



RESEARCH ARTICLE

Multiple environmental filters and competition affect the spatial co-occurrence of pond-breeding anurans at both local and landscape scales in the Brazilian Cerrado

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Abstract

Context Environmental filtering and limiting similarity have both been hypothesized to influence patterns of species co-occurrence, but in contrasting ways. While environmental filtering results in a greater similarity of functional traits among co-occurring species, limiting similarity predicts that only species with different functional traits can co-occur.

Objectives We evaluated the roles of environmental filtering versus competition in shaping patterns of species co-occurrence in terrestrial versus arboreal species of pond-breeding anurans, and also the influence of local and landscape environmental factors on those patterns, in the Brazilian Cerrado.

Methods We surveyed anurans within 85 ponds and adopted trait-based approaches to investigate patterns

of co-occurrence within terrestrial and arboreal species groups.

Results Local-scale environmental filters related to hydroperiod were more important than landscape factors. Habitat split was an important landscape filter, as was the amount of forest relative to pasture cover for arboreal species and the number of water bodies for terrestrial species. Habitat filtering was trait-mediated for arboreal species within ponds of similar size, hydroperiod, and degree of habitat split. Competition was weaker than environmental filters and led to a checkerboard distribution in arboreal species, whereas terrestrial species exhibited limiting similarity within small ponds.

Conclusions The processes that shape species co-occurrence patterns are dependent on spatial scale, degree of habitat degradation, and relative habitat use of species (terrestrial vs. arboreal), such that environmental changes as a result of land-use intensification have the potential to profoundly alter the structure and dynamics of pond-breeding anuran communities in the Cerrado.

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Keywords Amphibians · Limiting similarity · Fragmented landscapes · Habitat filtering · Habitat split · Niche aggregation

Introduction

Identifying the processes that drive spatial patterns of species co-occurrence remains a critically important challenge in community ecology, especially if we hope to predict how communities will change in response to future environmental changes due to land-use intensification and climate change. Ever since Diamond (1975) proposed a set of assembly rules founded on the role of competition in structuring communities, ecologists have sought to understand how various processes can contribute to species coexistence (Connor and Simberloff 1979; Wilson 1987; Hubbell 2001; Gotelli and Mccabe 2002; Mouillot et al. 2007; Ulrich et al. 2012; D'Amen et al. 2018; Kohli et al. 2018). In particular, trait-based approaches, which evaluate the relationship between patterns of species co-occurrence and environmental factors in view of species' functional or life-history traits, have been advanced for disentangling the relative influence of environmental constraints versus competition in structuring communities (Mouchet et al. 2013; Ulrich et al. 2017, 2018; Kohli et al. 2018).

These two major processes of community assembly—environmental filtering versus competition—predict contrasting patterns in the spatial distribution of co-occurring species (Ulrich et al. 2017, 2018). Environmental or habitat filtering permits only species with certain traits (e.g., ecological, morphological, or behavioral) to occur within a given environment (Whittaker 1967; Zobel 1997). Environmental filtering should thus result in greater similarity (i.e., clustering or aggregation) of functional or life-history traits among co-occurring species than expected by chance (i.e., if co-occurring species represented a random assemblage of the larger species pool; Zobel 1997; Mouillot et al. 2007). Conversely, the theory of limiting similarity (MacArthur and Levins 1967; Abrams 1983) predicts that if competition is primarily important in structuring communities, then the expected pattern is one of trait overdispersion or segregation (temporally, spatially, or environmentally), where only species with different functional traits can co-occur (Wilson and Stubbs 2004). Alternatively, the co-occurrence of species may be independent of their ecological similarity or functional traits, such that

patterns of species co-occurrence are entirely random (Hubbell 2001; Mouchet et al. 2013).

In a meta-analysis of 96 published studies, Gotelli and McCabe (2002) found evidence of nonrandom structure (either segregated or clustered patterns of species co-occurrence) in birds, bats, mammals, and plants, but not in fish, amphibians/reptiles, or invertebrates (except for ants). From these results, the authors suggested that patterns of co-occurrence in ectothermic species may often be random (Gotelli and McCabe 2002; see also Gotelli and Rohde 2002, Gotelli and Ulrich 2010). However, studies that used trait-based approaches (e.g. dividing species into different guilds or including information on species' functional traits) have revealed that communities of ectothermic species may indeed possess structure (Behangana and Luiselli 2008; Heino 2009; Both et al. 2011; Moreira and Maltchik 2012; McCreddie and Bedwell 2013; Mouchet et al. 2013; Arnhold et al. 2019). In the case of amphibians, some studies have reported that species co-occurrence patterns were aggregated (e.g., Melo et al. 2014), whereas other studies that adopted a trait-based approach using information on trophic guild (Both et al. 2011) or ontogenetic stage (Moreira and Maltchik 2012) revealed that competition may play an important role in structuring spatial patterns of co-occurrence. For example, Both et al. (2011) found segregated patterns of species co-occurrence among pond-breeding anurans in southern Brazil, but only for the larval (tadpole) stage of a single guild (benthic or nektonic tadpoles) and among non-breeding adults having similar pond-area requirements. Conversely, Behangana and Luiselli (2008) found that checkerboard (segregated) patterns of co-occurrence, in which two species are never found together, were generated by environmental variability rather than interspecific competition among amphibians in an African savanna. In addition, some studies have found evidence of abiotic factors (e.g., hydroperiod, number of vegetation types, distance to the nearest water body) acting as environmental filters in structuring patterns of amphibian occurrence at both local (site) and landscape scales (Moreira and Maltchik 2012; Prado and Rossa-Feres 2014a, b). Thus, we still have much to learn about the relative influence of environmental filtering versus competition in shaping patterns of species co-occurrence, especially in amphibian communities where both terrestrial and aquatic factors may play a

role and which could therefore vary as a function of scale between local breeding sites (e.g., ponds) and the broader landscape context in which those sites are embedded.

To that end, we adopted a trait-based approach to investigate spatial patterns of co-occurrence among pond-breeding anurans in the Brazilian Cerrado, a tropical savanna and global biodiversity hotspot (Myers et al. 2000). The Cerrado comprises about 20% of Brazil's land area, but is critically endangered by habitat loss and fragmentation due to agricultural expansion and intensification in recent decades (Françoso et al. 2015; Oliveira et al. 2019; Rausch et al. 2019; Grande et al. 2020). The Cerrado contains >200 amphibian species (Valdujo et al. 2012), many of which are still being described and their distributions mapped (Haga et al. 2017; Andrade et al. 2020). Amphibians have exhibited global declines and are threatened with extinction in many places, including the Cerrado (Hopkins 2007). Amphibians—and anurans in particular—are thus excellent subjects for the study of how local and landscape environmental factors influence community assembly: pond-breeding anurans occur in aquatic environments for part of their life cycle and are thus critical components of both aquatic and terrestrial communities; they exhibit a diversity of biological traits, which may differ between larval and adult life stages; and, they are good ecological indicators that are likely to be sensitive to environmental changes due to habitat loss, fragmentation, and agricultural intensification, which affect both their terrestrial and aquatic habitats (Becker et al. 2007, 2010; Prado and Rossa-Feres 2014b; Signorelli et al. 2016; Marques and Nomura 2018).

Our goal in this paper is to evaluate the relative roles of environmental filtering versus competition in shaping patterns of species co-occurrence in terrestrial versus arboreal species of pond-breeding anurans, as well as the relative influence of local-scale (pond) and landscape-scale (habitat amount and fragmentation) environmental factors on species co-occurrence patterns. We used an approach developed by Ulrich et al. (2012) that distinguishes between co-occurrence structures that capture different patterns of community assembly: a clumped (aggregated) versus a checkerboard (segregated) distribution. The analysis of these different types of patterns may uncover

dependencies between species co-occurrence and various environmental or functional traits, which could provide new insights into how these communities are assembled and thus whether or how future landscape or environmental changes are likely to restructure communities (Ulrich et al. 2012, 2018). For example, spatial aggregation of functional traits among co-occurring species provides evidence of habitat filtering, in which species with similar functional traits are jointly colonizing suitable ponds. Conversely, spatial segregation among species could occur either because of competition (limiting similarity) or because of differences in the pond environment or the amount and fragmentation of habitat in the surrounding landscape (i.e., environmental variability). By comparing the relationship between the variability in functional traits and environmental conditions, we can separate which process (limiting similarity or environmental variability) is likely responsible for the observed pattern of co-occurrence, as competitive effects are expected to segregate traits even when environmental variability is low, whereas habitat-induced trait segregation should correlate with environmental variability (Ulrich et al. 2017).

In our analysis, we evaluated co-occurrence patterns for all species combined, as well as separately for arboreal versus terrestrial species. We performed separate analyses for arboreal and terrestrial species because species co-occurrence in these groups is hypothesized to depend on factors that influence movement and habitat use along either the vertical or horizontal dimensions, respectively (Gonçalves et al. 2015; Scheffers et al. 2017; Oliveira and Scheffers 2019), which in turn should differentially influence a particular species' response to local- or landscape-scale variables (Dixo and Martins 2008; Basham et al. 2019; Cayuela et al. 2020). For example, we anticipated that while arboreal species would be more likely influenced by environmental filtering at both local and landscape scales given their general habitat affinity (i.e., for trees in an otherwise open-grassland system), their pattern of co-occurrence could ultimately reflect segregation with respect to species that possess similar functional traits (i.e., evidence for limiting similarity) given that past studies have documented vertical stratification among arboreal frog species (Farneda et al. 2015; Fonseca-Pérez et al. 2017; Basham et al. 2019; López-Rojas 2019).

Furthermore, many arboreal species exhibit continuous or prolonged reproduction (Prado et al. 2005; Oda et al. 2009; Kopp et al. 2010; de Sá et al. 2014), such that species are more likely to overlap in space and time within breeding areas, which could increase competitive interactions (Donnelly and Guyer 1994; Borzée et al. 2016; Garey et al. 2018). In contrast, we anticipated that terrestrial species would be more prone to environmental or habitat filtering and exhibit more aggregated patterns of co-occurrence because of their greater dependence on ephemeral or temporary ponds for reproduction (Rittenhouse et al. 2008; Child et al. 2009; Pereira et al. 2015), which are only available during the wet season in the Cerrado (Giaretta et al. 2008; Valdujo et al. 2013). This has apparently led to the evolution of rapid, synchronous (explosive) reproduction in some terrestrial groups (e.g. Leptodactylidae; Prado et al. 2005; Giaretta et al. 2008; Pereira et al. 2017), resulting in a greater dependence on water availability and species co-occurrence at the local site scale.

Material and methods

Study area

The study area is located in the center of the Brazilian Cerrado in the state of Goiás, between the municipalities of Goiânia ($16^{\circ}35'13.66''\text{S}$, $49^{\circ}11'01.43''\text{W}$), Terezópolis de Goiás ($16^{\circ}28'4.62''\text{S}$, $49^{\circ}7'58.97''\text{W}$) and Itauçu ($16^{\circ}13'23.16''\text{S}$, $49^{\circ}34'09.82''\text{W}$) (Fig. 1). This region is characterized mainly by remnants of forest vegetation, including seasonal semi-deciduous forest and gallery forest, surrounded by pastures (grazed rangeland), agricultural fields, and urban areas. The main river systems in this region are the João Leite and Meia Ponte rivers and their tributaries, which make up the Paranaíba river basin. The climate is tropical (Aw de Köppen), with two distinct seasons characterized as either wet (October–March) or dry (April–September) (Peel et al. 2007). The average monthly air temperature is 24.8°C (obtained for the period 2008–2017; Brasil 2018), but averages

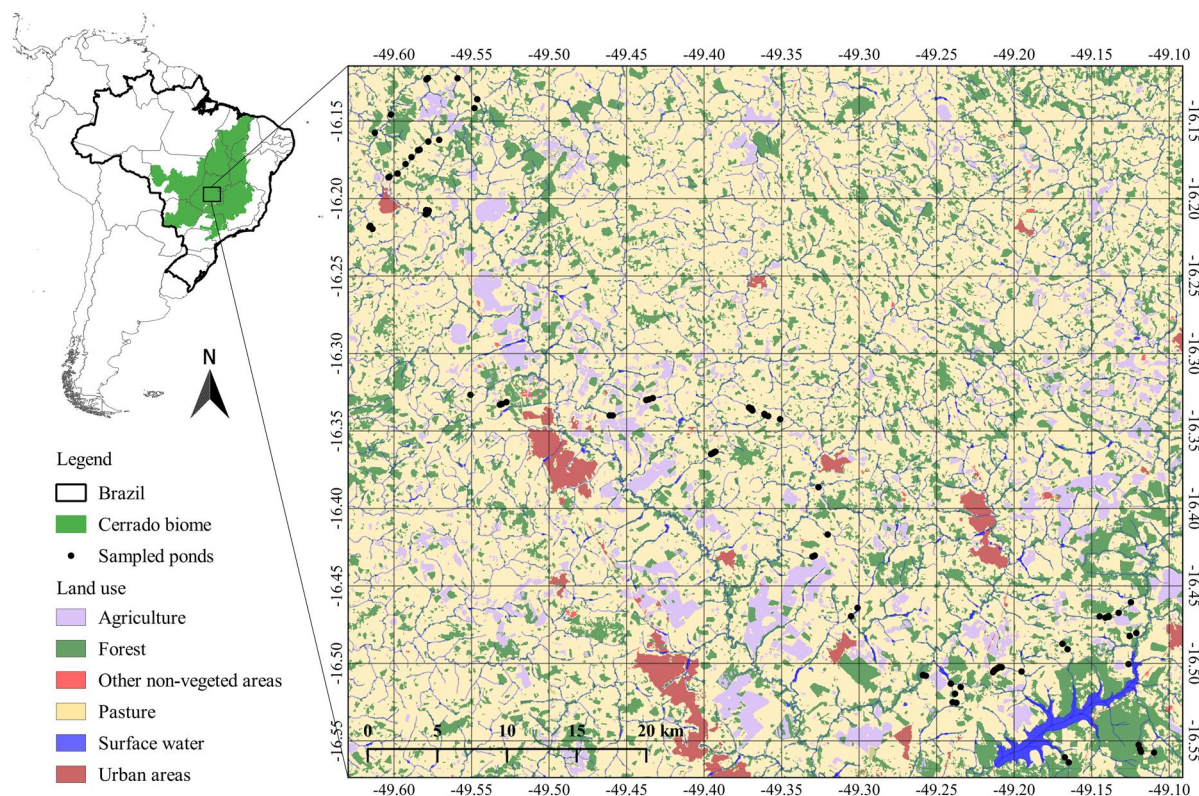


Fig. 1 Geographic location of the study area, showing the distribution of land-cover types, and the 85 ponds sampled in the Brazilian Cerrado

higher during the dry season in September (26.9 °C) and lowest in June (22.8 °C). The average monthly precipitation is 137.8 mm, with the highest rainfall occurring in December (319.7 mm) and the lowest in August during the dry season (2.3 mm).

Data collection

We surveyed pond-breeding anurans within 85 ponds, which represented a wide range of environmental conditions and landscape contexts (Fig. 1). Ponds included natural ponds (both permanent and temporary), impoundments (streams that had been dammed), palm swamps (*veredas*) and other marshy habitats, such as excavated ponds and low-lying areas that accumulate rainwater. We surveyed each pond three times, during the beginning (3–22 Dec 2016), middle (9 Jan–3 Feb 2017), and end (13 Mar–7 Apr 2017) of the rainy season. Surveys involved active search and the anuran species present were identified via a combination of visual and acoustic (Heyer et al. 1994) means by one of us (WPR) to avoid observer bias. All surveys were performed in the evenings between 19:00 and 00:00 h when anurans tended to call most actively (Guerra et al. 2020). The average duration of each pond survey was 30 ± 10 min, although sampling time was dependent on the size of the pond. In addition to the pond itself, anuran surveys also included the perimeter of ponds that were <0.5 ha in size, and a transect along the perimeter of the pond up to 100 m for larger ponds (>0.5 ha). Voucher specimens were obtained by first anesthetizing individuals, which were then killed with an injection of 5% xylocaine and fixed in 10% formalin, before being preserved in 70% ethanol and deposited in the Coleção Zoológica da Universidade Federal de Goiás (ZUFG), Goiânia, Goiás, Brazil.

Species functional traits

For each anuran species, we assembled a dataset of functional traits, using the ecological traits suggested in the AmphibiO global database (Oliveira et al. 2017). This database includes a suite of traits related to the ecology, morphology, and reproductive characteristics of amphibians, including the anuran species found in the Cerrado. In particular, we focused on the relationship between post-metamorphic traits (e.g., adult anuran body size, reproductive mode) and

various environmental or landscape factors (e.g., our local site and landscape variables, see next section) because these are expected to affect anuran dispersal (Cayuela et al. 2020), and thus, should have the greatest effect on patterns of species co-occurrence.

We characterized anuran species based on five adult functional traits: (1) diel period of activity; (2) seasonal period of activity; (3) toxicity; (4) body size; (5) habitat; and, (6) reproductive mode (Supplementary material S1). For the diel period of activity, we classified species as diurnal, nocturnal, or crepuscular, with some species falling into more than one category (e.g., some species sporadically call during the day but are most commonly active at night). The seasonal period of activity was based on a combination of precipitation (wet or dry) and temperature (warm or cold) conditions as wet/warm, wet/cold, dry/warm, and dry/cold in relation to the average climatic conditions over the year. For this particular trait, we based our assessment on our own observations as well as information obtained from other studies conducted near our study area (e.g., Oda et al. 2009; Kopp et al. 2010). As with diel period of activity, some species were characterized by more than one category (e.g., wet/warm and dry/warm). The seasonal period of activity is important because it relates to the length of the reproductive period, which varies among species from protracted (season-long) to explosive breeding in which all individuals reproduce at once over a short period of time (Wells 2013). Toxicity was characterized relative to the effect on predators as toxic (causing death if eaten), unpalatable or bad-tasting (resulting in predator avoidance), or non-toxic (Wells 2013). The similarity or dissimilarity of body sizes between co-occurring species may be a good metric of current or past competition (May and MacArthur 1972; Dayan and Simberloff 2005), and so we obtained the maximum adult body size (snout-to-vent length) for each species using the AmphibiO database (Oliveira et al. 2017) or published species accounts (e.g., De Carvalho et al. 2010; Andrade and De Carvalho 2013; Brasileiro and Haddad 2015). We classified the main habitat of each species as either forest, open areas, or both. Finally, we classified the reproductive mode of each species using the classification proposed by Pombal Jr. and Haddad (2007) and Crump (2015). The reproductive mode was characterized in terms of how eggs are deposited, whether in (1) water, (2) aquatic foam nests, (3) terrestrial foam

nests at the edge of the pond, or (4) attached to arboreal substrates (leaves, twigs) at the edge of the pond. Although these are pond-breeding anurans, the mode of reproduction may influence the response of different species to habitat loss and fragmentation because each mode requires different environmental conditions for success (Becker et al. 2007; Crump 2015).

Local environmental and landscape-scale variables

At the local site (pond) scale, we measured several environmental variables that are expected to influence the occurrence of anuran species. Previous research has found that the amount of vegetation cover within ponds and along the pond's edge are important determinants of species occurrence and abundance (Vasconcelos et al. 2009; Signorelli et al. 2016). Furthermore, the variation in pond area and hydroperiod creates an environmental gradient in habitat suitability, ranging from small ephemeral ponds that are subject to drying up to large permanent ponds that have high predation pressure because of the presence of fish and other aquatic predators (Prado and Rossa-Feres 2014b; Pintar and Resatarits Jr. 2017). We therefore focused on the following variables to characterize the local environment of each pond: area (m^2), hydroperiod (Hydro: ephemeral, temporary, semi-permanent, and permanent, as defined below), percentage of pond covered by vegetation (Veg_{in}), and percentage of pond edge covered by vegetation (Veg_{ed}). Local environmental variables were estimated visually during each of the three sampling periods. Pond hydroperiod was categorized as: ephemeral, pond dries up repeatedly outside of the rainy season; temporary, pond eventually dries up at some point during the dry season; semi-permanent, pond retains water all year, but experiences a marked reduction in depth ($>70\%$) during the dry season; and, permanent, the pond retains water all year, with little reduction in depth during the dry season (Prado and Rossa-Feres 2014b; Semlitsch et al. 2015). We based our assessment of pond hydroperiod on the observed water level within ponds at each visit during the sampling period and during multiple visits outside of the sampling period (i.e., during the dry season).

We defined landscape-scale variables in relation to the expected dispersal range of anurans. Owing to the lack of dispersal information for Cerrado species, we assumed a general dispersal range of 1 km,

as reported for some other anuran species (Gagné and Fahrig 2007). To characterize the landscape surrounding each pond, we first manually digitized satellite imagery using the world imagery basemap in ArcGIS 10.5 (ESRI 2018) and then calculated a number of landscape metrics within a 1-km buffer centered on each pond using the *landscapemetrics* package (Hesselbarth et al. 2019) in R (R Development Core Team 2019). Within each landscape, we calculated the relative amount (class area, CA) of forest (CA_f ; both seasonal and riparian forest combined), water bodies (CA_w ; all streams, river, ponds, dams, and swamps combined), and pasture (CA_p). Because habitat fragmentation has been linked to extensive declines in some anurans (Cushman 2006; Becker et al. 2007), we also quantified the number of patches (NP) of forest (NP_f), water bodies (NP_w), and pasture (NP_p) as a measure of fragmentation or dispersion for each cover type. In addition, we also calculated the straight-line distance (m) from the pond to the nearest forest fragment (DF) as a measure of “habitat split”, given that these pond-breeding anurans spend much of their lives outside of the breeding season in the forest (Becker et al. 2007, 2010). We do not include land covers such as agricultural fields, urban areas, or other non-vegetated areas (e.g., roads) in our analysis because they are not very prevalent in the study area within this region of the Cerrado, and because our focus here is on species associated with native vegetation types (e.g., forest).

Data analyses

Species co-occurrence patterns

Species occurrence data were summarized into three presence-absence matrices: (1) all species combined, (2) arboreal species only, and (3) terrestrial species only. We considered arboreal species to be those that have the ability to use the arboreal stratum to disperse between ponds (although they can also disperse along the ground), while terrestrial species are those who cannot use the arboreal stratum, which includes semi-aquatic species (e.g., *Pseudis bolbodactyla*). The resulting matrix dimensions were thus 32 species \times 85 ponds in the full matrix (all species combined), 14 species \times 81 ponds for arboreal species, and 18 species \times 80 ponds for terrestrial species.

Analysis of species co-occurrence patterns

We analyzed the co-occurrence patterns for each anuran group (arboreal, terrestrial, or all species combined) using the trait-based approach introduced by Ulrich et al. (2012) and modified by Ulrich et al. (2017), and implemented within the Niche software (Ulrich 2012). First, we organized the data on species functional traits, local- and landscape-scale environmental factors, and species occurrence within ponds into three types of matrices: (1) an environmental variable \times ponds matrix \mathbf{V} , (2) a species \times traits matrix \mathbf{T} , and (3) a species presence-absence \times ponds matrix \mathbf{M} , for each of the three groups (all species combined, terrestrial species only, and arboreal species only). These matrices were used to produce two distance matrices (Fig. 2): (1) an environmental dissimilarity matrix obtained by calculating the Euclidean distance

between sites' environmental variables (Δ_{env}) from the environmental matrix \mathbf{V} , and (2) a trait dissimilarity matrix obtained by calculating the Euclidian distance between species' traits (Δ_{trait}) from the trait matrix \mathbf{T} .

Each of these dissimilarity matrices was then contrasted with the co-occurrence patterns obtained from the species' presence-absence matrices (\mathbf{M}) to make inferences about the underlying process responsible for the observed co-occurrence pattern (e.g., habitat segregation vs. habitat filtering, trait segregation vs. trait aggregation, trait-based habitat filtering vs. limiting similarity), as we explain next. This involves counting the number of pairs of species for each group that exhibited either a clumped (\mathbf{A}_Δ , aggregated) or checkerboard (\mathbf{C}_Δ , segregated) pattern of co-occurrence (Stone and Roberts 1992; Ulrich et al. 2012; Ulrich and Gotelli 2013). The clumping score

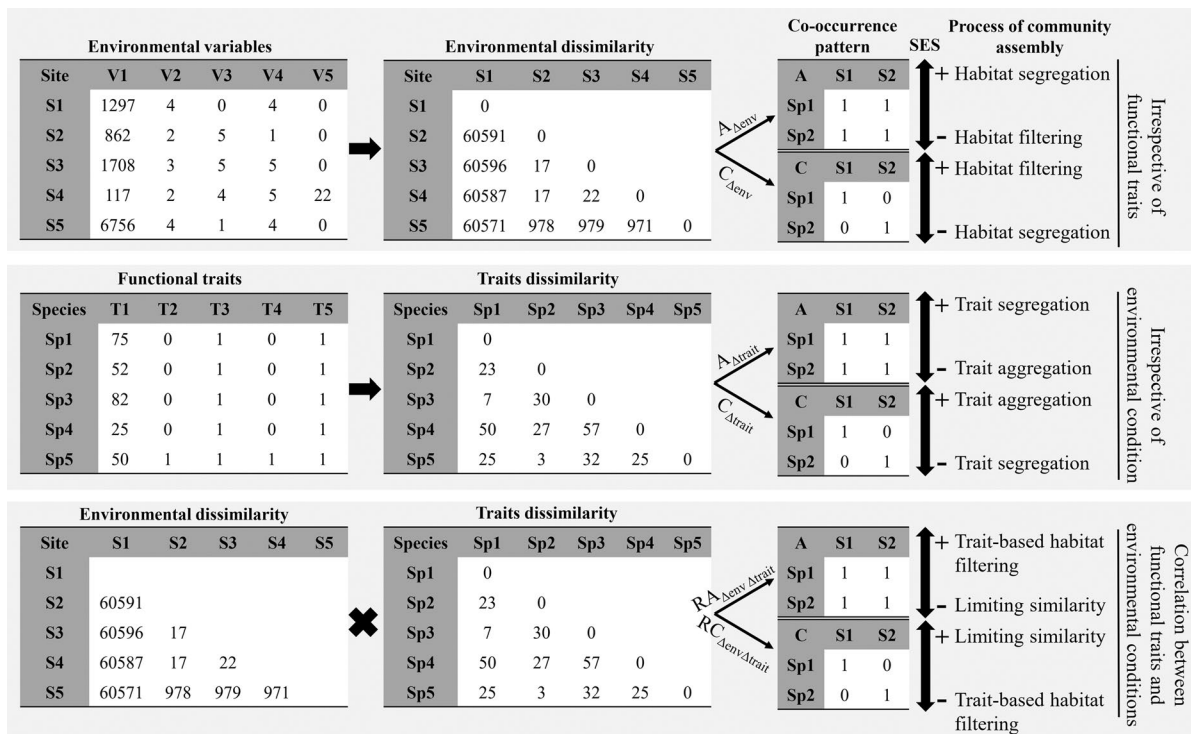


Fig. 2 A representation of the relationship between environmental condition, functional traits, and species co-occurrence patterns based on the Ulrich et al. (2012) methodology. The metrics $A_{\Delta_{env}}$ vs. $A_{\Delta_{trait}}$ (the clumping or aggregation scores) and $C_{\Delta_{env}}$ vs. $C_{\Delta_{trait}}$ (the C-scores for a checkerboard or segregated distribution) are defined as the average Euclidean difference of all pairwise differences in habitat conditions (Δ_{env}) and

distances between species' traits (Δ_{trait}), respectively. Positive and negative values of standardized effect size (SES) refer to the comparison of the observed scores to the respective null-model expectations and provide evidence of the following processes: habitat segregation, habitat filtering, trait segregation, trait aggregation, trait-based habitat filtering, and trait-based habitat segregation (i.e., limiting similarity)

(A_{Δ}) is the number of M submatrices (the 2×2 presence-absence combinations for each species pair) having the form $\{1,1\}\{1,1\}$, in which a pair of species is found to co-occur within the same ponds (Ulrich and Gotelli 2013; Ulrich et al. 2017). The clumping score is thus indicative of environmental or habitat filtering effects (Ulrich et al. 2012, 2017). By contrast, the C-score (C_{Δ}) is a normalized count of the M submatrices having the form $\{1, 0\}\{0, 1\}$, in which a pair of species exhibits a checkerboard distribution (i.e., the two species do not co-occur in the same ponds; Stone and Roberts 1992; Ulrich et al. 2017). We then calculated the average environmental distances and trait distances for all species pairs having either a clumped or checkerboard pattern of co-occurrence, as measured by the standardized effect size (SES, see procedure described below; Fig. 2). For aggregated species pairs, large differences ($SES > 1.96$) between sites in a certain environmental variable ($A_{\Delta env}$) indicate habitat segregation, whereas small differences ($SES < -1.96$) indicate habitat filtering, irrespective of the species' functional traits. Similarly, large distances ($SES > 1.96$) between the functional traits of co-occurring species ($A_{\Delta trait}$) indicate trait segregation, whereas small functional-trait distances ($SES < -1.96$) indicate trait aggregation, regardless of environmental conditions. For checkerboard patterns of co-occurrence, the reverse occurs: large SES scores between sites for a certain environmental variable ($C_{\Delta env}$) indicate habitat filtering, whereas small SES scores suggest habitat segregation, irrespective of species' functional traits. Likewise, a large SES score between functional traits of co-occurring species ($C_{\Delta trait}$) indicates trait aggregation, whereas small SES scores indicate trait segregation, regardless of environmental conditions (Fig. 2).

Because a checkerboard distribution could result either from competitive interactions (leading to trait segregation) or environmental variability (causing habitat segregation), we can infer which process is likely responsible for the observed pattern by evaluating how the pairwise differences between species functional traits correlate with the pairwise differences between pond environments and landscape features (i.e., as distance matrices Δ_{trait} and Δ_{env} , respectively; Fig. 2). Therefore, a positive correlation between species' traits and environmental variability ($SES > 1.96$) for checkerboard distributions ($RC_{\Delta env \Delta trait}$) would indicate limiting similarity

(functionally similar species are segregated within similar environments), whereas a negative correlation ($SES < -1.96$) instead suggests that trait-mediated habitat filtering (functionally similar species are found within dissimilar environments) is likely responsible for the checkerboard distribution of these species pairs (Fig. 2). For clumped species co-occurrence patterns, a positive correlation between species traits and environmental variability ($RA_{\Delta env \Delta trait}$) results in functionally similar species being found in similar environments (i.e., evidence of habitat filtering), whereas the existence of large trait differences between species pairs found in similar environments (a negative correlation between species traits and environmental variability) suggests that competition (i.e. limiting similarity) is likely playing a greater role (Ulrich et al. 2017). These last metrics, $RA_{\Delta env \Delta trait}$ and $RC_{\Delta env \Delta trait}$, are defined as the Pearson coefficient of the correlation between all the clumped or checkerboard submatrices, respectively, that are present in the species \times species matrix M , and the distance matrices Δ_{trait} and Δ_{env} (Fig. 2).

We used a null model approach to test the statistical significance of the observed clumping and C-score metrics for each anuran group with those obtained from 999 randomizations of the respective M matrices. We used a fixed-fixed (FF) null model, in which the row and column total of the M matrix are maintained. This FF null model performs well because it preserves the observed heterogeneity in species occurrence and species richness at sites (Ulrich and Gotelli 2013). The significance of each of the six metrics (four averages: $A_{\Delta env}$, $A_{\Delta trait}$, $C_{\Delta env}$, and $C_{\Delta trait}$); and two correlations: $RA_{\Delta env \Delta trait}$ and $RC_{\Delta env \Delta trait}$) was based on the respective tail distribution of 999 randomized matrices at the two-sided 5% and 1% error levels. In addition, we calculated standardized effect sizes (SES) = (observed score – expected score) / standard deviation of expectations. Significant SES scores have values below -1.96 and above $+1.96$ at the two-sided 5% error level under the assumption that the respective null distribution is approximately normal (Ulrich et al. 2012, 2018).

The relationships between species occurrences, functional traits, and local- and landscape-scale variables were analyzed graphically using the RLQ method (Dolédéc et al. 1996). This analysis was used to verify the magnitude and direction of significant effects when we uncovered evidence of habitat filtering,

trait segregation, trait-mediated habitat filtering, and limiting similarity. The RLQ is a three-step ordination procedure in which the relationship between the local and landscape variables (**R**), species occurrences (**L**), and functional trait (**Q**) matrices are combined into major linear correspondence axes. First, a correspondence analysis was computed on the **L** matrix. Second, a principal component analysis was used to summarize the **Q** matrix. Finally, the local and landscape variables (**R**) were ordinated using a Hill-Smith ordination. We tested the statistical significance of associations between functional traits and local and landscape variables in each RLQ analysis using a global Monte-Carlo test of the rows in the **R** (model 2) and **Q** (model 4) matrices (Dray and Legendre 2008). This analysis was performed using the R package *ade4* (Dray and Dufour 2007). To identify how the RLQ axes represented the observed environmental gradients, we correlated the coordinates of the most significant axes of the RLQ for the sites (ponds) with the original **R** matrix (i.e., the local and landscape variables). To determine which functional trait is significantly associated with environmental gradients, we (1) tested the association between the scores of the species for the most-significant axis of the RLQ and the adult snout-to-vent length using a Pearson correlation analysis; and (2) carried out a permutation test for multichoice functional traits, since each species can have more than one characteristic within each trait (e.g., diel period of activity; seasonal period of activity; toxicity; main habitat; and reproductive mode).

Results

Anuran communities showed clear evidence of environmental (habitat) filtering at both the local site (pond) and landscape scales. At the local scale, aggregated species co-occurred more often in ponds with similar hydroperiod and inside-vegetation cover than expected by chance for all three anuran groupings (significant $A_{\Delta env}$ scores, Table 1). Checkerboard species pairs also showed evidence of habitat filtering, albeit such species were segregated among ponds having dissimilar hydroperiods and vegetation cover (both inside and along the pond's edge) for all species combined and for terrestrial species, whereas arboreal species were segregated

only by dissimilar hydroperiod and inside-vegetation cover (significant $C_{\Delta env}$ scores, Table 1).

At the landscape scale, habitat split (the distance from the pond to the nearest forest, DF) is clearly acting as an environmental filter for all anuran groups (Table 1). Aggregated species pairs were more likely to co-occur in landscapes having a similar degree of habitat split, whereas checkerboard species were segregated by landscapes having different levels of habitat split. In addition, arboreal species were more likely to co-occur in landscapes having similar amounts of forest and pasture cover (significant $A_{\Delta env}$ scores), whereas aggregated terrestrial species were more likely to be filtered by landscapes having different numbers of water bodies (significant $A_{\Delta env}$ and $C_{\Delta env}$ scores, Table 1).

Although evidence for the role of competition in structuring the co-occurrence of pond-breeding anurans was weaker than for environmental filtering, we found consistent support for functional-trait segregation among arboreal species across both local and landscape scales, irrespective of environmental conditions (significant $A_{\Delta trait}$ and $C_{\Delta trait}$ scores, Table 1). Aggregated species pairs were more likely to differ in their functional traits than expected by chance (i.e., trait segregation) and checkerboard species pairs (which tend not to co-occur in the same ponds) had similar functional traits (again, consistent with trait segregation). A significant positive correlation indicates that arboreal species that exhibited a checkerboard pattern of co-occurrence were also more likely to exhibit trait-based segregation (limiting similarity) in landscapes that possessed a similar degree of pasture fragmentation (in terms of the number of pasture patches; significant positive $RC_{\Delta env \Delta trait}$ score for NPg, Table 1). As evidence of trait-based habitat filtering, arboreal species with similar traits exhibited an aggregated pattern in ponds of similar size (significant positive $RA_{\Delta env \Delta trait}$ score for area, Table 1). In addition, checkerboard arboreal species with similar traits were segregated among ponds that differed in hydroperiod and degree of habitat split (distance from pond to the nearest forest; significant negative $RC_{\Delta env \Delta trait}$ scores, Table 1). Co-occurring terrestrial species, by contrast, exhibited trait segregation in ponds of similar size, suggesting a role for competition in limiting the degree of similarity found among species able to coexist within ponds of

Table 1 Average Standardized Effects Size (SES) of the clumped and checkerboard (segregated) patterns of species co-occurrence for different anuran groups (all species combined,

arboreal species only, terrestrial species only) and their relationship with trait and environmental (local- and landscape-scale variables) dissimilarities

Metrics	Local scale ^a				Landscape scale ^b						
	Area	Hydro	Veg _{in}	Veg _{ed}	DF	CA _f	CA _p	CA _w	NP _f	NP _p	NP _w
All species											
A Δ_{env}	- 0.04	- 6.12	- 3.62	- 0.59	- 3.14	- 1.41	- 1.99	- 1.06	- 0.90	- 0.23	- 2.62
A Δ_{trait}	0.12	0.10	0.10	0.07	0.11	0.14	0.11	0.09	0.13	0.10	0.08
C Δ_{env}	1.03	11.28	5.51	2.35	5.45	- 0.18	0.48	0.33	0.22	- 0.27	2.11
C Δ_{trait}	- 1.03	- 1.00	- 1.02	- 0.98	- 1.04	- 1.06	- 1.02	- 1.02	- 1.05	- 1.03	- 1.00
RA $\Delta_{env\Delta trait}$	1.38	- 0.12	0.15	- 1.20	- 1.10	1.18	1.08	0.57	- 0.51	0.19	- 1.13
RC $\Delta_{env\Delta trait}$	0.99	- 1.56	- 0.47	- 1.05	- 1.63	0.09	- 0.23	- 0.22	0.53	1.08	- 0.62
Arboreal species											
A Δ_{env}	- 0.22	- 5.61	- 2.13	0.28	- 2.20	- 2.06	- 1.98	- 1.58	- 0.35	- 0.48	- 1.29
A Δ_{trait}	2.19	2.34	2.23	2.26	2.25	2.26	2.28	2.24	2.23	2.27	2.15
C Δ_{env}	1.87	10.61	5.02	0.98	4.00	- 0.02	0.36	0.28	- 0.57	- 1.01	- 0.07
C Δ_{trait}	- 2.08	- 2.27	- 2.17	- 2.16	- 2.24	- 2.21	- 2.23	- 2.17	- 2.13	- 2.18	- 2.16
RA $\Delta_{env\Delta trait}$	2.34	1.48	0.07	- 1.56	- 0.50	- 0.39	- 0.07	0.20	- 0.43	0.40	- 0.98
RC $\Delta_{env\Delta trait}$	0.05	- 2.78	- 0.91	- 0.98	- 2.02	0.49	- 0.10	0.94	1.14	2.36	0.02
Terrestrial species											
A Δ_{env}	1.08	- 2.27	- 3.04	- 0.87	- 2.18	- 1.13	- 1.20	- 0.54	- 1.4	0.05	- 2.42
A Δ_{trait}	0.02	0.04	- 0.02	- 0.01	0.03	0.01	- 0.04	0.07	0.02	0.05	- 0.01
C Δ_{env}	- 0.51	5.60	3.14	2.91	3.36	- 0.26	0.69	0.51	0.84	0.43	2.38
C Δ_{trait}	- 0.54	- 0.53	- 0.51	- 0.50	- 0.55	- 0.54	- 0.52	- 0.60	- 0.53	- 0.57	- 0.52
RA $\Delta_{env\Delta trait}$	0.56	- 0.51	0.29	- 0.39	- 0.92	1.37	1.08	0.43	- 0.14	- 0.04	- 0.63
RC $\Delta_{env\Delta trait}$	2.13	0.08	0.25	- 1.36	- 1.71	0.18	0.78	- 0.79	- 0.80	0.37	- 1.83

^aLocal-scale variables: Area=pond area; Hydro=hydroperiod; Veg_{in}=vegetation cover inside the pond; Veg_{ed}=vegetation cover along the pond's edge

^bLandscape-scale variables: DF = distance to the nearest forest fragment, CA_f = forest cover, CA_p = pasture cover, CA_w = water bodies cover, NP_f = number of forest patches, NP_p = number of pasture patches, NP_w = number of water bodies

Bold-face values indicate significant SES in relation to the confidence limits produced by a fixed-fixed null model distribution

a given size (significant positive **RC $\Delta_{env\Delta trait}$** score for area, Table 1).

The results of the RLQ analysis reinforced the trait-based analysis of co-occurrence and additionally revealed the direction and magnitude of environmental-filter effects on species. The first axis of the RLQ analysis explained 87.6% and 59.1% of the relationship between environmental variables (local and landscape), functional traits, and species co-occurrence for arboreal species and terrestrial species, respectively. The first RLQ axis summarized a gradient of local and landscape degradation (Figs. 3 and 4). For arboreal species, the first RLQ axis was positively correlated with distance to the nearest forest fragment ($r=0.82$, $p<0.01$) and pasture cover ($r=0.24$,

$p=0.03$), and negatively related to forest cover ($r=-0.23$, $p=0.04$), pond area ($r=-0.54$, $p<0.01$), hydroperiod ($r=-0.88$, $p<0.01$), and vegetation cover inside the pond ($r=-0.34$, $p<0.01$; Fig. 3). For terrestrial species, the first RLQ axis was positively correlated with the distance to the nearest forest fragment ($r=0.82$, $p<0.01$) and number of water bodies ($r=0.29$, $p<0.01$), and negatively correlated with pond area ($r=-0.48$, $p<0.01$), hydroperiod ($r=-0.87$, $p<0.01$) and vegetation cover along the pond's edge ($r=-0.54$, $p<0.01$; Fig. 4).

The relationship between environmental variables (both local and landscape) and functional traits was significant for both arboreal and terrestrial species (models 2 and 4: $p<0.01$). Several functional traits

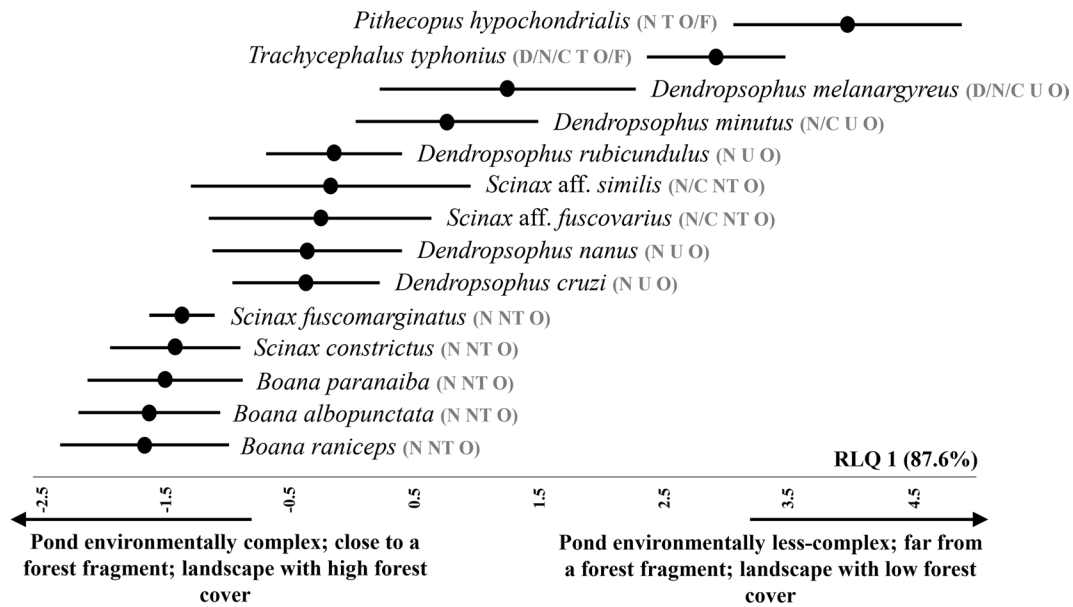


Fig. 3 Average position of arboreal species along the gradient of local environmental complexity and landscape structure (dark circles). The horizontal bars indicate the standard deviation of the mean position of each species. Pond environmental complexity is related to the variables of pond area, hydroperiod, and vegetation cover inside the pond (i.e., environmentally complex ponds are larger and have a longer hydroperiod,

which supports greater vegetation cover inside the pond, than less environmentally complex ponds). Grey letters refer to the functional traits that were significantly correlated ($P < 0.05$) with the first RQL axis (Habitat categories: F=Forest, O=Open; Toxicity: NT=Non-toxic, T=Toxic, U=Unpalatable or bad-tasting; Daily activity: C=Crepuscular, D=Diurnal, N=Nocturnal)

influenced the position of anurans along the habitat-degradation gradient, including their main habitat, toxicity, and diel period of activity, all of which were significantly correlated with the first RLQ axis ($p < 0.05$; Figs. 5 and 6). Non-toxic arboreal species that were active at night and inhabited open environments were associated with more environmentally complex ponds that were close to forest fragments and embedded within landscapes having high forest cover. Forest-dwelling arboreal species that were toxic and active for more than one diel period were associated with environmentally less-complex ponds that were far from a forest fragment and embedded in landscapes with less forest cover (Fig. 5). Forest-dwelling terrestrial species that were nocturnal and toxic were associated with more environmentally complex ponds that were close to forest fragments and embedded in landscapes with a smaller number of water bodies (Fig. 6). Diurnal terrestrial species that were non-toxic and inhabited open environments were associated with environmentally less-complex ponds that were far from a forest fragment and

embedded in landscapes having more water bodies (Fig. 6). Body size was also a significant trait for terrestrial species; larger species occurred in more environmentally complex ponds that were close to forest fragments and embedded in landscapes having fewer water bodies (Fig. 7). Body size was not a significant trait for arboreal species.

Discussion

Using complementary metrics of species co-occurrence structure (the clumping and C-score indices; Ulrich et al. 2012, 2017), we found that environmental filtering at both local and landscape scales was primarily responsible for community assembly in pond-breeding anurans of the Brazilian Cerrado. The relative effects of these local and landscape environmental filters, as well as their relationship with functional traits, varied between anuran groups depending on whether species were primarily arboreal or terrestrial. Species in both groups were distributed across

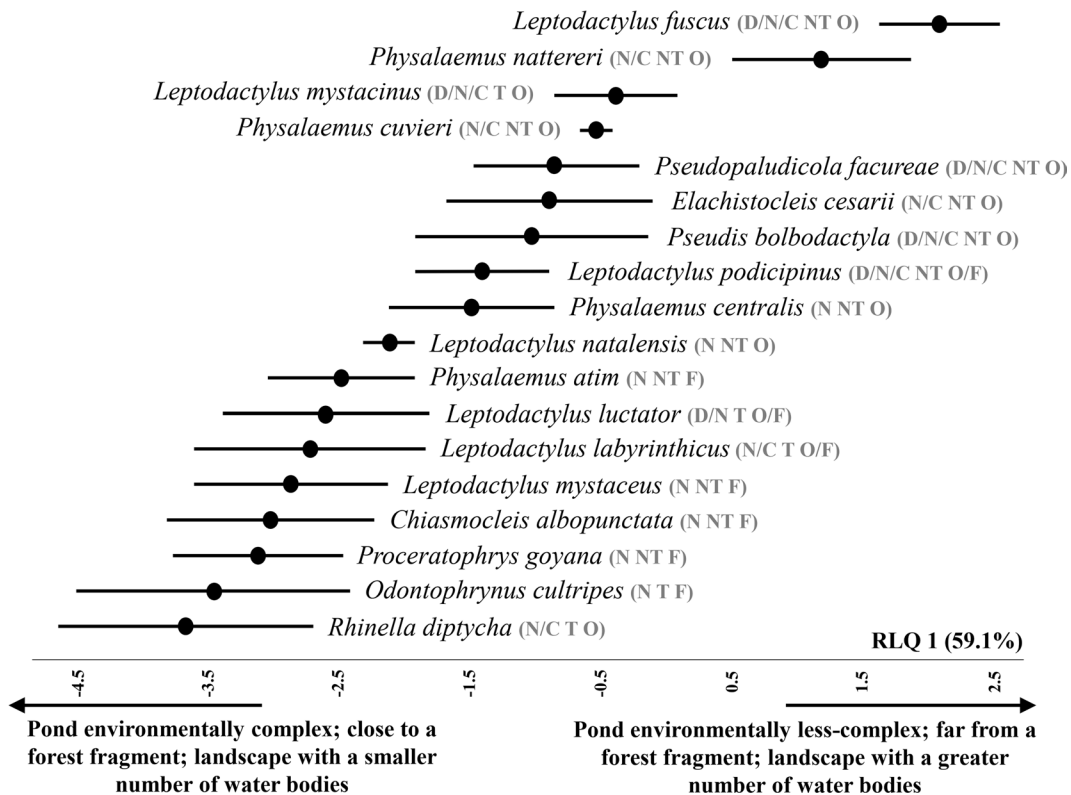


Fig. 4 Average position of terrestrial species along the gradient of local environmental complexity and landscape structure (dark circles). The horizontal bars indicate the standard deviation of the mean position of each species. Pond environmental complexity is related to the variables of pond area, hydroperiod, and vegetation cover along the pond's edge (i.e., environmentally complex ponds are larger and have a longer hydro-

period, which supports greater vegetation cover inside the pond, than less environmentally complex ponds). Grey letters refer to the functional traits that were significantly correlated ($P < 0.05$) with the first RQL axis (Habitat categories: F=Forest, O=Open; Toxicity: NT=Non-toxic, T=Toxic; Daily activity: C=Crepuscular, D=Diurnal, N=Nocturnal)

a gradient of habitat degradation, with environmental factors related to the complexity of the pond environment (pond area, hydroperiod, vegetation cover inside or along the pond's margin), amount of forest cover, and degree of habitat split (proximity of ponds to forest) filtering species along this gradient.

Although environmental filters at local and landscape scales were both important, the influence of local-scale filters was larger than landscape-scale filters on species co-occurrence patterns (as reflected by the higher standardized effect sizes for local-scale factors). At the local scale, species were filtered by pond hydroperiod and interior vegetation cover, irrespective of species' functional traits; vegetation along the pond's edge was an additional filter for terrestrial species. These three local-scale filters have been previously identified as important determinants

of species occurrence within pond-breeding anuran communities (Moreira and Maltchik 2012; Prado and Rossa-Feres 2014a, b; Signorelli et al. 2016; Marques and Nomura 2018). Hydroperiod in particular is important (as denoted by its high effect size) and is associated with other environmental factors, such as habitat complexity (e.g., a longer hydroperiod supports greater habitat complexity, such as greater vegetation cover and diversity of vegetation types including shrubs and trees) and predation risk, given that permanent ponds are more likely to have fish (Wellborn et al. 1996). For example, aggregated (clumped) patterns of species co-occurrence amongst tadpoles have been found in permanent ponds, which was attributed to the accumulation of species with certain functional traits (e.g., species are toxic/unpalatable or their tadpoles have effective antipredator

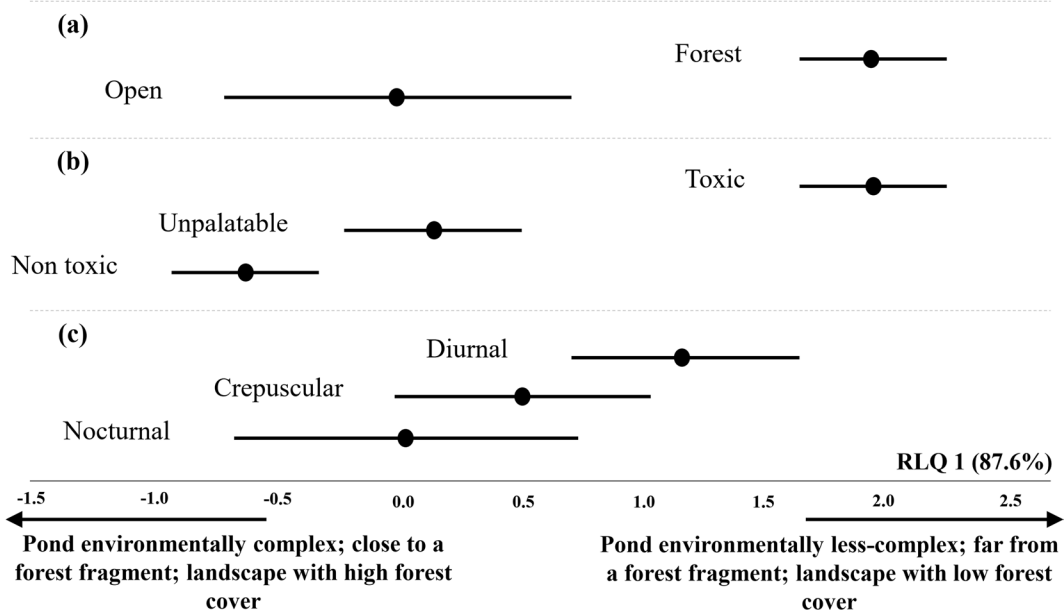


Fig. 5 Comparison of how functional traits that were significantly ($P < 0.05$) associated with the first RLQ axis varied along the environmental gradient for arboreal species. Mean values and standard deviations are given for habitat categories (a), toxicity (b), and daily activity (c) of species in relation to scores on the first RLQ axis. Pond environmental complex-

ity is related to pond area, hydroperiod, and vegetation cover inside the pond (i.e., environmentally complex ponds are larger and have a longer hydroperiod, which supports greater vegetation cover inside the pond, than less environmentally complex ponds)

behaviors) that reduce their predation risk (Moreira and Maltchik 2012). Hydroperiod is extremely variable among ponds within the Cerrado (Giaretta et al. 2008; Valdujo et al. 2013), and is thus an effective environmental filter of pond-breeding anurans, which end up being clustered within ponds of similar hydroperiod owing to their specific habitat requirements.

In addition to local-scale factors, landscape filters also played a role in structuring patterns of co-occurrence in these pond-breeding anurans. Habitat split—measured as the distance from ponds to the nearest forest fragment—was an important landscape filter for both arboreal and terrestrial species. Many of these pond-breeding anurans are associated with forests and other upland habitats for the majority of their life cycle (Lourenço-de-Moraes et al. 2020). Forest-dwelling amphibians with aquatic life stages are expected to be particularly sensitive to landscape modifications, such as forest clearing for agriculture, which increases the “split” between their terrestrial and aquatic habitats (Becker et al. 2007, 2010). Breeding dispersal between terrestrial and aquatic habitats becomes riskier as habitat split increases,

especially for amphibians that are highly susceptible to desiccation (Watling and Braga 2015). Our results agree with recent studies that found a complex relationship between pond-breeding anurans and habitat split (Lion et al. 2014; Prado and Rossa-Feres 2014b; Signorelli et al. 2016), with some species (e.g., *Boana raniceps*, *B. albopunctata*, *B. paranaiba*, *Odontophrynus cultripes*, *Proceratophrys goyana*, and *Chiasmocleis albopunctata*) negatively influenced by increasing habitat split, but others (e.g., *Pithecopus hypochondrialis*, *Trachycephalus typhonius*, *Dendropsophus melanargyreus*, *Leptodactylus fuscus*, and *Physalaemus nattereri*) seemingly benefitting from increased isolation between forests and breeding ponds. In fact, terrestrial species negatively affected by habitat split are, in general, more associated with forested environments in the Cerrado (Ramalho et al. 2018). However, we found that even two forest-dwelling arboreal species (*P. hypochondrialis* and *T. typhonius*) exhibited a positive relationship with increasing habitat split. The occurrence of some species may be greater in isolated ponds because isolation prevents the establishment of predators like fish (Scheffer et al.

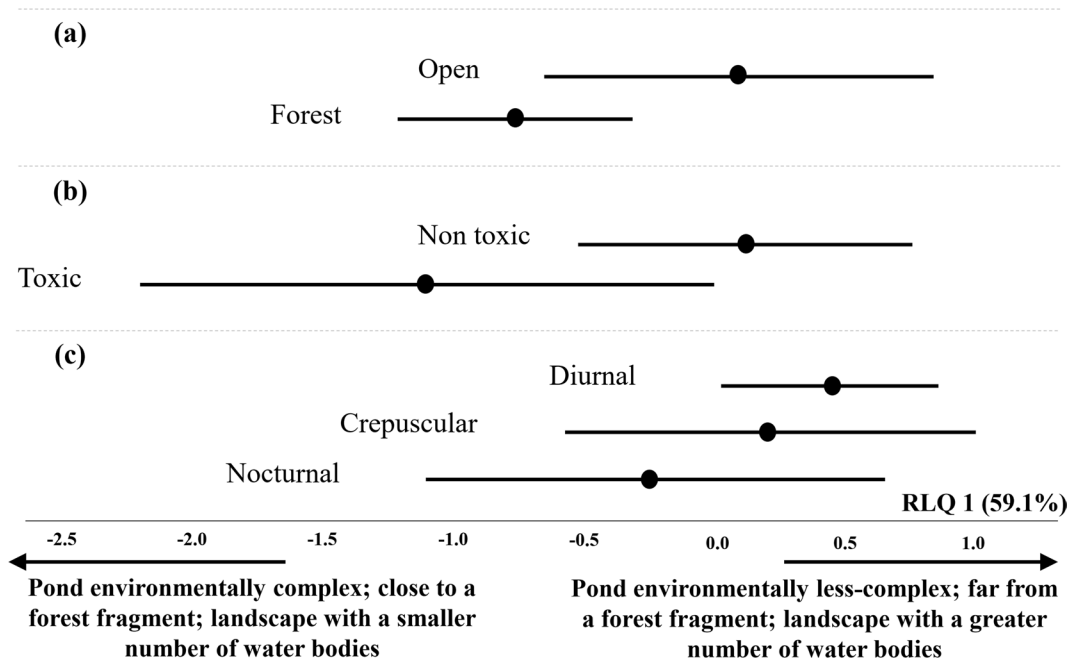


Fig. 6 Comparison of how functional traits that were significantly ($P < 0.05$) associated with the first RLQ axis varied along the environmental gradient for terrestrial species. Mean values and standard deviations are given for habitat categories (a), toxicity (b) and daily activity (c) in relation to scores on the first RLQ axis. Pond environmental complexity is related

to variables of pond area, hydroperiod and, vegetation cover along the pond's edge (i.e., environmentally complex ponds are larger and have a longer hydroperiod, which supports greater vegetation cover inside the pond, than less environmentally complex ponds)

2006), or highly mobile species may simply be better at colonizing isolated ponds (explained more fully below). In the case of the arboreal *P. hypochondrialis* and *T. typhonius*, their positive relationship with increasing habitat split, as well as their association with less-complex pond environments, reflects their generalist breeding-habitat requirements and greater tolerance for landscape disturbance. It thus appears that habitat split filters most of these pond-breeding anurans independently of their functional traits or primary habitat use (i.e., whether they were arboreal or terrestrial).

The co-occurrence of arboreal anurans was also influenced by another landscape-scale filter, the amount of forest relative to pasture cover. Arboreal species were distributed across a gradient of landscapes varying from high forest/low pasture to high pasture/low forest cover. Forest cover has been previously identified as an important environmental filter for both arboreal and terrestrial anurans, selecting for species that can occur at either extreme of habitat loss

(Almeida-Gomes and Rocha 2014; Signorelli et al. 2016). Because the benefits of vegetation cover differ among species (Signorelli et al. 2016; Cayuela et al. 2020), however, the response of anurans to habitat loss will also be species-specific, reflecting their reproductive potential, dispersal ability, home-range size, habitat specificity, and other characteristics (Fahrig 2001; Cushman 2006). Thus, the connectivity of forest habitat (as assayed by forest cover and the number of forest patches) may still represent an important environmental filter in landscapes fragmented by agricultural land uses (e.g., pastures; Adams et al. 2017), considering that the negative effects of habitat fragmentation for anurans may be greatest within landscapes with low or intermediate amounts of habitat (Püttker et al. 2020). Despite the importance of forest cover for biodiversity within the Cerrado, the agricultural conversion of this tropical savanna, especially for soy production (Rausch et al. 2019), has increased over the past two decades (Strassburg et al. 2017), resulting in habitat losses of

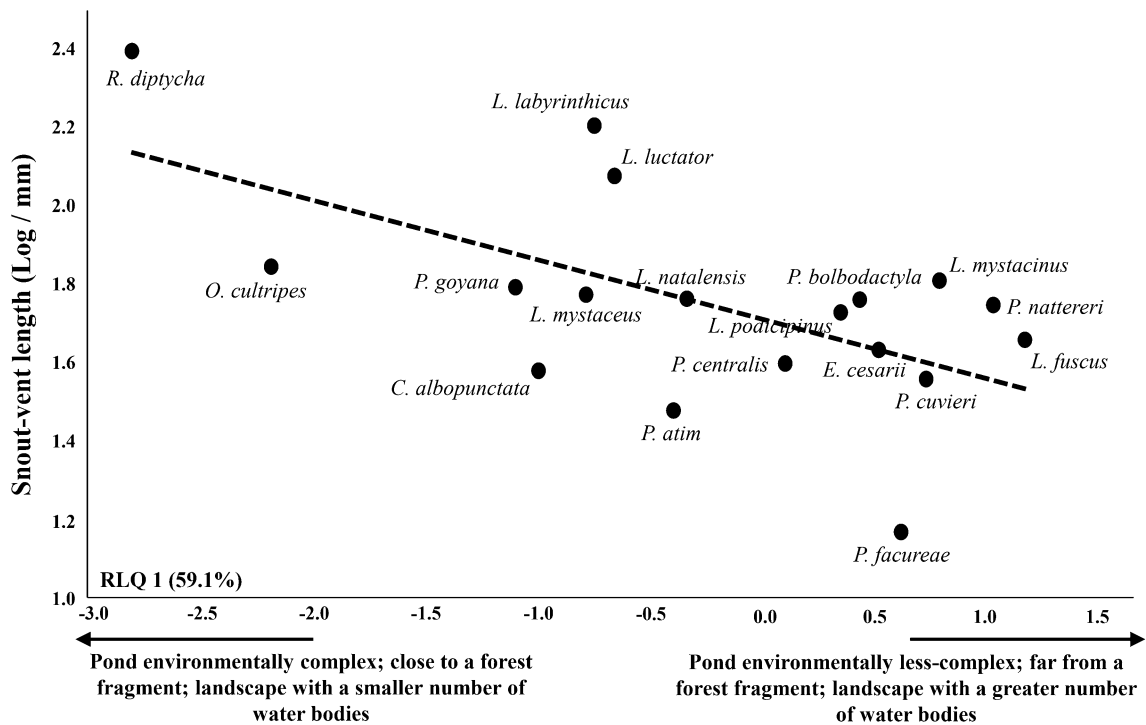


Fig. 7 Relationship between snout-vent length of terrestrial anuran species and their position along the first RLQ axis representing a gradient in pond environmental complexity and landscape structure (Pearson correlation; $r = -0.65$, $P < 0.01$). Pond environmental complexity is related to pond area, hydro-

period, and vegetation cover along the pond's edge (i.e., environmentally complex ponds are larger and have a longer hydroperiod, which supports greater vegetation cover inside the pond, than less environmentally complex ponds)

about 25% along with a significant decrease in connectivity across the biome (Grande et al. 2020). This trend is likely to continue for the foreseeable future, given that the Cerrado receives little legal protection compared to other biomes in Brazil (e.g., 8% vs. 46% in the Brazilian Amazon; Rausch et al. 2019).

Habitat filtering also appears to be trait-mediated in arboreal species (a significant correlation between environmental conditions and functional traits), as species with similar traits co-occurred in ponds of similar areas, hydroperiod, and degree of habitat split. In particular, trait-based habitat filtering appears more prevalent within environmentally complex ponds with a low to moderate degree of habitat split. Ponds with large areas tend to have long hydroperiods, with more vegetation inside and along the edge, which consequently leads to a higher richness of anurans (Gonçalves et al. 2015; Figueiredo et al. 2019). This increase in vegetation and availability of microhabitats, along with a low degree of habitat split,

favors the colonization and vertical segregation of arboreal species, which reduces competitive interactions among ecologically similar species (Gonçalves et al. 2015; Fonseca-Pérez et al. 2017; Basham et al. 2019; López-Rojas 2019).

At the landscape scale, arboreal species-pairs that are already spatially segregated (i.e., a checkerboard pattern of co-occurrence) exhibited significant trait-based segregation in landscapes with a certain degree of pasture fragmentation. In other words, arboreal species that are too similar in functional traits are unlikely to be found together in landscapes that are fragmented by many small pastures. Small pastures tend to be dotted with trees or contain small stands of trees that could act as refugia for arboreal species and may facilitate dispersal and colonization of nearby ponds. If arboreal species are necessarily concentrated within a limited number of trees, this could result in greater competition and lead to trait-based segregation (limiting similarity) among species

in fragmented landscapes. However, the absence of a correlation between the number of pastures patches and the first axis of the RLQ suggests either that (1) limiting similarity acts only at intermediate levels, rather than at the extremes, of the landscape-fragmentation gradient, or (2) the influence of fragmentation is sufficiently low as not to be reflected in the axis gradient. Regardless, competition appears to lead to a checkerboard distribution in the co-occurrence of arboreal species irrespective of environmental or landscape conditions.

In contrast to arboreal species, habitat filtering in terrestrial species was influenced by the number of water bodies at the landscape scale. For anuran species that move over land, even small or seemingly isolated water bodies may offer temporary refuge or function as stepping-stones during dispersal (Semlitsch and Bodie 1998). Reducing the number or density of water bodies in the landscape could thus decrease the likelihood of direct or indirect dispersal between ponds and lower the probability of colonization, thereby reducing site occupancy and potentially enhancing species extinction risk (Cosentino and Schooley 2018). Also, the connectivity between upland habitats and water bodies is important for the migratory movements of semiaquatic species (Semlitsch and Bodie 1998) such as anurans (Becker et al. 2007), and also serves to promote energy and nutrient transfers between terrestrial and aquatic systems (Regester et al. 2008). Not surprisingly, then, we found that habitat split (the distance between the pond to the nearest forest fragment) was an important habitat filter for terrestrial pond-breeding anurans in the Cerrado, which reinforces the importance of maintaining water surfaces-upland linkages for these types of species (Cosentino and Schooley 2018). Even species that were found to co-occur in landscapes with few ponds or other aquatic environments (e.g., *Rhinella diptycha*, *Odontophrynus cultripes*, *Proceratophrys goyana*, and *Chiasmocleis albopunctata*) tended to favor ponds that were environmentally complex (e.g., permanent ponds) and located close to forest fragments. Thus, connectivity between aquatic habitats and upland habitats may facilitate dispersal and survival even for these species, especially if survival during the dry season is greater within more-complex or more-permanent pond environments or for species such as *R. diptycha* that have the potential to disperse over long distances during extended

dry periods (Cayuela et al. 2020). In contrast, some species (e.g., *Physalaemus nattereri* and *Leptodactylus fuscus*) tend to co-occur within landscapes with numerous water bodies but in less-complex pond environments (ephemeral or temporary ponds) that may be located far from a forest fragment. Such species tend to have morphological or physiological traits that enhance their potential for dispersal across dry or open environments (Cayuela et al. 2020), as well as reproductive traits (e.g. explosive breeding) adapted to less-complex pond environments that may only be available seasonally (i.e., ephemeral or temporary ponds). However, we found that the spatial co-occurrence of these species was largely independent of their functional traits.

The distribution of terrestrial anurans also reflects the role of limiting similarity, given that species with similar functional traits were segregated among ponds of similar areas. This segregation occurred among crepuscular/nocturnal, non-toxic, and smaller-bodied species associated with open habitats (e.g., *Leptodactylus fuscus*, *L. mystacinus*, *Physalaemus cuvieri*, *P. nattereri*) along that first environmental gradient of the RLQ analysis, which summarizes environmentally less-complex ponds. If pond area is limited, the lack of vegetation structure could increase competitive interactions among ecologically similar species, especially for species of similar reproductive characteristics (e.g., explosive breeding; although reproductive mode was not important in explaining the RLQ variation). Species of similar reproductive strategy (foam nests and accelerated rates of development; Crump 2015) that reproduce in smaller and less-complex ponds tend not to co-occur due to competition (Dayton and Fitzgerald 2001; Buxton and Sperry 2017), although such patterns may be due to stochastic processes, such as priority effects (Leibold et al. 2004). While habitat filtering appears to occur at low-to-moderate levels of habitat degradation, limiting similarity appears to be more important at extreme levels of degradation. Therefore, habitat simplification in smaller, less environmentally complex ponds should filter species adapted to temporary or ephemeral conditions, but species coexistence may nevertheless be limited by competition for resources.

Competition may also play a role in structuring the co-occurrence patterns of arboreal species. Recall that at the local site scale, habitat filtering was evidenced by the fact that species with similar traits tended to

co-occur within ponds having similar environmental conditions (in terms of pond area, hydroperiod, and distance to the nearest forested fragment). However, we also found that arboreal species exhibited significant overdispersion in their functional traits irrespective of environmental conditions, and we found significant trait-based segregation of species at the landscape scale, especially in landscapes having a similar degree of pasture fragmentation. We therefore posit that both mechanisms could be acting simultaneously in arboreal species, just at different scales and perhaps along different dimensions (i.e., horizontally vs. vertically). All these arboreal species, except *P. hypochondrialis* (Phyllomedusiae), are in the Hylidae (treefrog) family, which are known to exhibit vertical stratification (Fonseca-Pérez et al. 2017; Basham et al. 2019). Reproduction in these species is often continuous or protracted throughout the season, and many species exhibit territorial behavior (Prado et al. 2005; Kopp et al. 2010; de Sá et al. 2014), which suggests that these species are likely competitors in both space and time (Donnelly and Guyer 1994; Borzée et al. 2016; Garey et al. 2018).

In conclusion, the co-occurrence patterns of pond-breeding anurans at a local and landscape scale may or may not be trait-mediated and the specific mechanisms involved—whether habitat filtering, competition, or some combination of the two—depend on whether the species are primarily arboreal or terrestrial. The new insights provided by this study suggest that anuran communities are formed by diverse assembly rules, in which habitat degradation due to agricultural intensification produces environmental filters at both local and landscape scales, while competition appears to be a secondary process or manifests only at extreme levels of degradation. These processes that shape patterns of species-co-occurrence are dependent on spatial scale, the degree of habitat degradation, and the primary habitat use of each species (whether terrestrial or arboreal), such that environmental changes resulting from land-use intensification will necessarily alter the structure and dynamics of pond-breeding anuran communities in the Cerrado. Based on these results, we can expect arboreal species and more specialized terrestrial species to be the most affected if deforestation and land-use change in the

Cerrado continues at fast pace. Given that environmental filtering was found to be such an important mechanism of community assembly in these anurans, management and conservation strategies should prioritize the protection or restoration of large and environmentally complex ponds located close to forests, which ideally would be situated within landscapes having large amounts of forest cover remaining and that maintain water surfaces-upland linkages, so as to support the greatest diversity of species.

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Author contributions All authors contributed to the conceptualization and design of the project. WPR collected the data, performed the data analysis, and led the writing of the text. LS provided additional expertise on anurans and data interpretation. KAW assisted with data interpretation and writing. VHMP and KAW supervised this research. All authors critiqued the manuscript and gave final approval for submission.

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Data Availability Will be available after the early review process.

Code availability Will be available after the early review process.

Compliance with ethical standards

Conflicts of interest The authors declare that they have no conflict of interest.

Research involving human and/or animal rights Permission to handle and collect animals was given by the Ministério do Meio Ambiente/Instituto Chico Mendes de Conservação da Biodiversidade (#55420-1) and Conselho Estadual do Meio Ambiente/Secretaria de Estado de Meio Ambiente e Desenvolvimento Sustentável (#015/2016).

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