CrossMark

RESEARCH ARTICLE

Landscape context affects site occupancy of pond-breeding anurans across a disturbance gradient in the Brazilian Cerrado

Luciana Signorelli · Rogério P. Bastos ·
Paulo De Marco Jr · Kimberly A. With

Abstract

Context   The Brazilian Cerrado, a global biodiversity hotspot, is being converted to agricultural production. Amphibians in particular are susceptible to agricultural practices that threaten both their wetland and upland habitats. Although local site variables are important for determining species occurrence, site occupancy is also mediated by the broader landscape and management context in which the site occurs.

Objectives   Investigate the relative effects of broad-, intermediate-, and local-scale factors on species occurrence for pond-breeding anurans within different landscapes across an agricultural-disturbance gradient in the Cerrado.

Methods   Ponds were surveyed for adult anurans over 3 years within 18 landscapes (each 625 km^2) that varied in their degree of agricultural land use (landscape context). We analyzed species distribution models for eight pond-breeding anurans, using hierarchical binomial generalized linear models.

Results   The broader landscape context had a significant effect on the incidence of pond-breeding anurans, even after accounting for variation in other environmental factors at more local (pond) or intermediate (1-km^2) scales. The top-ranked models for most species included some combination of broad-, intermediate- and local-scale factors, however. These covariates influenced species occurrence in different ways, with the response to agricultural disturbance varying among species. Although some species were negatively affected, others appeared to benefit from agricultural activities that increased breeding habitat (e.g., impoundments to provide water for cattle).

Conclusions   Landscape context, the degree to which landscapes have been transformed by agricultural land use, has a major influence on the distribution of pond-breeding anurans in the Brazilian Cerrado.

L. Signorelli (✉) · K. A. With
Laboratory for Landscape and Conservation Ecology,
Division of Biology, Kansas State University, Manhattan,
KS 66506, USA
e-mail: lfl.signorelli@gmail.com

L. Signorelli · R. P. Bastos · P. De Marco Jr
Ecology Department, Biological Sciences Institute,
Federal University of Goiás, Campus II, Goiânia,
GO 74001-970, Brazil

Introduction

The probability that a species is present at a given site (site occupancy or species occurrence) is dependent on various landscape and environmental factors that

operate across a range of scales. Although local site variables are expected to be important determinants of site occupancy, species occurrence may still be mediated by the broader landscape context in which the site occurs (Blevins and With 2011). For example, agricultural and range-management practices are typically implemented at broad landscape or regional scales, and can thus alter the suitability of whatever native habitat remains within that landscape or region (Carvalho et al. 2009). This may be caused by a reduction in available habitat, owing to a decrease in the amount and/or increasing isolation of habitat remnants, and through more subtle changes that alter ecological flows or functional linkages among habitat remnants (Cushman 2006; Becker et al. 2007). Land-use changes may alter the permeability or resistance of the matrix to movement, thereby exacerbating isolation-by-distance effects on dispersal, colonization success, and gene flow among habitat remnants (Chetkiewicz et al. 2006; Gilbert-Norton et al. 2010). Land-use change may also introduce new or different stressors that decrease habitat suitability (e.g., increased competition or predation, decreased food availability), which can then lead to lower abundance, higher mortality rates, and lower reproductive success within habitat remnants (Becker et al. 2010; Baudron and Giller 2014). Subsequently, site avoidance and local extinctions may reduce the occurrence of the species across the landscape (Nilsson et al. 2008; Becker et al. 2010). Thus, simply mapping the availability of suitable habitat is unlikely to be sufficient for evaluating a species' probable occurrence or distribution across the landscape, unless due consideration is given to the broader landscape context in which that habitat occurs (Blevins and With 2011; Scherer et al. 2012).

Landscape context is well known to influence aquatic habitats (Naiman et al. 1993). Agricultural land use may alter allochthonous inputs and nutrient loads into these systems: some nutrient inputs may be increased as a consequence of run-off (e.g., nitrogen and phosphorus from fertilizers), others may be substantially reduced (e.g., dead organic matter from leaf litter or terrestrial insects that subsidize aquatic food webs), and new threats (e.g., chemical pollutants from herbicides and pesticides or the introduction of predatory species, such as fish) may render entire systems uninhabitable for a given species (Foley et al. 2005; Baudron and Giller 2014). Even if the apparent availability of habitat is unaltered by land use (the wetlands are still present), the suitability of these habitats may have been compromised. Furthermore, some wetland species, such as amphibians, have different habitat requirements during different stages of their life cycle (tadpoles vs. adults) or at different times of the year (breeding vs. non-breeding season), and thus wetlands must also be functionally connected to other upland habitats (Pope et al. 2000). Agricultural land use thus poses a double jeopardy for amphibians, by impacting the suitability of both their wetland and terrestrial habitats, as well as the possibility that the altered land-use matrix may disrupt the functional connectivity (dispersal and gene flow) among these habitats (Becker et al. 2007, 2010).

The relationship between local- and landscape-scale effects on site occupancy has previously been explored for amphibians in temperate regions (e.g., Mazerolle and Desrochers 2005; Zanini et al. 2008; Scherer et al. 2012; Cayuela et al. 2015), but not in tropical regions. As the results among studies are quite varied, few generalizations have yet emerged as to which factors—and at what scales—influence site occupancy in amphibians (Zanini et al. 2008). Some studies have demonstrated the importance of landscape-scale factors (at both intermediate and broad scales) on species occurrence (Mazerolle and Desrochers 2005; Birx-Raybuck et al. 2010; Collier et al. 2012; Scherer et al. 2012; Cayuela et al. 2015). Specifically, many of these studies reinforce the positive effects of wetland habitat amount and connectivity (Scherer et al. 2012; Cayuela et al. 2015), as well as the negative effect of isolation between ponds or riparian zones (Birx-Raybuck et al. 2010), on the occurrence of some amphibian species. These findings do not mean that local variables are unimportant to the occurrence and persistence of amphibians, however, especially for species with indirect development (i.e., possessing an aquatic larval stage) in which the characteristics of the water body are vital to their successful development and survival (Scherer et al. 2012). Clearly, patterns of species occurrence can be related to factors at local (pond), intermediate (pond context) and broad (landscape context) scales, but the intensity and the direction of this relationship will vary depending on the species (Cunningham et al. 2007).

In this study, we considered the relationship between landscape context and site occupancy for

pond-breeding frogs in the Brazilian Cerrado. The Cerrado is a vast tropical savanna that covers about a quarter of the land area in Brazil (~ 2 m km^2), making it the country's second largest ecoregion after the Amazon rainforest (Ratter et al. 1997). The Cerrado is characterized by a variety of vegetation types, ranging from open grasslands to dense woodlands (Oliveira and Marquis 2002). Among the major habitat types within the Cerrado are *campo limpo* ("clean field"), *campo sujo* ("dirty field"), *campo cerrado* ("closed field"), *cerrado* sensu stricto (woody savanna), and *cerradão* (forest-like savanna). Gallery forests line the streams and rivers, and a variety of wetland habitats (temporary and permanent ponds, puddles, and swampy areas) occur throughout the Cerrado (Felfili 1995). As a consequence of this habitat diversity, the Cerrado supports a high level of biological diversity, including 209 amphibian species (Valdujo et al. 2012). Like many grasslands and savannas around the world, the Cerrado is being used for agricultural production, including cattle grazing, which has intensified in recent decades owing to government incentives (Ratter et al. 1997; Carvalho et al. 2009; Sano et al. 2010). Nearly 50 % of the Cerrado region has been converted to agricultural land use (MMA-IBAMA 2011), and only about 8 % of it is protected (MMA 2015).

To investigate the effects of landscape disturbance on the occurrence of pond-breeding frogs in the Brazilian Cerrado, we developed and analyzed species distribution models, using binomial generalized linear models, to evaluate various landscape and environmental factors on site occupancy for eight species. Our model analysis was designed to assess the relative effects of broad-, intermediate-, and local-scale factors on species occurrence in ponds within different landscapes across an agricultural-disturbance gradient in the Cerrado. We considered several hypotheses in constructing our candidate set of models. At broad and intermediate scales, a species' probability of occurrence was expected to increase with the total amount of native habitat in that landscape. Because of the inverse relationship between the amount of native habitat and agricultural land use, this hypothesis enables us to assess landscape effects on species occurrence across a disturbance gradient. Habitat amount is not the only factor that might affect species occurrence, however. Habitat-isolation effects are also important, especially since many amphibians are critically dependent on terrestrial habitats in close proximity to their aquatic breeding sites (Becker et al. 2007). Amphibians may spend a majority of their adult lives in upland habitats or utilize these during dispersal (Cushman 2006). Increased isolation of both native habitat remnants and water bodies is therefore expected to disrupt habitat connectivity and negatively influence site occupancy in pond-breeding anurans. Finally, we consider the role that local environmental factors play on the occurrence of anurans within their breeding habitat (Werner et al. 2007). Local characteristics of the breeding habitat (pond size and the relative amount of emergent vegetation within or along the edge of ponds) can play a significant role in determining species occurrence, especially given the physiological, ecological and behavioral constraints that restrict dispersal ability in this group (Mazerolle and Desrochers 2005; Titon et al. 2010).

Methods

Study area

Because of the vast extent of the Cerrado biome (~ 2 million km^2), we restricted our surveys to 18 landscapes (25×25 km $= 625$ km^2), located in the heart of the Cerrado region. Based on a systematic grid-survey and landscape analysis of the region, we selected landscapes that collectively represented a gradient in landscape disturbance (Supplemental Materials, Methods; Fig. S1). We used aerial photographs and field reconnaissance to identify ponds to survey in each landscape. We selected ponds non-randomly to ensure that a mix of sites were surveyed within either a predominantly agricultural or native-habitat context. In total, we surveyed 62 ponds within a native-habitat context and 65 within an agricultural context, although the broader landscape context (degree of agricultural disturbance) ultimately constrained how many of each kind we could survey within a given landscape (range 1–6 ponds/context/landscape). To ensure independence among sites, we selected ponds that were at least 1 km apart, as this distance exceeds the maximum annual dispersal for most anuran species (Smith and Green 2005). Thus, we ultimately surveyed four to nine ponds in each landscape, for a total of 127 ponds across all 18 landscapes (Fig. 1). The number of ponds surveyed in

each landscape varied as a result of constraints on site access and availability.

Anuran survey methods

Pond surveys were conducted during the rainy season (October–March) between 2010 and 2013. Up to four trained observers conducted anuran surveys in a given year, with one observer (L. Signorelli) participating in surveys all 3 years. Each observer was responsible for surveying all ponds in a given landscape. To assess the presence of individual species, observers spent 1 h at each pond between the hours of 1900 and 2400. Adult frogs were surveyed via a combination of acoustic and visual means (Rödel and Ernst 2004), by walking

slowly around the pond and systematically searching or listening for calling males (Heyer et al. 1994).

Target species

Of the 57 pond-breeding species we identified over the course of the study, our analysis here is centered on eight species that had an apparent occupancy of 20–85 % of ponds: *Dendropsophus cruzi*, *D. nanus* (dwarf tree frog), *D. rubicundulus* (Lagoa Santa tree frog), *Hypsiboas albopunctatus* (white-spotted tree frog), *Phyllomedusa azurea* (southern orange-legged leaf frog), *Scinax fuscomarginatus* (brown-bordered snouted tree frog), *Elachistocleis cesarii*, and *Leptodactylus fuscus* (whistling frog; Table S1). All eight of

Fig. 1 Landscapes (*n* = 18) surveyed throughout the state of Goiás in central Brazil. The locations of ponds surveyed for anurans (*n* = 127) are also indicated within the individual landscapes. The distribution of native Cerrado habitat is highlighted in *gray*
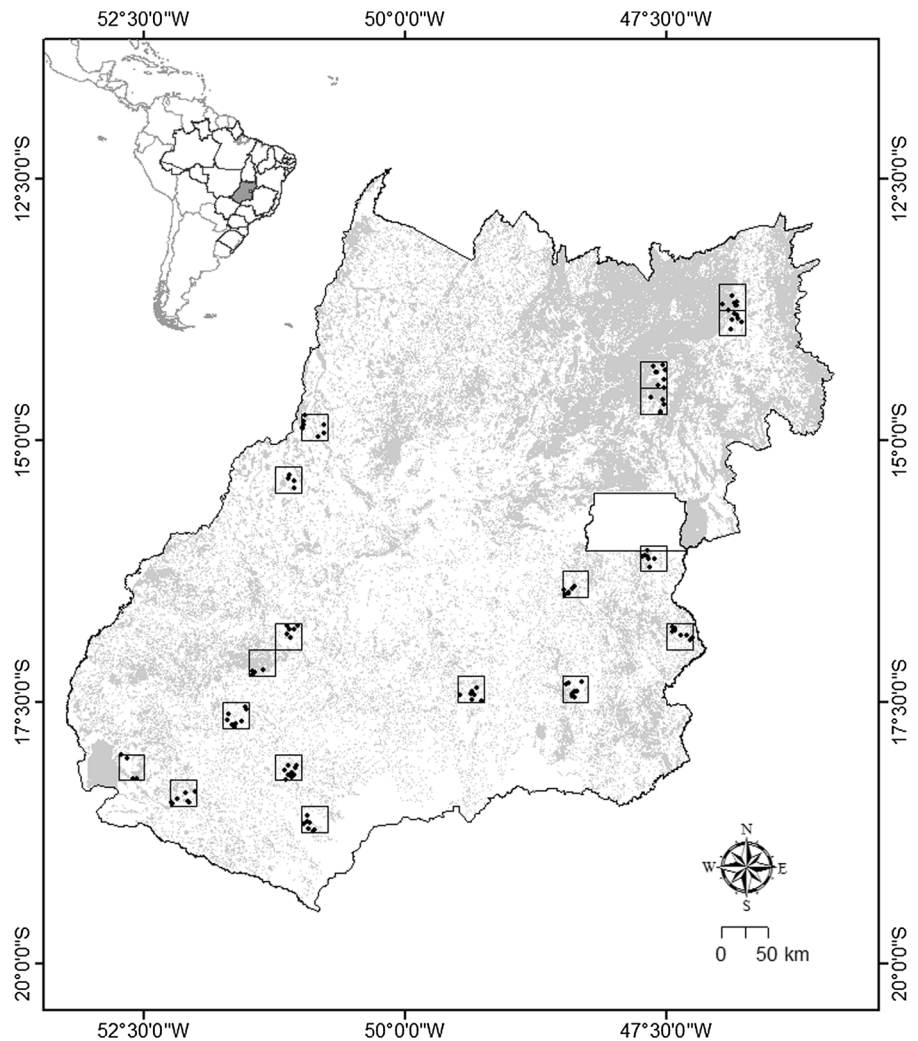
these species depend on water to reproduce and are considered to be open-habitat species. Three of these species (*D. cruzi*, *D. rubicundulus*, and *P. azurea*) are Cerrado endemics. We focused on species with at least 20 % apparent occupancy so as to minimize potential biases in the estimation of species occurrence (Kendall and White 2009).

Species distribution modeling and model selection

To model the influence of various covariates on species distributions (probability of occurrence), we adopted a hierarchical approach in which we first developed and assessed a series of candidate models at each of three scales (local, intermediate, or broad scale) using binomial generalized linear models (GLM). At the local scale, we included environmental variables that may be directly influencing the occurrence of species within ponds. Previous research indicated that vegetation in and around ponds was an important correlate of anuran species diversity within these Cerrado wetlands, more so than either pond area or depth, probably because vegetation provides breeding habitat and shelter (Becker et al. 2007; Vasconcelos et al. 2009). We therefore focused on the vegetation attributes of ponds as a local-scale factor influencing site occupancy, which we characterized in terms of the proportion of vegetation cover on the water's surface (pond-interior vegetation) and the proportion of vegetation at the edge of the surveyed pond (i.e., within 2 m of the water line; pond-edge vegetation). Although our survey methods are generally considered sufficient for detecting pond-breeding anurans (Pellet and Schmidt 2005), we also included two covariates known to influence detection of these species: air temperature (recorded at the end of each pond survey; temperature) and the amount of rainfall (recorded on the day of the survey; rain) in our candidate model set, in an effort to account for factors that might influence the apparent site occupancy of a given species.

We defined intermediate-scale covariates in relation to the expected dispersal range of anurans. Although we lack dispersal data for our target species, we assumed a dispersal range of 1 km, consistent with the reported dispersal range for most anurans (e.g., Houlahan et al. 2006; Gagné and Fahrig 2007). We thus calculated the amount of native Cerrado habitat within a buffer of 1 km around the centroid of each

pond (cover-1) using Fragstats 4.2 (McGarigal et al. 2012; Table S2). In addition, we calculated the straight-line distance to the nearest pond (nearest pond distance; Table S2) and assessed whether ponds were obviously connected to other wetlands (pond isolation) through a careful analysis of satellite imagery (Google Earth™). Ponds connected by wetlands, creeks, streams or other water sources were considered to be "connected," whereas ponds surrounded by agricultural land use or native habitats (e.g., Cerrado sensu stricto, *Cerradão*, and other dry habitat types) were considered to be "isolated." The latter ponds were either created to provide water for livestock, or were ephemeral pools that formed only during the wet season.

At the broadest scale (25×25 km^2), we calculated the proportion of native Cerrado habitat (cover-25) and the mean straight-line nearest-neighbor distance between native-habitat remnants (landscape configuration; config-25) from a 2011 Landsat ETM + satellite image using Fragstats 4.2 (McGarigal et al. 2012; Table S2). Because agriculture is the primary driver of land-use change in this region (i.e., cattle grazing, soybean, and sugar-cane production), we find that the proportion of native habitat decreases, and the mean nearest-neighbor distance between native-habitat remnants increases, with increasing agricultural land use. These covariates (cover-25 and config-25) thus correlate with the degree of landscape disturbance, and provide the broader landscape context for assessing species occurrence.

Prior to analysis, we calculated Pearson correlation coefficients between all pairs of variables within each scale (local, intermediate, and broad scales) out of concern for possible collinearities. Only the cover and configuration of native habitat at the broadest scale (cover-25 and config-25) exhibited a significant correlation ($r = -0.26$, $P < 0.003$). This result was expected, however, since habitat amount (cover) and configuration tend to be linked (i.e., landscapes with a large amount of habitat have larger patches that are closer together than landscapes with little habitat), and our study landscapes were specifically chosen to represent a gradient in landscape disturbance that was defined in terms of decreasing habitat cover and increasing mean nearest-neighbor distance (Fig. S1). Thus, we ended up using both variables because it was not clear a priori which measure—cover or configuration—might best explain how landscape disturbance

influenced species occurrence in these pond-breeding anurans.

The binomial GLM with a logit link function (Eq. 1; Kindt and Coe 2005) provides a flexible framework to describe how a dependent variable (presence or absence of a given species) can be explained by a range of explanatory variables (Calcagno and de Mazancourt 2010). The logit link is defined as:

$$logit(\mu) = \log\left(\frac{\mu}{1 - \mu}\right)$$
$$= b_0 + b_1 \times x_{i1} + b_2 \times x_{i2} + \cdots + b_n \times x_{in},$$
(1)

where μ is the probability of the site being occupied, $x_{i1}, x_{i2}, \ldots, x_{in}$ are the values for the n covariates of interest measured at the ith sampling unit, b_0 is the intercept term, and $b_1, b_2, \ldots, b_n$ are the regression coefficients that determine the effect of the respective covariates. Because response and predictor variables were standardized (i.e., converted to z-scores) prior to analysis, b_i is called the standardized partial regression coefficient or beta weight (Abdi 2004). Beta weights are comparable among covariates, and account for the relative contribution by each covariates to the model regression. Beta weights are ranked by each covariate's contribution to the model, and indicate how that covariate is expected to influence the dependent variable (e.g., whether they increase or decrease the probability of species occurrence). We therefore evaluated the beta weights from the global multi-scale model for each species to assess the relative importance of each covariate on species occurrence. We also analyzed the influence of covariates on species occurrence separately by scale. For each scale, we investigated the individual and additive effects of all covariates measured at that scale, which required a comparison of 16 candidate models at the local scale, eight at the intermediate scale, and four at the broadest scale.

Model selection was based on Akaike's Information Criterion (AIC), in which we identified the top-ranked models with ΔAIC < 2 at each scale (ΔAIC is the difference in AIC with respect to the AIC of the best candidate model). In addition, we calculated model probabilities or Akaike weights (w_i), which give the relative weight of evidence in support of each model, given the candidate set of models. In other words, it provides the probability that a specific model is the best for the observed data (Johnson and Omland 2004; Wagenmakers and Farrell 2004). The w_i is defined as:

$$w_i = \frac{\exp(-\frac{1}{2} \times \Delta_i AIC)}{\sum_{k=1}^{k} \exp(-\frac{1}{2} \times \Delta_k AIC)}$$
(2)

where $\sum w_i = 1$. Finally, to explore the combined effects of these scale-dependent covariates on the probability of species occurrence, we constructed a set of candidate models containing just the covariates from the top-ranked models at each scale (local, intermediate, and broad) from our previous analyses. We then used model-selection procedures to identify the best multi-scale model(s) of site occupancy for each of our eight target species. Models were constructed and explored using package glmulti (Calcagno and de Mazancourt 2010) and Biodiversi-tyR (Kindt 2015) in the R statistical computing environment.

Results

Based on the multi-scale analysis, which included just the covariates from the top-ranked models at each scale (ΔAIC = 0.0), we found that the top-ranked multi-scale models for most species included some combination of broad-, intermediate- and local-scale factors. The exception was *P. azurea*, whose occurrence was related to a single local-scale predictor (pond-interior vegetation; Table 1). The broad-scale covariates (cover-25 and/or config-25) explained the occurrence of six of the eight target species (all but *P. azurea* and *S. fuscomarginatus*; Table 1). Broad-scale covariates had a greater influence on site occupancy than either local or intermediate covariates for four of these six species (i.e., beta weights were largest for broad-scale covariates): *D. cruzi*, *D. rubicundulus*, *E. cesarii*, and *L. fuscus* (Table 2). In other words, the broader landscape context had a significant effect on the occurrence of these pond-breeding amphibians, even after accounting for variation in other environmental factors at more local or intermediate scales (Table S3). In the case of *D. nanus* and *H. albopunctatus*, local- and broad-scale covariates were of equal importance in explaining the occurrence of these species. Given that covariates at different scales

Table 1 Multi-scale, model-selection results for the probability of site occurrence by eight pond-breeding anurans in the Brazilian Cerrado

Species models	AIC	ΔAIC	w_i
Dendropsophus cruzi			
1, cover-25, config-25, cover-1, pond isolation	335.3	0.00	0.38
1, cover-25, config-25, pond isolation	336.0	0.66	0.28
D. nanus			
1, config-25, pond-edge vegetation, temperature	344.6	0.00	0.92
D. rubicundulus			
1, cover-25, pond-interior vegetation	359.0	0.00	0.19
1, cover-25, pond-interior vegetation, rain	359.5	0.47	0.15
1, cover-25, pond-edge vegetation, pond-interior vegetation	359.7	0.69	0.13
1, cover-25, pond-edge vegetation, pond-interior vegetation, rain	360.1	1.10	0.11
1, cover-25	360.8	1.85	0.08
Hypsiboas albopunctatus			
1, pond isolation, nearest pond distance, cover-25, config-25, cover-1, pond-interior vegetation, rain, temperature	317.3	0.00	0.38
1, pond isolation, cover-25, config-25, cover-1, pond-interior vegetation, rain, temperature	318.7	1.43	0.19
Phyllomedusa azurea			
1, pond-interior vegetation	362.7	0.00	0.60
1	363.5	0.78	0.40
Scinax fuscomarginatus			
1, nearest pond distance, pond-interior vegetation, rain, temperature	351.6	0.00	0.19
1, pond isolation, nearest pond distance, pond-interior vegetation, rain, temperature	351.8	0.12	0.18
1, pond isolation, nearest pond distance, pond-interior vegetation, rain	352.4	0.78	0.13
1, nearest pond distance, pond-interior vegetation, rain	352.5	0.87	0.12
Elachistocleis cesarii			
1, config-25, cover-1	358.9	0.00	0.55
1, cover-1	360.6	1.64	0.24
Leptodactylus fuscus			
1, config-25	347.4	0.00	0.70
1, config-25, pond-edge vegetation	349.0	1.65	0.30

Only the top-ranked models (ΔAIC <2) for each species are presented

explained site occupancy in most of our species, however, we next consider how covariates at a given scale variously influenced species occurrence, focusing on just those effects that had a significant relationship with site occupancy (i.e., the 95 % CI of beta weights does not include zero; Table 2).

Local-scale covariates

Local-scale covariates were in the top-ranked models (ΔAIC <2.0) of most species, with the exception of *D. cruzi* and *E. cesarii*, whose occurrence was not explained by any of the local-scale covariates

Table 2 The standardized partial regression coefficients (beta weights) and 95 % confidence intervals (lower confidence level; upper confidence level) across the global multi-scale models for covariates used to determine site occurrence by pond-breeding anurans in the Brazilian Cerrado

	Local-scale covariates				Intermediate-scale covariates			Broad-scale covariates	
	Temperature	Rain	Pond-edge vegetation	Pond-interior vegetation	Nearest pond distance	Pond isolation	Cover-1	Cover-25	Config-25
Dendropsophus cruzi						**−0.19**	−0.14	**−0.38**	**−0.22**
						−0.36; −0.01	−0.31; 0.03	**−0.58; −0.19**	**−0.39; −0.05**
D. nanus	**0.27**		**0.25**						0.27
	0.11; 0.44		**0.08; 0.42**						0.10; 0.44
D. rubicundulus		−0.12	0.11	−0.17				0.20	
		−0.29; 0.06	−0.07; 0.29	−0.35; 0.00				0.02; 0.37	
Hypsiboas albopunctatus	**−0.28**	**−0.16**		**0.19**	0.14	**−0.28**	**−0.21**	**−0.22**	**−0.28**
	−0.44; −0.13	**−0.31; −0.02**		**0.04; 0.34**	−0.01; 0.29	**−0.44; −0.11**	**−0.37; −0.05**	**−0.40; −0.03**	**−0.45; −0.11**
Phyllomedusa azurea				−0.15					
				−0.32; 0.03					
Scinax fuscomarginatus	−0.14	**−0.22**		**0.19**	**0.19**	−0.13			
	−0.31; 0.03	**−0.38; −0.05**		**0.02; 0.36**	**0.03; 0.36**	−0.29; 0.04			
Elachistocleis cesarii							−0.17		
							−0.34; 0.00		
Leptodactylus fuscus			−0.06					0.19	**0.36**
			−0.23; 0.11					0.02; 0.36	**0.19; 0.53**

Significant beta weights (i.e., confidence intervals that did not overlap zero) are highlighted in boldface
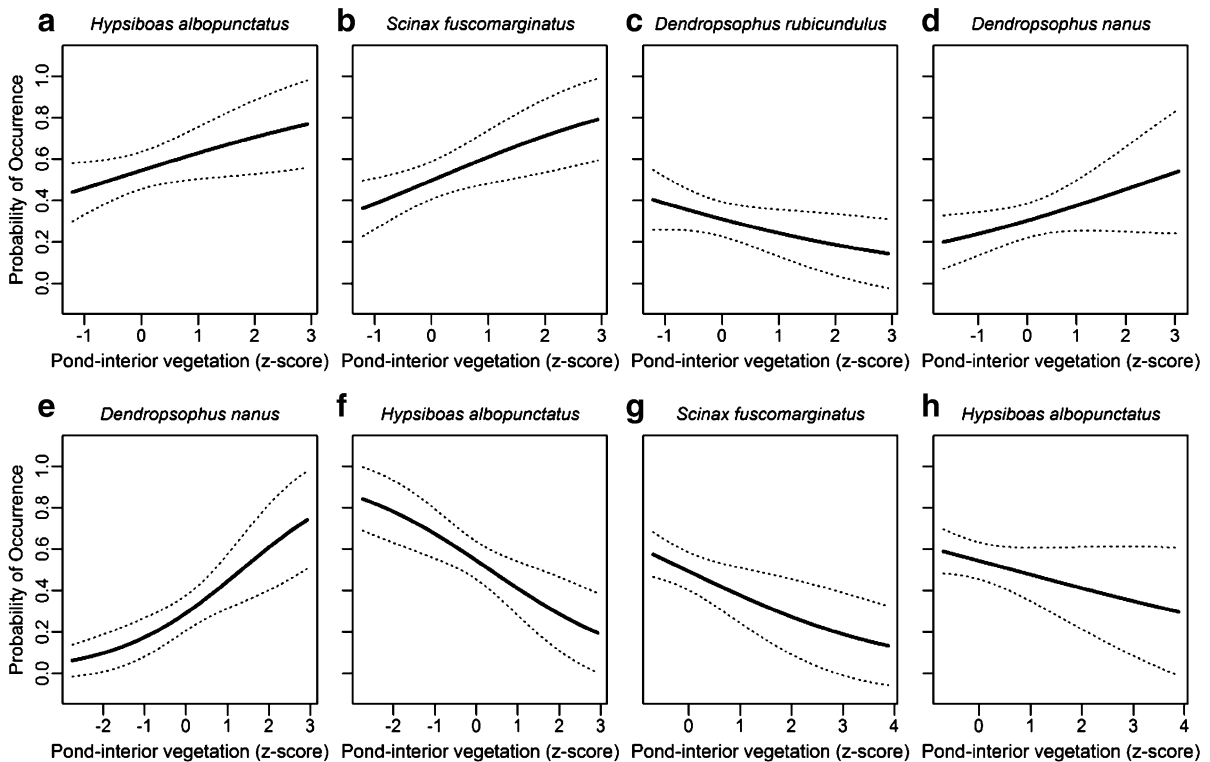
Fig. 2 Probability of occurrence for anurans in the Brazilian Cerrado as a function of local-scale covariates: proportion of emergent vegetation within ponds for **a** *Hypsiboas albopunctatus,* **b** *Scinax fuscomarginatus,* and **c** *Dendropsophus rubicundulus*; proportion of pond-edge vegetation for **d** *D. nanus*; air temperature for **e** *D. nanus* and **f** *H. albopunctatus*; and, rainfall for **g** *Scinax fuscomarginatus* and **h** *H. albopunctatus*. Predicted values (*line*) and the 95 % confidence interval (*dashed lines*) are depicted from the binomial GLM models for each species

(Table 1). For three species, emergent vegetation (pond-interior vegetation) was significantly related (95 % CI for beta weights does not include 0; Table 2) to their probability of occurrence in either a positive (*H. albopunctatus* and *S. fuscomarginatus*; Fig. 2a, b) or negative (*D. rubicundulus*; Fig. 2c) fashion. In contrast, the occurrence of *D. nanus* was positively correlated with the amount of vegetation along the pond's edge (pond-edge vegetation; Table 2; Fig. 2d). In addition, air temperature significantly increased the apparent occurrence of *D. nanus*, but significantly decreased the occurrence of *H. albopunctatus*, (Table 2; Fig. 2e, f). Rainfall was negatively related to the occurrence of both *S. fuscomarginatus* and *H. albopunctatus* (Table 2; Fig. 2g, h).

Intermediate-scale covariates

The probability of occurrence for four species was found to be correlated with covariates assessed at an intermediate scale (1 km around ponds; Table 1). One of these four species (*H. albopunctatus*) exhibited a significant negative relationship with the amount of native habitat (cover-1, >50 % probability of occurrence when cover <40 % = z-scores <0.5; Table 2; Fig. 3a). The occurrence of two species, *D. cruzi* and *H. albopunctatus,* exhibited a negative correlation with the isolation of ponds from other water sources (pond isolation), meaning that site occupancy was more likely in isolated ponds. Finally, the occurrence of *S. fuscomarginatus* increased with increasing
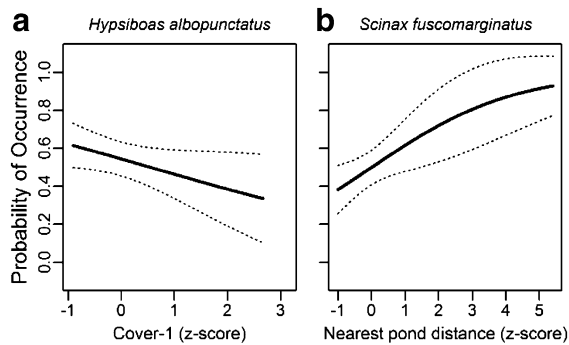
Fig. 3 Probability of occurrence for anurans in the Brazilian Cerrado as a function of intermediate-scale covariates: proportion of native habitat within 1-km² landscapes surrounding ponds for **a** *Hypsiboas albopunctatus*; and, nearest pond distance for **b** *Scinax fuscomarginatus*. Predicted values (*line*) and the 95 % confidence interval (*dashed lines*) are depicted from the binomial GLM models for each species

distance between ponds (>50 % occupancy when >270 m nearest pond distance = z-scores > 0; Table 2; Fig. 3b).

Broad-scale covariates

The probability of occurrence for all but two species was significantly correlated with one or both of the broad-scale landscape factors (25 × 25 km²; Table 2). Two species (*D. cruzi* and *H. albopunctatus,* Fig. 4a, b) exhibited a negative relationship with mean distance between native-habitat remnants (config-25), but three other species (*D. nanus, E. cesarii,* and *L. fuscus*) were positively correlated with this measure (Table 2; Fig. 4c, e). In addition, the occurrence of three species was either positively (*D. rubicundulus*) or negatively (*D. cruzi* and *H. albopunctatus*) influenced by the amount of native
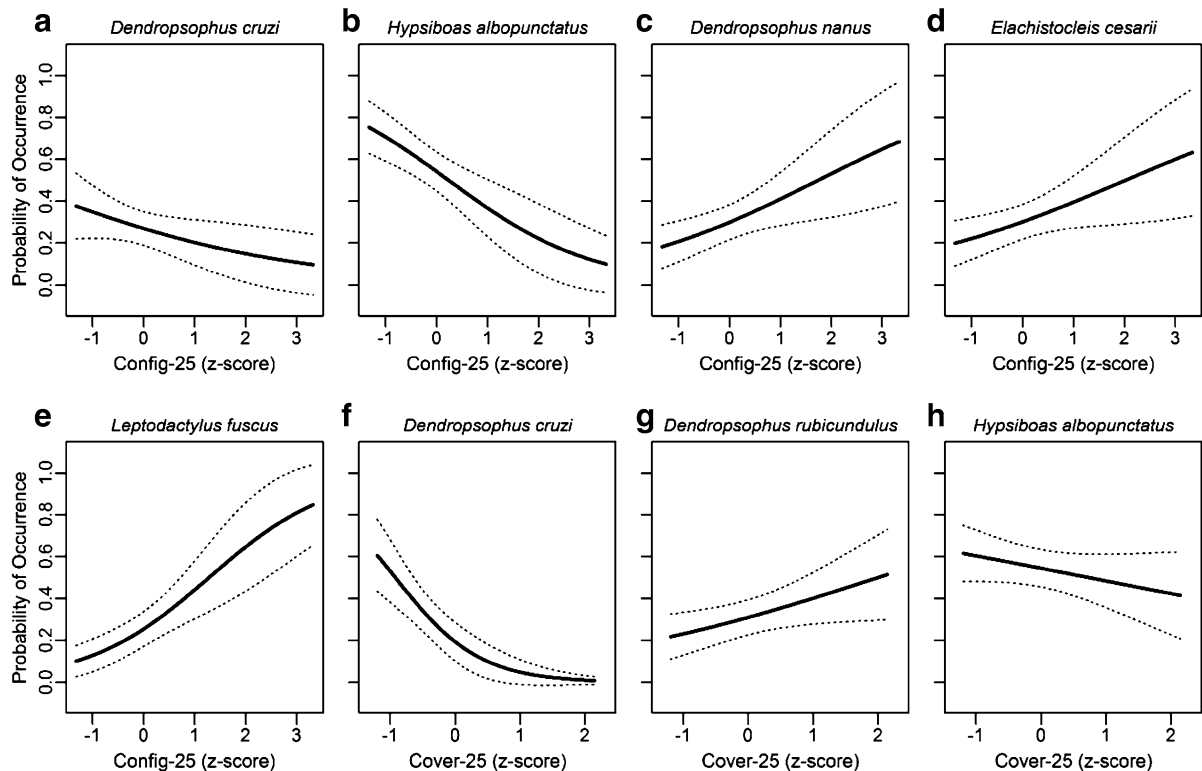

Fig. 4 Probability of occurrence for anurans in the Brazilian Cerrado as a function of broad-scale covariates: mean distance between native-habitat patches (config-25) for **a** *Dendropsophus cruzi,* **b** *Hypsiboas albopunctatus,* **c** *D. nanus,* **d** *Elachistocleis cesarii,* and **e** *Leptodactylus fuscus*; and, proportion of native habitat within 625-km² landscapes for **f** *D. cruzi,* **g** *H. albopunctatus,* and **h** *D. rubicundulus.* Predicted values (*line*) and the 95 % confidence interval (*dashed lines*) from the binomial GLM models are depicted for each species

habitat on the landscape (cover-25; Table 2; Fig. 4f, h). Thus, the incidence of *D. rubicundulus* was higher within landscapes having abundant native habitat (>50 % probability of occurrence when cover >60 % = z-scores >1.8; Fig. 4h), whereas *D. cruzi* and *H. albopunctatus* occurred mainly in landscapes that had a low proportion of native habitat (*D. cruzi*: >50 % occupancy when <16 % native cover = z-scores < −0.93, Fig. 4f; *H. albopunctatus*: >50 % occupancy when <44 % native cover = z-scores <0.83; Fig. 4g), but in which habitat remnants were still fairly close together (*D. cruzi*: >37 % occurrence when patch distance <1.6 km = z-scores < −1.3; Fig. 4a; *H. albopunctatus:* >50 % occurrence when patch distance <3.5 km = z-scores <0.2, Fig. 4b). In contrast, the incidence of *D. nanus, E. cesarii* and *L. fuscus* increased as a function of increasing patch distance (>50 % occurrence when patch distance >5.4 km = z-scores >2; Fig. 4c, e).

Discussion

Landscape context exerted a major influence on the distribution of most of the pond-breeding anurans we studied in the Brazilian Cerrado. For six of our eight target species, landscape factors were as or more important (based on relative beta weights) than the local- or intermediate-scale variables describing the pond habitat and surrounding environment (i.e., within a 1-km radius of ponds). This finding is all the more surprising given that the landscape context of these small wetlands was assessed at a very broad scale, in terms of the overall amount and configuration of native Cerrado habitat. Of the two broad-scale landscape factors, landscape configuration—the average distance between native-habitat remnants—had a greater effect on species distributions than native-habitat area (based on their relative beta weights). Habitat configuration was featured in the top-ranked models of five species (*D. cruzi*, *D. nanus*, *H. albopunctatus*, *E. cesarii*, and *L. fuscus*), whereas the amount of native habitat was featured in the top-ranked models of three species (*D. cruzi, D. rubicundulus*, and *H. albopunctatus*). It is worth noting that two of these species influenced by landscape context (*D. cruzi* and *D. rubicundulus*) are also Cerrado endemics (Valdujo et al. 2012). Given that our assessment of landscape context captures the relative

degree to which landscapes have been converted to agricultural land use, we suggest that agricultural practices related to cattle grazing and cash-crop production are influencing the occurrence of these pond-breeding anurans in the Cerrado.

Landscapes altered by agricultural and grazing practices may reduce species occurrence by creating a more open, drier environment that puts amphibians at increased risk of evaporative water loss and desiccation (Cosentino et al. 2011; Watling and Braga 2015). Amphibians are especially vulnerable to evaporative water loss because they require environmental moisture to maintain gas exchange (Wells 2007). For example, *H. raniceps*, a species from the *H. albopunctatus* group (Faivovich et al. 2005), was found to suffer greater evaporative water loss in open savanna than in forest. Thus, a susceptibility to desiccation may well be important in determining an anuran's response to habitat loss and the isolation of habitat remnants (Watling and Braga 2015), even in species that are considered habitat generalists (La Marca et al. 2004), including the Cerrado species we studied. Consistent with our expectations, then, the occurrence of *D. rubicundulus* increased with native-habitat cover, whereas the occurrences of both *D. cruzi* and *H. albopunctatus* were negatively influenced by the increasing isolation of native-habitat remnants. The occurrence of *H. albopunctatus* has previously been shown to exhibit a negative relationship with the increasing isolation of forest fragments in an agricultural region of southeastern Brazil (São Paulo state; Prado and Rossa-Feres 2014).

Still, not all anurans responded as expected to this landscape-disturbance gradient in the Cerrado. The occurrence of three species (*D. nanus*, *E. cesarii*, and *L. fuscus*) was positively associated with increasing distance among habitat remnants, whereas the occurrence of three other species (*D. cruzi*, *H. albopunctatus*, and *E. cesarii*) was negatively related to the proportion of native-habitat cover on the landscape. Many anurans found within the South American Dry Diagonal region (Werneck et al. 2012), which is formed by the Caatinga, Cerrado, and Chaco biomes, are habitat generalists that possess reproductive strategies that minimize the risk of desiccation (Prado and Rossa-Feres 2014). Although most of the species we studied from the Cerrado region have a generalized mode of reproduction, in that they lay their eggs directly in water (*D. cruzi, D. nanus, D. rubicundulus,*

H. albopunctatus, E. cesarii, and *S. fuscomarginatus*), others lay their eggs in vegetation above water (*P. azurea* lays its eggs on leaves, which it folds to form a closed nest) or underground (*L. fuscus* lays its eggs in foam nests in underground chambers at the margins of ponds) to prevent desiccation (Haddad and Prado 2005), and so may not be especially sensitive to broad-scale landscape changes resulting from grazing and agricultural land use. The Cerrado is by definition an open habitat, and thus pond-breeding anurans associated with this biome might be less susceptible to human-modified landscapes than, for example, forest-interior species. Species such as *D. nanus, H. albopunctatus, E. cesarii*, and *L. fuscus* are known to be tolerant of human disturbance (IUCN 2015), and might actually be benefiting from agricultural land-use activities that create small or temporary water bodies that can be used for breeding (e.g., cattle watering holes, roadside ditches, and skidder ruts; da Silva et al. 2011; De Marco et al. 2013).

Even for species that exhibited a positive association with more-intact Cerrado landscapes, however, the occurrence of these species had less to do with the amount of native habitat than the configuration of those habitats on the landscape. Although habitat loss is generally expected to have a deleterious effect on the distribution and abundance of amphibians (Riley et al. 2005; Rubbo and Kiesecker 2005), the configuration of terrestrial habitats may be a more important determinant of species occurrence for pond-breeding amphibians (Cayuela et al. 2015). Fragments of native habitat, independent of their size, could help facilitate dispersal across the landscape (e.g., habitat stepping stones) or provide other resources, such as suitable habitat during the non-breeding season or foraging areas in close proximity to breeding ponds (da Silva and Rossa-Feres 2011). In addition, wetlands within landscapes that have experienced less agricultural conversion may have better water quality (something we did not measure directly), as a consequence of less runoff, for example (De Marco et al. 2013). Thus, the occurrence of species in heavily disturbed landscapes dominated by agricultural land use does not mean that these species will be able to persist in those landscapes (i.e., that populations are in fact viable). Wetlands within a predominantly agricultural context could function as ecological traps (Rotem et al. 2013), which is a possibility that should

be addressed by future research on anurans in the Cerrado.

Although the occurrence of most pond-breeding anurans we studied was predominantly influenced by landscape context, factors at the local and intermediate scales were also important to some species. Indeed, the occurrence of *P. azurea* was best explained by a single local-site variable (pond-interior vegetation). The occurrence of *D. rubicundulus* was negatively associated with vegetation inside the pond, reflecting the preference of this species for open water. *Dendropsophus rubicundulus* and *P. azurea* are widely distributed throughout the Cerrado (Napoli and Caramaschi 1999; Silva et al. 2011), and thus might be expected to occur in a wide variety of pond habitats. We do know that *P. azurea* can be found in open areas within native Cerrado habitats as well as in highly disturbed environments elsewhere (e.g., Nomura et al. 2012; Bruschi et al. 2013), which reinforces the results of our occupancy model analysis.

At the intermediate scale, isolation of water bodies was expected to disrupt habitat connectivity and negatively influence site occupancy in these pond-breeding anurans. Our results do not support that prediction, however. We found that the incidence of just one species (*S. fuscomarginatus*) was related to the nearest pond distance, and in that case, the association was a positive one (i.e., site occupancy increased with increasing nearest-pond distance). An increase in species occurrence as a function of increasing pond isolation was also found for five frog species (*D. elianeae, D. minutus, Pseudis platensis, S. fuscovarius*, and *E. bicolor*) in an agricultural region in southeastern Brazil, a region characterized by fragments of semi-deciduous forest and savanna surrounded by a matrix of agricultural land use (Prado and Rossa-Feres 2014). It may be that isolated ponds that are not hydrologically connected to other water sources can better prevent the establishment of predators, such as fish (Scheffer et al. 2006). Further, pond isolation-by-distance is a relative concept, and it may be that the observed inter-pond distances do not in fact limit movement and dispersal for these species. Unlike true oceanic islands, habitat patches (e.g. ponds) in terrestrial landscapes are not surrounded by a uniformly hostile matrix. Thus, species attempting to move through the matrix may still find habitat in which to live and reproduce (Prugh et al. 2008), such as in

ephemeral water sources, for example. We therefore should not expect pond isolation to have a consistent effect across species. Moreover, we did not assess the amount and configuration of native Cerrado habitat among breeding ponds. "Habitat split," the degree to which wetlands are isolated from terrestrial habitats, is linked to lower amphibian richness in the Atlantic forest, for example (Becker et al. 2007, 2010), where humans settlement are concentrated next to water sources (Fonseca et al. 2013). Habitat split results in a disconnection between habitats needed by adults (forests) and their aquatic larvae (ponds and streams), which compels individuals to travel farther through the intervening matrix to reach breeding sites and/or resources, leading to lower dispersal success, colonization rates, and thus, species occurrence (Becker et al. 2007). Future research should thus assess the effect of habitat split on amphibian species from open areas, like the Cerrado and in other savannas and grasslands.

Conclusions and implications

Conservation for pond-breeding anurans typically focuses on the local-site level (the pond), and although that might still be necessary, especially for species like *P. azurea* whose occurrence was only linked to local-site variables, the results of our analysis highlight the importance of managing the broader landscape context. Landscape context had a significant effect on the occurrence of most of the pond-breeding species we studied in the Brazilian Cerrado. Much of this effect was due to the configuration of native-habitat remnants rather than the amount of native habitat remaining on the landscape. Because the Cerrado is undergoing widespread conversion to agricultural land use, our results suggest that agricultural practices are influencing the occurrence of these species. Contrary to general expectations, however, agricultural land use had contrasting effects on species, with the occurrence of some species actually increasing in response to the degree of landscape disturbance. This does not mean that agriculture *per se* is beneficial to these species, only that these species may be tolerant of the sorts of disturbances created by agriculture or can utilize habitats created as a byproduct of agricultural land use (e.g., cattle watering holes).

This nevertheless poses something of a conservation dilemma (Prado and Rossa-Feres 2014), in which management recommendations for one species might well conflict with another. As mentioned previously, many of our target species are widespread and habitat generalists (Table S1), and are therefore expected to occur in a wide variety of habitats, including human-modified ones. In developing management recommendations, we might therefore focus on just those species that have more specialized habitat requirements and/or are Cerrado endemics, bearing in mind that the fact a species is currently widespread does not guarantee its long-term persistence. For example, although *Physalaemus cuvieri* is a common and widely distributed pond-breeding frog from the Cerrado region, habitat loss has been shown to have a negative effect on the population genetic structure of this species (Telles et al. 2007).

Therefore, if we use our model results for two Cerrado endemics (*D. cruzi* and *D. rubicundulus*) as a guide, since the occurrence of both species was strongly affected by landscape context, it would be ideal if future land use could minimize isolation among native-habitat remnants by keeping these clustered and within 1.6 km of each other (i.e., the threshold distance at which *D. cruzi* exhibited greatest site occupancy). Developing a recommendation for the amount of native habitat to maintain is admittedly more difficult, given the conflicting response of these species to native-habitat cover (i.e., the occurrence of *D. rubicindulus* increased, but that of *D. cruzi* decreased, with increasing native-habitat cover) and the large size of the landscapes considered (625-km^2), which likely exceeds the scale of management by individual landowners. It might therefore be best to maintain a diversity of landscapes across the region, in which the amount of native-habitat cover varies, but is reduced to no less than 16 % of the total landscape (the threshold level at which *D. cruzi* had 50 % occupancy) but ideally would be far more than this in other landscapes (e.g., *D. rubicundulus* did not achieve >50 % occupancy unless there was >60 % native-habitat cover). According to Brazilian environmental law (12.651/12), landowners are supposed to maintain at least 20 % of native vegetation on private lands (Brasil 2012). Based on our analysis, this amount of native habitat may be reasonable for some species (e.g., *D. cruzi*), but would clearly be insufficient for others (*D. rubicunduls*).

As in many tropical regions of the world, research on anurans in the Brazilian Cerrado is still in its infancy. We lack basic information on the distribution and possible threats to most of these pond-breeding species. Species distribution modeling at least offers one way of exploring the threat posed by land-use change, such as from the agricultural conversion of the Cerrado, to the expected occurrence of these species in the meantime.

References

Abdi H (2004) Partial regression coefficients. In: Lewis-Beck M, Bryman A, Futing T (eds) Encyclopedia of social sciences research methods. Sage, Thousand Oaks, pp 1–4

Baudron F, Giller KE (2014) Agriculture and nature: trouble and strife? Biol Conserv 170:232–245

Becker CG, Fonseca CR, Haddad CFB, Batista RF, Prado PI (2007) Habitat split and the global decline of amphibians. Science 318(5857):1775–1777

Becker CG, Fonseca CR, Haddad CFB, Prado PI (2010) Habitat split as a cause of local population declines of amphibians with aquatic larvae. Conserv Biol 24:287–294

Birx-Raybuck DA, Price SJ, Dorcas ME (2010) Pond age and riparian zone proximity influence anuran occupancy of urban retention ponds. Urban Ecosyst 13:181–190

Blevins E, With KA (2011) Landscape context matters: local habitat and landscape effects on the abundance and patch occupancy of collared lizards in managed grasslands. Landscape Ecol 26:837–850

Brasil (2012) Lei n° 12.651, de maio de 2012. http://www.planalto.gov.br/ccivil_03/_ato2011-2014/2012/lei/l12651.htm. Accessed Dec 2015

Bruschi DP, Busin CS, Toledo LF, Vasconcellos GA, Strussmann C, Weber LN, Recco-Pimentel SM (2013) Evaluation of the taxonomic status of populations assigned to *Phyllomedusa hypochondrialis* (Anura, Hylidae, Phyllomedusinae) based on molecular, chromosomal, and morphological approach. BMC Genet 14:1–14

Calcagno V, de Mazancourt C (2010) glmulti: an R package for easy automated model selection with (generalized) linear models. J Stat Softw 34:1–29

Carvalho FMV, De Marco P, Ferreira LG (2009) The Cerrado into-pieces: habitat fragmentation as a function of landscape use in the savannas of central Brazil. Biol Conserv 7(142):1392–1403

Cayuela H, Lambrey J, Vacher JP, Miaud C (2015) Highlighting the effects of land-use change on a threatened amphibian in a human-dominated landscape. Popul Ecol 57:433–443

Chetkiewicz CLB, St Clair CC, Boyce MS (2006) Corridors for conservation: integrating pattern and process. Annu Rev Ecol Evol Syst 37:317–342

Collier BA, Groce JE, Morrison ML, Newnam JC, Campomizzi AJ, Farrell SL, Wilkins RN (2012) Predicting patch occupancy in fragmented landscapes at the rangewide scale for an endangered species: an example of an American warbler. Divers Distrib 18:158–167

Cosentino BJ, Schooley RL, Phillips CA (2011) Connectivity of agroecosystems: dispersal costs can vary among crops. Landscape Ecol 26:371–379

Cunningham JM, Calhoun AJK, Glanz WE (2007) Modified landscape pond-breeding amphibian species richness and habitat selection in a beaver-modified landscape. J Wildl Manage 71:2517–2526

Cushman SA (2006) Effects of habitat loss and fragmentation on amphibians: a review and prospectus. Biol Conserv 128:231–240

da Silva FR, Gibbs JP, Rossa-Feres DDC (2011) Breeding habitat and landscape correlates of frog diversity and abundance in a tropical agricultural landscape. Wetlands 31:1079–1087

da Silva FR, Rossa-Feres DC (2011) Influence of terrestrial habitat isolation on the diversity and temporal distribution of anurans in an agricultural landscape. J Trop Ecol 27:327–331

De Marco P, Nogueira DS, Correa CC, Vieira TB, Silva KD, Pinto NS, de Oliveira AAB (2013) Patterns in the organization of Cerrado pond biodiversity in Brazilian pasture landscapes. Hydrobiologia 723:87–101

Faivovich J, Haddad CFB, Garcia PCA, Frost DR, Campbell JA, Wheeler WC (2005) Systematic review of the frog family Hylidae, with special reference to Hylinae: phylogenetic analysis and taxonomic revision. Bull Am Mus Nat Hist 294:1–240

Felfili JM (1995) Diversity, structure and dynamics of a gallery forest in central Brazil. Vegetatio 117:1–15

Foley JA, DeFries R, Asner GP, Barford C, Bonan G, Carpenter SR, Helkowski JH (2005) Global consequences of land use. Science 309:570–574

Fonseca CR, Coutinho RM, Azevedo F, Berbert JM, Corso G, Kraenkel RA (2013) Modeling habitat split: landscape and

life history traits determine amphibian extinction thresholds. PloS One 8:1–7

Gagné SA, Fahrig L (2007) Effect of landscape context on anuran communities in breeding ponds in the National Capital Region, Canada. Landscape Ecol 22:205–215

Gilbert-Norton L, Wilson R, Stevens JR, Beard KH (2010) A meta-analytic review of corridor effectiveness. Conserv Biol 24:660–668

Haddad CFB, Prado CPA (2005) Reproductive modes in frogs and their unexpected diversity in the Atlantic Forest of Brazil. BioScience 55:207–217

Heyer WR, Donnelly MA, Foster M, McDiarmid RW (1994) Measuring and monitoring biological diversity: standard methods for amphibians. Smithsonian Institution Press, Washington

Houlahan J, Keddy PA, Makkay K, Findlay CS (2006) The effects of adjacent land use on wetland species richness and community composition. Wetlands 26:79–96

IUCN (2015) An analysis of amphibians on the 2015 IUCN red list. http://www.iucnredlist.org. Accessed Nov 2015

Johnson JB, Omland KS (2004) Model selection in ecology and evolution. Trends Ecol Evol 19:101–108

Kendall WL, White GC (2009) A cautionary note on substituting spatial subunits for repeated temporal sampling in studies of site occupancy. J Appl Ecol 46:1182–1188

Kindt R (2015) R package "biodiversityR." Package for community ecology and suitability analysis. Version 2.5-2. http://vps.fmvz.usp.br/CRAN/web/packages/BiodiversityR/BiodiversityR.pdf. Accessed Mar 2015

Kindt R, Coe R (2005) Tree diversity analysis: a manual and software for common statistical methods for ecological and biodiversity studies. World Agroforestry Centre, Nairobi

La Marca E, Azevedo-Ramos C, Silvano D, Scott N, Aquino L, Faivovich J (2004). *Hypsiboas raniceps*. The IUCN red list of threatened species. Version 2015.1. http://www.iucnredlist.org. Accessed Nov 2015

Mazerolle MJ, Desrochers A (2005) Landscape resistance to frog movements. Can J Zool 83:455–464

McGarigal K, Cushman SA, Ene E (2012) FRAGSTATS v4: spatial pattern analysis program for categorical and continuous maps. Computer software program produced by the authors at the University of Massachusetts, Amherst. http://www.umass.edu/landeco/research/fragstats/fragstats.html. Accessed Jan 2015

MMA (2015) O bioma Cerrado. http://www.mma.gov.br/biomas/cerrado. Accessed Oct 2015

MMA-IBAMA (2011) Monitoramento do desmatamento nos biomas brasileiros por Satélite. Acordo de cooperação técnica MMA/IBAMA. Monitoramento do bioma Cerrado: 2008–2009. http://www.mma.gov.br/estruturas/sbf_chm_rbbio/_arquivos/relatoriofinal_cerrado_2010_final_72_1.pdf. Accessed Oct 2015

Naiman RJ, Decamps H, Pollock M (1993) The role of riparian corridors in maintaining regional biodiversity. Ecol Appl 3:209–212

Napoli MF, Caramaschi U (1999) Geographic variation of *Hyla rubicundula* and *Hyla anataliasiasi*, with the description of a new species (Anura, Hylidae). Alytes 16:165–189

Nilsson SG, Franzén M, Jönsson E (2008) Long-term land-use changes and extinction of specialised butterflies. Insect Conserv Diver 1:197–207

Nomura F, Maciel N, Pereira E, Bastos RP (2012) Diversidade de anuros (Amphibia) em áreas recuperada de atividade mineradora no Cerrado e de plantio de Eucalyptus urophyla no Brasil Central Anura diversity. Bioscience J 28:312–324

Oliveira PS, Marquis RJ (2002) The Cerrados of Brazil: ecology and natural history of a neotropical savanna. Columbia University Press, New York

Pellet J, Schmidt BR (2005) Monitoring distributions using call surveys: estimating site occupancy, detection probabilities and inferring absence. Biol Conserv 123:27–35

Pope S, Fahrig L, Merriam H (2000) Landscape complementation and metapopulation effects on leopard frog populations. Ecology 81:2498–2508

Prado VHM, Rossa-Feres DC (2014) Multiple determinants of anuran richness and occurrence in an agricultural region in South-eastern Brazil. Environ Manag 53:823–837

Prugh LR, Hodges KE, Sinclair ARE, Brashares JS (2008) Effect of habitat area and isolation on fragmented animal populations. Proc Natl Acad Sci 105:20770–20775

Ratter J, Ribeiro J, Bridgewater S (1997) The Brazilian Cerrado vegetation and threats to its biodiversity. Ann Bot 80:223–230

Riley SP, Busteed GT, Kats LB, Vandergon TL, Lee LF, Dagit RG, Sauvajot RM (2005) Effects of urbanization on the distribution and abundance of amphibians and invasive species in southern California streams. Conserv Biol 29:1894–1907

Rödel M, Ernst R (2004) Measuring and monitoring amphibian diversity in tropical forests. I. An evaluation of methods with recommendations for standardization. Ecotropica 10:1–14

Rotem G, Ziv Y, Giladi I, Bouskila A (2013) Wheat fields as an ecological trap for reptiles in a semiarid agroecosystem. Biol Conserv 167:349–353

Rubbo M, Kiesecker J (2005) Amphibian breeding distribution in an urbanized landscape. Conserv Biol 19:504–511

Sano EE, Rosa R, Brito JLS, Ferreira LG (2010) Land cover mapping of the tropical savanna region in Brazil. Environ Monit Assess 166:113–124

Scheffer M, Van Geest GJ, Zimmer K, Jeppesen E, Søndergaard M, Butler MG, De Meester L (2006) Small habitat size and isolation can promote species richness: second-order effects on biodiversity in shallow lakes and ponds. Oikos 112:227–231

Scherer RD, Muths E, Noon BR (2012) The importance of local and landscape-scale processes to the occupancy of wetlands by pond-breeding amphibians. Popul Ecol 54:487–498

Silva G, Vieira J, Alves M (2011) Amphibia, Anura, Hylidae, *Dendropsophus rubicundulus* (Reinhardt and Lütken, 1862): distribution extension in northeastern Brazil. Check List 7:843–844

Smith MA, Green DM (2005) Dispersal and the metapopulation paradigm in amphibian ecology and conservation: are all amphibian populations metapopulations? Ecography 28:110–128

Telles MP, Diniz-Filho JAF, Bastos RP, Soares TN, Guimarães LDA, Lima LP (2007) Landscape genetics of *Physalaemus cuvieri* in Brazilian Cerrado: correspondence between population structure and patterns of human occupation and habitat loss. Biol Conserv 139:37–46

Titon B, Navas CA, Jim J, Gomes FR (2010) Water balance and locomotor performance in three species of neotropical toads that differ in geographical distribution. Comp Biochem Physiol 156:129–135

Valdujo PH, Silvano DL, Colli G, Martins M (2012) Anuran species composition and distribution patterns in Brazilian Cerrado, a Neotropical hotspot. S Am J Herpetol 7:63–78

Vasconcelos TS, Santos TG, Rossa-Feres DC, Haddad CFB (2009) Influence of the environmental heterogeneity of breeding ponds on anuran assemblages from southeastern Brazil. Can J Zool 87:699–707

Wagenmakers E-J, Farrell S (2004) AIC model selection using Akaike weights. Psychon Bull Rev 11:192–196

Watling J, Braga L (2015) Desiccation resistance explains amphibian distributions in a fragmented tropical forest landscape. Landscape Ecol 30:1449–1459

Wells KD (2007) The ecology and behavior of amphibians. The University of Chicago Press, Chicago

Werneck FP, Gamble T, Colli GR, Rodrigues MT, Sites JW Jr (2012) Deep diversification and long-term persistence in the South American "dry diagonal": integrating continent-wide phylogeography and distribution modeling of geckos. Evolution 66:3014–3034

Werner EE, Yurewicz KL, Skelly DK, Relyea RA (2007) Turnover in an amphibian metacommunity: the role of local and regional factors. Oikos 116:1713–1725

Zanini F, Klingemann A, Schlaepfer R, Schmidt BR (2008) Landscape effects on anuran pond occupancy in an agricultural countryside: barrier-based buffers predict distributions better than circular buffers. Can J Zool 86:692–699

Erratum

The axes in Fig. 2 are incorrect, and thus I have attached the corrected figure.