Effects of agriculture and topography on tropical amphibian species and communities

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Abstract. Habitat loss is the greatest threat to the persistence of forest-dependent amphibians, but it is not the only factor influencing species occurrences. The composition of the surrounding matrix, structure of stream networks, and topography are also important landscape characteristics influencing amphibian distributions. Tropical forests have high diversity and endemism of amphibians, but little is known about the specific responses of many of these species to landscape features. In this paper, we quantify the response of amphibian species and communities to landscape-scale characteristics in streams within the fragmented Brazilian Atlantic Forest. We surveyed amphibian communities during a rainy season in 50 independent stream segments using Standardized Acoustic and Visual Transect Sampling (active) and Automated Acoustic Recorders (passive) methods. We developed a hierarchical multi-species occupancy model to quantify the influence of landscape-scale characteristics (forest cover, agriculture, catchment area, stream density, and slope) on amphibian occurrence probabilities while accounting for imperfect detection of species using the two survey methods. At the community level, we estimated an overall mean positive relationship between amphibian occurrence probabilities and forest cover, and a negative relationship with agriculture. Catchment area and slope were negatively related with amphibian community structure (95% credible interval [CI] did not overlap zero). The species-level relationships with landscape covariates were highly variable but showed similar patterns to those at the community level. Species detection probabilities varied widely and were influenced by the sampling method. For most species, the active method resulted in higher detection probabilities than the passive approach. Our findings suggest that small streams and flat topography lead to higher amphibian occurrence probabilities for many species in Brazil's Atlantic Forest. Our results combined with land use and topographic maps can be used to make predictions of amphibian occurrences and distributions beyond our study area. Such projections can be useful to determine where to conduct future research and prioritize conservation efforts in human-modified landscapes.

Key words: anuran; Atlantic Forest; automated acoustic recorders; community model; deforestation; detection error; habitat loss; hierarchical model; landscape; matrix habitat; tropical forest.

Introduction

The conversion of native forest to human-modified landscapes reduces and fragments natural habitats and is a major driver of biodiversity loss at multiple scales (Collins and Crump 2009, Newbold et al. 2015). Native forest loss directly affects the characteristics of terrestrial and aquatic habitats by changing microclimate conditions and decreasing water quality and vegetation diversity (Ewers and Banks-Leite 2013, Clément et al. 2017, Matos et al. 2017). For example, forest areas act as buffers for the aboveground microclimate (Ewers and Banks-Leite 2013), providing more stable habitats for terrestrial fauna. The amount of forest cover within a landscape is typically used as a proxy of habitat availability for forest specialist species (Fahrig 2013, Quesnelle et al. 2015). As such, we might expect a direct decline of species abundance and richness with reductions in the proportion of forested habitats, triggering local extirpation of populations and low diversity in remaining forest

fragments (Fahrig 2013, Almeida-Gomes and Rocha 2014, Quesnelle et al. 2015).

The composition of the surrounding matrix differentially influences species occurrences within forest fragments by affecting population persistence, intra- and inter-specific interactions, habitat connectivity, dispersal success, edging crossing, and movement behavior (Prevedello and Vieira 2010, Popescu and Hunter 2011, Driscoll et al. 2013). For instance, open areas can be less permeable for forest specialist species than more vertically stratified uses, such as silviculture (Popescu and Hunter 2011). Yet, landscape cover is not the only factor influencing species occurrence and abundance. Landscapes with dense stream networks may have higher local occurrences of aquatic and semiaquatic species because they increase habitat availability and connectivity between habitats (Ficetola et al. 2009, 2011, Durães et al. 2016). Moreover, topographic features, such as slope, influence the movement of individuals (Lowe et al. 2006, Westgate et al. 2012) and are linked with habitat characteristics such as soil composition, stream depth and width, and vegetation structure (Kinupp and Magnusson 2005, Allan and Castillo 2007). These features can cause a gradient of habitat suitability, which influences the distribution of many species (Parris and McCarthy 1999, Menin et al. 2007, Keller et al. 2009).

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Amphibians have complex life cycles, occupying both aquatic and terrestrial habitats, making them especially vulnerable to habitat loss as compared to other terrestrial vertebrates (Collins and Crump 2009, Hoffmann et al. 2010). Nearly one-third of amphibian species are formally classified as threatened, with forest loss being the greatest threat to their persistence (IUCN 2017). Deforestation affects forest specialist amphibians by directly causing habitat loss and indirectly decreasing habitat quality (Ficetola et al. 2011, Quesnelle et al. 2015), creating habitat splits (i.e., disconnection of forest and aquatic habitats; Becker et al. 2007), reducing connectivity (Metzger et al. 2009) and decreasing individual movement and dispersal success (Popescu and Hunter 2011). Forest loss can also impact amphibians by operating synergistically with other factors, such as climate change (Brook et al. 2008, Collins and Crump 2009). Studies focused on tropical amphibian species are critically needed because tropical forests harbor the highest diversity and most of the threatened species worldwide (Hoffmann et al. 2010, Hof et al. 2011) and are continual diminished and fragmented (Hansen et al. 2013). However, most studies examining the relationship between landscape characteristics and amphibians of riparian zones are primarily focused on temperate systems (Ficetola et al. 2009, 2011, Quesnelle et al. 2015, Surasinghe and Baldwin 2015).

It can be difficult to determine the impacts of habitat loss on amphibians because the detection probabilities of amphibian species during sampling events are nearly always imperfect (Mackenzie et al. 2002, Zipkin et al. 2012, Walls et al. 2014). Many studies investigating the effects of landscape characteristics on amphibian populations and communities fail to consider that observational data may be biased due to detection errors in field surveys (Becker et al. 2007, Ficetola et al. 2009, 2011, Mendenhall et al. 2014, Quesnelle et al. 2015, Ferrante et al. 2017). If detection error is not properly incorporated, parameter estimates in models may be biased and results can be misleading (Ruiz-Gutiérrez and Zipkin 2011, Tingley and Beissinger 2013). The hierarchical multispecies occupancy model is a powerful modeling framework that allows estimation of both species-specific and community-level processes, while accounting for biases during the observational process (Dorazio and Royle 2005, Dorazio et al. 2010). Multi-species occupancy models can additionally estimate occurrence probabilities of rare and inconspicuous species with few or even zero records (Zipkin et al. 2009, Dorazio et al. 2010, Kéry and Royle 2015), which is especially advantageous in tropical systems that harbor high anuran diversity and many rare species (Villalobos et al. 2013).

Here, we developed a hierarchical multi-species occupancy model to investigate the influence of landscape characteristics on amphibian occurrence probabilities in Brazil's Atlantic Forest streams. Atlantic Forest streams have high diversity and endemism of amphibians (Haddad et al. 2013), but this tropical forest is drastically reduced to about 12% of its original area with more than 80% of its remaining area distributed as small fragments (<50 ha; Ribeiro et al. 2009). We quantified both species- and community-level responses of amphibians to important landscape-scale characteristics (forest cover, agriculture, catchment area, stream density, and slope) across 50 independent headwater drainages. Due to the tremendous body of research demonstrating a negative impact of forest loss on amphibian forest specialist species and communities (e.g., Herrmann et al. 2005, Ficetola et al. 2011, Quesnelle et al. 2015, Villaseñor et al. 2017), we hypothesized that forest cover would be positively related with forest specialist amphibians in Atlantic Forest streams. Similarly, we expected a positive relationship between amphibian occurrence probabilities and the density of stream networks, which is a proxy of aquatic habitat availability and connectivity (Ficetola et al. 2009, Durães et al. 2016). Alternatively, we hypothesized that the amount of agricultural lands surrounding the sampling sites would reduce habitat availability and negatively influence species and communities (Dixo and Metzger 2010, Almeida-Gomes and Rocha 2014). Because a steep slope may affect amphibian dispersal by demanding more energy to move between places compared to flat areas (Lowe et al. 2006, Westgate et al. 2012), we also hypothesized that species would respond negatively to slope. Catchment area is a proxy for many local habitat characteristics, such as stream physical habitats, that have been shown to have both positive and negative effects on individual amphibian species (Parris and McCarthy 1999, Eterovick and Barata 2006, Keller et al. 2009, Ribeiro et al. 2012, Konopik et al. 2015, Villaseñor et al. 2017). Therefore, we did not have a specific expectation as to the direction of catchment area effect on amphibians in Brazil's Atlantic Forest streams, although we expected this could be an important environmental covariate to some species.

METHODS

Study area

The Alto Paranapanema basin is in the São Paulo State Crystalline Plateau, southeastern Brazil, and covers approximately 22,700 km² (Kronka et al. 2005). This region harbors one of the most extensive areas of Brazil's Atlantic Forest remnants, including several contiguous reserve areas as part of Carlos Botelho State Park, Intervales State Park, Nascentes do Paranapanema State Park, and Xituê Ecological Station (approximately 40,000 ha of protected forest; Kronka et al. 2005, Ribeiro et al. 2009). The study region is characterized by a tropical wet climate with rainy season during the Southern Hemisphere spring and summer (October–March) with annual mean precipitation and temperature of approximately 1,600 mm and 20°C, respectively.

We conducted anuran surveys in 50 sites. Each site was in an independent headwater stream within the Carlos Botelho State Park or in surrounding forest fragments in the mountainous region within 5 km of the park (range from 23°59.710′ S to 24°8.106′ S and from 47°56.900′ W to 48°7.432′ W; Fig. 1). The predominant land cover in the study area is the Atlantic Forest (primary and secondary native forest), comprising approximately 69% of the region (Fig. 1). Our sampling sites have minimal variation in elevation, ranging from 688 to 813 m. The primary anthropogenic disturbances in our study area are silviculture of exotic plantations (mainly trees of genus *Pinus* and *Eucalyptus;* 19% of the region) and agriculture (dominated by vineyards, cattle ranching, and pastures; 11% of the region; Fig. 1). Our study area contains a small proportion of rural construction, villages, lentic water, and non-identifiable cover use (<1%).
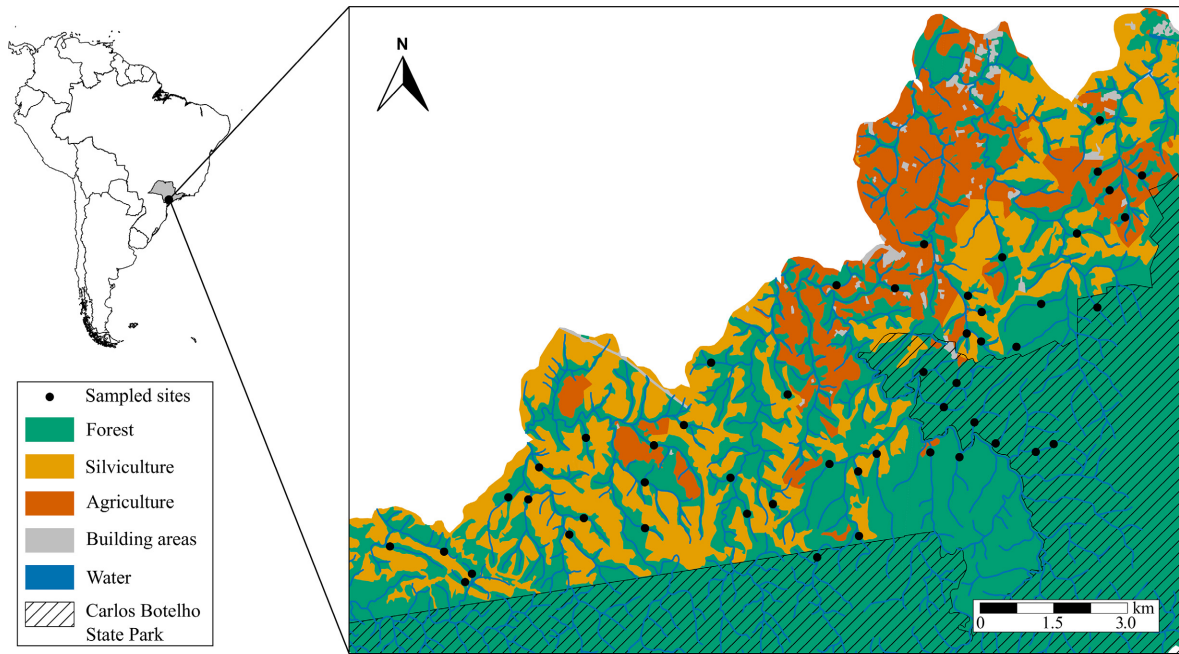
Fig. 1. Map of land cover types and locations of 50 headwater streams that were surveyed for amphibians in São Paulo state, southeastern Brazil (latitude 23°59.710′–24°8.106′ S; longitude 47°56.900′–48°7.432′ W).

Anuran data sampling

We surveyed anuran communities during a single rainy season, from October 2015 to March 2016 (total length was 165 d). All surveyed streams were flowing during this period. We used two survey methods: an active approach of Standardized Acoustic and Visual Transect Sampling (SAVTS) and a passive method using Automated Acoustic Recorders (AAR; Parris 2004). Most sites (96%) were surveyed a total of five times: two with the active method and three with the passive method (two sites were surveyed just once with the active method due to logistical issues). The minimum distance between sampling sites was 250 m, which we assumed to be sufficient for independence for tropical amphibian communities (Mendenhall et al. 2014), and the maximum distance was approximately 17,500 m.

For the active method (SAVTS), we established a 100 m transect segment in which two to three people systematically walked (J. W. Ribeiro, Jr. participated in all survey events) and recorded all observed individuals within approximately 10 m on each side. During each sampling event, we visually searched for amphibians in the stream channel, surrounding vegetation, and ground, and recorded all calling individuals (Parris 2004, Ficetola et al. 2011, Konopik et al. 2015). The amphibian species observed during SAVTS were identified in the field when possible, and the specimens that we could not identify in the field were collected, euthanized, preserved in 10% buffered formalin and deposited in the Célio F. B. Haddad anuran collection (CFBH-Institute of Biosciences, São Paulo State University, Rio Claro, Brazil) for later identification in comparison to museum specimens. Every site (except for two) was surveyed twice with the active method (from dusk to 01:00) with a minimum effort of two person-hours searching per sampling occasion.

For the passive survey, we placed an AAR (Song Meter SM3; Wildlife Acoustics, Maynard, Massachusetts, USA) approximately 1.5 m above the ground in the middle of a transect segment at each of 50 sampling sites (Parris 2004, Alix et al. 2014, Walls et al. 2014). Most tropical amphibians are vocally active during early evening, however some stream-dwelling amphibians of the Brazil's Atlantic Forest are active diurnally (Haddad et al. 2013). Therefore, we programmed the AAR to record 5-min periods each hour from 16 to 23 h (four periods in daytime and four in nighttime) for three days (Walls et al. 2014). We considered the eight periods recorded during a given day as a single sampling event (40 min length total), such that each site had three replicate survey events (one on each of the three days in which the AAR was present).

We identified amphibian advertisement calls to species by listening to the audio-recorded files and visually investigating the spectrograms using the software Raven Pro version 1.4 (Bioacoustics Research Program 2011). The audio files were identified through comparison to those from published calls of species when available. We also used audio files recorded during the field sampling and from other scientific collections to assist in identification of AAR-recorded calls.

Environmental data sampling

We delineated catchment perimeter and stream channel using a topography map produced by the Brazilian Institute of Geography and Statistics based on the scale 1:50,000. We defined the catchment area above each sampling site using the furthest downstream point from each transect. Hence, catchment area is the complete surface area that contributes to the stream channel in the downstream point from each sampling site (range 4.9–480 ha; Allan and Castillo 2007).

We classified land use and cover using EMPLASA aerial photographs with a scale of 1:25,000 (EMPLASA 2011) into six categories: native vegetation, silviculture, agriculture, lentic water system, buildings, and non-identifiable area. We also used the EMPLASA images to identify main paved and unpaved roads. The terrain slope was derived from the Digital Elevation Model raster image (30-m resolution) from Shuttle Radar Topography Mission (SRTM). For each site, we estimated land use, stream density, and mean reach slope within a 200 m radius buffer (Fig. 1). We used a 200 m radius buffer because Semlitsch and Bodie (2003) showed that the overall core terrestrial habitat for amphibians ranged from 159 to 290 m from the edge of the aquatic site, and we expected that the effect of land use on stream quality and amphibian occurrence would be influential at this scale (Ficetola et al. 2011, Alix et al. 2014, Villaseñor et al. 2017). Some studies have shown that species respond to habitat loss at much greater spatial scales, multiple times that of their dispersal distances (e.g., Fahrig 2013). As such, we additionally ran our model with covariates estimated within a 500 m radius buffer (2.5 times bigger than 200 m), but found comparatively weaker relationships between our response variables and forest cover (Appendix S1). Thus, our analyses suggest that a 200 m radius is an appropriate scale for amphibians, which is consistent with other studies (Semlitsch and Bodie 2003, Ficetola et al. 2011, Alix et al. 2014). All geoprocessing analyses were carried out in ArcGIS 10.3.1 (ESRI 2015).

We obtained precipitation data from the meteorological station in the city of São Miguel Arcanjo, located approximately 25 km away from the study area, which we hypothesized could have influenced detection during sampling. The station collects meteorological data each hour and is maintained by the National Institute of Metrology (INMET), Brazil. We summed each survey day's full 24 h of precipitation to use as a covariate of daily precipitation (range from 0 to 39 mm/d).

To avoid bias due to collinearity of covariates, we checked for correlations between all covariates using Kendall's tau coefficient (Sokal and Rohlf 1994). Because silviculture was strongly correlated with forest cover ($r = -0.64$), we removed silviculture as a covariate. Forest cover was weakly correlated to agriculture ($r < -0.25$), suggesting that collinearity between these covariates was not a source of bias in our model (Appendix S2). All covariates used in our model had low pairwise correlations (<0.42; see Appendix S2). Forest cover ranged from 30.9% to 100% and agriculture ranged from 0% to 64.5% in our sampling sites (200 m radius buffer). Reach slope in each buffer varied from 8.2% to 31.3%. Stream density was defined as the stream length (m) within 200 m buffer and ranged from 26.2 to 89.2 m/ha. Roads, lentic water, buildings, and non-identifiable area were rare landscape features in our study area, and were thus not included in our model.

Spatial autocorrelation can reduce precision and predictive power in statistical models when it occurs in both response and predictor variables (Legendre et al. 2002). Spatial autocorrelation in species occurrence or abundance is often linked to spatial correlations in covariates themselves (e.g., habitat type). As such, we carefully chose the covariates for our model. Even so, we evaluated any potential spurious effects of spatial correlations on species occurrence and richness patterns using spline correlograms on the raw data (using only species that were observed in at least 5% of sites). The spline correlogram is a nonparametric covariance function that estimates spatial dependence as a continuous function of distance (Bjørnstad and Falck 2001, Bjørnstad 2016). We followed Burton et al. (2012) who used detection data to evaluate spatial autocorrelation in a hierarchical multi-species modeling framework. The confidence intervals of all spline correlograms included zero across all distances suggesting no evidence of spatial correlation on species observations or richness (see Appendix S3). Thus, spatial autocorrelation was unlikely to be a source of bias in our analysis and was not further considered.

Multi-species model

We built a hierarchical multi-species occupancy model to investigate the relationships between landscape characteristics and occurrence probabilities of individual species, while accounting for detection biases during the survey process (Dorazio and Royle 2005, Zipkin et al. 2009). As with all occupancy models, we distinguish absence at a site from a missed detection (false negative) through repeated sampling over a timeframe during which the community is closed (Mackenzie et al. 2002, Kéry and Royle 2015). We assume that our survey period (six months) was sufficiently short such that there were no extinction or colonization events in the local communities (i.e., no changes to species occupancy across all survey events). We assumed all species were correctly identified with AAR because (1) audio-recorded files were exhaustively investigated and compared with other audio files, (2) all audio files were checked by the same researcher minimizing bias introduced by observer skill, and (3) we recorded species calling during transect sampling to assist with identifications (which allowed us to link the field identification with audio-recorded identification).

We denoted the presence of species i at site j as a binary latent state variable where $z_{i,j} = 1$ if the species was present and zero otherwise. The occurrence probability of species i at site j ($\psi_{i,j}$) was then modeled as a Bernoulli random process: $z_{i,j} \sim$ Bernoulli ($\psi_{i,j}$). A species i could only be detected ($y_{i,j,k} = 1$) during sampling if it occurred at the site j ($z_{i,j} = 1$). The probability that species i was observed at site j during the kth survey period ($p_{i,j,k}$) was modeled as a Bernoulli random variable conditional on occurrence: $y_{i,j,k}|z_{i,j} \sim$ Bernoulli ($z_{i,j} \cdot p_{i,j,k}$). Thus, if a species was absent at a site ($z_{i,j} = 0$) then the detection probability of that species was necessarily zero. To estimate the occurrence probability of each species at each site ($\psi_{i,j}$), we included site-specific covariates using a logit link function:

$$\text{logit}(\psi_{i,j}) = a0_i + a1_i \times \text{forest}_j + a2_i \times \text{agriculture}_j$$
$$+ a3_i \times \text{catchment area}_j + a4_i \times \text{stream density}_j$$
$$+ a5_i \times \text{slope}_j.$$

The parameters $a1$–$a5$ were the individual effects of forest cover, agriculture, catchment area, stream density, and slope, respectively, on species-specific occupancy. Note that each of the parameters were indexed by species (i) and were thus

estimated separately for all species in the community. Similarly, we incorporated the effect of survey type (active vs. passive), survey date, and precipitation on species-specific detection probabilities ($p_{i,j,k}$) using a logit link function:

$$\text{logit}\ (p_{i,j,k}) = b0_{i,\text{type}} + b1_i \times \text{date}_{j,k} + b2_i \times \text{date}^2_{j,k} + b3_i \times \text{precipitation}_{j,k}.$$

The intercept, parameter $b0_{i,\text{type}}$, was the detection probability (on the logit scale) for each species depending on the survey type (i.e., SAVTS or AAR). The coefficients $b1$ and $b2$ were the linear and quadratic effects of day of year (we assumed the first day as the beginning of Southern Hemisphere spring), and $b3$ was the effect of daily precipitation. Because precipitation influences the calling activity of many anurans (Heard et al. 2015), it can play an important role for detection probability of species (Johnson et al. 2016). We standardized all continuous covariates for both ecological and survey processes to have a mean of 0 and a standard deviation equal to 1 (Zipkin et al. 2009, Kéry and Royle 2015). We used community-level distributions (i.e., hyper-distributions) to link the species-specific parameters, such that each of the species-specific effects ($a0$–$a5$ and $b0$–$b3$) came from common, community-level, normal distributions with a mean and variance that was estimated along with the species parameters (e.g., $a0_i \sim N(\mu_{a0,\sigma^2_{a0}})$; Kéry and Royle 2015). This approach allows us to "borrow strength" across all species in the community and additionally produces community level parameters (e.g., mean and variance), which can be used to summarize an overall community response to individual covariates.

The hierarchical multi-species occupancy model allows for inference on species not detected during surveys through data augmentation (Dorazio and Royle 2005, Kéry and Royle 2015). The goal of data augmentation is to estimate the true (unobserved, latent) species richness of the community, N. Species richness can be equal to or bigger than the number of observed species, n such that $N \geq n$. To estimate N, we augmented the data with 120 potential species (nz) to the n observed species by adding in 120 all zero encounter histories. This creates a supercommunity of $M = n + nz$ possible species. The value of M is not critical to estimate N as long as it is greater than the possible value of species in the region (Dorazio et al. 2006); we chose M much greater than the number of potential species in the region (Forlani et al. 2010, Araujo et al. 2013). We assumed that $N \sim$ uniform $(0,M)$ and added an additional random variable (ω_i) to our model such that $z_{i,j} \sim$ Bernoulli($\omega_i \cdot \psi_{i,j}$) where $\omega_i \sim$ Bernoulli(Ω). We then estimated Ω along with all the other parameters in our model. Thus, if species i was a member of the community then $\omega_i = 1$, otherwise, it was a fixed zero and the probability that it occurred at any of the j sampling locations was zero (Zipkin et al. 2009, Kéry and Royle 2015). The use of community-level distributions on individual species parameters allows estimates of occurrence, detection, and covariate effects for unobserved species through data augmentation.

We fit our multi-species community occupancy model using a Bayesian approach with JAGS version 4.2.0 (Plummer 2016) called from R version 3.3.1 (R Core Team 2016) and the jagsUI package version 1.4.4 (Kellner 2016, see Data S1 for JAGS and R code; all data is publicly available at https://github.com/Xuletajr/Community-occupancy-model-amphibians-atlantic-forest-streams). We ran the model using three Markov chains with 50,000 iterations, burn-in of 30,000 iterations, 10,000 iterations for the adaptation phase, and thinned by 20. We used non-informative prior distributions for community-level model parameters. We evaluated the convergence of Markov chains using R-hat statistic values (<1.1) and by visually inspecting the chains for each monitored parameter (see Data S1 for JAGS and R code).

Results

We observed 36 amphibian species across all sampled sites (Appendix S4). Most observed species were classified as forest specialists (29 species), while only seven were categorized as habitat generalists (Haddad et al. 2013, Appendix S4). Our community model estimated a mean richness of 51 species in the study area (95% credible interval [CI]: 38–79 species; Fig. 2).

Community-level occupancy

The mean response of the community (i.e., the mean of the community-level distribution) was negative to slope, catchment area, and agriculture, and positive to forest cover and stream density at the landscape scale (Fig. 3; Appendix S5). Catchment area and slope had a significant negative relationship with amphibian occupancy probability at the community level (i.e., 95% credible intervals, CI, did not overlap zero; Fig. 3; Appendix S5). For forest cover, the 95% CI of the community-level parameter slightly overlapped zero, yet most values of the posterior distribution (83%) were positive, suggesting forest loss can negatively impact amphibians. For agriculture, the 95% CI of the community-level parameter slightly overlapped zero, but most values of the posterior distribution (92%) were negative, suggesting that matrix type can influence the communities, albeit differentially by species (Fig. 3). Community-level
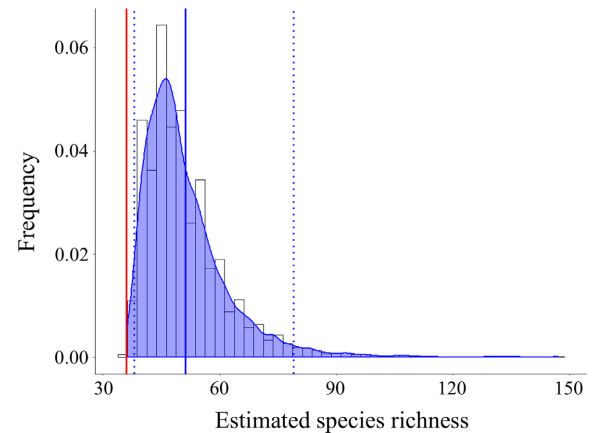

Fig. 2. The estimated number of amphibian species in our sampling region in Brazil's Atlantic Forest. Solid blue line represents estimated mean richness (51 species), blue dotted lines represent the 95% credible interval (38–79 species), and the red line represents the observed number of species (36 species).
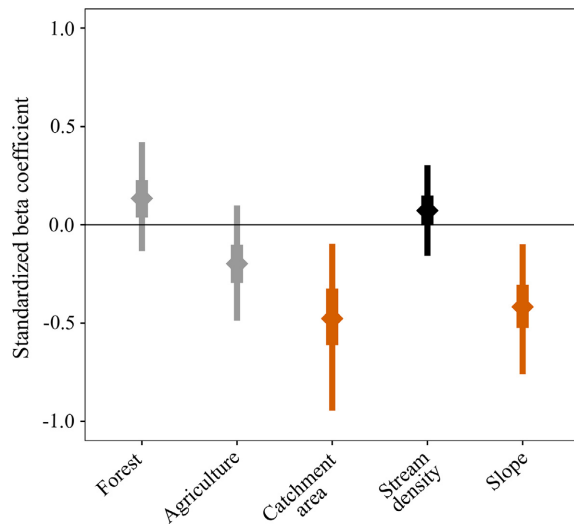
FIG. 3. Estimated beta coefficients for community-level mean occurrence probabilities (posterior means with 95% and 50% Bayesian credible intervals) in Brazil's Atlantic Forest streams. Black bars show relationships in which the 50% credible intervals (CI) overlap zero, gray bars indicate that the 50% CI does not overlap zero but the 95% CI does, and bright red bars indicate that the 95% CI does not overlap zero.

estimates for stream density were positive, but with more than 25% of CIs less than zero, indicating more variable responses of amphibians to this covariate (Fig. 3).

Species-level occupancy

Mean species-level estimates of occurrence probability varied widely, ranging from 0.02 to 0.93 (Appendix S4). Most species had a negative relationship with catchment area, with posterior probability distributions of four observed species not overlapping zero (*Adenomera marmorata*, *Crossodactylus caramaschii*, *Hylodes* gr. *lateristrigatus*, and *Paratelmatobius* sp.), and a positive relationship with four arboreal habit species (only *Vitreorana uranoscopa* 95% CI did not overlap zero; Fig. 4; Appendix S6). Most species responded negatively to slope, with three (*Paratelmatobius* sp., *Physalaemus lateristriga*, and *Proceratophrys boiei*) having 95% CIs that did not overlap zero (Fig. 4; Appendix S6). Eighty-one percent of observed species were negatively related to agriculture, but only *Fritziana* cf. *fissilis* had a 95% CI that did not overlap zero, while 15 other species had negative estimates in which the 75% CI did not overlap zero (Fig. 4). Most species had a positive mean relationship with forest cover and stream density, but relationships were generally small and weak (with more than 25% of CIs less than zero; Fig. 4; Appendix S6).

Detection process

At the community level, the active SAVTS (mean detection = 0.34; 95% CI: 0.19–0.50) was a more effective sampling method than the passive AAR (mean detection = 0.08; 95% CI: 0.02–0.18). Average community detection probability peaked slightly before the middle of the rainy season (Fig. 5; Appendix S5), which occurs around the 73rd day

after the beginning of spring. Daily precipitation had little influence on detection probabilities at both the community and species levels, except for *Proceratophrys boiei*, which was positively linked with daily precipitation and with 95% CI not overlapping zero (Appendix S7).

Average species detection probabilities were highly variable and influenced by the sampling method. Mean species detection probabilities ranged from 0.07 to 0.80 using SAVTS and from 0.01 to 0.88 with the AAR method (Appendix S8). The SAVTS method produced significantly higher detection probabilities for six species compared to the AAR method (*Hypsiboas bischoffi*, *Paratelmatobius* sp., *Rhinella icterica*, *Bokermannohyla circumdata*, *Haddadus binotatus*, and *Ischnocnema guentheri*), while the reverse was true for only two species (*Hylodes* gr. *lateristrigatus*, and *Adenomera marmorata*; Appendix S8). The 95% CIs for species detection probabilities were overlapping for the remaining 28 species, but average detection was higher for the active SAVTS method for most species, which is consistent with the community level-results (Appendix S8).

DISCUSSION

Habitat loss is the greatest threat to the persistence of amphibians (IUCN 2017) and several studies have found that amphibian richness and forest specialist species are positively related to the amount of forest cover (Herrmann et al. 2005, Ficetola et al. 2011, Almeida-Gomes and Rocha 2014, Quesnelle et al. 2015). Likewise, we found a positive relationship between amphibian communities and forest cover in riparian zones of Brazil's Atlantic Forest. Moreover, our results show that streams surrounded by agriculture may have comparatively lower amphibian occurrence probabilities, indicating the importance of the surrounding matrix. The area surrounding forest fragments, and how it is used, is a key element that determines whether a fragment can support species (Melo et al. 2013, Ferrante et al. 2017). Most observed species (80%) in our study are forest specialists (Appendix S4) that are expected to avoid open areas, such as agricultural lands (Dixo and Metzger 2010, Almeida-Gomes and Rocha 2014). Many amphibians require about 200 m of terrestrial habitat surrounding aquatic environments to maintain suitable habitats for refuge, overwintering and foraging (Semlitsch and Bodie 2003). Matrix type can further impact dispersal success, edge crossing, and movement behavior of individuals, which in turn influences population abundance, species occurrences, and metapopulation dynamics of plants, invertebrates, and vertebrates (Prevedello and Vieira 2010). For instance, our multi-species occupancy model shows that treefrog species associated with streams (i.e., *Aplastodiscus albosignatus*, *Phasmahyla cochranae*, and *V. uranoscopa*) respond weakly to forest cover (posterior mean estimates 0, −0.04, and 0.09, respectively), but strongly to agriculture (posterior mean estimates −0.28, −0.37, and −0.36, respectively; Fig. 4; Appendix S6). These results suggest some species may not always respond to forest cover amount per se, but the type of anthropogenic land use surrounding focal forest fragments.

Although our findings highlight the positive influence of forest cover and negative impact of agriculture on amphibian communities and on most individual species, the effects of
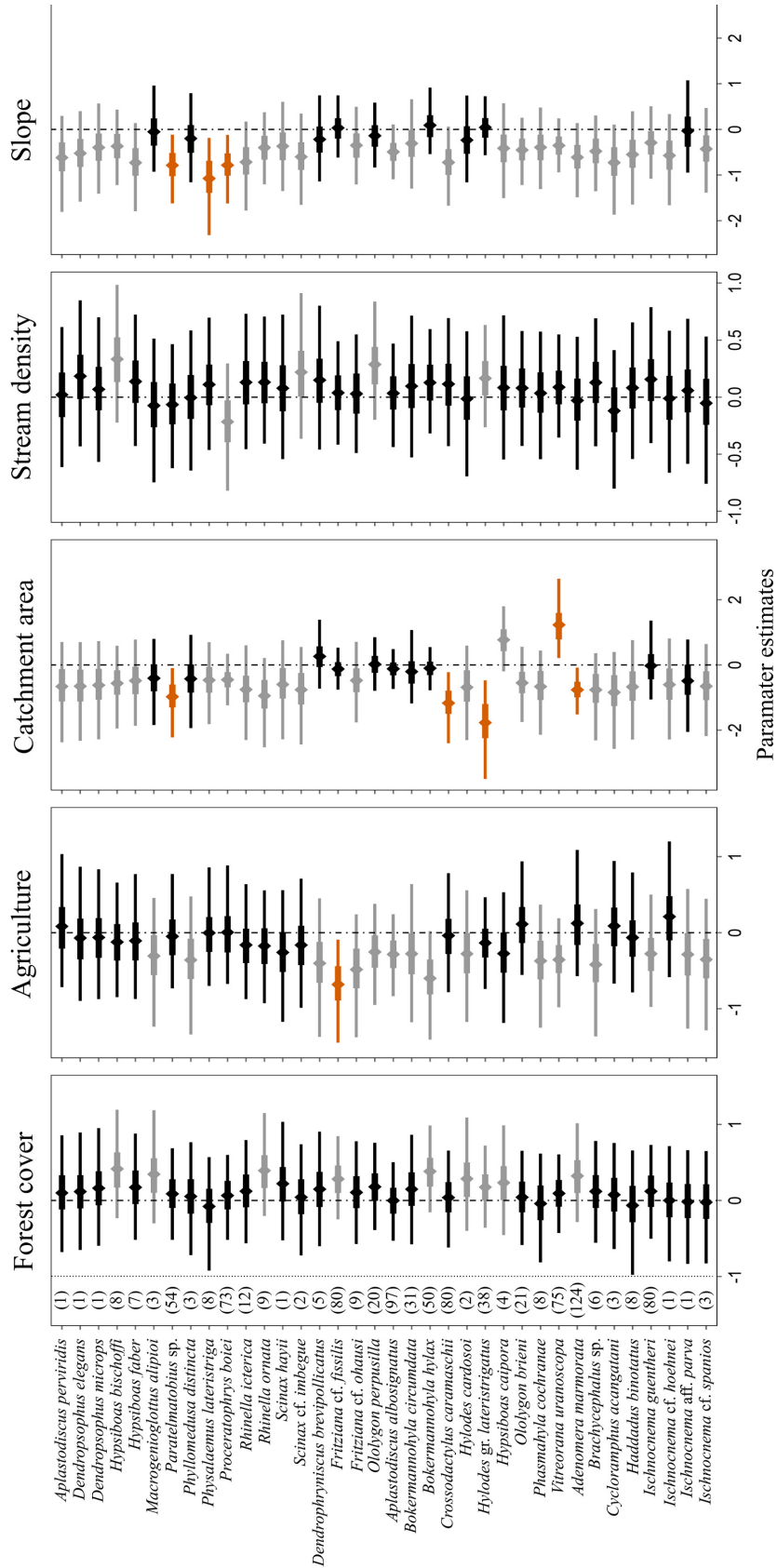
FIG. 4. Species-level mean occurrence probabilities (posterior means with 95% and 50% Bayesian credible intervals for each site-specific covariate) in Brazil's Atlantic Forest streams. Black bars show relationships in which the 50% credible intervals (CI) overlap zero, gray bars indicate that the 50% CI does not overlap zero but the 95% CI does, and bright red bars indicate that the 95% CI does not overlap zero. The numbers in brackets are the number of occasions each species was observed.
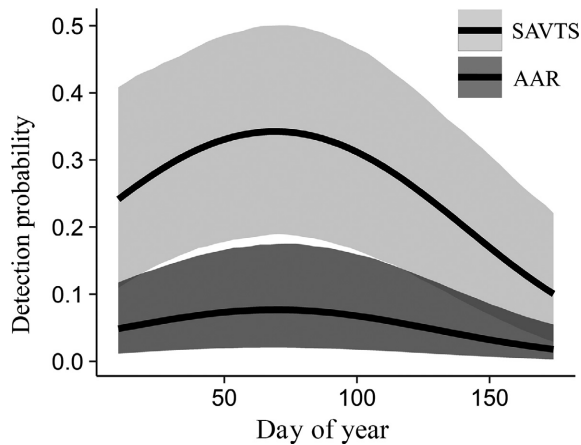
Fig. 5.   Relationships between survey date and estimated community-level detection probability (with shaded 95% credible intervals) for the two survey methods: Standardized Acoustic and Visual Transect Sampling (SAVTS; active approach; light gray), and Automated Acoustic Recorders (AAR; passive approach; dark gray). Day of the year begins the first day of Southern Hemisphere spring of 2015.

these land uses were generally small and weak for many species, including both forest specialists and habitat generalist species (with more than 25% of CIs overlapping zero), indicating a diffuse response of amphibians to these landscape features (only for *Fritziana* cf. *fissilis* the agriculture parameter did not overlap zero; Figs. 3, 4). The study area occurs in a highly forested region and it is possible that we did not obtain a large enough sample size for locations with low forest cover. Additionally, high connectivity between fragments can facilitate movement and dispersal among forest remnants, mitigating effects of forest habitat loss (Driscoll et al. 2013, Melo et al. 2013). Dispersal between breeding sites dramatically decreases extinction risk for American toad (*Anaxyrus americanus*) populations, demonstrating a critical process to the persistence of metapopulations through source–sink dynamics (Willson and Hopkins 2013). Source-sink dynamics can maintain species in suboptimal sites (sink habitats), or even outside their environmental range, through constant and intense dispersal from high-quality source habitats (Willson and Hopkins 2013, Durães et al. 2016). Through this process, riparian zones along the edge of continuous forest (i.e., suboptimal environmental) may be maintaining amphibian populations and communities by way of dispersal from source habitats (i.e., forested habitats). Metzger et al. (2009) showed that the abundance of forest amphibian species in Brazil's Atlantic Forest was positively related to the connectivity between fragments, while forest cover alone had no influence, suggesting that movement is key to maintaining amphibians within tropical fragments.

There was little evidence that stream density is an important covariate for amphibian species and communities in this forest dominated landscape. Stream density is likely more important in highly fragmented landscapes where this variable may be negatively related with habitat split, as low stream density may reduce the likelihood of connection between forest remnants and the hydrological network. Habitat split is triggered by deforestation that disconnects aquatic and forested habitat forcing amphibian species with aquatic reproduction to move from forest fragments to breeding sites

through open areas (Becker et al. 2007, 2010). This is one of the main threats for aquatic-breeding amphibians in tropical fragmented landscapes (Becker et al. 2007, 2010).

Our results indicate that many amphibian species have the highest occurrence probabilities in riparian zones with small catchment area within flat landscapes. Catchment area and slope are proxies of many habitat characteristics, including physical in-stream characteristics and variations in riparian vegetation composition and structure (Richards et al. 1996, Kinupp and Magnusson 2005, Costa 2006, Allan and Castillo 2007). For example, catchment area was strongly correlated with stream width in our study (Kendall's tau coefficient 0.63). Stream size (width, depth, and volume), presence of waterfalls, and stream slope influence species and communities of both tadpole and adult amphibians in tropical forests because they provide different microhabitats (Parris and McCarthy 1999, Eterovick and Barata 2006, Keller et al. 2009, Ribeiro et al. 2012). Slope may negatively affect amphibian dispersal because high slopes lead to higher energetic costs for moving compared to flat locations with low slope values (Lowe et al. 2006, Westgate et al. 2012). For example, stream slope positively influenced the genetic distance of stream salamanders *Gyrinophilus porphyriticus*, indicating that high slope may inhibit the dispersal of individuals (Lowe et al. 2006). In addition, variations in topography are directly linked with variations in vegetation composition in tropical forests (Kinupp and Magnusson 2005, Costa 2006), which can indirectly influence amphibian species distributions. Riparian understory and tree vegetation provide calling microhabitat and shelter for many species of amphibians and act as a buffer for microclimatic conditions (Parris and McCarthy 1999, Keller et al. 2009).

Detection probabilities of all amphibian species were less than one and varied widely between species, influenced by both survey type (active vs. passive) and survey date (Appendices S7, S8). Many studies on tropical amphibian species assume that surveys conducted within one breeding season are sufficient to avoid consideration of species detectability (Metzger et al. 2009, Pardini et al. 2009, Ferrante et al. 2017). However, our results show that detection probability is far below perfect for all species and variable across the rainy season (i.e., the amphibian breeding season). Our results suggest that the active method (SAVTS) is more effective than the passive one (AAR) to sample amphibians in streams and riparian zones. This was an expected outcome because the active method has the advantage of sampling species through both aural and visual surveys, allowing us to detect individuals that were not vocally active such as females, froglets, and individuals resting on leaves, branches, and litter. One third of the observed species were detected only visually with SAVTS and were never recorded calling in our sampling sites during the study period. The active sampling approach we used, SAVTS, is a common and well-established method (Parris 2004, Keller et al. 2009, Ribeiro et al. 2012), while the passive method, AAR, is a more recent approach to survey anurans (Walls et al. 2014, Ribeiro et al. 2017). Although our results suggest SAVTS is a superior method to survey amphibians in tropical riparian zones, this method is limited by the number of available specialists to conduct field surveys. Therefore, AAR is a potential alternative to enhance the number of sampled sites in a region and/or the number of

visits to each site. AAR devices can easily be programmed to record more hours in a day and/or more days during the rainy season without massively increasing field efforts. However, there are data processing concerns with the use of AAR devices, as it generates numerous recording files that require active listening or development of automated species identification algorithms (Ribeiro et al. 2017). Additionally, potentially lower levels of detection necessitate that appropriate analytical models be used with passive survey approaches (e.g., occupancy modeling).

The hierarchical multi-species model is a valuable approach that can model the true occurrence state while accounting for the survey process. Our modeling framework allowed us to estimate the mean response of amphibian communities in addition to species-specific responses to environmental gradients in riparian zones of the Atlantic Forest, without excluding those species that were rare. Our findings suggest that the reduction of forest cover surrounding tropical streams decreases mean occupancy probability at the community level. However, riparian forest fragments may also retain an important fraction of species because some species were not as influenced by forest cover amount. Riparian forest fragments in a forested dominated landscape can help maintain amphibian diversity, highlighting an important strategy for preserving amphibian diversity in human-modified landscapes (Pardini et al. 2009, Rodríguez-Mendoza and Pineda 2010, Almeida-Gomes and Rocha 2014, Mendenhall et al. 2014). Yet, fragments surrounded by agriculture may negatively impact the occurrence probabilities of some species, something that should be considered when developing conservation plans in human-modified landscapes. The negative effects of the surrounding matrix increase with structural differences between the matrix and the focal habitat fragment (Prevedello and Vieira 2010). Thus, we can expect that changes in land use, for instance, from silviculture to agricultural activities are likely to decrease the occurrence probabilities of many amphibian species in riparian fragments because of increased structural differences between fragments and the matrix. Additionally, we showed that slope and catchment area are important environmental covariates influencing the occurrence probabilities of tropical amphibians. Our results combined with land use and topographic maps (which can be produced by Digital Elevation Model raster images, freely available for download [e.g., Topodata database]) can be used to make predictions of amphibian occurrences and distributions in the larger Atlantic Forest. Such projections can be useful to determine where to conduct future research and prioritize conservation efforts.

Literature Cited

Alix, D. M., C. J. Anderson, J. B. Grand, and C. Guyer. 2014. Evaluating the effects of land use on headwater wetland amphibian assemblages in coastal Alabama. Wetlands 34:917–926.

Allan, J. D., and M. M. Castillo. 2007. Stream ecology: structure and function of running waters. Springer, Dordrecht, The Netherlands.

Almeida-Gomes, M., and C. F. D. Rocha. 2014. Landscape connectivity may explain anuran species distribution in an Atlantic forest fragmented area. Landscape Ecology 29:29–40.

Araujo, C. de O., C. K. Matsukuma, and S. M. de A. Santos. 2013. Composição taxonômica e distribuição de anuros no Alto e Médio Paranapanema, estado de São Paulo. Biota Neotropica 13:241–258.

Becker, C. G., C. R. Fonseca, C. F. B. Haddad, R. F. Batista, and P. I. Prado. 2007. Habitat split and the global decline of amphibians. Science 318:1775–1777.

Becker, C. G., C. R. Fonseca, C. F. B. Haddad, and P. I. Prado. 2010. Habitat split as a cause of local population declines of amphibians with aquatic larvae. Conservation Biology 24:287–294.

Bioacoustics Research Program. 2011. Raven Pro: interactive sound analysis software (version 1.4). The Cornell Lab of Ornithology, Ithaca, New York, USA.

Bjørnstad, O. N. 2016. Package "ncf". Spatial nonparametric covariance functions. R package version 1.1-7.

Bjørnstad, O. N., and W. Falck. 2001. Nonparametric spatial covariance functions: estimation and testing. Environmental and Ecological Statistics 8:53–70.

Brook, B. W., N. S. Sodhi, and C. J. A. Bradshaw. 2008. Synergies among extinction drivers under global change. Trends in Ecology & Evolution 23:453–460.

Burton, A. C., M. K. Sam, C. Balangtaa, and J. S. Brashares. 2012. Hierarchical multi-species modeling of carnivore responses to hunting, habitat and prey in a West African protected area. PLoS ONE 7:e38007.

Clément, F., J. Ruiz, M. A. Rodríguez, D. Blais, and S. Campeau. 2017. Landscape diversity and forest edge density regulate stream water quality in agricultural catchments. Ecological Indicators 72:627–639.

Collins, J. P., and M. L. Crump. 2009. Extinction in our times. Global amphibian decline. Oxford University Press, Oxford, UK.

Costa, F. R. C. 2006. Mesoscale gradients of herb richness and abundance in central Amazonia. Biotropica 38:711–717.

Dixo, M., and J. P. Metzger. 2010. The matrix-tolerance hypothesis: an empirical test with frogs in the Atlantic Forest. Biodiversity and Conservation 19:3059–3071.

Dorazio, R. M., and J. A. Royle. 2005. Estimating size and composition of biological communities by modeling the occurrence of species. Journal of the American Statistical Association 100:389–398.

Dorazio, R. M., J. A. Royle, B. Söderström, and A. Glimskär. 2006. Estimating species richness and accumulation by modeling species occurrence and detectability. Ecology 87:842–854.

Dorazio, R. M., M. Kéry, J. A. Royle, and M. Plattner. 2010. Models for inference in dynamic metacommunity systems. Ecology 91:2466–2475.

Driscoll, D. A., S. C. Banks, P. S. Barton, D. B. Lindenmayer, and A. L. Smith. 2013. Conceptual domain of the matrix in fragmented landscapes. Trends in Ecology & Evolution 28:605–613.

Durães, L., F. O. Roque, T. Siqueira, A. M. Santos, M. A. Borges, and R. S. Rezende. 2016. Simulating the role of connectivity in shaping stream insect metacommunities under colonization cycle dynamics. Ecological Modelling 334:19–26.

EMPLASA. 2011. Projeto de Atualização Cartográfica do Estado de São Paulo: Projeto Mapeia São Paulo, São Paulo, Brazil.

ESRI. 2015. ArcGIS Professional GIS for the desktop, version 10.3.1. ESRI, Redlands, California, USA.

Eterovick, P. C., and I. M. Barata. 2006. Distribution of tadpoles within and among Brazilian streams: the influence of predators, habitat size and heterogeneity. Herpetologica 62:365–377.

Ewers, R. M., and C. Banks-Leite. 2013. Fragmentation impairs the microclimate buffering effect of tropical forests. PLoS ONE 8: e58093.

Fahrig, L. 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. Journal of Biogeography 40:1649–1663.

Ferrante, L., F. B. Baccaro, E. B. Ferreira, M. F. de. O. Sampaio, T. Santos, R. C. Justino, and A. Angulo. 2017. The matrix effect: how agricultural matrices shape forest fragment structure and amphibian composition. Journal of Biogeography 44:1911–1922.

Ficetola, G. F., E. Padoa-Schioppa, and F. De Bernardi. 2009. Influence of landscape elements in riparian buffers on the conservation of semiaquatic amphibians. Conservation Biology 23:114–123.

Ficetola, G. F., L. Marziali, B. Rossaro, F. de Bernardi, and E. Padoa-Schioppa. 2011. Landscape-stream interactions and habitat conservation for amphibians. Ecological Applications 21:1272–1282.

Forlani, M. da. C., P. H. Bernardo, C. F. B. Haddad, and H. Zaher. 2010. Herpetofauna do Parque Estadual Carlos Botelho, São Paulo, Brasil. Biota Neotropica 10:265–309.

Haddad, C. F. B., L. F. Toledo, dePrado C. P. A., D. Loebmann, J. L. Gasparini, and I. Sazima. 2013. Guia dos anfíbios da Mata Atlântica: diversidade e biologia. Anolisbook, São Paulo, Brazil.

Hansen, M. C., et al. 2013. High-resolution global maps of 21st-century forest cover change. Science 342:850–853.

Heard, G. W., S. Canessa, and K. M. Parris. 2015. Interspecific variation in the phenology of advertisement calling in a temperate Australian frog community. Ecology and Evolution 5:3927–3938.

Herrmann, H. L., K. J. Babbitt, M. J. Baber, and R. G. Congalton. 2005. Effects of landscape characteristics on amphibian distribution in a forest-dominated landscape. Biological Conservation 123:139–149.

Hof, C., M. B. Araújo, W. Jetz, and C. Rahbek. 2011. Additive threats from pathogens, climate and land-use change for global amphibian diversity. Nature 480:516–519.

Hoffmann, M., et al. 2010. The impact of conservation on the status of the world's vertebrates. Science 330:1503–1509.

IUCN. 2017. The IUCN Red List of Threatened Species. Version 2017-3. http://www.iucnredlist.org

Johnson, B. A., K. Barrett, J. A. Homyack, and R. F. Baldwin. 2016. Anuran occupancy and breeding site use of aquatic systems in a managed pine landscape. Forest Ecology and Management 368:45–54.

Keller, A., M.-O. Rödel, K. E. Linsenmair, and T. U. Grafe. 2009. The importance of environmental heterogeneity for species diversity and assemblage structure in Bornean stream frogs. Journal of Animal Ecology 78:305–314.

Kellner, K. 2016. jagsUI: A Wrapper Around rjags to Streamline JAGS Analyses. R package version 1.4.4. https://github.com/kenkellner/jagsUI

Kéry, M., and J. A. Royle. 2015. Applied hierarchical modeling in ecology: analysis of distribution, abundance and species richness in R and BUGS. First edition. Academic Press, Amsterdam, The Netherlands.

Kinupp, V. F., and W. E. Magnusson. 2005. Spatial patterns in the understorey shrub genus Psychotria in central Amazonia: effects of distance and topography. Journal of Tropical Ecology 21:363–374.

Konopik, O., I. Steffen-Dewenter, and T. U. Grafe. 2015. Effects of logging and oil palm expansion on stream frog communities on Borneo, Southeast Asia. Biotropica 47:636–643.

Kronka, F. J. N., et al. 2005. Inventário florestal da vegetação natural do estado de São Paulo. Imprensa Oficial, Secretaria do Meio Ambiente, Instituto Florestal, São Paulo, Brazil.

Legendre, P., M. R. T. Dale, M.-J. Fortin, J. Gurevitch, M. Hohn, and D. Myers. 2002. The consequences of spatial structure for the design and analysis of ecological field surveys. Ecography 5:601–615.

Lowe, W. H., G. E. Likens, M. A. Mcpeek, D. C. Buso, and M. A. McPeek. 2006. Linking direct and indirect data on dispersal: isolation by slope in a headwater stream Salamander. Ecology 87:334–339.

Mackenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rate when detection probabilities are less than one. Ecology 83:2248–2255.

Matos, F. A. R., L. F. S. Magnago, M. Gastauer, J. M. B. Carreiras, M. Simonelli, J. A. A. Meira-Neto, and D. P. Edwards. 2017. Effects of landscape configuration and composition on phylogenetic diversity of trees in a highly fragmented tropical forest. Journal of Ecology 105:265–276.

Melo, F. P. L., V. Arroyo-Rodríguez, L. Fahrig, M. Martínez-Ramos, and M. Tabarelli. 2013. On the hope for biodiversity-friendly tropical landscapes. Trends in Ecology & Evolution 28:461–468.

Mendenhall, C. D., L. O. Frishkoff, G. Santos-Barrera, J. Pacheco, E. Mesfun, F. M. Quijano, P. R. Ehrlich, G. Ceballos, G. C. Daily, and R. M. Pringle. 2014. Countryside biogeography of Neotropical reptiles and amphibians. Ecology 95:856–870.

Menin, M., A. P. Lima, W. E. Magnusson, and F. Waldez. 2007. Topographic and edaphic effects on the distribution of terrestrially reproducing anurans in Central Amazonia: mesoscale spatial patterns. Journal of Tropical Ecology 23:539–547.

Metzger, J. P., A. C. Martensen, M. Dixo, L. C. Bernacci, M. C. Ribeiro, A. M. G. Teixeira, and R. Pardini. 2009. Time-lag in biological responses to landscape changes in a highly dynamic Atlantic forest region. Biological Conservation 142:1166–1177.

Newbold, T., et al. 2015. Global effects of land use on local terrestrial biodiversity. Nature 520:45–50.

Pardini, R., D. Faria, G. M. Accacio, R. R. Laps, E. Mariano-Neto, M. L. B. Paciencia, M. Dixo, and J. Baumgarten. 2009. The challenge of maintaining Atlantic forest biodiversity: a multi-taxa conservation assessment of specialist and generalist species in an agro-forestry mosaic in southern Bahia. Biological Conservation 142:1178–1190.

Parris, K. M. 2004. Environmental and spatial variables influence the composition of frog assemblages in sub-tropical eastern Australia. Ecography 27:392–400.

Parris, K. M., and M. A. McCarthy. 1999. What influences the structure of frog assemblages at forest streams? Australian Journal of Ecology 24:495–502.

Plummer, M. 2016. JAGS: A program for analysis of Bayesian graphical models using Gibbs Sampling. Proceedings of the 3rd International Workshop on Distributed Statistical Computing, Vienna, Austria.

Popescu, V. D., and M. L. Hunter. 2011. Clear-cutting affects habitat connectivity for a forest amphibian by decreasing permeability to juvenile movements. Ecological Applications 21:1283–1295.

Prevedello, J. A., and M. V. Vieira. 2010. Does the type of matrix matter? A quantitative review of the evidence. Biodiversity and Conservation 19:1205–1223.

Quesnelle, P. E., K. E. Lindsay, and L. Fahrig. 2015. Relative effects of landscape-scale wetland amount and landscape matrix quality on wetland vertebrates: a meta-analysis. Ecological Applications 25:812–825.

R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ribeiro, M. C., J. P. Metzger, A. C. Martensen, F. J. Ponzoni, and M. M. Hirota. 2009. The Brazilian Atlantic forest: how much is left, and how is the remaining forest distributed? Implications for conservation. Biological Conservation 142:1141–1153.

Ribeiro, J. W., A. P. Lima, and W. E. Magnusson. 2012. The effect of Riparian zones on species diversity of frogs in Amazonian forests. Copeia 2012:375–381.

Ribeiro, J. W., L. S. M. Sugai, and M. Campos-Cerqueira. 2017. Passive acoustic monitoring as a complementary strategy to assess biodiversity in the Brazilian Amazonia. Biodiversity and Conservation 26:2999–3002.

Richards, C., L. B. Johnson, and G. E. Host. 1996. Landscape-scale influences on stream habitats and biota. Canadian Journal of Fisheries and Aquatic Science 53:295–311.

Rodríguez-Mendoza, C., and E. Pineda. 2010. Importance of riparian remnants for frog species diversity in a highly fragmented rainforest. Biology Letters 6:781–784.

Ruiz-Gutiérrez, V., and E. F. Zipkin. 2011. Detection biases yield misleading patterns of species persistence and colonization in fragmented landscapes. Ecosphere 2:art61.

Semlitsch, R. D., and J. R. Bodie. 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conservation Biology 17:1219–1228.

Sokal, R. R., and F. J. Rohlf. 1994. Biometry: the principles and practices of statistics in biological research. Third Edition. W.H. Freeman and Company, San Francisco, California, USA.

Surasinghe, T. D., and R. F. Baldwin. 2015. Importance of riparian forest buffers in conservation of stream biodiversity: responses to land uses by stream-associated salamanders across two southeastern temperate ecoregions. Journal of Herpetology 49:83–94.

Tingley, M. W., and S. R. Beissinger. 2013. Cryptic loss of montane avian richness and high community turnover over 100 years. Ecology 94:598–609.

Villalobos, F., R. Dobrovolski, D. B. Provete, and S. F. Gouveia. 2013. Is rich and rare the common share? Describing biodiversity patterns to inform conservation practices for South American anurans. PLoS ONE 8:e56073.

Villaseñor, N. R., D. A. Driscoll, P. Gibbons, A. J. K. Calhoun, and D. B. Lindenmayer. 2017. The relative importance of aquatic and terrestrial variables for frogs in an urbanizing landscape: key insights for sustainable urban development. Landscape and Urban Planning 157:26–35.

Walls, S. C., J. Hardin Waddle, W. J. Barichivich, I. A. Bartoszek, M. E. Brown, J. M. Hefner, and M. J. Schuman. 2014. Anuran site occupancy and species richness as tools for evaluating restoration of a hydrologically-modified landscape. Wetlands Ecology and Management 22:625–639.

Westgate, M. J., D. A. Driscoll, and D. B. Lindenmayer. 2012. Limited influence of stream networks on the terrestrial movements of three wetland-dependent frog species. Biological Conservation 153:169–176.

Willson, J. D., and W. A. Hopkins. 2013. Evaluating the effects of anthropogenic stressors on source-sink dynamics in pond-breeding amphibians. Conservation Biology 27:595–604.

Zipkin, E. F., A. Dewan, and J. Andrew Royle. 2009. Impacts of forest fragmentation on species richness: a hierarchical approach to community modelling. Journal of Applied Ecology 46:815–822.

Zipkin, E. F., E. H. C. Grant, and W. F. Fagan. 2012. Evaluating the predictive abilities of community occupancy models using AUC while accounting for imperfect detection. Ecological Applications 22:1962–1972.

Supporting Information

Data Availability