#### **ORIGINAL RESEARCH**



# The role of seasonal migration in predicting amphibian population persistence across fragmented tropical landscapes: an individual-based model

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#### Abstract

Anthropogenic habitat disturbances often create discontinuity between the multiple classes of natural habitats that many species need to complete their life cycles. This process, termed *habitat split*, is common across Neotropical landscapes and negatively impacts several classes of vertebrates and invertebrates. For instance, habitat split—often arising from habitat loss and fragmentation—exposes aquatic-breeding amphibians to risky migrations through disturbed environments as they move between natural terrestrial habitats and aquatic breeding sites, contributing to population declines. In contrast, terrestrial-breeding amphibians should not be impacted by this form of habitat split because they may spend their entire life cycle in the same terrestrial habitat. We used available field data and natural history information to develop Individual-Based Models (IBM) that account for seasonal migrations to quantify the impact of different levels of habitat split on population survival of Brazilian amphibians. Our IBM results align with our observed field data, indicating a disproportionate decline in the occurrence and population abundances of migrating aquatic-breeding amphibians compared to non-migratory terrestrial-breeding amphibians in regions with high habitat split. An intermediate dispersal optimum for aquatic-breeding frogs was suggested by our IBM, indicating that long-distance dispersal might not always be advantageous for population persistence, likely due to tradeoffs between reproduction and migration risk. Our spatial model framework factoring breeding migration could be applied widely across ecoregions of interest and help inform targeted habitat restoration strategies to curb localized amphibian declines and extinctions.

**Keywords** Dispersal · Migration · Reproductive mode · Amphibian declines · Deforestation · Amphibia · Anura · Atlantic forest

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#### Introduction

Animal movement plays a crucial role in determining the long-term viability of wildlife populations (Morales et al. 2010; Jeltsch et al. 2013). Movement can be affected by ecological and biogeographical factors, such as the spatiotemporal distribution of resources, habitat quality, predation, and competition interactions (Dingle & Drake 2007; Alerstam et al. 2003). While animal movement broadly supports population viability, migrations—defined as seasonal movements between habitats, particularly to breeding sites—are especially critical for the persistence of local populations (Bauer and Hoye 2014). However, the accelerated change in land cover and land use has disrupted natural landscapes and negatively impacted the migration of hundreds of invertebrate and vertebrate species (Robinson et al. 2001, 2009; Wilcove & Wikelski 2008; Lennox et al. 2016).

Most amphibian species (Class Amphibia), which are the most threatened group among vertebrates, have a biphasic life cycle with an aquatic larval phase and a post-metamorphic terrestrial phase (hereafter aquatic-breeding amphibians; Haddad & Prado 2005; Nunesde-Almeida et al. 2021). During the reproductive period, adults of several aquatic-breeding amphibian species leave terrestrial habitats in search of breeding sites such as streams or ponds. After reproduction, adults and juveniles of the year migrate to forage and overwinter in adjacent terrestrial habitats. However, breeding migrations can be disrupted in landscapes where aquatic breeding sites and remnants of natural terrestrial vegetation are disconnected through agriculture, livestock, or other anthropogenic activities (Cushman 2006; Compton et al. 2007). This human-induced discontinuity between terrestrial and aquatic habitats that are used by different amphibian life stages (termed habitat split) forces many amphibian species to migrate through disturbed environments (Pope et al. 2000), ultimately leading to population declines (Becker et al. 2007; 2010). Conversely, amphibian species that complete their ontogeny entirely in terrestrial habitats either through (i) direct development within the egg, (ii) endotrophic larval development in terrestrial chambers, or (iii) those that reproduce in water cavities of terrestrial plants (phytotelma) (hereafter terrestrial-breeding amphibians) do not need to migrate to lentic or lotic water bodies to complete their life cycle (Haddad & Prado 2005; Nunes-de-Almeida et al. 2021). In summary, habitat split is predicted to negatively impact aquatic-breeding amphibians, while it is expected not to affect their terrestrial-breeding counterparts. Consequently, the potential decline and extinction of aquatic-breeding populations may lead to significant shifts in amphibian community structure (Becker et al. 2007; Fonseca et al. 2008).

In several tropical landscapes with high topographic complexity, habitat fragmentation often results in high levels of habitat split (Viana et al. 1997; Ribeiro et al. 2009). These landscapes often have human settlements concentrated in valleys where water is available for human use, including agriculture and livestock production (Ribeiro et al. 2011). In contrast, forest remnants are concentrated on steep slopes and mountaintops with poor-quality soils (Silva et al. 2007). This is the case in sections of the Brazilian Atlantic Rainforest, where a large fraction of forest fragments is spatially disconnected from permanent water bodies and the adjacent drainage network (Becker et al. 2010; Vancine et al. 2024). The lack of spatial connectivity between forest and riparian zones impairs seasonal migrations of a myriad of aquatic-breeding amphibian species, where post-metamorphic frogs are forced to cross inhospitable habitats to complete their life cycle (Becker et al. 2007; 2010). A theoretical model was developed to predict the impact of split distance—the distance between natural terrestrial and aquatic habitats—on population demographics (Fonseca et al. 2013), with an empirical application (Lion et al. 2014). The model also suggested that

higher dispersal abilities reduced the negative effects of habitat split on aquatic-breeding amphibian populations, supporting the idea that dispersal ability is a critical factor in mitigating fragmentation impacts. While previous studies have modeled the effects of habitat split, few have integrated empirical field data with spatially explicit demographic models accounting for amphibian migrations. Our study contributes to this body of literature by forecasting the impact of habitat split on amphibians with contrasting reproductive modes and migratory behaviors.

Here, we employed an Individual-Based Model (IBM) framework to quantify the differences in the effects of habitat split on both aquatic-breeding and terrestrial-breeding amphibians, each with varying dispersal abilities. We used available natural history information for model parametrization and empirical field data for model validation. We applied our model framework that factors seasonal amphibian migrations to: (i) a focal disturbed landscape in the Brazilian Atlantic Forest, and (ii) four hypothetical landscapes with different levels of habitat split that enabled us to manipulate the degree of split distance while controlling for habitat loss. Specifically, we hypothesized that our models would show reduced relative abundance of migrating aquatic-breeding amphibian species in landscapes with high levels of habitat split while non-migratory terrestrial-breeding amphibians would show stable population abundances independent of landscape-scale habitat split. Finally, we evaluated the effect of reproductive modes and dispersal ability as predictors of amphibian population abundance (number of individuals per cell) and occurrence (presence of at least one individual in a cell) under varying levels of habitat split. We anticipated that as the distance of habitat split increases, the impacts on the abundance and occurrence of aquatic-breeding amphibians intensifies, while terrestrial-breeding amphibians were expected to show no response regardless of the degree of habitat split. Moreover, we hypothesized that, in both the focal and hypothetical models, aquatic-breeding amphibians with greater dispersal ability experienced less impact from habitat split in disturbed landscapes compared to their lower-dispersing counterparts. In contrast, dispersal ability was not expected to influence the population dynamics of terrestrial-breeding amphibians under any scenario. Our results provide a spatial modeling framework that incorporates the impact of anthropogenic habitat disturbance on amphibian migratory behavior and could be applied to predict amphibian population persistence/viability in regions with limited data on population demographics.

# Methods

To begin, it is crucial to distinguish between habitat fragmentation and habitat split. While fragmentation can lead to habitat split, the latter specifically pertains to the disruption of spatial connectivity between critical habitats required for a species to complete its life cycle.

### Study landscape, field sampling, and amphibian reproductive strategies

Our focal study landscape encompasses a severely disturbed area (hereafter disturbed forest), and an adjacent area of mature Atlantic Rainforest at Parque Estadual da Serra do Mar—Núcleo Santa Virgínia (hereafter continuous forest) in the municipality of São Luiz do Paraitinga, state of São Paulo, Brazil (23° 13' S, 45° 18' W; Fig. 1A). Forest fragments in the disturbed area cover~12% of our focal study landscape and are located at higher



#### A Study landscape

Fig. 1 Study landscape of São Luiz do Paraitinga, State of São Paulo (A). The square on the globe image highlights the approximate location of the focal study landscape in Brazil. Depiction of the hypothetical landscapes (B). Four representations of the same area under different degrees of habitat split, where OC=lack of habitat split, 1C=low split distance, 2C=intermediate split distance, and 3C=high split distance (C). Green represents natural forest habitats in both landscapes, white represents non-natural vegetation, and lines represent riparian zones

elevations ( $844 \pm 8.0$  m a.s.l) compared with the anthropogenic matrix ( $816 \pm 7.7$  m a.s.l). The matrix comprises pastures and other non-natural vegetation types covering the mostly flat, fertile, and irrigated areas commonly used for agriculture, while forest fragments are often disconnected from perennial water bodies (Becker et al. 2007). Riparian zones and associated aquatic habitats, such as streams, ponds, and swamps, are the main breeding sites for aquatic-breeding amphibians while understory and forest floor are the main breeding sites for terrestrial-breeding amphibians. Thus, terrestrial-breeding species can breed in any remnant of natural forest, microclimate permitting (Haddad et al. 2013; Toledo et al. 2021).

We used available field survey data of forest-associated leaf-litter frogs in our focal study landscape, collected between 2003 and 2006 (Anjos 2008; Giasson 2008; Becker,

et al. 2010). Sampling for these independent studies consisted of both visual-encounter surveys and sampling using pitfall traps with drift fences. We did not include tree frogs in our analyses (Hylidae, Centrolenidae, and Hemiphractidae) due to the restricted trapping effectiveness of pitfall traps for this group of amphibians. Thus, we focused only on leaf-litter amphibian species. We classified frog species as aquatic-breeding or terrestrial-breeding based on the 39 reproductive modes of Neotropical anurans (Haddad & Prado 2005; Table S1). Data on relative abundance among species was lumped for each section (disturbed forest *vs.* continuous forest) of our focal study landscape. These data were used to validate our IBM for the focal study landscape by comparing patterns of amphibian population abundance and occurrence of aquatic-breeding *vs.* terrestrial-breeding species among disturbed *vs.* continuous forests.

#### Land cover and hypothetical landscapes

To estimate the effect of discontinuity between natural forest and riparian zones (a habitat split for amphibians) on population survival, we categorized our focal study landscape into four land cover types: 1–riparian habitat in disturbed vegetation, 2–riparian habitat in natural forest, 3–disturbed vegetation, and 4–natural forest (Fig. 1A). For this classification we created a raster of 50 m resolution using a 2002 land-cover classification (5-m resolution SPOT image) and hydrographic maps (IBGE 1:50.000).

To estimate the effect of split distance on population survival, we also designed four hypothetical landscapes using the same land cover types of our focal study landscape, varying in split distance from one to three 50 m  $\times$  50 m cells (C). The first hypothetical landscape had continuous terrestrial and aquatic habitats (0C, no habitat split). The second hypothetical landscape had a habitat split of 50 m of distance (1C, low split distance), which is the lowest monthly dispersal estimated for aquatic-breeding tree frog *Boana faber* in a telemetry study conducted in the Atlantic Forest (see Supplementary Fig. S1; Neely 2023). The third hypothetical landscape had a split distance of 100 m (2C, intermediate split distance) and the fourth landscape had a split distance of 150 m (3C, high split distance); split distances rarely exceeded 150 m in our study landscape. Finally, to exclude the effect of habitat loss, we standardized the width of the riparian zone to 100 m and forest fragments to 400 m on our hypothetical landscapes (Fig. 1B, C). All these raster landscapes were created using ArcGIS 10.6.1.

#### Model description

We designed and implemented an Individual-Based Model (IBM) to simulate temporal abundance and occurrence of two amphibian groups with different reproductive strategies in our focal study landscape (Fig. 1A) and our hypothetical landscapes (Fig. 1B, C). We used the Overview, Design concepts, and Details (ODD) protocol for the IBMs description (Grimm et al. 2010, 2020). IBMs were implemented in Java with a Perl wrapper (Christiansen et al. 2012), and code is available in Supplementary Information. All model parameters were based on natural history information from the literature, author expertise, and direct field observation from previous studies (Table 1; Becker et al. 2007; Giasson et al., 2008; Anjos et al., 2008; Haddad et al. 2013).

Parameters Ab   Parameters Ab   Start brobability 0.5   Start breeding in month # 4	Tb	
Sex ratio probability 0.5 ( Start breeding in month # 4 4		Description/Keierence
Start breeding in month # 4 4 4 4 4 4 4 4 4 4 4 4 4 4 4 4 4 4	0.5	0.5 probability of being female (or male)
Fnd hreeding in month #	4	Breeding lasts for four months (Becker et al. 2010; Haddad et al. 2013)
	٢	Breeding lasts for four months (Becker et al. 2010; Haddad et al. 2013)
Dispersal probability per month 0.2–1	0.2 - 1	Dispersal given the seasonality of breeding migrations (Becker et al. 2007; Haddad et al. 2013)
Average sexual maturity (years) 2	0	Average sexual maturity for the amphibians present in the study landscape (Haddad et al. 2013)
Initial individuals per cell 5	5	Models started with 5 individuals in each cell
Maximum longevity (months) 36	36	Average longevity for the amphibians present in the study landscape (Haddad et al. 2013)
Carrying capacity for all cell types 10	10	Modeled carrying capacity for $50 \text{ m}^2$
Density independent death (%) per time step for different cell types		Density-independent death increase towards disturbed areas (Becker et al. 2010)
Cell type 1—riparian habitat in disturbed matrix 0.05 (	0.05	
Cell type 2—riparian habitat in natural forest 0.03 t	0.03	
Cell type 3—disturbed vegetation 0.08 t	0.08	
Cell type 4—natural forest 0.03 (	0.03	
Offspring per female for different cell types		The number of offspring is affected by reproductive mode and the availability of reproductive sites, which
Cell type 1—riparian habitat in disturbed matrix 2	0	are reduced in disturbed areas (Haddad & Prado 2005; Almeida-Gomes & Rocha 2015; Nunes-de-
Cell type 2—riparian habitat in natural forest 2	0	Almeida et al. 2021)
Cell type 3—disturbed vegetation 0 0	0	
Cell type 4—natural forest 0	0	

Table 1 (continued)			
Parameters	Ab	Tb	Description/Reference
Friction time 1			Friction (1) toward water bodies during breeding season for aquatic-breeding amphibians
Cell type 1-riparian habitat in disturbed matrix	0.01	66.0	Friction (2) toward forest during non-breeding season for aquatic-breeding amphibians, and during whole year for terrestrial-breeding amphibians
Cell type 2-riparian habitat in natural forest	0.01	0.01	Aquatic-breeding species embark on seasonal breeding migrations between terrestrial and aquatic habitats (Haddod & Brodo 2005, Beolear et al. 2007, Haddod et al. 2013)
Cell type 3-disturbed vegetation	0.99	0.99	Terrestrial-breeding species tend to avoid moving through disturbed environments or migrating (Haddad &
Cell type 4—natural forest	0.99	0.01	Prado 2005; Becker et al. 2007)
Friction time 2			
Cell type 1-riparian habitat in disturbed matrix	0.99	66.0	
Cell type 2—riparian habitat in natural forest	0.99	0.01	
Cell type 3-disturbed vegetation	0.01	0.99	
Cell type 4—natural forest	0.01	0.01	

#### Purpose

Our models aim to quantify the effect of habitat split on aquatic-breeding and terrestrialbreeding amphibians, and to determine how movement of aquatic-breeding amphibians could mitigate the adverse effects of habitat split on amphibian population abundance and occurrence.

#### Entities, parameters, and scales

IBM entities include cells (pixels), aquatic-breeding amphibians, and terrestrialbreeding amphibians. The study landscapes had dimensions of  $691 \times 380$  pixels, while the hypothetical landscapes had dimensions of  $705 \times 434$  pixels. State parameters for aquatic-breeding and terrestrial-breeding amphibians are listed in Table 1.

#### Process overview and scheduling

In our models, each time step represents one month, and simulations were run for 30 years. At each time step, individuals age, reproduce, disperse and die, and state parameters are updated accordingly. Our model also features a breeding season and a non-breeding season, aligning with the duration of the rainy season in our study land-scape (Becker et al. 2007; Haddad et al. 2013). The submodels describing these processes are listed in the submodels in Sect. "Submodels".

### Design concepts

**Basic principles** The model allows the categorization of animals according to their habitat complementation requirements for reproduction and other life history traits, thereby facilitating the assessment of disparities in various life history traits within a specified landscape. Additionally, the model enables the exploration of how different levels of mobility influence population resilience in disturbed environments. Although we had substantial natural history information for most of the local species, we did not implement species-specific IBMs for each species in the focal community due to the observed diversity in life histories among tropical amphibian communities. Instead, we ran IBMs independently for the two reproductive modes of interest in this study—aquatic-breeding and terrestrial-breeding—each incorporating varying dispersal abilities, while selecting other parameters based on overall life history attributes from our focal community (Table 1).

**Emergence** The survival and reproduction of aquatic-breeding and terrestrial-breeding amphibians (agents) emerge in response to suitable breeding conditions.

Adaptation and objectives To avoid competition for resources and predation or desiccation, individual amphibians (agents) refrain from moving to cells with maximum carrying capacity reached and to inhospitable cells, respectively. Additionally, agents are assumed to move towards cells favorable for breeding. In general, a friction matrix in the model guides amphibian migration toward favorable breeding cells or away from inhospitable cells during non-reproductive periods.

**Sensing** Amphibian agents are presumed to sense the habitat types of the cells and move through the landscape toward their desired habitat. In this way, inhospitable habitats are generally avoided (probability values can be adjusted in the model), and during the breeding season, animals search for suitable breeding habitats.

**Interaction** Individuals interact directly with their environment (*e.g.*, cell habitat type) and with each other, which can result in breeding if sexually mature males and females are in the same cell with suitable habitat. Individuals also interact indirectly with each other, which can result in death if the cell's carrying capacity is exceeded.

**Stochasticity** Stochasticity is used in initializing the model (Initialization, below) to create a random age distribution and sex ratio among amphibian agents in each cell. Additionally, during simulation, the direction of movement for each individual amphibian is randomized, as well as the occurrence of movement if the dispersal probability chosen by the modeler is less than 100%. In other words, if the dispersal probability is 40%, the movement may or may not occur at the end of each time step, which is also randomized in our model. While the general direction of migration for aquatic-breeding individuals is influenced by assigned friction values guiding them toward their breeding habitats during the breeding season and towards forest habitats during the non-breeding season (see Breeding Migration in Sect. "Submodels"), the precise path taken incorporates randomness, creating variability in routes. Finally, the number of offspring and deaths in each cell also factors some degree of stochasticity. The number of offspring in each cell depends on the cell type and the presence of sexually mature males and females, while deaths may be influenced by the type of habitat the animal occupies. Collectively, these processes enable each model run to generate distinct results.

While the model has the capacity to incorporate a stochastic extinction variable, it was not included in this study. Stochastic extinction operates by randomly removing individuals within a specified area, essentially creating a zone that results in the elimination of all individuals within it. This parameter represents instances of local extinctions due to factors such as natural disasters and disease outbreaks. The modeler has the flexibility to define both the minimum and maximum extinction areas.

**Observation** The number of individuals in each cell and the number of occupied cells is recorded for each time step. Additionally, if repetitions are requested by the modeler, a matrix is generated at the end of each repetition containing information about the number of animals in each cell. Finally, the graphical user interface (GUI) in our Java package provides real-time map displays (*i.e.*, the landscape provided by the modeler) of the number of individuals in each cell, the number of occupied cells, and the movement of individuals across the landscape.

Learning, prediction, and collectives None of these elements are included in our model.

#### Initialization

The IBM is initialized by uniformly seeding five individual amphibians per cell, with a sex ratio assigned with 50/50 probability and with age drawn uniformly from zero to the maximum defined longevity of three years (based on average longevity data for amphibians in our focal study site; Haddad et al. 2013; C.F.B. Haddad, unpublished data). Furthermore, the model presented here was initialized with both study and hypothetical landscape ASCII rasters, as described in Sects. "Land cover and hypothetical landscapes" and "Entities, parameters, and scales", but any landscape of interest to the modeler can be applied.

### Input data

Each input data was carefully selected to generalize patterns observed in different species within our focal study landscape. Some parameters values change according to the habitat type of the cell and season (Table 1). Dispersal probability (*i.e.*, 0.2 to 1) represents the likelihood of migrating to another cell and is assigned based on the modeler's interest. These input parameters values can be easily modified by users through the Perl model interface, enabling the application of this model to other species or landscapes of interest.

### Submodels

**Mortality** An individual dies when reaching maximum longevity of 3 years. Furthermore, individuals experience density-dependent death (DDD), which is determined by a carrying capacity of 10 individuals in each cell. That is, when the number of individuals within a cell surpasses 10, individuals are randomly removed from the model to prevent the cell from exceeding its carrying capacity. Additionally, individuals are susceptible to density-independent death (DID), which escalates in disturbed areas (Becker et al. 2010); hence, DID values are dependent on the habitat type of the occupied cell (Table 1).

**New offspring** Breeding occurs when a female of breeding age is in a suitable breeding habitat (*e.g.*, riparian habitats for aquatic-breeding amphibians and natural forests for terrestrial-breeding amphibians) during the breeding season, and a male is also present in the same cell. Individual frogs can breed once per month during the breeding period, in the same or in different cells. The number of offspring per female follows a Poisson distribution, resulting in random and independent birth events with the average number of offspring depending on the habitat type. In unsuitable cells for reproduction, the number of offspring is set to 0, whereas in suitable habitats for reproduction it is set to 2 (Table 1). These values are based on the author's expert opinion regarding amphibian survival, rather than the number of eggs laid. Finally, the sex of offspring is assigned with a 50% probability of being male or female.

**Dispersal** For each cell within our landscapes, dispersal is allowed to any of the eight surrounding cells, except for cells at the edge of our matrix (*i.e.*, the simulation had reflecting boundaries) or cells with maximum carrying capacity reached. Aquatic-breeding and terrestrial-breeding amphibians are allowed to move from one cell to another every month, and the frequency of this movement depends on the dispersal probability set for the model. However, the direction of dispersal may depend on breeding migration

(see below). We set dispersal probabilities for each model, and they remained constant throughout all time steps. Due to the overall short life cycle of amphibian species in our study landscape, juvenile amphibians disperse and move similarly to adults, with the difference that they do not breed.

**Breeding migration** The IBM model incorporates a friction matrix to induce migratory behavior in aquatic-breeding amphibians. During time steps corresponding to the breeding months (time steps 4 to 7; Friction time 1), aquatic-breeding amphibians move towards aquatic habitat cells, and during time steps corresponding to the non-breeding season (time steps 8 to 3; Friction time 2), they move towards natural forest cells. Each cell in the landscape receives probability values (*i.e.*, 0.01 or 0.99) depending on the habitat type and season. The value 0.01 attracts the animal's movement towards that cell, while 0.99 repels it. Therefore, if an animal has cells with values of 0.01 and 0.99 around it, the movement during dispersal will be biased towards cells with values of 0.01. Friction time 1 has values of 0.01 in riparian habitat cells and 0.99 in non-riparian habitat cells. Friction time 2 has values of 0.01 in forest habitat cells and 0.99 in riparian habitat cells (Table 1).

In contrast, terrestrial-breeding amphibians do not rely on breeding migrations, as they reproduce independently of water bodies (Haddad & Prado 2005), have presumably limited dispersal capabilities (Becker et al. 2007), and require natural forest vegetation to complete their life cycle (Haddad et al. 2013). Previous data from our study landscape indicate that terrestrial-breeding species avoid moving through disturbed environments (Becker et al. 2007). Thus, terrestrial-breeding individuals move toward undisturbed habitats throughout the year, and both friction time values for terrestrial-breeding amphibians support this directional movement, with undisturbed habitats having values of 0.01, while disturbed riparian and matrix habitats have values of 0.99 during all timesteps (Table 1).

**Survival within cell** Amphibian survival in each cell depends on both deaths and births. As mentioned earlier, deaths can occur when individuals reach their maximum longevity or due to DDD and DID. Therefore, only DID can vary according to the cell type. Births can occur in a cell with suitable habitat if there are sexually mature males and females. If breeding is successful, females likely have an average of 2 offspring. Therefore, the total number of offspring per cell also depends on the number of sexually mature females. After each time step, every state parameter is calculated and updated to continue with the same processes in the next time step.

**Movement among cells** Movement in this study includes aquatic-breeding and terrestrial-breeding amphibian dispersal and aquatic-breeding amphibian breeding migration throughout the landscape. Dispersal probabilities represent how likely individual amphibians leave their cell and move to another cell, while breeding migration (friction matrix) specifically promotes the movement of aquatic-breeding amphibians toward favorable habitats for both reproduction and overwintering. Given this movement dynamics, the model does not allow an individual to stay stationary in a cell when the dispersal probability is equal to 1, even if that cell is a favorable one. However, when the dispersal probability is less than 1, individuals may remain stationary in favorable cells or have to move based on the random outcomes of the model. If an individual ends up moving, the direction of movement always accounts for avoiding unfavorable cells.

#### Simulations

For each landscape, we ran models independently for both aquatic-breeding and terrestrial-breeding amphibians, with five dispersal probabilities (0.2, 0.4, 0.6, 0.8, and 1). Each model consisted of 30-year simulations, repeated 100 times. We chose a 30-year time frame because amphibian populations in our models generally stabilized after approximately 10-year simulations (Fig. S2). In our focal study landscape, half of the grid was deemed to be 'continuous' habitat and the other half 'disturbed' habitat (see Fig. 1A). We implemented IBMs in Java, with a Perl wrapper to facilitate running replicate simulations.

#### Statistical analysis

We calculated average amphibian population abundance and occurrence at the end of year 30 for each IBM for all landscapes (study and hypothetical landscapes); averages were based on 100 replicates per model (Table S2 and S3). We plotted IBM results for both our study and hypothetical landscapes. To validate our models, we compared the IBM results of our study landscape with the species' relative abundance data from published field surveys conducted within the same landscape (Tables S1, S2, S3). To compare estimated abundance between IBMs and field survey data, we transformed the values to z-scores (*i.e.*, a data standardization technique given by the formula: observed value—mean/stand-ard deviation). We used a likelihood ratio test to compare aquatic-breeding and terrestrial-breeding IBM occurrence rates in forest fragments disconnected from riparian zones vs. fragments connected to riparian zones.

# Results

Within our focal study landscape, previous independent field studies identified a total of 25 leaf-litter amphibian species. In our study, we selected only data from 18 species that were endemic to the Atlantic Forest, as shown in Table S1 for model validation. Non-endemic species associated with open-canopy vegetation, and thus often benefiting from forest clearing, were excluded from our analysis (*i.e.*, *Elachistocleis cesarii*, *Leptodactylus furnarius*, *L. fuscus*, *L. labyrinthicus*, *L. luctator*, *L. mystacinus*, and *Physalaemus cuvieri*).

The validation of IBMs for our focal study landscape showed that the modeled abundance patterns of both aquatic-breeding and terrestrial-breeding amphibian species in both disturbed and continuous forests aligned with the data obtained from the field surveys conducted within the same focal study landscape (Fig. 2A, B). While the field survey data showed greater variability than the estimates generated by the IBMs, this outcome was anticipated; while the IBMs employed a generalized pattern for a range of species (aquatic or terrestrial), the field data was collected for each specific species, accounting for their individual variability. Furthermore, we observed a consistent pattern for the number of species in the study landscape, with a higher proportion of aquatic-breeding species in the continuous (67%) compared to the disturbed section of the landscape (44%). Conversely, there was a lower proportion of terrestrial-breeding amphibian species in the continuous forest (33%) compared to the disturbed section of the landscape (56%; Fig. 3).

In our study landscape, our models indicated lower abundance and occurrence of aquatic-breeding frogs in the disturbed half of the landscape, where habitat split



Fig. 2 Boxplot displaying the median and quartiles of population abundance (z-scores) for aquatic-breeding and terrestrial-breeding amphibians, derived from both IBM and field-collected data in the disturbed forest (A) and continuous forest (B) within our study landscape

Fig. 3 Absolute number of aquatic-breeding (blue) and terrestrial-breeding (red) species endemic to the Brazilian Atlantic Forest recorded in both disturbed and continuous forest areas of the study landscape. The percentages within the bars indicate the relative abundance of each breeding strategy

![](_page_12_Figure_4.jpeg)

is pervasive, when compared to the continuous forest (Likelihood ratio test: Chisquare = 166.733, P < 0.001; Fig. 4A, B). In contrast, terrestrial-breeding amphibians persisted in all forest fragments (Fig. 4A, B). Our model results indicated that aquatic-breeding amphibians with higher dispersal probabilities (0.6, 0.8, and 1.0) in the disturbed area had higher population sizes than those with lower dispersal rates (Fig. 4A). The modeled abundance and occurrence of terrestrial-breeding amphibians remained constant in both

![](_page_13_Figure_1.jpeg)

Fig. 4 Population abundance (log-transformed) for aquatic-breeding amphibians (blue line) and terrestrialbreeding amphibians (red line) is shown across different probabilities of dispersal in disturbed forest ( $\mathbf{A}$ ) and continuous forest ( $\mathbf{B}$ ) within the study landscape and hypothetical landscapes with varying split distances ( $\mathbf{C}$ )

disturbed and continuous sections of the landscape, independent of their dispersal probability (Fig. 4A, B). Detailed outputs of our models are reported in Tables S2, S3 and Fig. S3.

IBM results obtained from the hypothetical landscapes (controlling for total amount of natural habitat) indicated that the population abundance of aquatic-breeding amphibians was positively affected by dispersal probabilities, especially in split distances of 50 and 100 m; at the same time, population abundance decreased with split distance (Fig. 4C). However, IBM estimates revealed that aquatic-breeding amphibian populations with high dispersal probabilities, such as those above 0.8, also experienced a decline in abundance in split habitats (Fig. 4C). Populations of terrestrial-breeding amphibians were not affected by dispersal or split distance (Fig. 4C). IBMs showed a similar general pattern for occurrence data (presence/absence).

#### Discussion

Results from IBMs applied to our focal study landscape agreed with data from previous field surveys (Anjos 2008; Giasson 2008; Becker et al. 2010), where amphibian population abundance and occurrence were lower in disturbed areas that show high levels of habitat split, and where population declines were disproportionately higher for aquatic-breeding species. Additionally, our IBM results also agreed with a landscape-scale study showing proportionally lower occurrence rates and population abundances of aquatic-breeding compared with terrestrial-breeding amphibians across gradients of habitat split (Becker et al. 2007), further highlighting the applicability of our modeling framework. Our IBM results suggest that as the split distance between the forest edge and the drainage network increases, population abundance decreases in our hypothetical landscapes, and these findings were exacerbated under scenarios of low amphibian dispersal probability (see Lion et al. 2014). Interestingly, the highest dispersal rate bracket led to a reduction in population abundances under high split distances for aquatic-breeding frogs, suggesting an

intermediate dispersal optimum for breeding migrations rather than indicating that longdistance dispersal is always advantageous.

Amphibians with different life histories (e.g., reproductive modes) vary in their responses to environmental disturbances, including fragmentation and habitat split (Werner & Gilliam 1984; Gascon et al. 1999; Tocher et al. 2001; Bell & Donnelly 2006). Aquaticbreeding amphibian species often need landscape complementation, relying on the integrity and connectivity between terrestrial and aquatic habitats to complete their biphasic life cycles (Werner & Gilliam 1984; Pope et al 2000; Becker et al. 2010). Adults and newly metamorphosed individuals of aquatic-breeding amphibians cross disturbed environments migrating during the reproductive season when natural terrestrial and aquatic habitats are spatially split (Becker et al. 2010), being exposed to dehydration, predation, parasites, pathogens, high UV-B radiation, agrochemicals, and other pollutants that reduce their fitness or lead to death (Mazerolle & Desrochers 2005; Relyea et al., 2005; Bancroft et al. 2008; Cosentino et al. 2011; Becker et al. 2023). In contrast, many terrestrial-breeding amphibians reproduce in the interior of forest fragments and often avoid crossing open environments, which allows them to tolerate fragmented and split natural habitats (Gascon, 1999; Pardini, 2009; Dixo & Metzger 2010; Ferreira et al. 2016). Our IBM results indicated that dispersal and habitat split were not associated with population abundance or occurrence of terrestrial-breeding amphibians. Thus, our study emphasizes that habitat split and migratory breeding behavior are both good proxies for occurrence and abundance of aquaticbreeding amphibians in our study system.

Our IBMs, incorporating seasonal breeding migrations, support earlier results from a comprehensive model that underscore split distance as a pivotal landscape metric explaining species richness and abundance of amphibians in tropical forest fragments (Fonseca et al. 2013). Empirical field data also supports the negative correlation between the split distance among forested areas and ponds in temperate systems (e.g., Loman 1988; Laan & Verboom 1990; Lehtinen et al. 1999; Lion et al. 2014). In real-life conditions, larger split distances could lead to population declines in aquatic-breeding amphibians through several mechanisms: (i) higher split distances involve greater exposure to non-natural habitats and consequently higher probability of mortality (e.g., through increased dehydration, predation, parasitism, and exposure to UV-B radiation; Becker et al. 2023); (ii) in disturbed habitats, amphibian dispersal ability may be three to four times lower when compared to pristine habitats (Rothermel & Semlitsch 2002), potentially affecting seasonal breeding migrations while also increasing the risk of inbreeding depression due to reduced gene flow (Andersen et al. 2004; Allentoft & O'Brien 2010); (iii) longer travel distances raise the cost of dispersal (Fahrig 2003; Kokko & Lopez-Sepulcre 2006; Schtickzelle et al. 2006; Bonte et al. 2012), potentially reducing clutch and egg sizes, and lowering reproductive success (Kinnison et al. 2001; Crossin et al. 2004); and (iv) habitat split could drive a reduction in waterborne pathogen exposure and immune gene upregulation during nonbreeding months, which may lead to a lack of acquired resistance to pathogens, such as the deadly chytrid fungus (Carvalho et al. 2017), at the onset of the breeding season (Becker et al. 2023).

Many aquatic-breeding amphibian populations often forage or overwinter in natural terrestrial habitats 300–1000 m away from aquatic breeding sites (Semlitsch & Bodie 2003; Schabetsberger et al. 2004; Crawford & Semlitsch 2007; Sinsch et al. 2012), making dispersal ability a determining attribute for population persistence (Gulve 1994; Trenham et al. 2001; Becker et al. 2007; Werner et al. 2009; Campbell Grant, 2010; Pitman et al., 2014). Although anthropogenic environmental change profoundly impacts the ability of animals to disperse through the landscape (Rothermel & Semlitsch 2002;

Fahrig 2007), greater rates of dispersal can decrease the negative effects of deforestation on population persistence in disturbed landscapes with high levels of habitat split, as demonstrated here and in previous studies (Fonseca et al. 2013). Our modeling results, however, indicate that individual amphibians that disperse through very long distances might also suffer from enhanced risk of mortality while moving through disturbed environments, which indicates an ecologically-realistic trade-off between dispersal and fitness in our models (see Fig. 4C). Prolonged exposure to disturbed environments caused by habitat split will likely reduce fitness in amphibians, as it raises dispersal costs and reduces dispersal ability (Rothermel & Semlitsch 2002; Kokko & Lopez-Sepulcre 2006; Schtickzelle, 2006; Bonte et al. 2012). Long dispersal events could certainly be advantageous for amphibians recolonizing areas following local extinction events (Hanski & Thomas 1994; Tscharntke et al. 2002; Grimm et al. 2004), but our modeling results agree with empirical data linking costly dispersal with higher mortality rates (Casagrandi and Gatto 1999; Fahrig 2001; Flather and Bevers 2002). Thus, incorporating seasonal migrations (to and from breeding sites) into our modeling framework led to more ecologically realistic estimates of population persistence for distinct amphibian reproductive modes and throughout ecologically realistic heterogeneous landscapes.

Predicting optimal migrations in newly modified landscapes can be challenging because previous dispersal patterns that evolved in pristine habitats may no longer be optimal under current scenarios of anthropogenic land use (Fahrig 2007). This mismatch could also help explain population declines, as individuals exhibiting historical dispersal behaviors might be exposed to higher mortality risks in modified environments. Thus, our modeling results align with the idea that vagile aquatic-breeding and endemic amphibians of the Atlantic Forest, which evolved in continuous forest, may continue to exhibit these long-distance dispersal behaviors, crossing extensive stretches of non-natural habitats and moving through inhospitable matrix environments, which could increase mortality rates (Fahrig 2003, 2007). These findings also suggest that our model can provide valuable insights into how selection pressures might act on dispersal behavior in newly altered landscapes, offering enhanced predictions of future population dynamics.

In conclusion, although we did not incorporate variation in species-specific life history traits such as longevity, clutch size, or stress tolerance due to the complexity of tropical communities, we opted to focus on broader reproductive strategies (aquatic-breeding and terrestrial-breeding) and dispersal abilities to generalize patterns across the amphibian community. We acknowledge that this simplification may introduce bias by overlooking species-specific behaviors and ecological traits that could influence population dynamics. Despite this, our general IBMs closely matched recent trends in Neotropical amphibian populations in the wild. This link included our focal study landscape, with reproductive mode and dispersal ability being important predictors of population persistence in disturbed landscapes and under scenarios of habitat split. Spatially explicit IBMs, such as the ones presented here, that incorporate migratory behavior among multiple classes of natural habitats, could enhance our ability to forecast amphibian population persistence in varying scenarios of anthropogenic interference, landscape structure, and spatial connectivity. Furthermore, integrating population genetics parameters, such as pairwise Fst, allelic richness, inbreeding, and genetic drift, into our models could significantly improve predictions of amphibian population resilience over longer time scales. We hope that our model framework could be applied to understudied regions or ecosystems and help target habitat restoration efforts and mitigation programs before the onset of silent population declines and local extinctions.

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Author contributions TC and NF executed model experiments, analyzed, interpreted the data, and wrote the manuscript. TW developed the mathematical models and coding. LAA, LOMG, and CFBH contributed with field survey data. CGB and CFBH conceived the idea and revised the final manuscript. LFT and MHV participated in interpreting the data and helped with writing. All authors critically revised the final manuscript version, provided editorial advice, and approved it for publication.

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**Data availability** Individual-Based Models, including the Perl code, parameter estimates, and ASCII files, are available on Dryad (https://doi.org/10.5061/dryad.g1jwstr2d).

# Declarations

Conflict of interest The authors declare no competing interests.

**Ethical approval** This modeling paper utilizes data from published amphibian surveys. Model validation utilizes data from a recent radio telemetry study conducted under the following permits (SISBio #70883, SISGEN-AC88222, CEUA-Unisinos#10.2019, CEUA-Unesp 08/2021, IACUC #19-07-2547).

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