of amphibian species endemism and phylogenetic endemism (Vasconcelos et al., 2019). In southern Brazil, elements of the Atlantic Forest replace the subtropical grasslands of the Uruguayan Savanna (equivalent to the Brazilian Pampa Biome; Project MapBiomas, 2021). Along this grassland-forest transition, the type of dominant vegetation has effects on the regional amphibian species pool (Alvares et al., 2022), with patterns of β diversity associated with distinct factors in each ecoregion (Knauth et al., 2019). As in most near-shore habitats across the globe, Brazilian coastal wetlands are experiencing substantial urban and agricultural expansion. Such land use intensification is already affecting the morphology of some species and how amphibian assemblages are structured (Boelter et al., 2022; Moreira et al., 2021). Therefore, an interesting question is whether human land use affects similarly functional traits from distinct species pools.

Given the small surface water area (<1ha), many coastal wetlands are tightly bound to surrounding terrestrial environments. Therefore, several stressors can interact synergistically with biodiversity (crop chemicals, hydrological regime changes, vegetation homogenisation). Species sensitivity to agrochemicals seems independent of phylogenetic relationships in amphibians (Egea-Serrano et al., 2012). However, dehydration can result in morphological alterations to tadpoles, even excluding certain species according to their plasticity to desiccation (Venturelli et al., 2021). Wetland water drainage is driven mainly by agriculture (Stirling et al., 2020). Thus, drought events in agricultural wetlands can be particularly harsh for freshwater communities. Here, we investigated amphibian assemblages along 500 km of coastal wetlands in southern Brazil. Explicitly, we explored whether human land use would affect functional diversity patterns based on tadpole traits. We assessed three aspects of functional diversity (FRic, FEve, and FDiv) while considering spatial autocorrelation and phylogenetic relatedness among species. We posit that FDiv and FEve would decline with land conversion to crop areas but without significant change in FRic.

2 | METHODS

2.1 | Study area and data collection

We studied tadpole communities inhabiting the southern Brazilian Coastal Plain (states of Rio Grande do Sul and Santa Catarina; Figure 1), which includes a mosaic of grasslands, shrubby vegetation (Restinga), and forests (Marques et al., 2015). Along its extension, the Coastal Plain has a humid subtropical climate without dry seasons and hot summers (Alvares et al., 2013). Wetland environments encompass various types, such as marshes, coastal lagoons,

inland lagoons, and estuaries. The sampled coastal wetlands (hereafter ponds) were at least 10km apart and were chosen based on accessibility (i.e., private landowners willing to participate in the study). Ponds were close to 0.4 ha (± 0.19), although two large ponds were included in the sampling (c. 0.75 ha). In the spring of 2015, we sampled tadpoles twice (September and November) in 16 ponds across the transition zone between the Pampa and Atlantic Forest (Figure 1). We took samples with dip nets (30cm wide, 250 μ m mesh size). Twelve standardised 1-m sweeps were distributed at different pond depths (i.e., six sweeps near the margin and six in deep water near the center). We pooled these sweeps into one sample (3.5-L plastic bucket), where tadpoles were anaesthetised with clove oil solution and preserved in the field.

We digitally measured specimens between Gosner's stages 31 and 39 without tail injuries. We took digital photos of lateral and dorsal views with a camera mounted to a copy stand (Canon Rebel T5i; 150mm). Seven morphological measures (Figure S1) were digitised from each image using tpsDig2 software, version 2.16 (Rohlf, 2010). We chose four functional traits related to habitat use and predator avoidance (Azizi et al., 2007; Marques & Nomura, 2015; Melo et al., 2018). For example, agricultural land use affects dragonflies and fish communities (Pires et al., 2022; Yofukuji et al., 2023). Tadpoles tend to develop large tails and smaller bodies when they are under predation pressure (Kruger & Morin, 2020; Relyea, 2002;

Sergio et al., 2021). By contrast, some tadpole species showed longer fins and large body sizes in ponds surrounded by larger crop areas (Boelter et al., 2022; Marques et al., 2019). Therefore, these traits are potentially associated with amphibian responses to environmental changes (i.e., response traits).

All traits used were ratios between morphological measures to accommodate differences across tadpole developmental stages (Table 1). We used a time-calibrated phylogenetic tree by Jetz and Pyron (2018) to obtain the phylogenetic relationship among species. We pruned the phylogeny to match the species pool recorded in the study. When the resolution for our taxa was not present in the phylogeny, we manually incorporated our species following a range of published sources for between-species relationships (Figure S2). To adjust branch lengths, we used mean path length calibration.

We defined circular buffers (1,000m radius) and measured land use data (Table S1) using Qgis (ver. 3.22.6, <https://qgis.org/en/site/>, accessed 20 May 2022). Although land use may affect freshwater biodiversity at multiple spatial scales, we selected a buffer of 1,000m based on assessments of tadpole occupancy and habitat split effects in areas from the Pampa and Atlantic Forest (Lion et al., 2014; Moreira et al., 2016). We used a classification produced within the scope of the MapBiomias initiative (Project MapBiomias, 2021). At first, we recorded five different land uses (temporary crop, cattle, crop/cattle mosaic, forest plantation, and urban area). The loblolly pine (*Pinus taeda*) and the slash pine (*Pinus elliotii*) cover most planted forests. A hybrid variety of *Eucalyptus* occurs to a lesser extent. Cattle farming also encompasses natural grasslands (mainly in the Pampa). Because it was hard to distinguish which natural grasslands had cattle, we did not assess the influence of land uses classified as cattle.

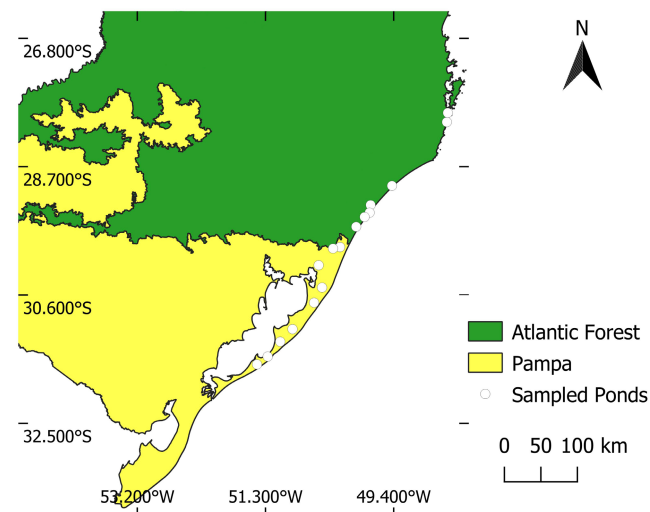


FIGURE 1 Location of the study region in a transition zone between Atlantic Forest and Pampa biome, in the southern Brazil.

2.2 | Data analysis

We assessed sampling saturation overall and per ecoregion with rarefaction and extrapolation curves with Hill numbers (Chao et al., 2014). We also estimated species richness per ecoregion with an incidence-based richness estimator (Chao 2). We used the iNext package (Hsieh et al., 2016) implemented in R (version 4.1.1, R Core Team, 2021) for generating the sampling curves.

To quantify changes in functional trait variation across ponds, we calculated three metrics based on the mean of measurements of the four traits (Table 1): FRic, FEve, and FDiv (Villéger et al., 2008).

TABLE 1 Traits and measurements of tadpoles used to calculate functional diversity indices.

Trait	Measure	Relevance
Lateral body form	BH/BL	Swimming type and endurance
Tail shape	MTaH/TaL	Position in the water column
Relative tail muscle height	TaMH/TL	Acceleration and manoeuvrability
Dorsal body form	BW/BL	Microhabitat use

Abbreviations: BH, body height; BL, body length; BW, body width; MTaH, maximum tail height; TaL, tail length; TaMH, tail muscle height; TL, total length.

The former describes a multidimensional trait space filled by the assemblage and is related to species richness. The other metrics are proportional to species' relative abundance, with FEve reflecting the regularity of the distribution in functional space and FDiv representing the proportion supported by species with the most extreme trait values. We calculate metrics only for ponds with a minimum of three species. To facilitate comparisons, we calculated the standardised effect size (SES; Gotelli & McCabe, 2002) using a null model that preserves regional species occurrence frequency and pond species richness (independent swap algorithm; Gotelli, 2000). We used the R packages *picante* (Kembel et al., 2010) and *FD* (Laliberté et al., 2014) for computing functional diversity.

Phylogenetic signal in traits may inflate type I error in the functional metrics used here (Duarte et al., 2018). Therefore, we assessed the phylogenetic signals in morphological traits using the *K* statistic (Blomberg et al., 2003). As the analysis did not detect evidence of a phylogenetic signal in the traits (Table S2), we did not perform the phylogenetic correction. We also investigated if observed species richness in the pond was associated with the values obtained by the different functional diversity metrics (Figure S3). Although there was weak evidence for the relationship between FRic and species richness, regressions showed no evidence for other functional diversity metrics. To account for spatial autocorrelation, we used the geographic coordinates of the ponds to construct distance-based Moran's eigenvector maps (MEMs) (Dray et al., 2006). We used the minimum spanning tree and the function f_{PCNM} to generate the connectivity and weighting matrices, respectively (Dray et al., 2006). The used threshold distance corresponded to the minimum distance connecting all sampling ponds (129 km). This procedure yielded three MEM variables, modelling positive correlations and corresponding to a specific spatial structure and scale (Figure S4). They represented the spatial components in the subsequent analysis to account for spatial autocorrelation. MEM1 can model broad-scale structures in the community data, whereas MEM2 and MEM3 progressively represent intermediate and finer-scale patterns.

We evaluated the effect of land use (crop, forest plantation, mosaic, and urban areas) on functional diversity metrics (SES.FRic, SES.FEve, and SES.FDiv) using generalised linear models with Gaussian distribution. Before analysis, we used logit transformation on land use because the data used here were proportions. We kept the candidate models simple because the data set was small. We built three blocks of models assuming that land use had either no effect, effects independent of spatial patterns, or additive to spatial predictors. The first set included each one of the three spatial predictors. Our second set contained only the land use classes. The third model set ($n=12$) combined each land use with spatial predictors. This framework gave us a candidate set of 19 models (Table S3), which we ranked using the corrected Akaike's information criteria (AIC_c).

We used multimodel inference to avoid relying on a single model to conclude the importance of variables on functional diversity metrics (Burnham et al., 2011). We retained only models within four AIC_c units of the most informative model. For the top-ranked models, we used AIC_c -weighted slope estimates $\pm 95\%$ confidence

intervals to judge the significance of each explanatory variable. To assess the variance explained by the top-ranked models, we calculated the McFadden pseudo- r^2 values. We used MASS, MuMIn, and AICcmodavg packages in R for multimodel inferences (Barton, 2020; Mazerolle, 2023; Venables & Ripley, 2002).

3 | RESULTS

Summarising data over all ponds sampled, we found tadpoles of 16 anuran species, representing eight genera from three families (Table 2). Because many specimens had tail injuries, we used 241 individual measurements of four traits for functional diversity indices. Measurements encompassed all species from the 16 ponds. Across all ponds, the most abundant species was *Scinax squilirostris*, corresponding to 34% of all the collected tadpoles (Table 2). Many species had a low occurrence (between three and six ponds). Ponds in the Pampa hosted about 60% of the tadpole abundance (Table 2). Across all ponds, the observed species richness was a lower bound of estimated richness. Indeed, the estimated richness was 16.9 (95% confidence interval: 16.1, 25.5). Rarefaction curves suggested that richness was lower in the Atlantic Forest ponds; however, 95% confidence intervals were wide in the Pampa (Figure S5).

The model that was most likely to explain FRic suggested that MEM1 influences SES.FRic (Table 3). Three further models showed Akaike weight >0.1 . All the models with a weight >0.1 included additive effects of broad-scale spatial predictor (MEM1) and different land uses (Table 3). The 95% confidence interval for the model-averaged regression excluded 0 (0.45, 1.41) and indicated that FRic increased with positive values of MEM1. Although land use variables were among the best-ranked models, the 95% confidence interval for the variables included 0 (Table 3).

For SES.FEve, the best-supported models included forest plantation alone and additive effects of plantation and spatial predictors (Table 4). FEve was higher in ponds surrounded by more forest plantation cover. The model containing only forest plantation explained 17% of the variation in SES.FEve. The 95% confidence interval for all three spatial predictors included 0 (Table 4). The effect of crop area on evenness was less marked (pseudo- r^2 : 0.11), but the 95% confidence interval (-1.69, -0.13) indicated that crop area negatively affects SES.FEve.

The FDiv was best explained by forest plantation data, followed by additive effects of forest plantation and MEM1 (Table 5). There was substantial evidence for a positive effect of forest plantation areas on SES.FDiv, as indicated by the 95% confidence interval for the variable. The spatial predictors did not influence the FDiv (Table 5).

4 | DISCUSSION

Our results showed that some human land uses have more pervasive impacts on amphibian communities, particularly reforestation

TABLE 2 Species occurrence and tadpole abundance in 16 ponds across the Pampa and Atlantic Forest transition zone, in the southern Brazil.

Species	Atlantic forest		Pampa	
	Occurrence	Abundance	Occurrence	Abundance
Hylidae				
<i>Boana pulchella</i>	0	0	5	48 (20)
<i>Dendropsophus minutus</i>	3	49 (12)	1	24 (4)
<i>Dendropsophus sanborni</i>	2	5 (2)	6	16 (9)
<i>Pseudis minuta</i>	1	3	5	16 (7)
<i>Scinax fuscovarius</i>	2	50 (4)	0	0
<i>Scinax granulatus</i>	4	20 (8)	4	9 (4)
<i>Scinax nasicus</i>	4	13 (1)	1	7 (5)
<i>Scinax squalirostris</i>	7	157 (30)	9	144 (62)
Leptodactylidae				
<i>Leptodactylus gracilis</i>	2	5 (5)	1	4 (4)
<i>Leptodactylus luctator</i>	0	0	1	65 (7)
<i>Leptodactylus mystacinus</i>	1	7 (4)	1	1 (1)
<i>Physalaemus biligonigerus</i>	0	0	1	84 (25)
<i>Physalaemus cuvieri</i>	4	38 (7)	2	20 (6)
<i>Physalaemus gracilis</i>	1	4	2	56 (6)
<i>Pseudopaludicola falcipes</i>	0	0	3	17 (3)
Odontophrynidae				
<i>Odontophrynus asper</i>	2	2 (1)	1	8 (4)

Note: Individuals measured for functional diversity indices are given in parentheses.

TABLE 3 Highest-ranked generalised linear models and estimates explaining the standard effect size for functional richness of tadpole communities in the Pampa and Atlantic Forest transition zone.

	Number of parameters	ΔAIC_c^a	Akaike weight	Model-averaged parameter (95% CI)
Model				
MEM1	3	0	0.39	
MEM1+Crop	4	0.6	0.29	
MEM1+Forest plantation	4	2.18	0.13	
MEM1+Mosaic	4	2.43	0.11	
MEM1+Urban	4	3.56	0.07	
Parameter				
MEM1				0.93 (0.45, 1.41)
Crop				-0.61 (-1.33, 0.12)
Forest plantation				0.32 (-0.21, 0.85)
Mosaic				-0.30 (-0.87, 0.27)
Urban				0.05 (-0.4, 0.5)

Note: Pseudo- r^2 of the best-ranked models was between 0.21 and 0.27. Estimates in boldface type indicate that 0 is excluded from the 95% confidence interval.

^aCorrected Akaike's information criteria (AIC_c) of the highest ranked model was 50.27.

with exotic species. Using tadpoles as a study model, we showed that most of the variation in the functional diversity dimensions was independent of species richness. Spatial components influenced FRic to a greater extent than land use. Although we did not

find an isolated effect of spatial processes on FEve and FDiv, our findings pointed out the spatially structured variation of land use (exotic reforestation or crops) within the three functional metrics. Compelling evidence shows that agricultural land use and exotic

TABLE 4 Highest-ranked generalised linear models and estimates explaining the standard effect size for functional evenness of tadpole communities in the Pampa and Atlantic Forest transition zone.

	Number of parameters	ΔAIC_c^a	Akaike weight	Model-averaged parameter (95% CI)
Model				
MEM1 + Forest plantation	4	0	0.27	
MEM3 + Forest plantation	4	0.12	0.25	
Forest plantation	3	0.13	0.25	
MEM2 + Forest plantation	4	2.11	0.09	
Crop	3	3.22	0.05	
Parameter				
Forest plantation				0.83 (0.34, 1.32)
Crop				-0.91 (-1.69, -0.13)
MEM1				0.3 (-0.25, 0.85)
MEM2				0.27 (-0.24, 0.78)
MEM3				0.39 (-0.02, 0.8)

Note: Pseudo- r^2 of the best-ranked models was between 0.1 and 0.25. Estimates in boldface type indicate that 0 is excluded from the 95% confidence interval.

^aCorrected Akaike's information criteria (AIC_c) of the highest ranked model was 48.13.

TABLE 5 Highest-ranked generalised linear models and estimates explaining the standard effect size for functional divergence of tadpole communities in the Pampa and Atlantic Forest transition zone.

	Number of parameters	ΔAIC_c^a	Akaike weight	Model-averaged parameter (95% CI)
Model				
Forest plantation	3	0	0.44	
MEM1 + Forest plantation	4	0.62	0.33	
MEM3 + Forest plantation	4	3.33	0.08	
MEM2 + Forest plantation	4	3.63	0.07	
Parameter				
Forest plantation				0.64 (0.25, 1.04)
MEM1				-0.28 (-0.62, 0.05)
MEM2				0.03 (-0.35, 0.41)
MEM3				0.11 (-0.25, 0.47)

Note: Pseudo- r^2 of the best-ranked models was between 0.22 and 0.29. Estimates in boldface type indicate that 0 is excluded from the 95% confidence interval.

^aCorrected Akaike's information criteria (AIC_c) of the highest ranked model was 40.55.

reforestation play a fundamental role in amphibian species loss and community structure segregation in southern Brazil (Machado et al., 2012; Moreira et al., 2021; Saccol et al., 2017, 2022). At least part of the results observed here might echo preferred environmental conditions for breeding. Habitat selection by adults is an interplay between climate-related environmental conditions (at broad scales) and local pond features, such as hydroperiod and pond vegetation structure (Garey et al., 2023; Knauth et al., 2018; Provete et al., 2014). In modified landscapes, adults may have to deal with constraints related to habitat split and altered hydrology (Lion et al., 2014; Machado et al., 2012). Our results highlight a need for more integrative approaches to understanding how amphibians cope with a changing habitat (i.e., tadpole and adult

responses). In this section, we focused on constraints related to the tadpole phase, keeping in mind the habitat suitability for adults.

Spatial processes are often related to the dispersal limitations of organisms (Almeida et al., 2015; Knauth et al., 2019), but they also may arise from unmeasured factors (Landeiro & Magnusson, 2011). The movement ecology of amphibians is poorly understood, but species' behavioural differences and desiccation resistance play crucial roles in movement decisions (Mazerolle & Desrochers, 2005; Oliveira et al., 2016; Watling & Braga, 2015). The positive association with the broad-scale spatial predictor indicated a latitudinal gradient in the FRic, where SES.FRic values seem to decrease towards the south. At first, this result suggests that dispersal limitations were associated more with environmental gradients (i.e., changes

from forests in the north to wooded Restinga/dunes in the south) than geographic distance or barriers (e.g., great rivers or mountain ranges). Recent studies with tadpoles favour similar interpretations at different Brazilian Biomes (e.g., Garey et al., 2023). In addition, tadpole distribution is a good indicator of habitats effectively used for reproduction. Therefore, results such as ours also reflect success in habitat selection after surpassing environmental filters.

Negative impacts of nonnative eucalypt and pine species on the development of amphibian larvae and other aspects related to physiology and behaviour are well known (Burraco et al., 2018; Earl et al., 2012; Haggerty et al., 2019). In southern Brazil, exotic reforestation areas directly affect species composition and abundances of amphibian communities in the tadpole and adult phases (Machado et al., 2012; Saccol et al., 2017). These works attributed the decreases in the abundances to constraints related to moisture and shorter hydroperiods. Theory predicts high values of FEve in competition or limiting similarity scenarios, where competitive exclusion would restrain the coexistence of functionally similar species (Mouchet et al., 2010). In addition, high levels of FDiv indicate that the most abundant species are dissimilar in the selected traits and would weakly compete. Here, tadpoles associated with the mid-water column (i.e., body triangular in lateral view, high dorsal fins) were more abundant in ponds surrounded by exotic plantations. Several studies have stressed the role of depth gradients enabling tadpoles of different guilds to co-occur in the same habitat (Melo et al., 2018; Queiroz et al., 2015). Our results indicate that exotic reforestation depletes the abundance of tadpoles with low dorsal fins and depressed bodies (i.e., benthic species associated with pond bottom). Given our trait choice, we posit a filter related to water depth in the reforestation ponds. While this is speculative, such constraints would be congruent with the performance filter hypothesis (Mouillot et al., 2013) and agree with a faster pond drying up in exotic reforestation ponds (Machado et al., 2012). However, we cannot rule out the importance of phenolic compounds leaked from exotic pine trees or local land management.

Jointly with reforestation, we found evidence for a crop area effect on FEve. Traits such as depressed bodies and low fins, as in *Boana pulchella* and *Leptodactylus luctator*, were dominant in ponds surrounded by crop areas. In the southern Brazilian Coastal Plain, temporary crops comprise mainly rice and soy that may sometimes be cultivated in rotation (Project MapBiomias, 2021). There is an ongoing debate about wetlands' conversion to grow crops, but rice fields are sometimes considered supplementary habitats for aquatic species (Maltchik et al., 2017). Although there are similar deleterious impacts in both crops (agrochemicals, land preparation, vegetation homogenisation), soy fields pose a harsher environment for tadpoles when compared to rice fields (Cunha et al., 2021; Moreira et al., 2014). Because rice fields retained water during most of the cultivation cycle (sometimes also in the off-season), differences in land management may favour the dominance of ground-dwelling species with benthonic tadpoles.

Habitat modification to human land use often results in vegetation homogenisation (inside and around wetlands) and alteration in

the hydrological regimes, so we deliberately chose traits related to depth gradients and habitat heterogeneity (e.g., Melo et al., 2018; Queiroz et al., 2015). For example, a depressed body with short tail fins is frequent in tadpoles inhabiting shallow habitats with sparse aquatic vegetation. We cannot rule out the possibility that land use might affect other tadpole traits. Traits associated with food acquisition are effect traits and, therefore, more likely to affect ecosystem services, such as nutrient cycling (e.g., Moreira et al., 2020; Sun et al., 2023). Sadly, the feeding ecology of Neotropical tadpoles is relatively poorly known (Gonçalves et al., 2023). The land use might also affect environmental components tracked by adults, such as canopy cover and water chemistry (Knauth et al., 2019; Proverte et al., 2014).

To conclude, this study showed that traits describing habitat use and predator avoidance mediate most responses of tadpole assemblages to land use in coastal wetlands from southern Brazil. Still, spatial aspects were crucial to functional diversity patterns. Regarding the forest plantation role observed here, many areas in southern Brazil, including the Coastal Plain, had massive increments in the exotic forestry areas in the last decade (Project MapBiomias, 2021). In addition, our study provides further evidence that land use may shape amphibian communities through filters related to the larval aquatic phase. Therefore, there is a need for approaches involving tadpoles and adult responses to habitat modification. We hope to contribute to the ongoing debate about land use change, biodiversity conservation, and ecosystem service provision.

AUTHOR CONTRIBUTIONS

Thaise Boelter: Conceptualisation; formal analysis; data curation; writing-original; writing-review and editing. Leonardo Moreira: Formal analysis; visualization; validation; writing-review and editing. Cristina Stenert: Funding acquisition; project administration; supervision; writing-writing review and editing. Leonardo Maltchik: Funding acquisition; project administration; supervision; writing-writing review and editing.

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CONFLICT OF INTEREST STATEMENT


The authors read and approved the final manuscript. We have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Amphibian data and scripts that support the findings of this study are available on request of the corresponding author.

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SUPPORTING INFORMATION

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