



The effects of edge influence on the microhabitat, diversity and life-history traits of amphibians in western Ecuador

Research Article

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Abstract

Edge effects change biodiversity patterns and ecological processes, particularly in tropical forests. To understand the synergistic impact of multiple edges, this study examines how edge influence (EI) is associated with life-history traits (snout-vent length and body temperature), diversity and microhabitat of amphibians as well as habitat characteristics in a tropical forest in Ecuador. We used EI, a metric that calculates cumulative effects across all nearby edges, in combination with five environmental variables that are part of the amphibians’ microhabitat (temperature, humidity, slope, canopy cover and leaf litter depth) to understand how their biodiversity patterns are impacted. Our results show that most amphibian species tend to be habitat specialists, and many had an affinity for forest edges and warmer habitats. We do not find significant correlations between EI and amphibian life-history traits and diversity. Our findings corroborate previous results that many amphibian species tend to be positively associated with habitat fragmentation and show that this association is likely driven by thermal regulation.

Introduction

Estimates suggest that tropical forests harbour more than half of the world’s terrestrial diversity (Latham 2014), with 40% of global species of flora and fauna found in the forests in South America and the Caribbean (Botero 2015). At the same time, however, these forests in South America experience a high rate of forest cover loss, threatening this diversity (García *et al.* 2014). Such destruction of tropical forests is usually accompanied by fragmentation where large areas of forest are divided, creating edges between forests and human-modified habitats (Laurance *et al.* 2011). Edges expose forest areas to external climatic conditions, altering the microclimate and biotic interactions up to 1 km into the forest, which means that a large proportion of remaining natural habitat is modified by edge effects (Ewers and Didham 2008, Ewers and Banks-Leite 2013, Haddad *et al.* 2015). Despite the ubiquity of such edge effects, previous research often fails to fully assess the impact of forest edges on species, because most studies only investigate the influence of the nearest edge (Pfeifer *et al.* 2017). However, abiotic and biotic elements, including the diversity of species living within this habitat, respond to the cumulative (additive or synergistic) effect of all edges in the vicinity, having an additive nature (Malcolm 1994, Fletcher 2005).

To overcome this limitation, Pfeifer *et al.* (2017) developed an approach to measure cumulative edge effects taking into account the influence from multiple edges within a patch and any nearby edge in an adjacent patch. This measure is represented by edge influence (EI) and edge sensitivity (S) (Pfeifer *et al.* 2017), which have been used in previous studies and have highlighted the extent to which various species can respond to edge effects (Betts *et al.* 2019, Parra-Sanchez and Banks-Leite 2020). To our knowledge, no other approach is able to account for multiple effects. Another advantage of this metric is the use of tree cover map rather than a classified map, meaning that the influence of the matrix on the native habitat is measured by how much it contrasts to tree cover inside forest patches.

The extent to which species respond to edge effect depends on their traits (Pfeifer *et al.* 2014) and the microclimate at the forest edge (Isaacs-Cubides and Urbina-Cardona 2011). Small-bodied amphibians are more likely to be negatively impacted by edges due to changes in microhabitat (Dixo and Martins 2008, Pfeifer *et al.* 2017). Without constant hydration, smaller amphibians can cool down below ambient temperature only for a few minutes in open habitats along forest edges (Nowakowski *et al.* 2017), exposing them to a greater risk of overheating and desiccation (Mokhatla *et al.* 2019). In contrast, larger amphibians are better able to maintain their body temperature below the critical thermal maximum and, for this reason, are less sensitive to warmer conditions at edge habitats (Nowakowski *et al.* 2018). In Andean ecosystems, amphibian species that inhabit cultivated areas have a greater body mass than those

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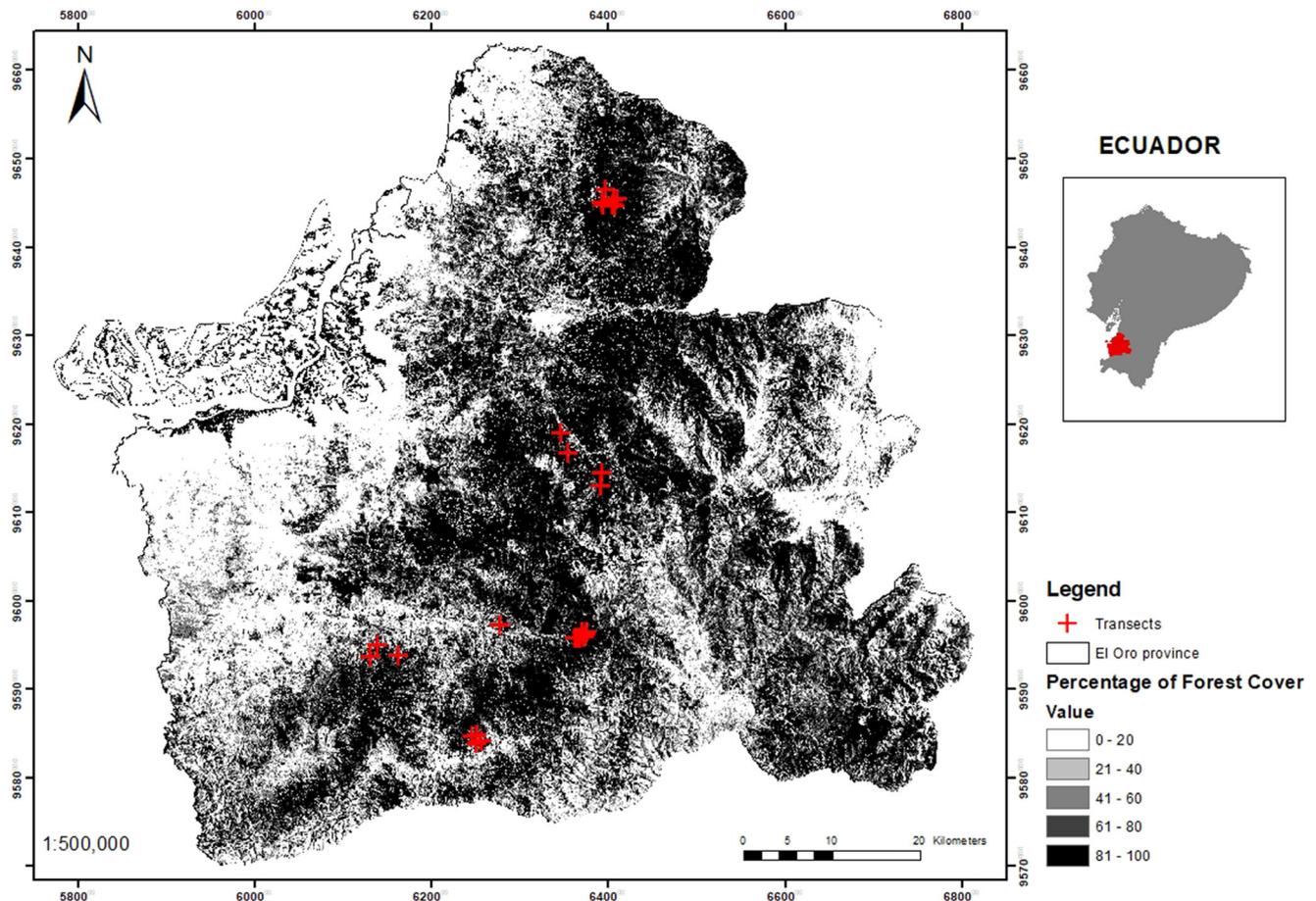


Figure 1. Study area and location of the transects used for the monitoring of amphibians in the province of El Oro, Ecuador. Darker colours indicate a higher tree cover in 2018.

that inhabit forest areas (Galindo-Uribe *et al.* 2022). Generalist species found along the vegetation gradient in neotropical forests have larger body sizes, reducing their ability to lose water and greater tolerance to desiccation (Zabala-Forero and Urbina-Cardona 2021, Galindo-Uribe *et al.* 2022). Habitat selection of amphibian species in tropical forests is also determined by tree and canopy cover, where microhabitats with a higher tree density offer more niches for species to develop in different vegetation strata (Roll *et al.* 2015).

Previous studies have shown mixed results of the impact of forest edges on amphibians. In Brazilian forests, breeding-guild proved to be a determinant in species distribution in response to edge effects (Prado *et al.* 2005). The study found that water-bodies breeders maintain stable abundances regardless of the distance from the edge, whereas leaf-litter and bromeliad breeders decreased in diversity as they approach the edge (Prado *et al.* 2005). In the Andean montane forests of Colombia, forest edges have lower species diversity of amphibians, although the configuration of the matrix surrounding the forest has a strong influence on how amphibians will use the edge (Cortés *et al.* 2008).

In Ecuador, studies in high Andean forests indicate an abrupt decrease in amphibian diversity upon reaching the edge of the forest and an agricultural matrix (Torales *et al.* 2002) or an increase in the abundance of diversity at the edge between a paramo-forest gradient (Celi and Posse-Sarmiento 2015). Taken together, the mixed results of the impact of edges on life-history traits, diversity and habitat selection of amphibians is often the result of the specific traits studied as well of using a methodology based on a binary classification of forest vs. non-forest habitat. These inconclusive

findings highlight the need to move beyond traditional edge effects measures that capture only simple information about the edge to one that such as EI, which incorporates more information about the patch as well as edges from neighbouring patches.

In this present study, we examine how edge effects are associated with life-history traits, and diversity of species, specifically amphibians, in a tropical forest in western Ecuador – one of the countries with the highest number of species per km² but also a country that lost about 12% of its natural forest cover in almost 30 years (1990–2018) (Tapia-Armijos *et al.* 2015, Kleeman *et al.* 2022). To better understand the species' response to the presence of a forest edge, we also analysed the influence of the edge on the microhabitat itself. We hypothesise that the microhabitat will become drier and hotter near the edge, reducing the diversity of amphibians. Further, we hypothesise that there will be two distinct anurofauna communities at the edge habitat and forest core as species vary in edge sensitivity, consisting of different species varying in body temperature and size.

Methods

Study area

The study was conducted between April and May 2019 in the piedmont forests of the province of El Oro in the southwest Andean slopes of Ecuador (Figure 1). This ecosystem is located between 400 and 1600 m a.s.l. and consists of forests with several strata and trees of more than 20 m in height (Morales *et al.* 2013).

These hyper-humid forests have an annual precipitation level of 1147 mm and an average annual temperature of 26°C (Melo *et al.* 2013). The topography is characterised by hills and slopes with abundant streams (Castro *et al.* 2013). Areas of cocoa crops, pastures for livestock and sectors for artisanal mining surround the remnants of the piedmont forests.

Amphibian sampling

To collect life-history traits (snout-vent length (SVL) and body temperature) and information about amphibians' diversity, we monitored transects using a methodology recommended by Urbina-Cardona *et al.* (2015). We determined the location of the transects using the Stratified Design Algorithm (SDA) (Bowler *et al.* 2022) which allowed us to place transects in a way that minimised the spatial autocorrelation of the data (Bowler *et al.* 2022). Using the SDA algorithm, we could establish 27 transects within 15 patches of forest. Each transect had a length of 30 m by 2 m wide and was surveyed by two people in the morning (9:00 to 11:00) and night (19:00 to 21:00) for two consecutive days. We did not sample transects outside the forest for safety reasons.

Each time we located an individual, we recorded their body temperature with an infrared thermometer with a Distance to Spot Size Ratio of 50:1 at a 10 cm distance from the target. Then, we collected each individual amphibian and took them to the base camp near our sampling area where we measured their body size (SVL). We kept the individuals overnight in well-ventilated and humid containers to avoid stress to the amphibian. This procedure further ensured that we were not taking the measurements of the same individual two nights in a row. On the morning of the third day, the amphibians were released into the transects where they were found.

Microhabitat survey

To characterise the microhabitat, we marked each transect in three sections: at 0 m, 15 m and 30 m. In each section, we recorded data on environmental temperature (°C, average temperature taken in the morning and evening of each sampling day), relative humidity (%), leaf litter depth (cm), and slope (%) and took hemispheric photographs to obtain a value of canopy cover (%). We obtained the percentage of canopy cover by analysing the photographs with the program ImageJ 1. x (Schneider *et al.* 2012) with the macro Hemispherical_2.0 (Beckschäfer 2015).

We used the data provided by Hansen *et al.* (2013) and Google Earth Engine (Gorelick *et al.* 2017) to create a map of the percentage of tree cover in the study area in 2018. Within this data set, tree coverage (per pixel) is defined as an estimate of the canopy cover of a forest that has trees with a height greater than 5 m. Combining the data sets of tree canopy cover and forest loss from Google Earth Engine allowed us to create a final map with a resolution of 30-m pixel percentage of tree cover.

EI and S calculation

We used the BioFrag Edge Response software (Lefebvre *et al.* 2016), developed by the BioFrag team, to calculate two metrics: edge influence (EI) and edge sensitivity (S). EI is calculated from maps of continuous gradient of tree cover per pixel across the landscape. It calculates the cumulative edge effects across multiple edges within the landscape (i.e., the influence of the matrix into the forest) and within the matrix (i.e., the influence of the forest into the matrix). By using both pieces of information, this measure is

not only based on a comparison of forest vs. matrix but takes into account the shape and size of every patch in the landscape, as well as additive and synergistic effects from nearby edge.

EI relies on information about the Depth of Edge Influence (DEI) which considers the shape and size of each forest patch and geographic location of the transects in our study. Generally, a higher value of DEI implies that a larger portion of the remaining habitat is under edge effects. Based on our map of the percentage of canopy cover and the location of our transects within the forest patches in our study, we used a value of 1250 m for DEI. This value influences the interpretation of EI, meaning that if a value of 0 is obtained for EI, there will be no edges in a radius of 1250 m and this area is considered a core zone. In contrast, a value of 100 reflects an edge habitat (Lefebvre *et al.* 2016).

The software also calculates edge sensitivity (S) which reflects amphibian' sensitivity to edges by analysing the area of EI that is not occupied by the species. Values of S vary between 0 and 1, where a value close to 0 is obtained for habitat generalists and values close to 1 are obtained for habitat specialists (e.g., edge or core of the forest) (Pfeifer *et al.* 2017).

Data analysis

Our data analysis strategy consisted out of two parts. First, we examined the association of EI with the amphibians' microhabitat (temperature, humidity, slope, canopy cover and leaf litter depth). Second, we investigate the association of EI, S and microhabitat on amphibian diversity. Specifically, we focus on amphibian abundance, which we defined as average number of individuals per transect, amphibian richness, which we defined as the number of different species detected in each transect, and amphibian life-history traits.

We ran four mixed-effect models using the R package lme4 (Bates *et al.* 2015) to test whether EI impacted the microhabitat of the amphibians. Each model had a similar structure with EI as an explanatory variable and a different characteristic of the microhabitat as the response variable (temperature, humidity, canopy cover and leaf litter depth). We excluded slope as a microhabitat characteristic from this analysis because of its intercorrelation with EI because of a measurement artefact. Each model included Transect ID as a random effect. We tested the statistical significance of each model by comparing it with a null model where the response variable was maintained, but the explanatory variable was 1.

We also ran two mixed-effect models to test whether EI impacted the diversity of amphibians as reflected in their richness and abundance. EI was the explanatory variable, with richness and abundance as the response variables in each of the models. We included Species ID as a random effect. We further tested how the microhabitat influences the abundance and diversity of amphibians with two quasi-Poisson GLM models which included six explanatory variables: environmental temperature, relative humidity, canopy cover, leaf litter depth, slope and EI. A quasi-Poisson model is used due to the presence of underdispersion in the data, allowing the dispersion parameter in the estimated model to deviate from 1. We report results as statistically significant when the p-value is equal to or less than 0.05. Variables that showed collinearity were excluded from the final model.

We used a linear mixed model (LMM) to test whether habitat specialists and generalists (as measured by edge sensitivity, S) vary in SVL and body temperature. The analyses only included categories that had more than two species. We performed two

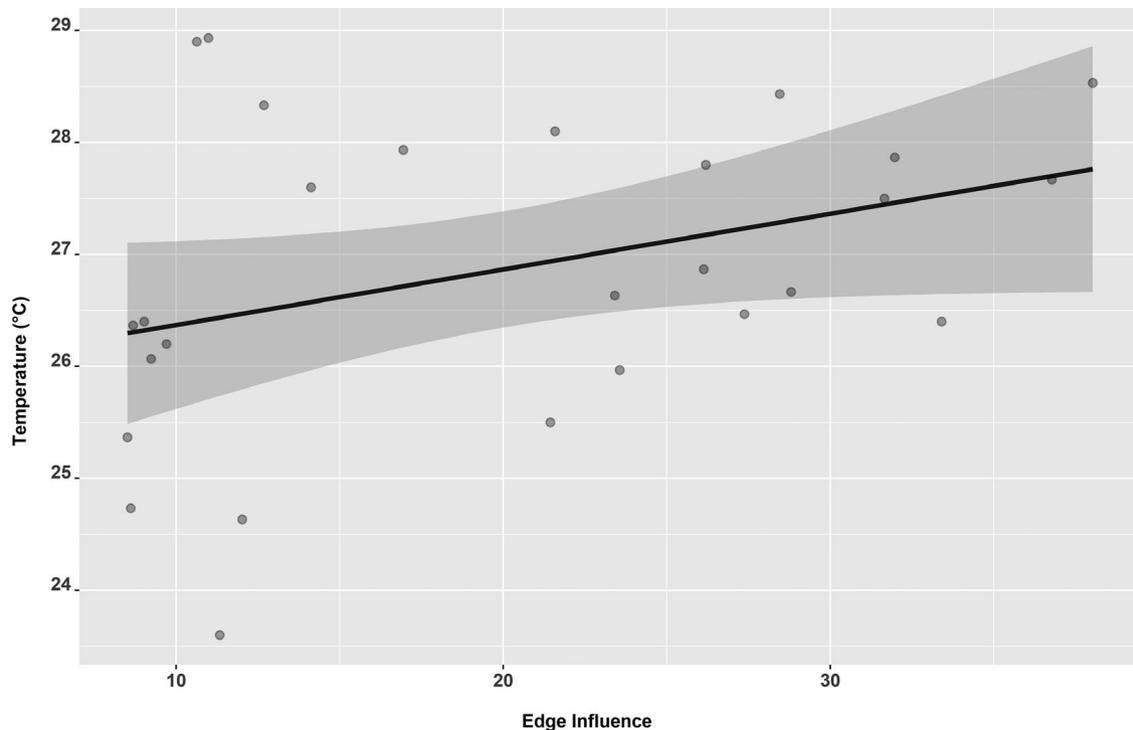


Figure 2. Graphical representation of the LMM. Microhabitat of amphibians. Temperature is shown in °C.

separate LMMs, one for SVL (mm) and one for body temperature (°C). We used R version 3.5.1 (R Core Team 2021) for all analysis and the R package ggplot2 (Wickham *et al.* 2016) for plotting.

Results

Microhabitat analysis

We recorded 332 individuals of 16 species of amphibians in 27 transects with a sampling effort of 216 person/hours. The most abundant species was *Pristimantis achatinus* (Cachabi robber frog), with 178 individuals, and the least abundant were *Agalychnis spurrelli* (Gliding Treefrog) and *Rhinella alata* (Forest toad), with one individual each.

We first tested whether EI is associated with characteristics of the amphibians' microhabitat and only found evidence for a statistically significant correlation between EI and temperature (0.58 SE, $R^2_{(m)} = 0.09$, $R^2_{(c)} = 0.72$, p-value = 0.001, Supplementary Table 1), with an average temperature was 25.9 °C. Transect ID explained 69% of the variance in the data. In an ecological context, these results show that for every unit increase in EI, the microhabitat temperature increases by 0.5 °C (Figure 2).

Amphibian diversity analysis

Next, we analysed the effect of EI on amphibian abundance and richness. None of the models showed any statistical significance (Supplementary Table 1). The model for amphibian richness revealed that the average number of species found per transect was 2.88, but transect ID explained 99% of all variance in the data. Similarly, the model for amphibian abundance also suggested that any variation in the explanatory variable is primarily explained by the transect.

We then investigated the association between microhabitat characteristics and amphibian diversity. The result of the best-fitted

quasi-Poisson model indicate that only temperature has an impact on amphibian richness (0.07 SE, p-value = <0.05) and none of the microhabitat characteristics have an association with amphibian abundance (Supplementary Table 2). When calculating the effect size of this association between temperature and amphibian richness, we can see that an increase in one degree in temperature is related to an increase in richness of 1.16 species of amphibians (Figure 3).

Amphibian life-history trait analysis

Lastly, we examined whether life-history traits differed across amphibians based on their habitat selection. We find that, on average, the species of amphibians recorded in our study have an S value of 0.71 (Figure 4), suggesting that most species tend to be habitat specialists. *P. achatinus* was associated with the lowest value ($S = 0.26$), indicating that this species is a habitat generalist. In contrast, *Rana bwana* (Rio Chipillico frog) was associated with the largest value ($S = 0.97$), indicating that this species is a habitat specialist. Based on their S scores, we classified eight out of the 16 species included in this study as belonging to the edge-response category Forest Edge and five as belonging to Forest Core. Two species were categorised as Non-Abundant and one was Unknown (Figure 5) (Supplementary Table 3; See also Wells 2010).

We then tested whether species' SVL and body temperature correlate with edge-response category and neither model showed statistical significance. The model revealed that the average SVL of Forest Core species was 31.77 mm (7.79 mm SE, Table 1) and 34.42 mm (9.91 SE, Table 1) for Forest Edge species. Species ID explained 91% of all variance in the response variable (Table 1).

The model for body temperature showed that the average temperature for Forest Core species was 25.02 °C (0.38 SE, Table 1), while for Forest Edge species, the average body temperature was 24.97 °C (0.46 SE, Table 1). Species ID explained

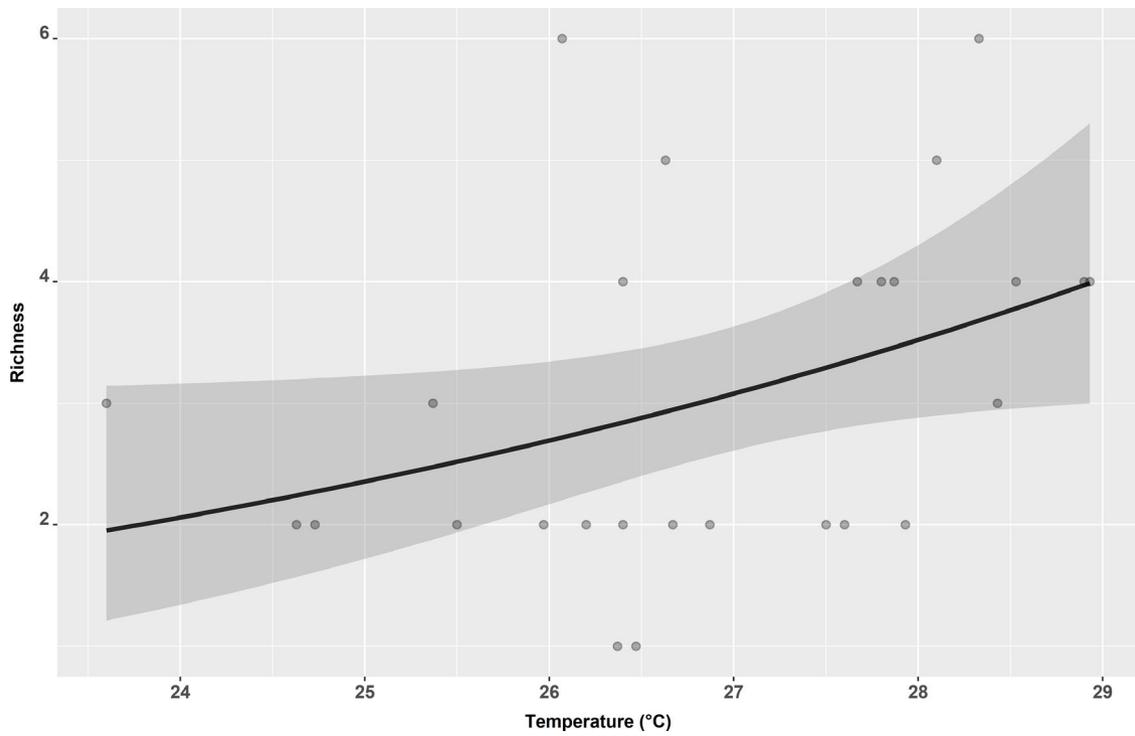


Figure 3. Graphical representation of the GLM. Richness of amphibians. Temperature is shown in °C.

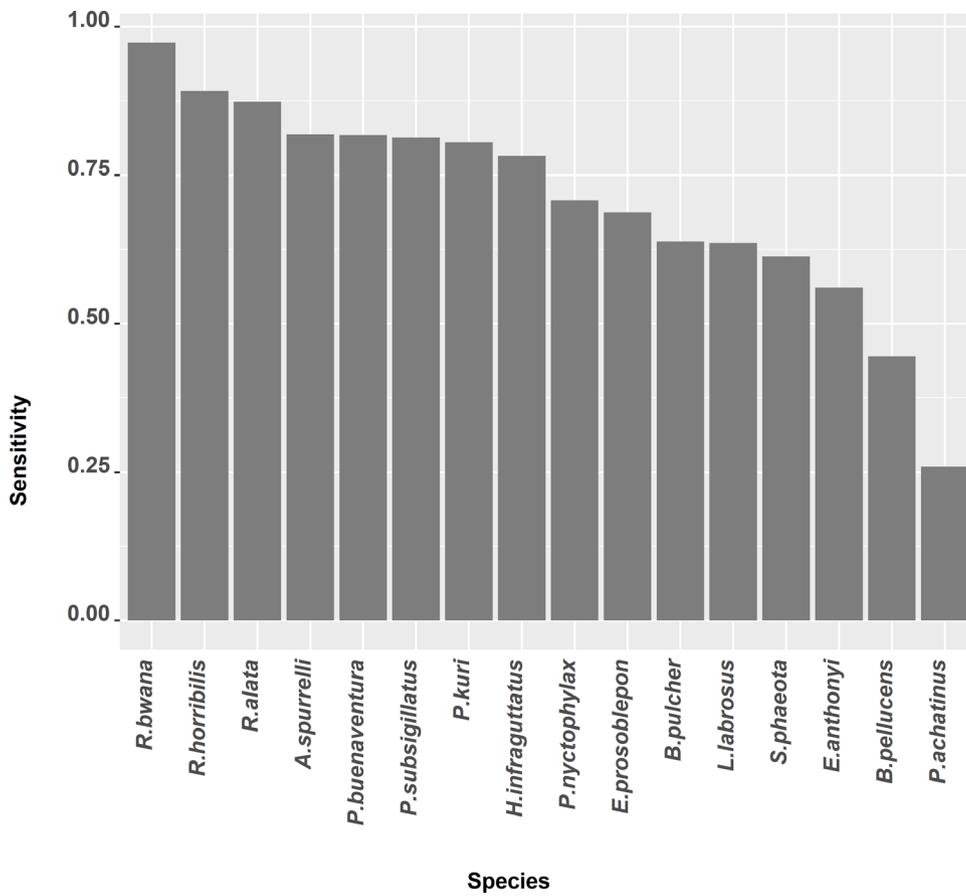


Figure 4. Values of edge sensitivity per species.

Table 1. Results of the LMM for amphibians SVL and body temperature. Model A) Amphibian SVL was the response variable, and the edge-response category was the explanatory variable. Model B) Amphibian body temperature was the response variable, and the edge-response category was the explanatory variable

A) Amphibian snout-vent length		
Variable	Estimate	Precision
Fixed effects	B	SE
Intercept (forest core)	31.77	7.79
Forest edge	2.65	9.91
Random effects	Variance	Standard deviation
Species	294.5	17.16
Residual	28.9	5.38
B) Amphibian body temperature		
Variable	Estimate	Precision
Fixed effects	B	SE
Intercept (forest core)	25.02	0.38
Forest edge	-0.05	0.46
Random effects	Variance	Standard deviation
Species	0.05	0.23
Residual	5.44	2.33

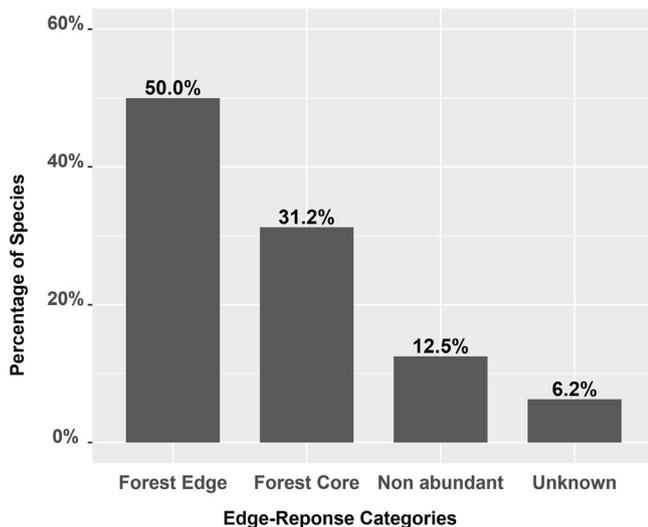


Figure 5. Percentage of species per edge-response categories.

0% of all variance in the data set, because there was not much variation within individuals or species.

Discussion

Forest edges are important landscape features in the western piedmont forests of Ecuador. Specifically, we found that EI positively influences ambient temperature which, in turn, has a positive association with amphibian species richness. Interestingly, we did not find evidence that EI impacts amphibian richness directly. We also found a strong turnover in species composition with 50% of the species preferring forest edges and 31% preferring forest cores. Together, our results show a complex relationship

between amphibians and habitat fragmentation but suggest that ultimately fragmentation negatively impacts the diversity of this community.

EI, microhabitat characteristics and amphibian diversity

Our study shows that EI is positively associated with temperature in the microhabitat of amphibians, supporting findings from prior research by Vieira *et al.* (2015) who studied changes in the Velvet ant's microhabitat in the Brazilian Amazon and found that transects closer to an edge recorded higher temperatures and further lower humidity. Ewers and Banks-Leite (2013) report that in the Atlantic Forest of Brazil, the capacity of the forests to buffer the maximum external temperature was reduced near the forest edges, where the edge effect extended up to 20 m inside the forest, making the temperatures higher, especially at a metre above the ground. Schneider-Maunoury *et al.* (2016) report an average depth of EI for amphibians in neotropical forests is 408 m (ranging from -11 m to 1900 m). These types of microclimatic changes tend to increase the mortality of trees and result in the creation of canopy gaps, further increasing temperature and decreasing humidity in an ever-expanding area (Laurance *et al.* 2007, Laurance *et al.* 2011).

When analysing the effects of microhabitat characteristics on amphibian diversity, our results showed that only temperature had an impact on amphibian richness, but none of the other habitat characteristics were statistically significant. A possible explanation is that temperature may function as a proxy for other microhabitat characteristics that correlate directly with amphibian diversity. This argument was put forward in a study by Urbina-Cardona and colleagues, conducted in Los Tuxtlas, Mexico, which also showed that amphibian diversity was significantly influenced by temperature in dry and wet seasons (Urbina-Cardona *et al.* 2006).

Amphibians' sensitivity to edges

Our study found high values of edge sensitivity (S) indicating that species either preferred forest edges or forest cores. These results may help explain why we did not find any effects of EI on amphibian richness and abundance, as there was a significant turnover in species composition between edge and interior transects, from edge to core specialists. Few of our recorded species were true generalists, with the leading example being *Pristimantis achatinus* – the most abundant species in the study which was recorded in 26 of the 27 transects analysed. Indeed, *P. achatinus* has been previously shown to have generalist habits regarding food, habitat selection and vertical stratum selection (Neira and Quezada 2016). On the other hand, *Rana bwana* was the amphibian species with the greatest sensitivity value. However, this species has been found in anthropogenically altered areas, as long as there are permanent bodies of water where their larvae can develop (Coloma *et al.* 2022). Since S is calculated using the abundance of each species, we believe that the result obtained may be due to a high abundance of this species in the only two transects where it was recorded, which were located near rivers. We believe that the degree of sensitivity of each species calculated using EI may vary as the sampling effort increases and the abundances of certain species increase.

Our results corroborate those from previous studies showing that although species richness may not be impacted, the species composition of amphibians can still be strongly influenced by habitat loss and fragmentation. For instance, Banks-Leite *et al.* (2014) showed evidence that forest cover does not affect the species richness of Atlantic Forest amphibians, but that species

composition varies dramatically along this gradient. In fact, changes in species composition along the gradient of habitat loss and fragmentation can be so dramatic that few species are shared between each side of the gradient (Banks-Leite *et al.* 2012). Similarly, about 50% of our amphibians inhabited the forest edge, while 31% inhabited the forest core (with another 12.5% not being abundant enough for analysis), highlighting the distinct composition of species within each type of habitat. In our findings, the greater richness at the Forest Edge could be due to species that are colonising this area from the matrix. Santos-Filho *et al.* (2008) found that of the 15 species of small mammals that they recorded in forest areas in Mato Grosso, Brazil, seven species constantly move between the edge and the matrix, so they were not exclusive to the forest edge. Our result likely reflects a group of species that use the matrix or the edge according to their convenience.

We would like to note that the duration of our study was reasonably brief as we only sampled in the wet season. It is possible that the forest edge specialists recorded in our study also use forest core habitats in other seasons, changing their edge sensitivity score. For instance, lizards of the genus *Norops* in Costa Rica likely migrate to forest edges during the dry season when they are not territorial (Schlaepfer and Gavin 2001). The same phenomenon has been observed in amphibians in Madagascar where species avoid forest edges in the dry season but use them in the rainy season (Lehtinen *et al.* 2003). In fact, researchers have suggested that amphibian species become more vulnerable to edges during dry periods (Demaynadier and Hunter 1998). The movement of amphibians during the rainy season may also respond to the preference of some species for warmer and deeper ponds which would benefit larval development (Ochoa-Ochoa and Whittaker 2014). These water bodies are generally found in more open or disturbed areas, so these amphibians would only use edge areas during the breeding season.

Piedmont forests in western Ecuador are one of the ecosystems with great richness of amphibians. Historical records indicate that throughout Ecuador, western piedmont forests can contain between 25 and 27 species of amphibians (Sánchez and Yáñez-Muñoz 2015, Ron *et al.* 2022). In contrast, we found only 16 species of amphibians during the course of our research. While the time frame of our study was limited to the wet season and we did not count species that were not identified at the species level (e.g., Sánchez and Yáñez-Muñoz 2015), it is highly plausible that the low number in species we encountered relative to historical numbers is the outcome of habitat loss and fragmentation, suggesting that species have already been lost in this ecosystem. We show that changes to amphibian microclimate (i.e., ambient temperature) can influence amphibian communities, especially their diversity. Given that edge effects have such strong documented influence on microclimate (Ewers and Banks-Leite 2013), it is critical that more studies assess the effects of habitat loss and fragmentation on amphibian diversity and microhabitat.

Supplementary material. For supplementary material accompanying this paper visit <https://doi.org/10.1017/S026646742400004X>

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Competing interests. The authors declare none

Ethical statement. The authors assert that all procedures contributing to this work comply with applicable ethical standards under the scientific research authorisation No. 007-2019-IC-FLORA/FAUNA-DPAEO-MAE granted by the Ministry of Environment of Ecuador.

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