Modeling Habitat Split: Landscape and Life History Traits Determine Amphibian Extinction Thresholds

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Abstract

Habitat split is a major force behind the worldwide decline of amphibian populations, causing community change in richness and species composition. In fragmented landscapes, natural remnants, the terrestrial habitat of the adults, are frequently separated from streams, the aquatic habitat of the larvae. An important question is how this landscape configuration affects population levels and if it can drive species to extinction locally. Here, we put forward the first theoretical model on habitat split which is particularly concerned on how split distance – the distance between the two required habitats – affects population size and persistence in isolated fragments. Our diffusive model shows that habitat split alone is able to generate extinction thresholds. Fragments occurring between the aquatic habitat and a given critical split distance are expected to hold viable populations, while fragments located farther away are expected to be unoccupied. Species with higher reproductive success and higher diffusion rate of post-metamorphic youngs are expected to have farther critical split distances. Furthermore, the model indicates that negative effects of habitat split are poorly compensated by positive effects of fragment size. The habitat split model improves our understanding about spatially structured populations and has relevant implications for landscape design for conservation. It puts on a firm theoretical basis the relation between habitat split and the decline of amphibian populations.

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Introduction

One-third of the world's amphibian species are threatened, more than 40% have declining populations, and 168 species probably went extinct in the last five centuries [1]. In biodiversity hotspots, 2841 amphibian species are facing an unprecedented contraction of their geographic area [2], being threatened by habitat loss and fragmentation [3]. Many theoretical models have been proposed to capture the complexity of such processes, from the theory of island biogeography [4,5] to complex spatially explicit metapopulation models [6,7]. The basic predictions of these models have been corroborated for different taxa, including protozoa [8], butterflies [9,10], birds [11], and mammals [12, but see 13,14,15]. However, since amphibian species exhibit marked ontogenetic habitat shifts, being strongly affected by habitat split [16], the predictive power of such models is limited.

Habitat split is defined as human-induced disconnection between habitats used by different life history stages of a species [16]. For forest-associated amphibians with aquatic larvae, deforestation causes spatial disjunction between the habitat of the larvae, ponds and streams, and the habitat of the adults, the forest fragments. At the local scale, habitat split compels adults to traverse the anthropogenic matrix to reach breeding sites and recently metamorphosed juveniles to walk haphazardly through

the matrix searching for an isolated forest fragment. This compulsory bi-directional migration causes drastic declines on amphibian populations [17].

At the landscape scale, habitat split decreases the richness of the amphibian community due to the extinction of aquatic larvae species [16]. More importantly, the richness of amphibians with aquatic larvae has been demonstrated to be more strongly affected by habitat split than by habitat loss and habitat fragmentation [16].This process causes bias in communities towards amphibians with terrestrial development, since these species are able to breed successfully in forest fragments even in the absence of a water source [16,18].

The habitat split concept has also contributed to conservation issues. In a recent complementarity exercise for the identification of key Neotropical ecoregions for amphibian conservation, the differentiation between species with aquatic and terrestrial developmental generated a more comprehensive coverage of priority ecoregions than when species were pooled together [19]. Also, by analyzing how the incidence of habitat loss and habitat split varies across a regional landscape, the selection of a minimum priority set of watersheds for amphibian conservation could be optimized [20].

Habitat split is a worldwide phenomenon, being particularly common in biodiversity hotspots where habitat fragmentation is

intense and human settlements are generally concentrated on the valleys where water is available for agriculture, industry, and human consumption [2]. The Brazilian Atlantic Forest, for instance, is now distributed in 245,173 forest fragments from which 83.4% are smaller than 50 ha [21]. In a typical Atlantic Forest landscape, less than 5% of the fragments are connected to streams [17]. In fact, "dry fragments" are the rule and their distance to the nearest stream can vary widely from a few meters to several kilometers. Predicting how the amphibian populations respond to such landscape alteration is essential for conservation.

We provide, here, the first theoretical model for habitat split. A minimum diffusion model shows that habitat split generates critical split distances for population persistence in forest fragments. The model predicts how life history traits, such as juvenile dispersal ability and recruitment, determine the extinction threshold. Furthermore, it predicts how population size is affected by the quality of the matrix and its distance from the breeding habitat. The model has relevant implications for amphibian conservation landscape design.

Materials and Methods

The Model

In this section we develop a model designed to capture the main consequences of habitat split on populations of amphibians with aquatic larvae. This means a model that has enough ingredients to provide a basis for predictions without, however, taking into account particularities of any specific amphibian species. The main point the model is set to address is that of population decline and local extinction. The spatial configuration of the model is shown in Figure 1. The reproductive site of the amphibians is at the river at $x = 0$, whereas the forest fragment, where the adults live, has a size $s = L_2 - L_1$. The shortest distance from the fragment to the river is L_1, from now on called *split distance*, a new metric for habitat fragmentation studies. We have chosen to work in a one-dimensional context. Extensions to a two-dimensional space can be implemented, but the main features are already present in our model.

Habitat split consequences on the amphibian population are directly connected to the fact that the population is stage-structured. Accordingly, we introduce two variables, $J(x,t)$ and $A(x,t)$, which represent juveniles and adults densities, respectively. We will assume that after leaving the reproductive site the juvenile amphibians move in a haphazard way through the matrix. This assumption is based on the fact that in the pristine environment they did not have to search for the terrestrial habitat, therefore they lack adaptations that allow them to find the forest fragments in a directional fashion. From the modeling point of view, this suggests that a diffusion equation is appropriate to describe the spatial aspects of the juveniles in the matrix. In the fragment, we

will posit that the adults also obey a diffusion equation, assuming that the forest fragment is spatially homogeneous and that the adults will haphazardly look for food and escape from their predators before reproduction. However, individuals walking in the matrix or in the forest fragment can exhibit different diffusion rates.

Juveniles that reach the fragment are dynamically equivalent to adults, so we will assume that there are no juveniles in the fragment, $J(x,t) = 0$ when $L_1 < x < L_2$. On the other hand, adults migrate through the matrix back to the river for reproduction. This however, is a directed movement, much more like advection rather than diffusion, and is not modeled explicitly. Mathematically, these assumptions translate into two diffusive equations. The first equation is defined for juveniles in the matrix and the second for adults in the forest fragment:

$$\frac{\partial J}{\partial t} = D_J \frac{\partial^2 J}{\partial x^2} - \mu_J J \qquad (1)$$

$$\frac{\partial A}{\partial t} = D_A \frac{\partial^2 A}{\partial x^2} - \mu_A A, \qquad (2)$$

Where D_J and D_A are the diffusion coefficients for juveniles and adults in the matrix and the forest, and μ_J and μ_A the respective mortality rates. At the fragment border L_2, several scenarios are possible, depending on the landscape beyond L_2: the boundary may be completely absorbing if there is a very hostile matrix, or totally reflexive if the environment is as good as in the fragment, or it can be something in between. This point will be discussed in detail in the next section and for now we consider a general formulation [22]:

$$-D_A \frac{\partial A}{\partial x}\Big|_{x=L_2} = bA\Big|_{x=L_2}. \qquad (3)$$

If $b = 0$, we have a completely closed patch at L_2 and the adults will turn back towards the fragment interior. This condition is used when we do not want to take into account size effects of habitat patch, that is, when the patch is large. The opposite limit, $b \to \infty$, corresponds to the situation in which all individuals that reach the border L_2 will leave the modeled landscape.

When juveniles reach the fragment, they become adults and, since adults cannot turn into juveniles, the border $x = L_1$ represents a completely absorbing boundary for juveniles. Moreover, the rate at which new adults arrive at the fragment must be the same as the rate of juveniles leaving the matrix. These conditions are expressed in the following boundary conditions:

$$D_A \frac{\partial A}{\partial x}\Big|_{x=L_1} = D_J \frac{\partial J}{\partial x}\Big|_{x=L_1} \qquad (4)$$

$$J\Big|_{x=L_1} = 0. \qquad (5)$$

The fourth and last boundary condition models the reproductive behavior of the amphibians. For simplicity, adults are assumed to exhibit a constant recruitment rate r, so that the rate at which new juveniles are generated at the river is proportional to the total number of adults in the fragment. We also take into account that it
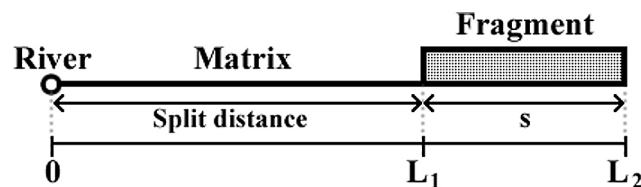

Figure 1. The spatial configuration for the habitat split model. The model has three main landscape elements: the river (or any aquatic breeding habitat), at L_0, the inhospitable matrix and the forest fragment. Split distance is defined by L_1 while fragment size (s) is defined by $L_2 - L_1$.
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2

takes a certain time, t_1, for the influx of juveniles to respond to a variation in the number of adults. Population size is controlled by competition at the river, so we introduce a saturation parameter K, which can be interpreted as the maximum rate of juveniles that can be generated. The mathematical expression of this condition is the following:

$$-D_J \frac{\partial J}{\partial x}|_{x=0} = \frac{rN}{1 + \frac{r}{K}N},$$ (6)

where r is the recruitment rate and N is the total number of adults in the fragment at a past time. Notice that the negative sign accounts for the fact that $J(x)$ is always a decreasing function of x. The total number of adults in the fragment at a past time is given by:

$$N = \int_{L_1}^{L_2} A(x, t - t_1) dx.$$ (7)

In this model we suppose that the most important factor limiting amphibian flow is of the juveniles that start at the river and cross the matrix to the forest fragment. The return of the adults to the river is assumed in equation (6) to be advective. These conditions introduce two phenomenological constants r and t_1. The first of them, the recruitment, takes into account the fertility of adults, the survival of tadpoles and the adult mortality in the matrix. The time t_1 is the sum of the time to cross the matrix, mate, reproduce, mature eggs and develop juveniles capable of crossing the matrix. Although describing a different system, this set of equations and boundary conditions is similar to the one presented in [23].

Results

Equations (1,2) do not contain any density dependent terms: they are linear. As discussed above, the population control term appears only in the boundary conditions, namely in equation (6). Moreover, the fact that these conditions include a time delay makes it impossible to obtain exact solutions in general. However, when we seek for stationary solutions, that is, solutions such that $\partial J/\partial t = 0$ and $\partial A/\partial t = 0$, the time delay plays no role anymore and we can find the solutions and – more important – the existence criteria for non-zero solutions.

The stationary solutions are obtained by setting to zero the time-derivatives in equations (1,2) which leads us to:

$$D_J \frac{d^2 J}{dx^2} = \mu_J J$$ (8)

$$D_A \frac{d^2 A}{dx^2} = \mu_A A,$$ (9)

where we have changed partial derivatives for ordinary ones as J and A depend only on x. The couple of linear equations (8,9) has the solution:

$$J(x) = c_1 e^{x\sqrt{\mu_J/D_J}} + c_2 e^{-x\sqrt{\mu_J/D_J}}$$
$$A(x) = f_1 e^{x\sqrt{\mu_A/D_A}} + f_2 e^{-x\sqrt{\mu_A/D_A}},$$ (10)

Where c_1, c_2, f_1 and f_2 are integration constants. With help of boundary conditions (5,6) we find explicitly their values. This result is found in the supplementary material S1. Equation (10) makes sense only for real positive solutions. We derive such conditions from $J|_{x=0} > 0$. If this condition is not satisfied the population will go extinct as the null solution turns out to be the only stable one in this case. We prove in supplementary material S1 that $J|_{x=0} > 0$ is equivalent to:

$$\frac{r}{\mu_A \cosh\left(\sqrt{\mu_J/D_J}L_1\right)} \left[1 - \frac{1 + \beta}{\beta e^{\sqrt{\mu_A/D_A}s} + e^{-\sqrt{\mu_A/D_A}s}}\right] > 1.$$ (11)

In this expression, $\beta = \frac{b + \sqrt{\mu_A D_A}}{b - \sqrt{\mu_A D_A}}$. This condition has a standard interpretation in population dynamics: the recruitment should be large enough to replace the population, otherwise, the population disappears. In the special case where we take to be zero, we have:

$$\frac{r}{\mu_A \cosh\left(\sqrt{\mu_J/D_J}L_1\right)} > 1.$$ (12)

Further, notice that $b = 0$ is the same as taking the limit $s \rightarrow \infty$, that is, considering an arbitrarily large patch.

Stationary Solutions

The general form of the stationary solution as a function of x, the distance from the river, is depicted in Fig. 2, where we assume now $b = 0$. To help the visualization we plot the juveniles and adults in the same figure; for $0 < x < L_1$ the density in the y-axis refers to juveniles while for $L_1 < x < L_2$ the density of the adults is plotted. As a first approach we assume that diffusion coefficients of adults and juveniles are the same: $D_J = D_A = 1$. On the other hand we suppose a large difference in mortalities of juveniles and adults, we use $\mu_A = 0.01 < < 0.01 < < \mu_J$. The values of μ_J are shown in the picture. In this and the following plot we use $L_1 = s = K = r = 1$. The general behavior of this solution points to populations that decrease in the matrix and tend to stabilize in the fragment.

We also explore in Fig. 2 the dependence of the population in the fragment on juvenile mortality. We plot solutions for three distinct μ_J, simulating matrixes of different quality. As expected, an increase in the mortality leads to smaller populations and, as a preview of the next subsection, this trend suggests the existence of a threshold in this model.

The Existence of a Critical Split Distance

The split distance, L_1, is an important landscape metric which has great influence on the existence of a non-zero stationary solution of the model and therefore on the viability of the population. At this point we explore the most important conceptual result of this work. The model introduced in this article predicts an extinction threshold for L_1. This means, there is a critical split distance L_1^* such that if $L_1 > L_1^*$ the amphibian population goes locally extinct. In other words, if the split distance is larger than a certain value, the population does not persist in this landscape.

In Fig. 3 we show the population size in the fragment as a function of the split distance L_1, for three different values of the juvenile mortality μ_J. The presence of a critical value L_1 (the point where the curves intercept the x-axis) is clearly seen. This figure
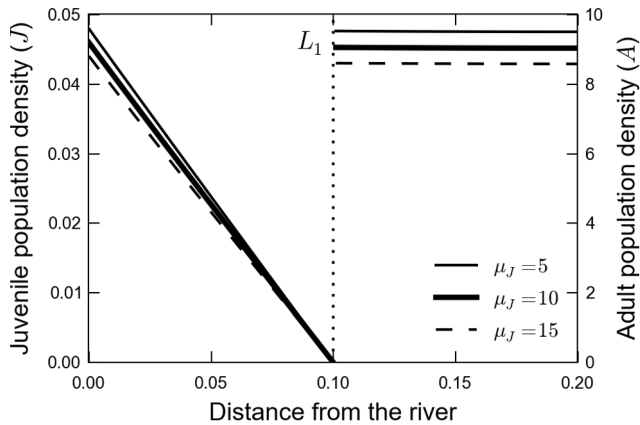
Figure 2. Stationary solutions of the model as a function of space. In the model, all distances are measured according to the reproductive site that is taken as zero. The fragment starts at L_1 and ends at L_2. Each curve refers to a given juvenile mortality in the matrix (μ_J). The parameters used were $r = K = \mu_J = D_J = D_A = 1$, $b = 0$ and $\mu_A = 0.01$.
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also explores the influence of μ_J on L_1^*; as expected there is an inverse relation between L_1^* and μ_J. A more inhospitable habitat (large μ_J) will make the critical split distance smaller.

Dependence of the Critical Split Distance on Life-history Parameters

One of the most relevant life-history traits for our analysis is the recruitment r, a parameter that measures the reproductive success of the amphibians. Indeed, in our model r encompasses three biological processes: fertility of the reproductive adults, the survival of the tadpoles until they emerge from the aquatic habitat to become able to cross the matrix and the adult mortality in their way back to the river to reproduce. In Fig. 4 we show the critical split distance, L_1^*, as a function of the recruitment, r, for three distinct values of diffusion coefficients of the juveniles D_J. The point ($L_1^* = 0, r = 1$) is a limit case; for this situation the recruitment

is the minimum to maintain the population ($r = 1$) when the favorable habitat is connected to the reproduction site ($L_1 = 0$). The curves of Fig. 4 show an increase of L_1^* with recruitment translating the fact that a higher reproductive success allows for larger split distances. The reason of this behavior is that the recruitment compensates the mortality in the matrix.

The three curves in Fig. 4 examine the influence of the diffusion of the juveniles, D_J; for a given r, a larger diffusion coefficient allows a larger split distance for the population. In this way D_J also counterbalances the mortality in the matrix: higher dispersal ability helps to deplete the effect of habitat split.

Dependence of the Critical Split Distance on Landscape Metrics

As we have seen in the previous sections, a critical split distance appears. When we took the border of the fragment as completely reflexive ($b = 0$), the dependence of the critical split distance on the size of the fragment disappeared: no matter how large the fragment, once a critical split distance is attained, the population goes locally extinct. On the other hand, we can introduce a non-zero value for b, representing a partially absorbing boundary at L_2. In this case, a flux of adults to the outside of the fragment exists, making it still more difficult for the population to persist. To illustrate this point, we plotted in Fig. 5 the adult population in the fragment as a function of the split distance for three different fragment sizes in the case where $b = 1$. It is clear that the population is always smaller the smaller the fragment is, representing a typical area effect.

Discussion

Amphibian populations are declining worldwide [24,25]. Several non-exclusive hypotheses have been proposed to explain such a widespread pattern, including the emergence of *Batrachochytrium dendrobatidis*, a highly virulent fungus [26,27], ultraviolet-B radiation, climate change [28], pollution [29], introduction of exotic species [30], habitat loss and fragmentation [1,31,32], and, more recently, habitat split [16]. Here, we explore the theoretical consequences of habitat split for the conservation of amphibian species with aquatic larvae. However, the model can be of relevance for other organisms exhibiting marked ontogenetic habitat shifts. For instance, insects with indirect development, such
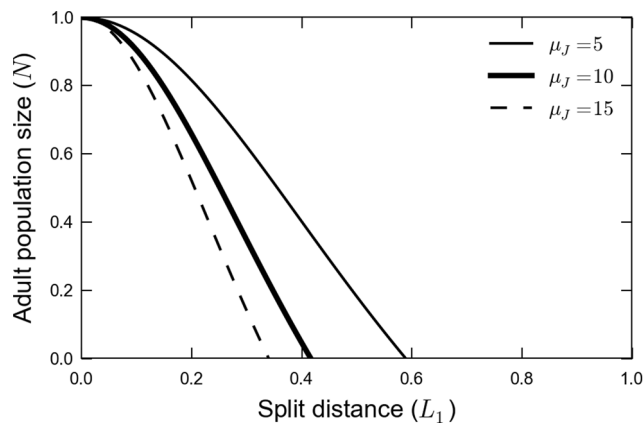

Figure 3. Population size of adults in the fragment as a function of the split distance, L_1 This picture points a critical split distance L_1^* above which the population gets extinct. The three curves indicated in the figure represent different values of the juvenile mortality μ_J that can be caused by differences in matrix quality. The parameters used were $r = K = D_J = D_A = 1$, $b = 0$ and $\mu_A = 0.01$.
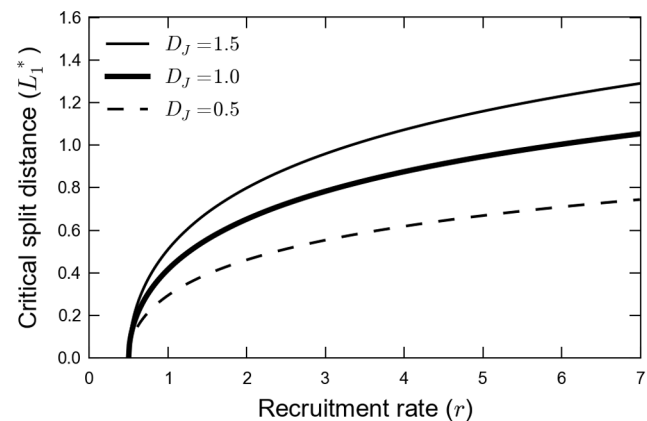doi:10.1371/journal.pone.0066806.g003

Figure 4. Critical split distance as a function of life history traits. The model explores two factors that modulate the habitat split effect: the recruitment rate and the diffusion coefficient of the juveniles. The parameters used were $r = K = \mu_J = D_A = 1$, $b = 0$ and $\mu_A = 0.01$.
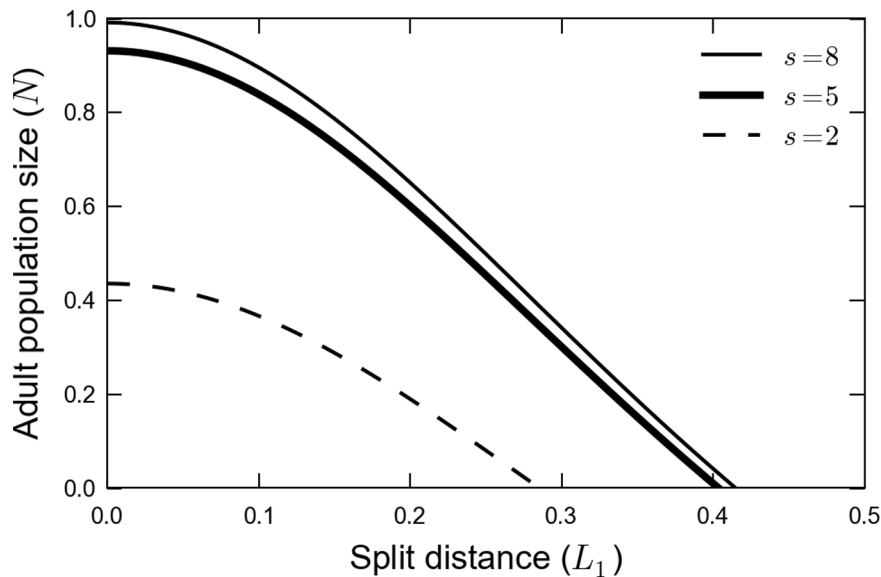doi:10.1371/journal.pone.0066806.g004

Figure 5. Curve of adult population size versus split distance. In this figure we point the effect of the size of the fragment on the critical split distance. This figures show that large forest fragments have only a limited effect to reduce the habitat split local extinction prevision. The parameters used $r = K = \mu_J = D_J = D_A = L_1 = b = 1$ and $\mu_A = 0.01$.
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as dragonflies and damselflies, have been recently demonstrated to suffer from alterations in the physical structure of the riparian vegetation that disconnect the aquatic habitat of the larvae from the terrestrial habitat of the adults [33].

Our diffusive model reveals that habitat split alone can generate extinction thresholds. Fragments located between the breeding site and a given critical split distance are expected to contain viable amphibian populations. In contrast, populations inhabiting fragments farther from such critical distance are expected to be extinct. The theoretical existence of extinction thresholds has been also demonstrated for habitat loss and fragmentation [6,34,35]. In this case, increase in the proportion of habitat loss above a certain level causes an abrupt non-linear decay in population size. Simulation models based on percolation theory suggest that this can be simply attributed to structural properties of the fragmentation process [36]. However, biological mechanisms such as minimal home range, minimal population size, and the Allee effect contribute to such extinction thresholds [35].

The model can be also interpreted from a breeding site perspective. Split distance is expected to have a negative impact on the occupancy of matrix-inserted ponds. Indeed, a field study with *Rana dalmatina* demonstrated that the number of egg-clutches in ponds declines exponentially with increasing distance from a deciduous forest. Ponds less than 200 m from the forest edge were considered the most valuable for the species conservation [37]. For *Rana temporaria*, the occupancy of ponds for breeding purposes is influenced by the distance from suitable summer habitats [38]. Furthermore, some studies have shown that the richness of amphibians in ponds is negatively related to the distance to forest patches [39,40].

The habitat split model predicts that amphibian species with different life history traits will exhibit different extinction proneness in response to a given landscape setting. One key feature determining the critical split distance (i.e. the distance value of L_1 at which the predicted abundance is zero) is the diffusion rate of the post-metamorphic juveniles in the matrix. Amphibian species with higher diffusion rate are expected to

exhibit farther extinction thresholds. Therefore, for a given fragmented landscape submitted to habitat split, species with lower diffusion ability are expected to be present in a smaller number of fragments and ultimately be regionally extinct earlier. Additionally, the probability of extinction in response to habitat split gradients can be expected to be higher for species with lower diffusion ability.

Amphibians vary considerably in dispersal ability. Across species, the frequency distribution of maximum dispersal distance fits an inverse power law [41].While 56% of the amphibian species presented maximum dispersal distances lower than one kilometer, 7% could disperse more than 10 km [41]. However, those are data for adults. For the habitat split model, the main parameter to be estimated is the diffusion rate of the post-metamorphic juveniles. Although such data is more difficult to be obtained, one expects that the mean dispersal ability of juveniles should be lower than of adults due to their smaller body size, lower energetic reserves and higher sensitivity to environmental stress [42].

The reproductive success is also a crucial life history parameter determining how far is the critical split distance for a given species. In the model, reproductive success is defined as the average number of post-metamorphic juveniles produced per adult living in the fragment. Since this parameter varies between species, we expect that species with higher reproductive success will be able to keep viable populations in forest fragments that are farther away from the breeding site in comparison to species with lower reproductive success. We envisage that in future individual-based models, recruitment could vary between individuals according to their conditions.

Reproductive success is positively correlated to clutch size but also a function of the survival rate of the aquatic larvae before metamorphosis. Body size is possibly a good inter-specific predictor of reproductive success. Body size has a strong positive inter-specific relationship with clutch size, even after controlling for the phylogeny [43]. Furthermore, for pond-breeding anurans of three different families (Bufonidae, Hylidae and Ranidae), there is a positive relationship between body size and egg-diameter [42].

Therefore, species with larger body size can be expected to exhibit larger critical split distances. The survival rate of the aquatic larvae, however, depends on biotic interactions, such as predation and competition. Furthermore, riverine systems are nowadays submitted to multiple anthropogenic generated stressors [44], agrochemicals [29], and emerging diseases [26] that can dramatically alter mortality rates.

The model predicts that the extinction threshold can be pushed away from the breeding site only at the cost of increasing the size of the fragment, depending on the kind of boundary at the interface habitat/exterior matrix. However, although enlarging the size of the fragment can allow for larger splits, even in the case of a very large fragment the critical split distance remains finite: local extinction can occur even for infinite fragments when the split distance is larger than a critical value. The implications of such results for conservation are straightforward. When habitat loss is intense and small fragments are the rule, the best landscape scenario for the conservation of forest-associated amphibians with aquatic larvae is the preservation of the riparian vegetation.

The quality of the matrix is also a key element defining the critical split distance. Higher quality matrix generates lower mortality rates of post-metamorphic juveniles enabling recruited individuals to successfully reach forest fragments that are farther away. For empirical studies this parameter is critical since anthropogenic matrix vary widely in quality, from intensively used cattle and crop fields to ecologically-managed tree monocultures [45]. Furthermore, roads are also important matrix elements that can jeopardize the bi-directional migration of amphibians [46].

In biodiversity hotspots [2], in particular, landscape design is expected to play a crucial role in the conservation of the aquatic larvae species. For instance, the Brazilian Atlantic Forest is home of one the most species rich amphibian fauna of the world [2], containing at least 300 endemic amphibian species [47]. Nowadays, only 11.7% of its original cover is left, and although the protection of the riparian vegetation was, until recently, insured by the Brazilian Forest Code (4771/65), habitat split is a common feature in the landscape [16]. Not surprisingly, several amphibian populations have declined recently [48,49,50] and many more are expected to pay the extinction debt [51]. The habitat split model reinforces the view that the conservation and restoration of riparian vegetation should be properly enforced [52].

Metapopulation models assume disjunct breeding patches containing individual populations that exist in a shifting balance between extinctions and recolonisations via dispersing individuals [6]. Realistic models on metapopulations have incorporated patch area, shape, isolation besides the quality of the intervening matrix [7]. The metapopulation concept has been applied to amphibians, showing even structured genetic outcomes [53]. Despite that, the application of metapopulation models to amphibians has been questioned in several grounds [14,41]. We envisage that future metapopulation models, when designed to species exhibiting marked ontogenetic habitat shifts, will generate more accurate predictions by the incorporation of habitat split effects.

Supporting Information

File S1   Mathematical formulation of the model, including the derivation of the stationary solution and a study of its stability.
(PDF)

Author Contributions

Conceived and designed the experiments: CRF GC RAK. Performed the experiments: CRF RMC FA JMB GC RAK. Analyzed the data: CRF RMC FA JMB GC RAK. Wrote the paper: CRF RMC FA JMB GC RAK.

References

1. Stuart SN, Chanson JS, Cox NA, Young BE, Rodrigues ASL et al. (2004) Status and trends of amphibian declines and extinctions worldwide. Science 306: 1783–1786.
2. Mittermeier RA, Gil PR, Hoffmann M, Pilgrim J, Brooks T et al. (2004) Hotspots revisited: earth's biologically richest and most endangered terrestrial ecoregions. Chicago: Cemex and University of Chicago Press.
3. Gardner TA, Barlow J, Chazdon R, Ewers RM, Harvey CA et al. (2009) Prospects for tropical forest biodiversity in a human-modified world. Ecol Lett 12: 561–582.
4. MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton: Princeton University Press.
5. Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Syst 34: 487–515.
6. Hanski I (1991) Single species metapopulation dynamics – concepts, models and observations. Biol J Linn Soc Lond 42: 17–38.
7. Hanski I (1999) Metapopulation ecology. Oxford: Oxford University Press.
8. Holyoak M, Lawler SP (1996) Persistence of an extinction-prone predator-prey interaction through metapopulation dynamic. Ecology 77: 1867–1879.
9. Harrison S, Murphy DD, Ehrlich PR (1988) Distribution of the bay checkerspot butterfly, *Euphydrias editha bayensis*: evidence for a metapopulation model. Am Nat 132: 360–382.
10. Hanski I, Thomas CD (1994) Metapopulation dynamics and conservation: a spatially explicit model applied to butterflies. Biol Conserv 68: 167–180.
11. Ferraz G, Nichols JD, Hines JE, Stouffer PC, Bierregaard RO Jr. et al. (2007) A large scale deforestation experiment: effects of patch area and isolation on Amazon birds. Science 315: 238–241.
12. Lomolino MV (2008) Mammalian community structure on islands: the importance of immigration, extinction and interactive effects. Biol J Linn Soc Lond 28: 1–21.
13. Harrison S, Bruna E (1999) Habitat fragmentation and large-scale conservation: what do we know for sure? Ecography 22: 225–232.
14. Marsh DM, Trenham PC (2001) Metapopulation dynamics and amphibian conservation. Conserv Bio 15: 40–49.
15. Harrison S (2008) Local extinction in a metapopulation context: an empirical evaluation. Biol J Linn Soc Lond 42: 73–88.
16. Becker CG, Fonseca CR, Haddad CFB, Batista RF, Prado PI (2007) Habitat split and the global decline of amphibians. Science 318: 1775–1777.
17. Becker CG, Fonseca CR, Haddad CFB, Prado PI (2010) Habitat split as a cause of local population declines of amphibians with aquatic larvae. Conserv Biol 24: 287–294.
18. Fonseca CR, Becker CG, Haddad CFB, Prado PI (2008) Response to comment on "Habitat split and the global decline of amphibians". Science 320: 874d.
19. Loyola RD, Becker CG, Kubota U, Haddad CFB, Fonseca CR et al. (2008) Hung out to dry: choice of priority ecoregions for conserving threatened Neotropical anurans depends on life-history traits. PLoS ONE 3: e2120.
20. Becker CG, Loyola RD, Haddad CFB, Zamudio KR (2009) Integrating species life-history traits and patterns of deforestation in amphibian conservation planning. Biodivers Conserv 16: 10–19.
21. Ribeiro MC, Metzger JP, Martensen AC, Ponzoni F, Hirota M (2009) Brazilian Atlantic forest: how much is left and how is the remaining forest distributed? Implications for conservation. Biol Conserv 142: 1141–1153.
22. Cantrell RS, Cosner C, Fagan WF (1998) Competitive reversals inside ecological reserves: the role of external habitat degradation. J Math Biol 37: 491–533.
23. Ananthasubramaniam B, Nisbet R, Nelson WA, McCauley E, Gurney WSC (2011) Stochastic growth reduces population fluctuations in *Daphnia*-algal systems. Ecology 92: 362–372.
24. Alford R, Richards SJ (1999) Global amphibian declines: A problem in applied ecology. Annu Rev Ecol Syst 30: 133–165.
25. Beebee TJC, Griffiths RA (2005) The amphibian decline crisis: a watershed for conservation biology? Biol Conserv 125: 271–285.
26. Lips KR, Brem F, Brenes R, Reeve JD, Alford RA et al. (2006) Emerging infectious disease and the loss of biodiversity in a neotropical amphibian community. Proc Natl Acad Sci U S A 103: 3165–3170.
27. Vredenburg VT, Knapp RA, Tunstall TS, Briggs CJ (2010) Dynamics of an emerging disease drive large-scale amphibian population extinctions. Proc Natl Acad Sci U S A 107: 9689–9694.

28. Pounds JA, Bustamante MR, Coloma LA, Consuegra JA, Fogden MPL et al. (2006) Widespread amphibian extinctions from epidemic disease driven by global warming. Nature 439: 161–167.

29. Relyea RA (2005) The lethal impact of roundup on aquatic and terrestrial amphibians. Ecol Appl 15: 1118–1124.

30. Kats LB, Ferrer RP (2003) Alien predators and amphibian declines: review of two decades of science and the transition to conservation. Divers Distrib 9: 99–110.

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

32. Gardner TA, Barlow J., Peres CA (2007) Paradox, presumption and pitfalls in conservation biology: the importance of habitat change for amphibians and reptiles. Biol Conserv 138: 166–179.

33. Remsburg AJ, Turner MG (2009) Aquatic and terrestrial drivers of dragonfly (Odonata) assemblages within and among north-temperate lakes. J N Amer Benthol Soc 28: 44–56.

34. Artiles W, Carvalho PGS, Kraenkel RA (2008) Patch-size and isolation effects in the Fisher–Kolmogorov equation. J Math Biol 57: 521–535.

35. Swift TL, Hannon SJ (2010) Critical thresholds associated with habitat loss: a review of the concepts, evidence, and applications. Biol Rev 85: 35–53.

36. Orbach R (1986) Dynamics of fractal networks. Science 231: 814–819.

37. Wederkinch E (1988) Population size, migration barriers, and other features of *Rana dalmatina* populations near Koge, Zealand, Denmark. Mem Soc pro Fauna et Flora Fenn 64: 101–103.

38. Loman J (1988) Breeding by *Rana temporaria*: the importance of pond size and isolation. Mem Soc pro Fauna et Flora Fenn 64: 113–15.

39. Laan R, Verboom B (1990) Effects of pool size and isolation on amphibian communities. Biol Conserv 54: 251–262.

40. Lehtinen RM, Galatowitsch SM, Tester JR (1999) Consequences of habitat loss and fragmentation for wetland amphibian assemblages. Wetlands 19: 1–19.

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

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

43. Cooper N, Bielby J, Thomas GH, Purvis A (2008) Macroecology and extinction risk correlates of frogs. Glob Ecol Biogeogr 17: 211–221.

44. Tockner K, Pusch M, Borchardt D, Lorang MS (2010) Multiple stressors in coupled river–floodplain ecosystems. Freshw Biol 55: 135–151.

45. Fonseca CR, Ganade G, Baldissera R, Becker CG, Boelter CR et al. (2009) Towards an ecologically-sustainable forestry in the Atlantic Forest. Biol Conserv 142: 1209–1219.

46. Glista DJ, DeVault TL, DeWoody JA (2008) Vertebrate road mortality predominately impacts amphibians. Herpetol Conserv Biol 3: 77–87.

47. Haddad CFB (1997) Biodiversidade dos anfíbios no estado de São Paulo. Biodiversidade do estado de São Paulo, Brasil: síntese do conhecimento ao final do século XX. In: Castro RMC, Joly CA, Bicudo CEM, editors. São Paulo: Editora FAPESP. 15–26.

48. Heyer WR, Rand AS, Cruz CAG, Peixoto OL (1988) Decimations, extinctions, and colonizations of frog populations in southeast Brazil and their evolutionary implications. Biotropica 20: 230–235.

49. Weygoldt P (1989) Changes in the composition of mountain stream frog communities in the Atlantic mountains of Brazil: frogs as indicators of environmental deterioration? Stud Neotrop Fauna Environ 243: 249–255.

50. Eterovick PC, Carnaval A, Borges-Nojosa DM, Silvano DL, Segalla MV et al. (2005) Amphibian declines in Brazil: an overview. Biotropica 37: 166–179.

51. Krauss J, Bommarco R, Guardiola M, Heikkinen RK, Helm A et al. (2010) Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. Ecol Lett 13: 597–605.

52. Wuethrich B (2007) Biodiversity–reconstructing Brazil's Atlantic rainforest. Science 315: 1070–1072.

53. Hale JM, Heard GW, Smith KL, Parris KM, Austin JJ et al. (2013) Structure and fragmentation of growling grass frog metapopulations. Conserv Genet 14: 313–322.

Supporting Information Material S1

Mathematical formulation of the model

We define again the equations for juveniles in the matrix, J, and for adults in the forest fragment, A:

$$\frac{\partial J}{\partial t} = D_J \frac{\partial^2 J}{\partial x^2} - \mu_J J \tag{S.1}$$

$$\frac{\partial A}{\partial t} = D_A \frac{\partial^2 A}{\partial x^2} - \mu_A A \;, \tag{S.2}$$

where D_J and D_A are the diffusion coefficients for juveniles in the matrix and for adults inside the forest, and μ_J and μ_A the respective mortality rates. For this system, we define boundary conditions considering that juveniles become adults when they reach the fragment (Eqs. (S.3) and (S.4)). Since adults do not become juveniles, that border is completely absorbing to the juvenile population:

$$J\big|_{x=L_1} = 0 \;. \tag{S.3}$$

We must also observe that the flux of adults that enter the fragment must be the same as the flux of juveniles leaving the matrix, so that

$$D_A \frac{\partial A}{\partial x}\bigg|_{x=L_1} = D_J \frac{\partial J}{\partial x}\bigg|_{x=L_1} \;. \tag{S.4}$$

Further, at the fragment border, several scenarios are possible according to the landscape beyond: (i) the boundary may be completely absorbing, if there is a very hostile matrix for $x > L_2$, or (ii) totally reflexive, if the environment is as good as in the fragment, or (iii) it can be something in between. This point yields the third condition:

$$-D_A \frac{\partial A}{\partial x}\bigg|_{x=L_2} = bA\bigg|_{x=L_2} \;, \tag{S.5}$$

where b defines how reflexive or absorbing the border at $x = L_2$ is. When $b = 0$ means that the patch is large, and it is used to avoid size effects of habitat patch.

1

The fourth boundary condition deals with the reproductive behavior of the amphibians. The population of juveniles generated at the river at time t is proportional to the total number of adults in the fragment at an earlier time $t - t_1$. To control the population size we include a saturation parameter K, that considers the intraspecific competition at the river. Then, we have:

$$-D_J \frac{\partial J}{\partial x}\bigg|_{x=0} = \frac{rN}{1 + \frac{r}{K}N} \, , \tag{S.6}$$

where r is the recruitment of new individuals and N is the total adult population at the fragment in a previous time t_1 given by:

$$N = \int_{L_1}^{L_2} A(x, t - t_1) dx \, . \tag{S.7}$$

This model has the diffusive behavior of juveniles crossing the matrix searching for the fragment and the advective movement of adults during their return to the river to mate and reproduce. The condition (S.6) introduces two important phenomenological constants r and t_1. The first is the recruitment depending on the fertility of adults, the survival of tadpoles and the adult mortality in the matrix. The second, t_1, is the sum of the time expent by adults to cross the matrix, mate, reproduce, plus the time to mature eggs and develop juveniles capable of crossing the matrix.

Derivation of the stationary solution

The model equations (1 and 2), along with the boundary conditions (3, 4, 5 and 6), are studied qualitatively through the analysis of fixed points, namely, through stationary solutions, which do not depend on time, thus $A(x,t) = A^*(x)$ and $J(x,t) = J^*(x)$. In this case, we have that $\partial J / \partial t = 0$ and $\partial A / \partial t = 0$, leading to equations (8 and 9):

$$D_J \frac{d^2 J}{dx^2} = \mu_J J$$

$$D_A \frac{d^2 A}{dx^2} = \mu_A A \, .$$

The solution yields equation (10):

$$\begin{cases} J(x) &= c_1 e^{\sqrt{\frac{\mu_J}{D_J}}x} + c_2 e^{-\sqrt{\frac{\mu_J}{D_J}}x} \\ A(x) &= f_1 e^{\sqrt{\frac{\mu_A}{D_A}}x} + f_2 e^{-\sqrt{\frac{\mu_A}{D_A}}x} \, , \end{cases}$$

2

where the constants c_1, c_2, f_1 and f_2 from integration are fixed by the boundary conditions, that do not depend on time:

$$J\big|_{x=L_1} = 0 \tag{S.8}$$

$$D_J \frac{\partial J}{\partial x}\bigg|_{x=L_1} = D_A \frac{\partial A}{\partial x}\bigg|_{x=L_1} \tag{S.9}$$

$$-D_A \frac{\partial A}{\partial x}\bigg|_{x=L_2} = bA\bigg|_{x=L_2} \ , \tag{S.10}$$

$$-D_J \frac{\partial J}{\partial x}\bigg|_{x=0} = \frac{rN}{1+\frac{r}{K}N} \tag{S.11}$$

Using the boundary condition (S.10), we find

$$f_2 = f_1 e^{2\sqrt{\frac{\mu_A}{D_A}}L_2} \left(\frac{\sqrt{\mu_A D_A}+b}{\sqrt{\mu_A D_A}-b} \right) \ , \tag{S.12}$$

with $\beta = (b+\sqrt{\mu_A D_A})/(b-\sqrt{\mu_A D_A})$, we rewrite :

$$f_2 = -f_1 e^{2\sqrt{\frac{\mu_A}{D_A}}L_2}\beta \ , \tag{S.13}$$

From equation (S.8)

$$c_1 = -c_2 e^{-2\sqrt{\frac{\mu_J}{D_J}}L_1} \ ,$$

then, from equation (S.9), we obtain c_1 and c_2 as functions of f_1:

$$c_1 = f_1 \frac{\sqrt{\mu_A D_A}}{\sqrt{\mu_J D_J}} \frac{e^{-\sqrt{\frac{\mu_J}{D_J}}L_1}e^{\sqrt{\frac{\mu_A}{D_A}}L_2}\left(e^{-\sqrt{\frac{\mu_A}{D_A}}s}+\beta e^{\sqrt{\frac{\mu_A}{D_A}}s}\right)}{2} \tag{S.14}$$

$$c_2 = -f_1 \frac{\sqrt{\mu_A D_A}}{\sqrt{\mu_J D_J}} \frac{e^{\sqrt{\frac{\mu_J}{D_J}}L_1}e^{\sqrt{\frac{\mu_A}{D_A}}L_2}\left(e^{-\sqrt{\frac{\mu_A}{D_A}}s}+\beta e^{\sqrt{\frac{\mu_A}{D_A}}s}\right)}{2} \ , \tag{S.15}$$

where $s = L_2 - L_1$ is the fragment size.

Calculating N as function of f_1:

$$\begin{aligned} N &= \int_{L_1}^{L_2} A(x)\,dx = \int_{L_1}^{L_2} f_1 e^{\sqrt{\frac{\mu_A}{D_A}}L_2}\left[e^{-\sqrt{\frac{\mu_A}{D_A}}(L_2-x)} - \beta e^{\sqrt{\frac{\mu_A}{D_A}}(L_2-x)}\right]dx \\ &= f_1\sqrt{\frac{D_A}{\mu_A}}e^{\sqrt{\frac{\mu_A}{D_A}}L_2}\left(1-e^{-\sqrt{\frac{\mu_A}{D_A}}s}+\beta-\beta e^{\sqrt{\frac{\mu_A}{D_A}}s}\right) \ , \end{aligned} \tag{S.16}$$

3

then, using the condition (S.11):

$$f_1 = \frac{K}{\sqrt{\mu_A D_A}\, e^{\sqrt{\frac{\mu_A}{D_A}}L_2}} \times \left\{ \frac{\mu_A}{r}\left[\beta\left(e^{\sqrt{\frac{\mu_A}{D_A}}s}-1\right) + e^{-\sqrt{\frac{\mu_A}{D_A}}s}-1\right]^{-1} - \right.$$

$$\left. \left[\cosh\left(\sqrt{\frac{\mu_J}{D_J}}L_1\right)\left(\beta e^{\sqrt{\frac{\mu_A}{D_A}}s}+e^{-\sqrt{\frac{\mu_A}{D_A}}s}\right)\right]^{-1}\right\}. \quad (S.17)$$

Substituting Eq. (S.17) into Eqs. (S.13), (S.14) and (S.15), all integration constants are specified as function of the model parameters. Consequently, one is able to write the stationary solution $J^*(x)$ and $A^*(x)$ in terms of the model parameters.

Existence and stability of the stationary solution

From the biological perspective, the stationary solutions shown in the previous section are significant only if their values are positive for all x. It means that $J^*(x) > 0$ and $A^*(x) > 0$. Since it can be shown that the condition for positive stationary solution at any x yields the same results, we consider the particular case $x = 0$, to derive conditions for our model to satisfy:

$$J^*(0) > 0 . \quad (S.18)$$

Thus, taking $x = 0$ in equation (10) leads to

$$c_1 + c_2 > 0 , \quad (S.19)$$

which is satisfied if, and only if

$$\frac{r}{\mu_A \cosh\left(\sqrt{\frac{\mu_J}{D_J}}L_1\right)}\left[1 - \frac{1+\beta}{\beta e^{\sqrt{\frac{\mu_A}{D_A}}s}+e^{-\sqrt{\frac{\mu_A}{D_A}}s}}\right] > 1 . \quad (S.20)$$

In the case where the fragment border at $x = L_2$ is completely absorbing, one has $b = 0$ and $\beta = -1$, so the condition (S.20) for population persistence becomes:

$$r > \mu_A \cosh\left(\sqrt{\frac{\mu_J}{D_J}}L_1\right), \quad (S.21)$$

One can easily see that as $L_1 \to 0$, $\cosh\left(\sqrt{\frac{\mu_J}{D_J}}L_1\right) \to 1$, it shows immediately that in the case where there is no split, the population persistence is possible if r satisfies

$$r > \mu_A , \quad (S.22)$$

4

which is a known result for population dynamics.

Further, the stability around the trivial solution $J = A = 0$ turns out to be unstable, once the stationary solution becomes positive and stable. Therefore, the conditions for stability (S.20) and (S.21) found above are also valid to analyse this particular case.