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Response to Comment on "Habitat Split and the Global Decline of Amphibians"

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Response to Comment on "Habitat Split and the Global Decline of Amphibians"

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Habitat split, defined as human-induced disconnection between habitats used by different life history stages of a species, is a strong factor negatively affecting the richness of Brazilian Atlantic Forest amphibians. Here, the disconnection between streams and forest fragments is shown to reduce the proportion of species with aquatic larvae in local communities.

Becker *et al*. (*1*) showed a strong effect of habitat split on the richness of species with aquatic larvae but no effect on the richness of species with terrestrial development, both when habitat split was analyzed alone in linear regressions and when it was analyzed together with habitat loss and fragmentation in more complex path analyses. Cannatella (*2*) argues that if species with aquatic larvae are indeed more affected by habitat split than species with terrestrial development, we would verify a negative relationship between the proportion of species with aquatic larvae (a binomial variable) and habitat split. By using a simple logistic regression, he did not find this effect.

The answer to this question, however, requires more complex approaches. One important point is that the total number of species is not a fixed factor, as assumed by Cannatella (*2*), but a random variable that is affected by habitat split (*3*–*5*). We built two alternative linear models to test whether habitat split affects species with distinct developmental modes equally (model 1) or differently (model 2). Both models combine the effect of habitat split on the total species richness and on the proportion of this total that is represented by species with aquatic larvae. In model 1, the expected number of aquatic species is a fixed proportion of the expected total species richness. Model 2 is similar, except that the proportion of total species richness is a linear function of habitat split. Total species richness is a Poisson variate whose expected value is a linear function of habitat split. The number of aquatic species is a binomial variable, with parameter N as the expected total number of species and the parameter p (probability of a single success) as a constant for model 1 or a linear function of habitat split for model 2. We obtained maximum likelihood estimates of the parameters of each model with optimization routines (*6*, *7*). The models were compared with deviance tests (*4*).

Both models predict a decrease in the richness of species with aquatic larvae with increasing habitat split (Fig. 1) due to the negative effect of habitat split on total richness [model 1, intercept a = 21.2 ± 3.0 (SEM), slope b = –0.099 ± 0.048; model 2, a = 21.2 ± 2.9, b = –0.095 ± 0.052]. In model 1, the proportion of species with aquatic larvae was estimated as 0.647 (± 0.062). In model 2, this proportion decreases with habitat split (a = 0.841 ± 0.109, b = –0.005 ± 0.002). Only model 2 provides a significant fit in relation to the null model (model 1, deviance $D = 2.92$, df = 2, $P = 0.23$; model 2, $D = 9.36$, df = 3, $P = 0.025$). Model 1 underestimates the expected number of species with aquatic larvae in sites where habitat split is lower and overestimates it where habitat split is higher. Model 2 provides a better fit in comparison to model 1 ($D = 6.44$, df = 1, $P = 0.011$) and estimates that an increase in habitat split from 10% to 80% decreases the proportion of aquatic species from 0.80 to 0.45 across the studied sites.

Cannatella (*2*) performed three independent logistic regressions to estimate the effect of habitat split, habitat loss, and fragmentation on the proportion of species with aquatic larvae, failing to consider them in a single analytical framework. We performed a path analysis (*8*), with the same structure used in Becker *et al*. (*1*), using the residuals of a regression between the number of species with aquatic larvae and the total number of species (both in log scale) as a continuous index of the prevalence of species with aquatic larvae in the community (Fig. 2). It shows a strong and negative effect of habitat split [standardized path coefficient = –2.187 ± 0.783 (SEM), $P < 0.01$] and a positive effect of habitat loss (standardized path coefficient = 1.807 ± 0.892, $P < 0.05$). Similar results emerged when we used a Poisson multiple regression model with a robust error variance (*9*–*12*). The positive influence of habitat loss can be explained by its negative influence on the richness of species with terrestrial development, as reported in (*1*).

The question raised by Cannatella can also be answered at the species level. It can be rephrased as: "Are species with distinct developmental modes occurring in the same position along the habitat split gradient?" To test this hypothesis, we built a null model (*13*) based on the site records of all 58 closed-forest species reported in Becker *et al*. (*1*). The 12 sites were ranked according to their level of habitat split (1 to 12, from lower to higher levels of habitat split). Each species record in the matrix was replaced by the rank value of that site. For each species i, its location along the habitat split gradient was represented by the median rank r_i, calculated based on the number of records of that species (N_i). The median location of species with aquatic larvae (m_a, $n = 34$ species) and species with terrestrial development (m_t, $n = 24$ species) along the habitat split gradient were determined by the median r_i values for each developmental mode. The difference between the location of aquatic and terrestrial developing species along the habitat split gradient (d) was estimated as $d = m_a - m_t$. The significance of d was tested by a Monte Carlo simulation (10,000 trials), where the occurrences of each species i were randomly allocated among sites, considering the observed number of records for each species (N_i). Observed d was –2.5, this being significantly lower than one could expect by chance ($P = 0.008$).

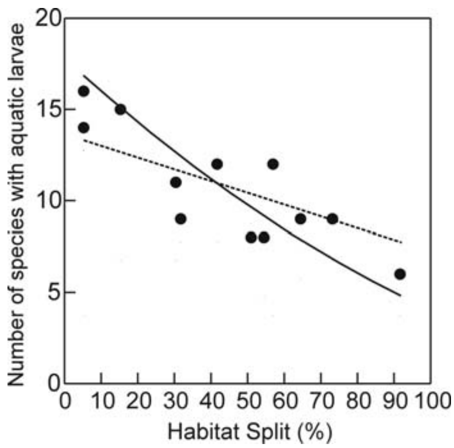

Fig. 1. Effect of habitat split on species richness of leaf-litter amphibians with aquatic larvae across 12 Brazilian Atlantic Forest landscapes. The dotted line represents the expected values for model 1, where the proportion of aquatic species out of the total number of species is constant [$S_{al} = (21.2 - 0.099\ S_t)(0.647)$]. The continuous line represents the expected values for model 2, where the proportion of aquatic species is a linear function of habitat split [$S_{al} = (21.2 - 0.095\ S_t)(0.841 - 0.005\ S_t)$]. Model 2 provides a better fit (deviance $D = 6.44$, df = 1, $P = 0.011$). S_t stands for total species richness and S_{al} for number of species with aquatic larvae.

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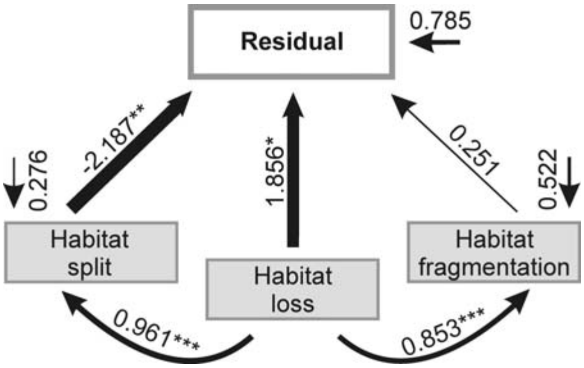

Fig. 2. Path analysis model showing the relative strength of habitat split, habitat loss, and habitat fragmentation on the prevalence of species with aquatic larvae. The prevalence is measured by the residuals of a linear regression between the number of species with aquatic larvae (log) and the total number of species (log) for 12 Brazilian Atlantic Forest landscapes.

We conclude that habitat split is inducing species with aquatic larvae to vanish from the Brazilian Atlantic Forest. Its influence on other organisms and ecological contexts remains to be tested. The concept of habitat split improves our ability to predict the effect of habitat changes on community structure and to design more efficient landscapes for amphibian conservation (*14*).

References and Notes

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12. An alternative approach to test the influence of habitat split, habitat loss, and habitat fragmentation on the proportion of amphibian species with aquatic larvae is the use of a Poisson multiple regression model with a robust error variance implemented in the module Proc Genmod in SAS (*9*). This method, which assumes a log link and a binomial distribution, has proven to perform better than logistic regression when frequencies are considerably high and sample sizes are small (*10*, *11*). In our data set, the proportions of species aquatic larvae in communities are high (minimum = 0.47, maximum = 0.80), and the number of independent data points is limited (N = 12 sites). The response variable is defined by the number of species with aquatic larvae (number of events) and by the total species richness (number of trials). The full model contained the three landscape variables and their higher-order interactions as explanatory variables; the minimal adequate model was established by a stepwise multiple regression, with backward deletion. The proportion of species with aquatic larvae was negatively associated to habitat split ($b = -0.0122 \pm 0.004$, $z = -3.06$, $P = 0.0022$) and positively associated to habitat loss ($b = 0.0102 \pm 0.0031$, $z = 3.32$, $P = 0.0009$). This reinforces the results presented by the path analysis.
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