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Research Article

Road-edge Effects on Herpetofauna in a Lowland Amazonian Rainforest

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Abstract

The impact of roads on the flora and fauna of Neotropical rainforest is perhaps the single biggest driver of habitat modification and population declines in these ecosystems. We investigated the road-edge effect of a low-use dirt road on amphibian and reptile abundance, diversity, and composition within adjacent lowland Amazonian rainforest at San José de Payamino, Ecuador. The road has been closed to vehicle traffic since its construction in 2010. Thus, effects from vehicle mortality, vehicle-related pollution, and road noise were not confounding factors. Herpetofauna were surveyed using both visual encounter surveys and drift fences with pitfall and funnel traps at varying distances from the road. Structural and microclimate features of the forest were measured at each sampling distance. Several habitat variables were found to differ at intermediate and interior sampling distances from the road compared to forest edge conditions, suggesting the road-edge effect began to attenuate by the intermediate sampling distance. However, the edge effect on amphibians and reptiles appeared to extend 100 m from the road edge, as abundance and diversity were significantly greater at the interior forest compared to the forest edge. Additionally, assemblage composition as well as the hierarchical position of species shifted between sampling distances. Habitat predictor models indicate that amphibian abundance was best predicted by vine abundance, while both vine and mature tree abundance were the best predictors for species richness and diversity. Overall, and contrary to what might otherwise be expected, our results demonstrate that small, little-used road disturbances can nonetheless have profound impacts on wildlife.

Key words: edge effects, herpetofauna, roads, Neotropical, amphibians, reptiles

Resumen

El impacto de carreteras sobre la flora y fauna de selvas es quizás el conductor más grande de la modificación de hábitat y disminución de poblaciones. Investigamos el efecto “orilla de la carretera” en una carretera de tierra de baja utilización sobre la abundancia, diversidad, e composición de anfibios y reptiles en la selva baja Amazónica en la vecindad de San José de Payamino, Ecuador. La carretera ha sido abandonada de tráfico vehicular desde su construcción en 2010, así efectos de mortalidad de vehículo, contaminación relacionada con vehículos, e ruido de carretera no era probable factores de confusión. La herpetofauna fue muestreada usando encuentro visual e cercas de desvío con trampas de caída e embudo a diferentes distancias de la carretera. Características de estructura e microclima fueron medidas en cada lugar. Varios variables de hábitat se encontraban a diferir a distancias de muestreo intermedios e interiores de la carretera a el bosque, comparada a condiciones de la orilla del bosque. Lo que sugiere es que el efecto “orilla de la carretera” empezó a atenuar desde la distancia de muestra intermedia de la carretera a el bosque. Sin embargo, el efecto de la “orilla de la carretera” sobre la herpetofauna aparecía extender 100 m del orilla de la carretera, así como abundancia e diversidad fueron significativamente mayor en el interior del bosque comparado con la orilla del bosque. Adicionalmente, composición de montaje también como posición jerárquica de especies desplazó entre distancias de muestreo. Modelos de predicción de hábitat indican que abundancia de anfibios fue mejor predicha por la abundancia de vides, mientras abundancias de vides e árboles maduras fueron los mejores predictores de la diversidad de especies. Sobre todo, y contrario a lo que de todos modos sería esperado, nuestros resultados demuestran que disturbios pequeñas, poco-usadas de carreteras pueden en todo caso tener impactos profundos sobre la fauna silvestre.

Palabras claves: efecto de orilla, herpetofauna, carreteras, Neotropical, anfibios, reptiles

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Introduction

Tropical forests harbor immense levels of biodiversity that includes roughly half of the world's terrestrial vertebrates [1]. However, habitat loss and degradation continue to be a great threat to tropical forest biota. Deforestation in the tropics is increasing the most in South America, with Ecuador suffering the greatest forest loss [2, 3]. Deforestation generally corresponds to an expanding regional road network, as a majority of deforestation occurs in close proximity to roads [4, 5]. Both legal and illegal road development associated with deforestation in the Amazon is driven by global demand for resources such as minerals, oil, timber, and gas [6-9]. An estimated 260,000 km of legal and illegal roads already penetrate the Amazon rainforest [5]. The relatively poor economic status of tropical South American countries—coupled with projected regional growths in economy and population—will likely exacerbate road development and resource exploitation in the Amazon as the 21st century progresses [1, 10, 11].

Despite the expanding road network in the region, studies of road impacts on Amazonian wildlife are relatively scarce, especially compared to temperate regions [12]. Existing research on tropical road ecology has demonstrated negative effects on wildlife from linear structures such as roads, which include: vehicle-related mortality [12-15]; elevated predation levels [12]; increased human hunting and exploitation [16, 17]; exotic species invasions [12]; and edge and barrier effects [1]. Road-edge effects can be particularly complex. Disturbances to forest adjacent to roads are not limited to changes in forest structure and microclimate [18]; road noise, artificial light, and road-related pollution also affect forest-edge habitat [12, 19]. The area of forest affected by these factors can vary depending on road location, road characteristics, and the focal taxa [1]. Furthermore, forest edges can act as barriers to species dispersal, because tropical rainforest biota typically evolve specialized life history traits specific to forest interiors [1, 12] and sub-populations may be genetically isolated and subjected to greater risk of local extinction [20]. However, current research has not sufficiently evaluated how road development impacts a majority of tropical animal species, assemblages, and communities.

With unpaved roads representing more than half of all roads in South America [14], it is particularly important to gauge the impact of primitive roads on biodiversity. Herpetofauna are especially diverse in the western Amazon Basin, which harbors the most diverse single-site herpetofauna assemblages on record [21-23], but these nonetheless remain underestimated [e.g., 24] and few road ecology studies center on Amazonian herpetofauna [25, 26]. In Neotropical humid forest, unpaved roads have less herpetofauna diversity than interior forest habitat [27]. However, it is unclear how primitive roads influence diversity and composition along the edge-interior forest gradient adjacent to a road. In fragmented landscapes, edge effects can vary depending on the region and focal species, and generally correspond to changes in forest structure and microclimate [28]. But how diversity and composition are impacted by a primitive road disturbance within otherwise intact forest—an increasingly common landscape feature—is poorly understood. Canopy dwelling anurans inhabiting epiphytic tank bromeliads have been shown to experience reduced abundance and occupancy in rainforest adjacent to an oil road compared to undisturbed forest [29]. Aside from this, little is known of the effects on herpetofauna and other taxa from low-impact dirt roads.

We examined the road-edge effect of a primitive dirt road on the abundance, diversity, and composition of amphibians and reptiles along the adjacent forest edge-interior gradient at a site in eastern Ecuador. Measures of forest structure and microclimate were quantified to explore any differences along the gradient, and models were created to determine which habitat variables, if any, have the greatest influence on herpetofauna abundance and diversity. Because the study road has experienced only foot traffic (*i.e.*, no vehicle traffic), any changes found in herpetofaunal variables are despite the absence of vehicle mortality, vehicle noise, road dust, and exhaust pollution since its construction.

Methods

Study Site

Fieldwork was conducted within the territory of the indigenous Kichwa community of San José de Payamino (Payamino hereafter) in the Amazonian province of Orellana, Ecuador, 300 m elevation (Fig. 1). Their extensive territory consists of ca. 17,000 hectares of lowland Amazonian rainforest and is bordered to the north by, and partially ranging within, the Gran Sumaco Biosphere Reserve. Much of their area is only used for hunting grounds, as most community members live near the forest bordering the Payamino River. The habitat is characterized by large tracts of primary *terra firme* forest, disturbed secondary forest primarily around the community square and near the Payamino River, and riparian forest and oxbow lakes along the Payamino River. Rainfall in the region is higher than that of the rest of the Amazon—averaging 3,711 mm over a 10-year period at a nearby site—and is generally considered aseasonal with irregular annual patterns [22].

Less than 10 years ago, Payamino was relatively isolated, and transportation to the nearest towns of Loreto and Coca was accomplished via river. This has now changed, as there has been a substantial amount of primitive road creation in the area within the past decade. One such road established in 2010 was poorly executed, as a river crossing with no bridge makes it inaccessible to most vehicles, and in multiple areas erosion has made the road impassable for vehicles since its construction (Paul Bamford, pers. comm.). Oriented north-south, this narrow stretch of dirt road (5-10 m wide) is about 4 km long and runs 1–2.5 km west of, and roughly parallel to, the Payamino River (Fig. 2; Appendix 1). Despite its size, the road leaves a noticeable scar in the landscape, creating a gap in the canopy (Appendix 1). Daily low-volume foot traffic occurs along the clearing, which, along with machete use, continues to maintain it as a road-sized disturbance.

Study Design

The project study area was restricted to secondary forest 110 m from each side of the dirt road (0°28'58"S, 77°17'5"W). Sampling greater distances from the road was not possible, as secondary forest occurred only as far

as ~125 m from both sides of the road (*i.e.*, primary forest began roughly 125 m interior from the forest edge in areas west of the road, but no primary forest was to the east side of the road). Therefore, sampling different habitat types from opposite sides of the road was avoided. We established eighteen alternating 100 m transects running perpendicular to the road, with the first running west of the road, the second running east, and so on (*i.e.*, nine transects per side; Fig. 2). A Garmin 62S model GPS unit was used to navigate the forest perpendicular to the road. Each transect was separated by 30–50 m from the nearest opposing transect. On each transect, three 20-m diameter plots were established at different distances from the road edge, with plot center-points marked at: 10 m (edge plot), 50 m (intermediate plot), and 100 m (interior plot). Plots did not extend onto roadside ditches or narrow grassy verges (*i.e.*, edge plots reached only to the forest edge) to avoid sampling individuals in standing water along the road periphery. Also, no plots overlapped small streams within the forest, although having some plots closer to streams than others was unavoidable.

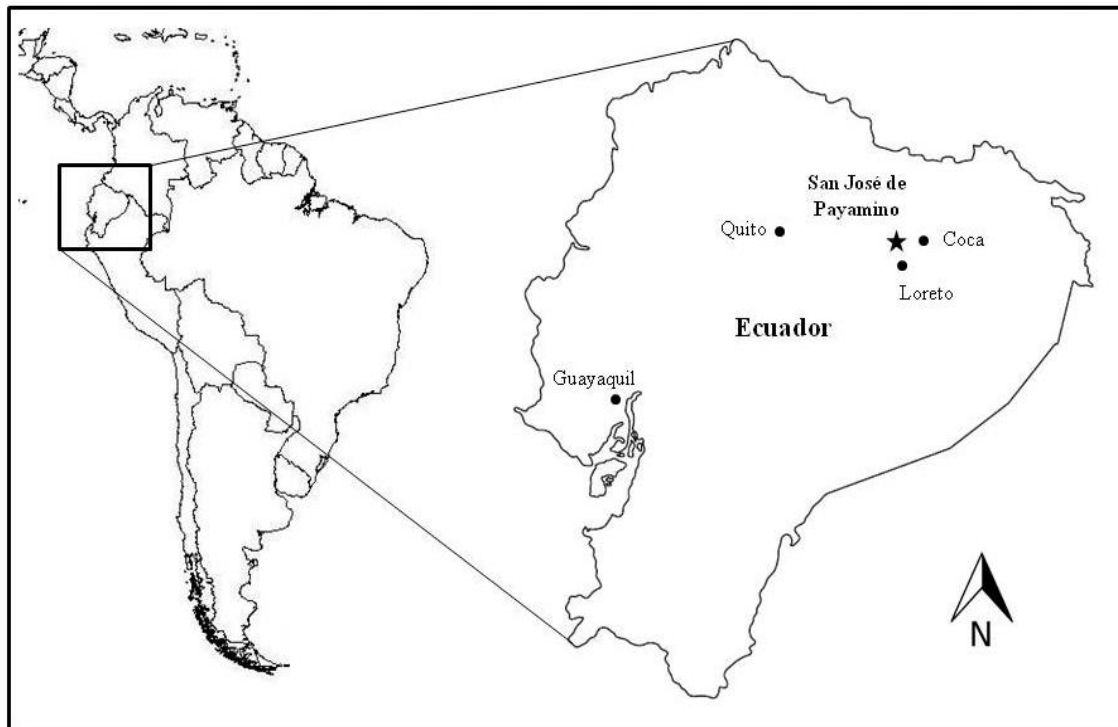


Fig. 1. Location of the study site, San José de Payamino (indicated by star), in Orellana, Ecuador, 300 m elevation.

Sampling Methods

All data were collected from June – August 2013. A nocturnal visual encounter survey (VES) was chosen as the primary sampling technique [30-31]. We performed two 30-minute VES sample efforts at least one week apart for each plot. All VES samples were conducted by the same two biologists (RJM and NCA). Each VES was performed between 1900 – 0030 h with the use of high-powered LED headlamps and a stopwatch to keep time. Prior to each night of surveys, the order at which plots were to be sampled along transects was selected at random to avoid bias in the timeframe sampling distances were surveyed.

Plots were 20 m in diameter with plot center points marked with flagging tape [32]. During a VES sample, a plot was surveyed as thoroughly as possible by both observers for 30 min. When an individual amphibian or reptile

was observed, the stopwatch was paused to allow data collection for the individual. Data collected on all animals were: *in situ* photographs, species identification, substrate or perch type, perch height (cm), perch diameter (cm), and a visual estimate of snout-to-vent length (mm). Although most individuals were not captured, all records from a plot were crosschecked via photographs to assure no individuals were counted twice during a survey.

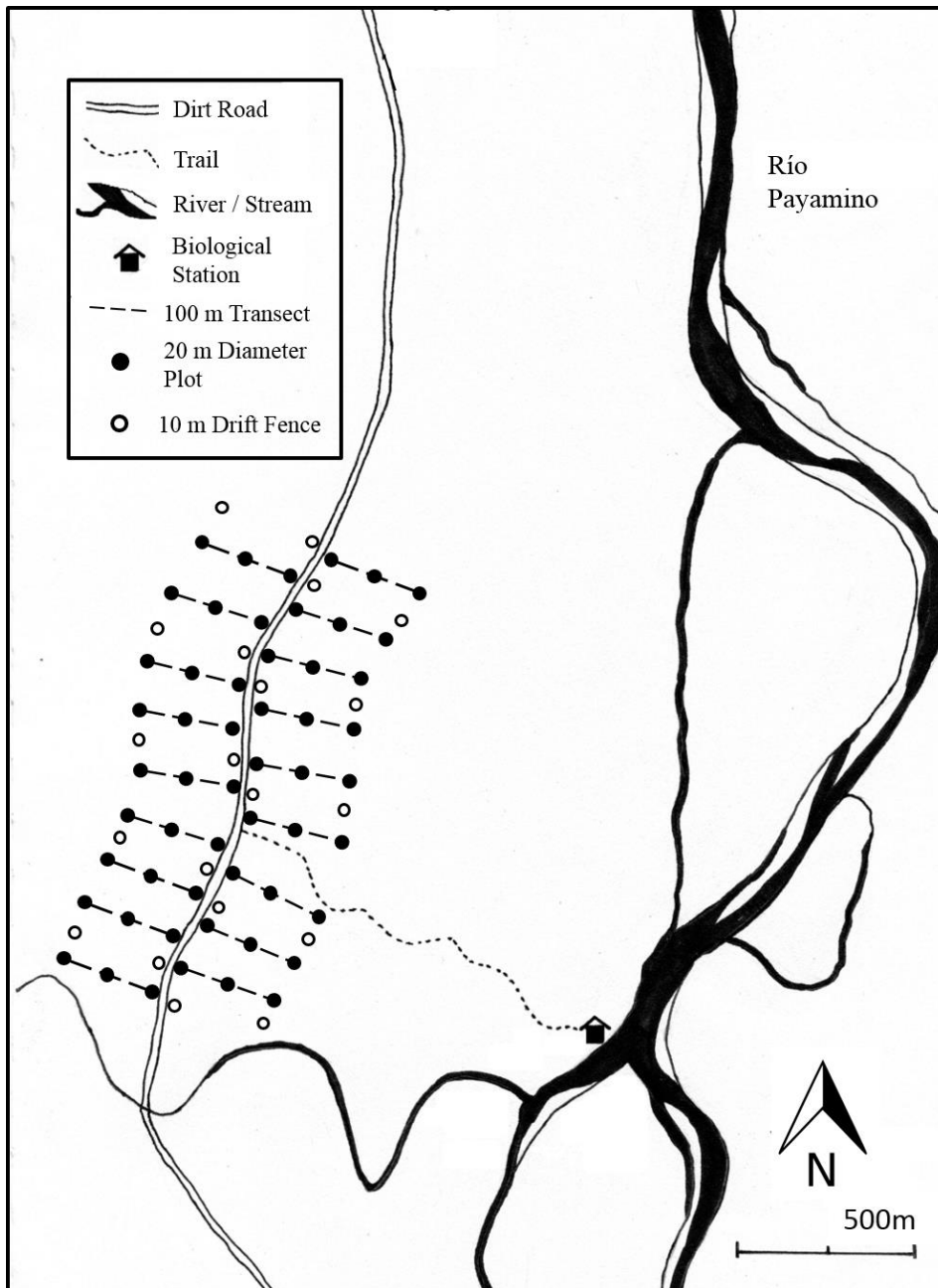


Fig. 2. Study design depicting sites of 20 m diameter plots and 10 m long drift fences. Plot center-points were situated at three perpendicular distances from the dirt road: 10 m (forest edge), 50 m (intermediate), and 100 m (interior forest). All sampling sites were restricted to secondary forest. Plot and drift fence locations are not to scale.

As a secondary sampling method, we constructed drift fences with both funnel and pitfall traps [33-34]. Combining this method with VES enabled a broader description of the herpetofauna assemblage along the sampled edge-interior forest gradient, since drift fences with traps are effective at capturing species easily overlooked by VES, such as those which are primarily fossorial or leaf litter inhabitants. Drift fence sites were chosen in a similar fashion to that of VES plots, however drift fences were constructed only at the forest edge (just inside the tree line) and interior forest (100 m), with 10 fences at each distance (Fig. 2). Drift fence sites did not overlap with plot sites and were distributed as evenly as possible from one another within the study area. Drift fences were 10 m in length, unidirectional, and oriented parallel to the road. Each fence had two mesh nylon funnel traps (25 X 46 X 25 cm; dual 6 cm entrances) placed at both ends of a fence on the side facing away from the road. Additionally, a large plastic bucket (40.5 l) was sunk flush to the ground at the center of each drift fence. All drift fences were open for a total of ten days and were checked at least once every 24 hours when open. Captured individuals were released after identification > 15 m away from the drift fence site to help avoid recaptures, corroborated by photos of captured individuals.

Six habitat variables were measured to determine structural differences along the forest edge-interior habitat gradient. At each plot site, we recorded leaf litter depth, understory density, percent canopy cover, vine abundance, abundance of mature trees (defined as number with DBH >12 cm), and number of downed trees (DBH \geq 20 cm). Leaf litter depth was measured by placing a graduated ruler into the leaf litter until it reached the soil. Understory density was calculated by vertically placing a 3.5-cm diameter and 2-m tall PVC pole on the ground and counting the number of contact points made on the pole by the vegetation (branches, stumps, leaves; [28]). Leaf litter and understory density were measured five meters from the center point of a plot in each of the four cardinal directions, and then averaged. Percent canopy cover was measured using a spherical densiometer held 0.5 m above the ground at the center of a plot. Vine abundance (woody and herbaceous) of plots was independently scored on a scale from 0 to 4 by both observers and then averaged, as outlined by Schlaepfer and Gavin [35]. Additionally, relative humidity and ambient temperature ($^{\circ}$ C) were recorded prior to each VES sample using a digital thermo-hygrometer.

Data Analysis

Analyses pertain to data from VES samples and are exclusive of drift fence data unless specified. Drift fence data are primarily used to compare sampling methods as well as to detect species that were unique to this method. A complete list of all individuals recorded by either method is reported (Appendix 2).

Abundance of amphibians and reptiles for each plot was calculated as the average of the total abundance values from each of the two VES samples of a plot. We calculated amphibian and reptile species richness in the same fashion. Diversity was also calculated for each plot using the Shannon-Weaver index, but only for amphibians, as sample sizes were generally too low for reptiles. We used Pearson correlation coefficients to identify correlated measures of the habitat. Pairwise permutation tests [36] were used to examine differences in habitat variables and herpetofauna abundance and diversity among habitat types. Each permutation test was performed for 9,999 iterations, using the *PopTools* 3.2 plugin for Microsoft Excel. Pairwise differences among sampling distances were calculated by taking the absolute difference between the mean values for the variable being tested. The original plot values were then randomly re-assigned (without replacement) to treatments, allowing an additional absolute difference to be calculated using the resampled data. Next, the distribution of absolute differences from resampled data was compared to the absolute difference from the actual observed values to determine the likelihood that the pattern found in the original data could be found by chance [36]. The *P*-value for the test represents the proportion of the 9,999 iterations that were greater than, or equal to, the observed difference in treatment means. Observed values were considered significant if the *P*-value was < 0.05.

We compared abundance patterns and species evenness between sampling distances using rank-abundance curves [37]. For each sampling distance, we plotted relative abundance of each species on a logarithmic scale against the rank order for the species from most to least abundant [28]. Relative abundance of a species was calculated as the total number of individuals of i species divided by the total number of individuals recorded at that sampling distance (n_i/N). Rank-abundance curves were calculated for amphibians and reptiles separately. All records were included for analysis from both surveys of each plot.

To better understand which measured habitat variables best predict animal abundance and diversity, we created models using stepwise multiple regressions in program JMP (v.10; SAS Institute). After consideration of collinearity, a standard least squares regression was used to obtain the parameter estimates, followed by forward stepwise multiple regressions. Habitat variables were included in models using the selection threshold of $P \leq 0.10$. We used the lowest Akaike's Information Criterion (AIC_c) score to select the model that best explains the dependent variable using the fewest habitat variables. Additional models that had a difference in AIC_c score (ΔAIC) within 2.0 of the best model (*i.e.*, that with the minimum AIC_c score) were also noted for consideration. Models were only created for amphibians due to the relatively small sample size for reptiles.

Ethics Statement

Field work was carried out in strict accordance with the recommendations in the guidelines for use of live amphibians and reptiles in field research compiled by the American Society of Ichthyologists and Herpetologists (ASIH). Research was conducted with permission of the Ministerio del Ambiente, Ecuador, (permit #: 001-11 IC-FAU-DNB/MA).

Results

A total of 672 individuals comprising 43 amphibian species from eight families and 21 reptile species from nine families were recorded from VES samples and drift fence captures within the secondary forest of the study area. These represent 58% and 36% of the amphibian and reptile fauna currently known from Payamino territory, respectively (Maynard, unpubl. data). Amphibians accounted for 89% ($n = 596$) and reptiles accounted for 11% ($n = 76$) of all records. Terrestrial-breeding frogs of the genus *Pristimantis* were the most commonly encountered group (73% of amphibian records; 64% of total records), and this genus represented the six most abundant species (Appendix 2). In contrast to the comparatively few abundant species, 24 amphibian and 17 reptile species were represented by \leq five individuals; of these, 12 amphibian and seven reptile species were represented by a single individual (Appendix 2).

The species accumulation curve from VES samples indicate that a majority of the herpetofauna within the study area were recorded, as it approaches an asymptote (Appendix 3D). However, curves plotted for each habitat type separately suggest that further sampling will likely yield additional species, particularly at the forest edge and interior forest sampling distances. The species accumulation curve for drift fence captures corroborates an incomplete sample of the study area (Appendix 5), and recorded three amphibian and five reptile species not detected during VES samples (Appendix 2).

VES surveys accounted for 588 records (87% of total records) consisting of 40 amphibian species from eight families and 16 reptile species from seven families. Amphibians were much more abundant ($n = 542$) than reptiles ($n = 46$). Amphibian abundance was highest at the interior forest ($n = 219$, 40% of VES observations) and intermediate habitats ($n = 186$, 34%), while forest edge habitat exhibited the least abundance ($n = 137$, 25%). Reptiles were also most abundant at the interior forest habitat ($n = 25$; 54%), while forest edge habitat was the next most abundant ($n = 12$; 26%) and intermediate habitat was the least abundant ($n = 9$; 20%). Pairwise permutation tests using mean plot values show that both amphibian and reptile abundances were significantly greater in the interior forest habitat than in forest edge habitat ($P = 0.0063$; $P = 0.0317$, respectively; Fig. 3).

Reptile abundance at the interior forest habitat was also significantly greater than that at the intermediate sampling distance ($P = 0.006$).

Of the 40 amphibian species recorded during plot surveys, 29 species (73%) were observed at the interior forest habitat, and 23 species (58%) were recorded at both the forest edge and intermediate habitats (Appendix 2). Of the 16 reptile species recorded, interior forest was again the most species rich with 14 species (88%), while the forest edge and intermediate habitats yielded seven species (44%) and four species (25%), respectively. Amphibian and reptile species richness were significantly greater at the interior forest habitat than at the forest edge habitat ($P = 0.0488$; $P = 0.0309$, respectively; Fig. 3). The same was true for amphibian diversity ($P = 0.0450$; Fig. 4).

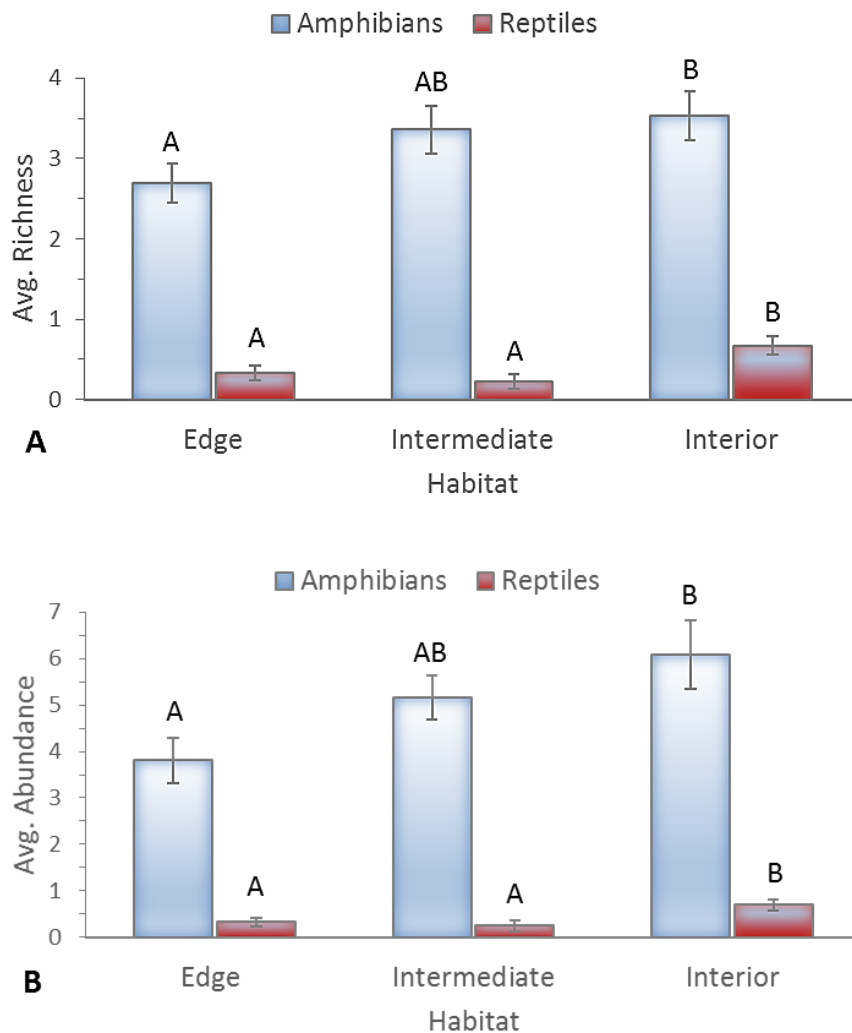


Fig. 3. (A) Comparison of mean values for amphibian and reptile abundance at each habitat type (i.e., each sampling distance from the road edge). (B) Comparison of mean values for amphibian and reptile richness at each habitat type. Bars with similar letters did not differ ($P \geq 0.05$) after pairwise tests comparing the absolute difference between observed values and permuted values. Error bars represent one standard error.

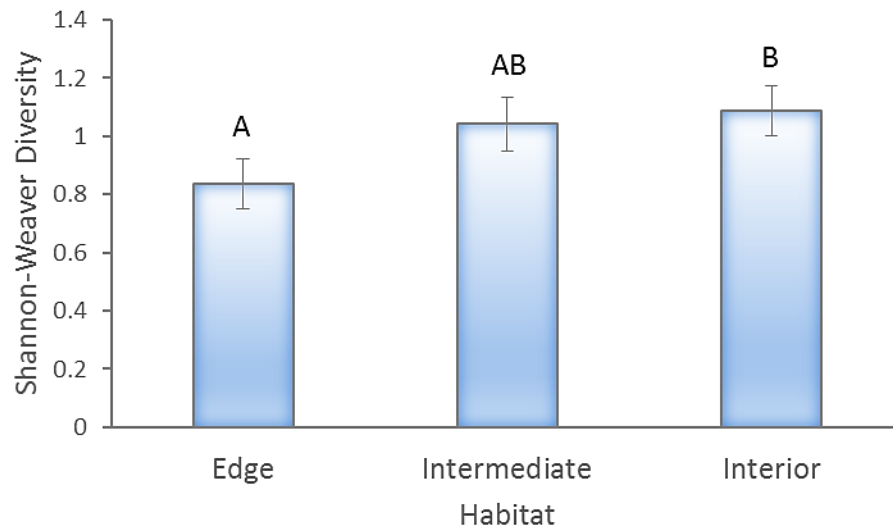


Fig. 4. Comparison of mean values for amphibian diversity at each habitat type (i.e., each sampling distance from the road edge). Bars with similar letter did not differ ($P \geq 0.05$) after pairwise tests comparing the absolute difference between observed values and permuted values. Error bars represent one standard error.

Further examination of the plot dataset shows that eight species were documented only within the forest edge habitat, four species were unique to the intermediate habitat, and 13 species were unique to the interior forest habitat (Appendix 2). Thirteen species were recorded in all three habitats; however, over half ($n = 7$) demonstrated increased abundance from the edge to the interior forest habitat, four showed no trend, and two declined in abundance. Using pairwise tests for species with sample sizes greater than 50, the abundances of *Pristimantis kichwarum*, Metallic Robber Frog (*P. lanthanites*), and *P. aff. martiae* were significantly greater in interior forest habitat than in edge habitat ($P = 0.0012$, $P = 0.0405$, and $P = 0.0027$, respectively). The difference in abundance for *P. aff. martiae* between edge habitat and intermediate habitat was also significant ($P = 0.0081$), and approached significance for the Metallic Robber Frog ($P = 0.0877$). *Pristimantis variabilis* demonstrated the opposite relationship, as its abundance was significantly greater in edge habitat than in interior habitat ($P = 0.0042$).

The slopes in rank-abundance curves for amphibians in all three habitat types mostly resemble a log series model, with few highly abundant species and many rare species (i.e., species having $n \leq 3$ individuals; Fig. 5). However, intermediate and interior forest habitats harbored a range of abundant species, suggesting greater evenness, whereas only one highly prolific species persisted at the forest edge habitat (*P. variabilis*). Rank-abundance curves for reptiles at the edge and interior forest are also distributed according to a log series model, and the most abundant species in both habitats was the same (Slender Anole [*Anolis fuscoauratus*]; Fig. 5). Intermediate habitat showed a rank-abundance curve that suggests greater species evenness, but this is based on only four species recorded at this sampling distance and relatively few records, making interpretation difficult.

Drift Fences

Drift fence captures accounted for 84 records (13% of total records) consisting of 14 amphibian species from four families and 10 reptile species from six families. More amphibians were captured ($n = 54$) than reptiles ($n = 30$). We experienced an overall capture rate of 0.42 animals per drift fence/day. In contrast to VES plot samples, there were more individuals and species of herpetofauna captured at drift fences within the forest edge (abundance = 58; richness = 18) than in interior forest habitat (abundance = 26; richness = 12); these differences were not significant ($P = 0.0880$; $P = 0.3186$; respectively).

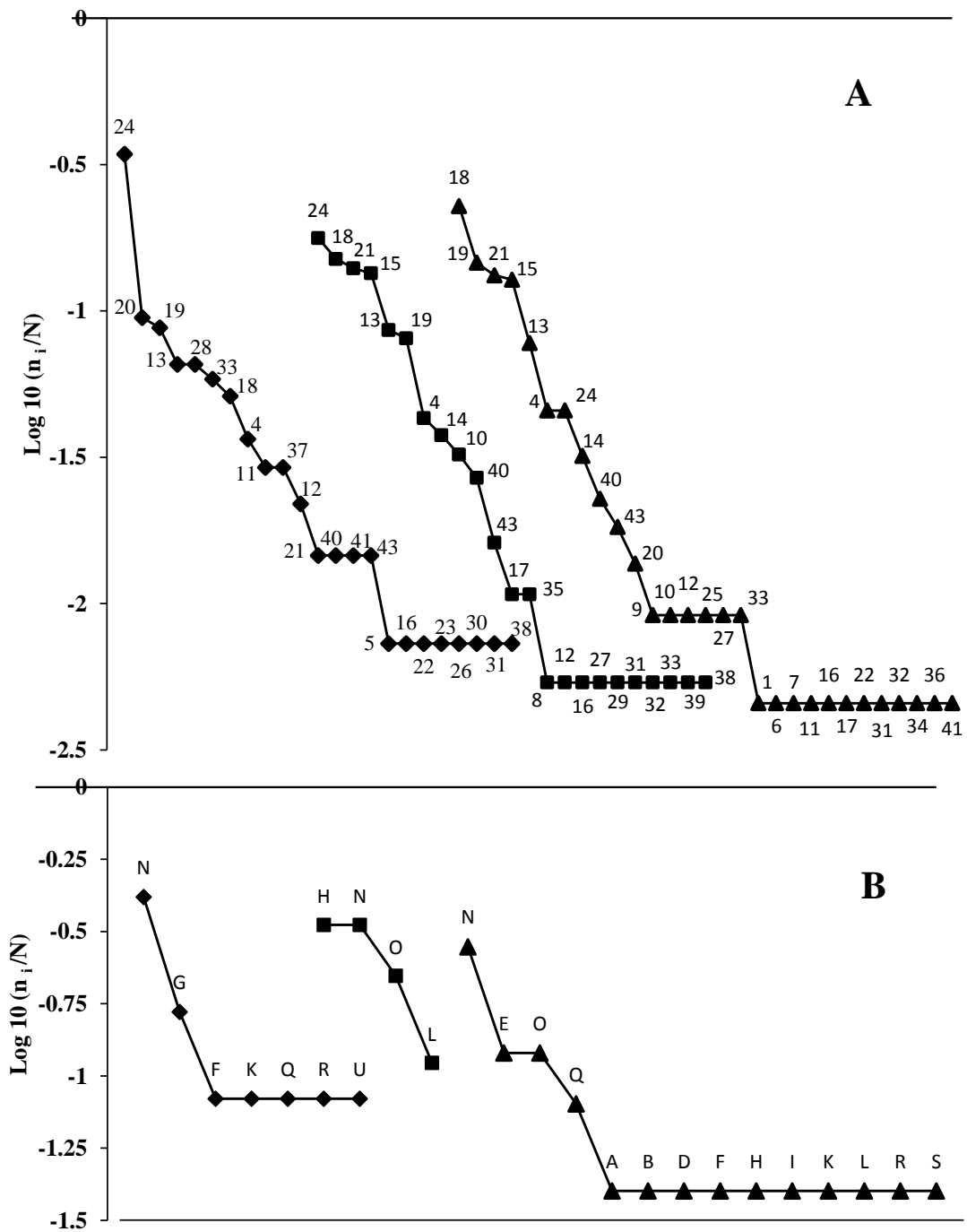


Fig. 5. Rank-abundance curves for amphibians (A) and reptiles (B) at the edge (♦), intermediate (■), and interior forest (▲) habitats. For each curve, relative abundance (n_i/N) of species is plotted on a logarithmic scale against the species rank, ordered from most (far left species on a given curve) to least abundant (far right). Numbers and letters next to symbols represent species codes, which are provided in Appendix 1.

Habitat Structure and Climate

There were various differences found in habitat structure across the forest edge-interior gradient (Table 1). Understory density and vine abundance decreased with increasing distance from the road; both variables were significantly greater at the forest edge habitat than in intermediate and interior forest habitats (all comparisons: $P < 0.001$; Table 1). Downed tree abundance and average temperature demonstrated a general decline with distance from the road, although differences between habitats were not significant. Mature tree abundance and relative humidity increased with distance from the road; mature tree abundance was significantly different between habitats (edge vs. intermediate: $P < 0.001$; edge vs. interior: $P < 0.001$). Canopy cover was greater at the intermediate habitat than at forest edge ($P = 0.004$). No trend in leaf litter depth was found relative to distance from the road (edge vs. intermediate: $P = 0.6639$; edge vs. interior: $P = 0.3570$; intermediate vs. interior: $P = 0.1719$).

Various habitat and climatic features were correlated (Table 2). Vine abundance was most strongly correlated with understory density, mature tree abundance, and distance from the road ($P < 0.001$). Mature tree abundance also had notable correlations with understory density and canopy cover. Correlations between distance from the road and both understory density and mature tree abundance were also highly correlated.

Abundance and Diversity Models

Stepwise regressions suggest that vine abundance is the single most important predictor variable for amphibian abundance, richness, and species diversity within the study area (Table 3). Models with the lowest AIC_c score for each of the dependent variables indicate a negative relationship with vine abundance. Models within two Δ AIC of the best model for amphibian abundance also include downed tree abundance and relative humidity. For amphibian richness and diversity, the model with the lowest AIC_c score includes vine abundance and mature tree abundance (Table 3). As vine abundance decreases and mature tree abundance increases, richness and diversity are predicted to increase.

Table 1. Habitat and environmental variables measured at each plot along the forest edge-interior gradient adjacent to a dirt road at San Jose de Payamino, Orellana, Ecuador. Values in a row with same letters did not differ ($P \geq 0.05$) after pairwise tests comparing the absolute difference between observed values and permuted values. LLD = leaf litter depth; USD = understory density; CC = canopy cover; VA = vine abundance; MT = mature tree abundance; DT = downed tree abundance; RH = relative humidity; AT = ambient temperature.

Habitat Variable	Edge (10 m)		Intermediate (50 m)		Interior (100 m)	
	Mean	SD	Mean	SD	Mean	SD
LLD (cm)	2.2 _A	±1.4	2.1 _A	±0.5	2.5 _A	±0.7
USD (pole contacts)	5.2 _A	±1.3	2.9 _B	±0.7	2.9 _B	±1.1
CC (%)	87.1 _A	±6.2	91.9 _B	±4.4	89.7 _{AB}	±3.5
VA (low 0-4 high)	3.0 _A	±0.8	2.0 _B	±0.8	2.0 _B	±0.8
MT (> 12 cm)	2.4 _A	±1.5	6.7 _B	±3.2	7.8 _B	±2.3
DT (> 20 cm)	1.6 _A	±1.0	1.1 _{AB}	±1.9	0.4 _B	±1.0
RH (%)	90.4 _A	±2.0	91.6 _{AB}	±2.5	92.0 _B	±2.6
AT (°C)	25.6 _A	±0.9	25.4 _A	±1.0	25.2 _A	±1.1

Table 2. Pearson correlation coefficients among nine environmental variables measured within the secondary rainforest bordering the primitive dirt road.

	DR	LLD	USD	CC	VA	MT	DT	RH	AT
Distance from road	1.00								
Leaf litter depth	0.14	1.00							
Understory density	-0.61 ^c	-0.18	1.00						
Canopy cover	0.19	-0.23	-0.19	1.00					
Vine abundance	-0.44 ^c	-0.25	0.48 ^c	-0.13	1.00				
Mature tree abundance	0.65 ^c	0.08	-0.40 ^b	0.36 ^b	-0.47 ^c	1.00			
Downed tree abundance	-0.32 ^a	-0.02	0.12	-0.31 ^a	0.33 ^a	-0.59 ^c	1.00		
Relative humidity	0.27 ^a	0.21	-0.27 ^a	0.04	-0.33 ^a	0.24	-0.29 ^a	1.00	
Temperature	-0.15	-0.14	0.08	-0.13	0.15	-0.05	0.18	-0.45 ^c	1.00

For *P*-values from pairwise correlations: a = < 0.05; b = < 0.01; c = < 0.001

Table 3. Best-supported habitat predictor model (using lowest AIC) for amphibian abundance, richness, and Shannon-Weaver (SW) diversity.

Model	Variables	Parameter				95% Confidence	
		Estimate	SE	r^2_{ADJ}	<i>P</i> -value	Lower	Upper
Abundance	VA			0.2458	< 0.0001		
	Intercept	8.3584	0.8385		< 0.0001	6.6757	10.041
	VA	-1.4201	0.3322		< 0.0001	-2.0868	-0.7534
Richness	VA, MT			0.1829	0.0022		
	Intercept	3.7177	0.6552		< 0.0001	2.4024	5.0331
	VA	-0.4204	0.1889		0.0305	-0.7997	-0.041
	MT	0.0829	0.0522		0.1185	-0.0219	0.1878
SW Diversity	VA, MT			0.2176	0.0019		
	Intercept	1.1234	0.2022		< 0.0001	0.7174	1.5294
	VA	-0.1242	0.0583		0.0381	-0.2412	-0.0071
	MT	0.0281	0.0161		0.0879	-0.0043	0.0604

VA = vine abundance; MT = mature tree abundance

Discussion

Amphibians and reptiles within the forest bordering the dirt road at Payamino demonstrated an overall negative response to the road-edge effect, as forest edge habitat harbored markedly fewer numbers of animals and species than the interior forest habitat (*i.e.*, 100 m). Assemblage composition of both groups shifted along the forest edge-interior gradient, as evident by changes to hierarchical positions of species among sampling distances. Distribution patterns of amphibians appear to have been influenced by substantial changes to the habitat structure, which in some cases occurred as close as 50 m inside the forest edge. The differences in reptile distribution were difficult to interpret due to low sample sizes.

Despite being a relatively small disturbance, the dirt road's impact on the structure of the adjacent forest was similar to that of a fragmented forest landscape. Changes found along the edge-interior forest gradient, such as decreasing vine abundance and understory density and increasing mature tree abundance, are also characteristic of Neotropical forest fragments; these changes correspond with substantial variations in local amphibian and reptile distributions [35, 38]. Temperature has also been correlated with species incidence along forest edge-interior gradients [28]. We did not detect a temperature difference, likely due to sampling only at night, although a difference potentially exists during the day due to greater penetration of sunlight at the forest edge [18]. Even so, a difference in climate was detected, as relative humidity increased with greater distance from the road-edge. However, determining the degree at which certain habitat characteristics influence animal distributions is difficult because of various combinations of synergistic interactions with other abiotic and biotic factors.

Amphibian Distribution Patterns

Corroborating similar studies, species-specific responses to differences in habitat strongly influenced amphibian abundance and diversity trends [28, 35, 39]. For example, both the highly disturbed forest-edge habitat and moderately disturbed intermediate habitat were dominated in relative abundance by a disturbance specialist (*Pristimantis variabilis*), particularly at the forest edge (Appendix 2). This same species was uncommon in the interior forest habitat and was observed only in the few plots that showed clear signs of disturbance. Such species are often indicative of forest disturbance levels, as their abundance along a forest gradient generally reflects the degree of disturbance at any given point. A similar trend has been found with the numerically dominant Cachabi Robber Frog (*P. achatinus*) at various sites in western Ecuador, where its abundance also declined in habitats with decreasing levels of disturbance [27; Paul Hamilton, unpubl. data].

Contrarily, many rainforest amphibians have likely evolved life history traits that are specific to interior forest conditions. Lower amphibian abundance, richness, and diversity at the forest edge is perhaps due to an inability of many interior forest specialists to persist there, due to lack of necessary resources or proper environmental conditions. In this study, 16 amphibian species were absent from the forest edge, seven of which were restricted to the interior forest habitat. Species that were found at the forest edge that are otherwise generally associated with interior forest habitat were often found in close proximity to, or directly on, old growth trees still standing adjacent to the road (*e.g.*, Brown-eyed Treefrog [*Nyctimantis rugiceps*]; *Osteocephalus deridens*; *Pristimantis paululus*). Whether or not mature trees at the forest edge remain healthy and persist over time could strongly influence how permeable the forest nearest the road is to such species.

In some cases, greater or equal animal abundance and diversity at the forest edge compared to interior forest are attributed in part to a source effect from the matrix in fragmented landscapes [40-43]. However, the little-disturbed interior forest at Payamino still harbored more individuals and species of amphibians than the highly-disturbed forest edge habitat, adding to the relatively few studies reporting negative effects on amphibian abundance and diversity from forest clearing or edge effects in Neotropical forests [29, 35, 44-45]. The source effect of matrix habitat is potentially reduced in situations where only a narrow linear disturbance bisects

otherwise mostly continuous tropical rainforest, such as that at Payamino. The road in this study is comprised of compact soil and lacks the vegetative substrate characteristic of open matrix conditions such as pastures, which might reduce or preclude certain matrix specialists. Interestingly, species known to use the open dirt road at Payamino, such as numerous hylid frogs that exploit water-filled roadside depressions as breeding sites, mostly avoided overlap within the forest edge. Of at least eight hylid species known to make use of such habitat in relatively high numbers at Payamino, only the Upper Amazon Treefrog (*Dendropsophus bifurcus*; $n = 1$), Basin Treefrog (*Hypsiboas lanciformis*; $n = 9$), and Red-snouted Treefrog (*Scinax ruber*; $n = 4$) were recorded in edge plots [Appendix 2; Ross Maynard, unpubl. data]. None of these species were recorded beyond the forest edge habitat. A similar pattern has been reported from forest fragments in central Amazonia, where nearly 20% of anurans were recorded exclusively in matrix habitat [46].

The increase in amphibian abundance along the forest edge-interior gradient was driven not only by greater assemblage diversity at the interior forest habitat, but this is also where five of the overall six most abundant species were most numerous. Although some studies have found either positive or neutral effects of edge on amphibians, the results generally reflect a particular species or guild [28, 45]. Nevertheless, terrestrial-breeding frogs in the genus *Pristimantis* played a large role in the patterns of distribution of amphibians reported herein due to their prominence in the dataset. *Pristimantis* was by far the most abundant and species rich of all the genera observed, with a majority of *Pristimantis* spp. demonstrating greater abundance with increasing distance from the forest edge. Three *Pristimantis* spp. were completely absent from the forest edge habitat.

Other studies have also found a negative effect of forest clearing or edge effects on abundance and diversity of Neotropical terrestrial-breeding frogs [29, 38, 45], perhaps because many species are highly sensitive to edge changes in moisture (*e.g.*, humidity in important microhabitats), microhabitat availability, and food availability. Such associations are presumably specific to interior forest conditions for many species. However, teasing apart which habitat components are most closely tied to patterns of abundance and diversity is difficult. McCracken and Forstner [29] found no relationships between several habitat variables and high-canopy anuran abundance, and Ernst and Rödel [47-48] found that habitat factors were not significant predictors of species incidence in tropical frog assemblages in Africa and South America. When models suggest significant habitat associations with patterns of animal distribution, they are generally drawn from broad-scale environmental measures rather than specific measures of quality and quantity of important microhabitats [*e.g.*, 28], which are unknown for many tropical taxa. In our models, the suggested importance of vine abundance is noteworthy, as it is a conspicuous element of disturbed secondary forest structure and likely serves as a proxy variable for other habitat factors that are more difficult to measure. Both vine abundance and understory density, which we found to be correlated, have had a negative impact on amphibians elsewhere in Neotropical forests [35, 38]. Rising vine abundance in the Neotropics has known negative effects on tree diversity, recruitment, growth, and survival [49], and its conspicuous structural influence at the forest edge presumably translates to differences in resource availability from that of interior forest conditions. Such differences likely have a profound impact on amphibian distribution patterns. For example, increased vine abundance at the forest edge could alter the quality and quantity of perch and oviposition sites, change the acoustics of the habitat and thereby influence the ability of frogs to effectively transmit or receive auditory signals, or alter inter-specific dynamics (*i.e.*, predator-prey relationships).

Regarding other habitat variables, the lack of difference in leaf litter depth among sampling distances was likely due to the high abundance of large, multi-lobed leaves shed from the many *Cecropia* at the forest edge, which formed a leaf litter layer comparable in depth to that of interior forest. Instead of depth, perhaps a difference is more likely to be found in leaf litter quality and composition. Since the large *Cecropia* leaves become gnarled and concave in shape after abscission, the leaf litter within the forest edge habitat is less compact and likely retains less moisture than leaf litter at the forest interior. Additionally, leaf litter at the forest edge is presumably

lower in compositional diversity, which could alter micro-fauna and flora diversity. Such differences, should they exist, could influence clutch success for terrestrial-breeding herpetofauna as well as the availability of essential microhabitats such as refuges during particularly hot temperatures or dry spells. Future studies could address these issues by measuring dried leaf litter mass in addition to leaf litter depth.

Reptile Distribution Patterns

The greater reptile abundance at the interior forest than at the forest edge habitat was somewhat unexpected, as tropical reptile species that thrive in open or disturbed habitat generally persist in greater abundances than forest interior species [50]. Also, light gaps are particularly important for heliothermic lizards [51], which are usually characteristic of disturbed areas of forest, such as that at the edge. Interestingly, reptile trapping with drift fences was more successful at the forest edge than at the interior forest and recorded species otherwise not detected by VES samples (Appendix 2). The conflicting results from the two survey methods underscores the importance of using multiple survey methods for reptiles, of surveying by both day and night, and of the difficulty of acquiring adequate samples of Neotropical reptile assemblages to properly assess their distribution patterns.

Lastly, even though the overall species accumulation curve for the herpetofauna suggests a nearly complete survey of the species in the study area, this is certainly not the case, as numerous amphibian and reptile species either known from outside the immediate study area or not yet recorded at Payamino but known from nearby sites, are still likely to be present [22, 39; Ross Maynard & Paul Hamilton, unpubl. data]. Even survey efforts spanning nearly 30 years have yet to completely sample the entire amphibian and reptile assemblage at a site close to Payamino, as additional species continue to be recorded there [22; Ross Maynard, Paul Hamilton, and Greg Vigle, unpubl. data].

Future Research

We suggest several avenues for future research: 1) with road creation increasing in the Amazon Basin [12] coupled with the paucity of information on road impacts on biota in the region, projects examining roads differing in width, position (*e.g.*, roads on gradients vs. upland vs. lowland), traffic intensity, and road type (dirt vs. gravel vs. pavement) are all necessary; 2) research needs to encompass extended timeframes to better survey the diverse biotic assemblages that characterize the region; 3) careful observations are needed for many taxa to determine their natural history. Such information is necessary to quantify vital habitat features for particular species or animal groups that are potentially altered by anthropogenic disturbances; and 4) additional distances from the edge as well as a road plot should be sampled to gain a clearer perspective of changes occurring throughout the ecotone.

Implications for conservation

Our results suggest that edge effects from a small, primitive road within lowland Amazon rainforest negatively influence herpetofauna abundance and diversity, and alter assemblage composition—a novel finding among published studies. The road-edge effect presumably acts as a partial barrier to dispersal, or at least creates a distributional gap for some species, particularly for amphibians. Previous studies suggesting a road-barrier effect have primarily used roads that have regular vehicle traffic and/or steep road verges [52-54], and generally attribute their results to synergistic effects of road traffic with other road impacts, including edge effects [55]. Moreover, many aspects of roads that are known or suspected to influence herpetofauna such as road salt [56], vehicle-related pollutants [57-58], road-traffic noise [59], and vehicle mortality [58, 60] are not confounding factors in our results since vehicle traffic is absent. Despite the road having a relatively moderate impact on the landscape, the edge effects have apparently been strong enough to influence amphibian and reptile distributions by maintaining a defined gap in the canopy, thereby exacerbating differences in forest structure and climate along the forest edge-interior gradient. Although unpaved roads are generally preferable to paved roads due to

their comparably reduced ecological impacts [11], we highlight the profound effects on herpetofauna distributions that stem from even a relatively obscure unpaved road. Therefore, minimizing small or unnecessary disturbances at Payamino (*e.g.*, construction of an undrivable road) will help mitigate negative impacts on local animal distributions.

Furthermore, these data show that biodiversity can differ in responses to a road. Such findings are likely not limited to amphibians and reptiles, and monitoring efforts should extend to other forms of biodiversity to better inform local management decisions. Involving local communities through citizen science initiatives [*e.g.*, 61] and research collaborations can help greatly to achieve these goals and encourage indigenous peoples to initiate programs of community-based management [*e.g.*, 62]. Ultimately, maintaining the natural integrity of biotic communities as much as possible should be a priority, as native flora and fauna are closely tied to the livelihoods of indigenous peoples throughout Amazonia, including the Kichwa.

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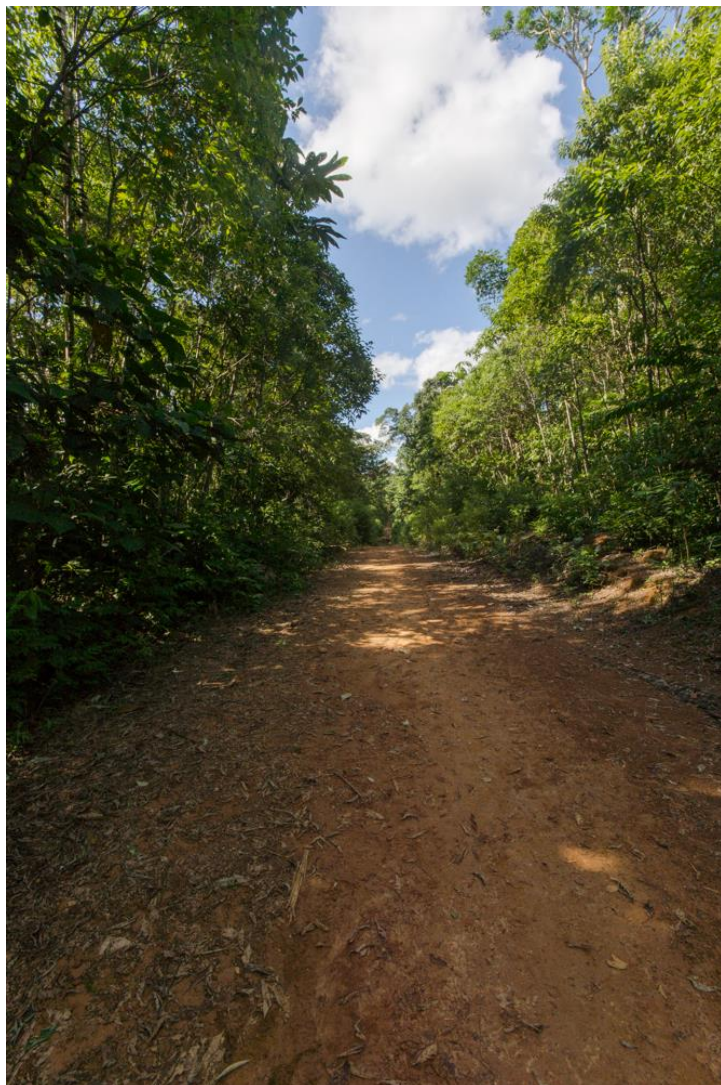
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Appendix 1. Image of the dirt road bisecting the secondary forest growth.



Appendix 2. List of species observed in the study area at Payamino. Subscripts after species names represent species' codes. Abundance values for each habitat type are as follows: W(X,Y,Z); where W = total abundance; X = VES observations; Y = pitfall captures; Z = funnel trap captures. Only one value is reported for the intermediate habitat, as only VES samples were obtained at that distance from the road. The conservation status by the IUCN is represented by the following categories: NE = not evaluated; LC = least concern; DD = data deficient. If available, vernacular names provided in parenthesis were sourced from the Encyclopedia of Life (eol.org).

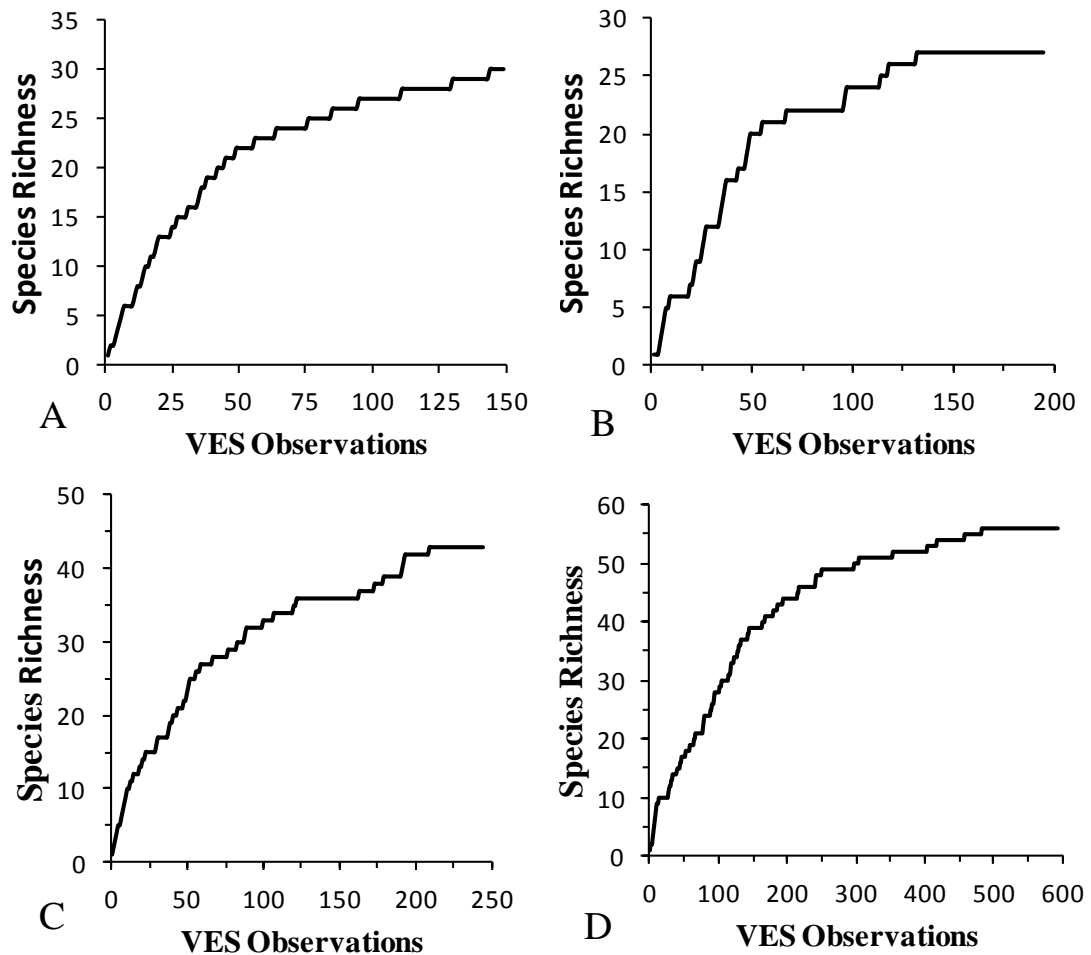
Scientific Name	Habitat			Total #	IUCN
	Edge	Intermediate	Interior		
ANURA					
Aromobatidae					
<i>Allobates femoralis</i> (complex) ₁	—	—	7 (1,6,0)	7	LC
(Brilliant-thighed Poison Frog)					
Bufo					
<i>Rhaebo ecuadorensis</i> ₂	1 (0,1,0)	—	—	1	NE
<i>Rhinella dapsilis</i> ₃	1 (0,1,0)	—	—	1	LC
(Bom Jardin Toad)					
<i>Rhinella margaritifera</i> ₄	8 (5,3,0)	8	10 (10,0,0)	26	LC
(Mitred Toad)					
<i>Rhinella marina</i> ₅	20 (1,13,6)	—	1 (0,1,0)	21	LC
(Cane Toad)					
Centrolenidae					
<i>Cochranella resplendens</i> ₆	—	—	1 (1,0,0)	1	LC
(Respendent Cochran Frog)					
<i>Hyalinobatrachium munozorum</i> ₇	—	—	1 (1,0,0)	1	NE
<i>Hyalinobatrachium sp. n.</i> ₈	—	1	—	1	NE
<i>Teratohyla midas</i> ₉	—	—	2 (2,0,0)	2	LC
(Santa Cecilia Cochran Frog)					
Craugastoridae					
<i>Hypodactylus nigrovittatus</i> ₁₀	1 (0,0,1)	6	2 (2,0,0)	9	LC
<i>Oreobates quixensis</i> ₁₁	10 (4,5,1)	—	1 (1,0,0)	11	LC
(Common Big-headed Frog)					
<i>Pristimantis acuminatus</i> ₁₂	3 (3,0,0)	1	2 (2,0,0)	6	LC
(Canelos Robber Frog)					
<i>Pristimantis altamazonicus</i> ₁₃	9 (9,0,0)	16	17 (17,0,0)	42	LC
(Amazon Robber Frog)					
<i>Pristimantis conspicillatus</i> ₁₄	—	7	7 (7,0,0)	14	LC
(Chirping Robber Frog)					
<i>Pristimantis croceinguinis</i> ₁₅	—	25	29 (28,1,0)	54	LC
(Santa Cecilia Robber Frog)					

<i>Pristimantis delius</i> ¹⁶	1 (1,0,0)	1	1 (1,0,0)	3	DD
<i>Pristimantis diadematus</i> ¹⁷	—	2	1 (1,0,0)	3	LC
<i>Pristimantis kichwarum</i> ¹⁸	7 (7,0,0)	28	50 (50,0,0)	85	LC
<i>Pristimantis lanthanites</i> ¹⁹	12 (12,0,0)	15	32 (32,0,0)	59	LC
(Metallic Robber Frog)					
<i>Pristimantis librarius</i> ²⁰	13 (13,0,0)	—	3 (1,0,0)	16	DD
<i>Pristimantis aff. martiae</i> ²¹	3 (2,1,0)	26	29 (29,0,0)	58	NE
<i>Pristimantis matidiktyo</i> ²²	1 (1,0,0)	—	1 (1,0,0)	2	NE
<i>Pristimantis paululus</i> ²³	1 (1,0,0)	—	—	1	LC
<i>Pristimantis variabilis</i> ²⁴	47 (47,0,0)	33	10 (10,0,0)	90	LC
Dendrobatidae					
<i>Ameerega bilinguis</i> ²⁵	—	—	2 (2,0,0)	2	LC
(Ecuadorian Poison Frog)					
Hylidae					
<i>Dendropsophus bifurcus</i> ²⁶	1 (1,0,0)	—	—	1	LC
(Upper Amazon Treefrog)					
<i>Hypsiboas geographicus</i> ²⁷	—	1	2 (2,0,0)	3	LC
(Map Treefrog)					
<i>Hypsiboas lanciformis</i> ²⁸	9 (9,0,0)	—	—	9	LC
(Basin Treefrog)					
<i>Hypsiboas punctatus</i> ²⁹	—	1	—	1	LC
(Polka-dot Treefrog)					
<i>Nyctimantis rugiceps</i> ³⁰	1 (1,0,0)	—	—	1	LC
(Brown-eyed Treefrog)					
<i>Osteocephalus deridens</i> ³¹	1 (1,0,0)	1	1 (1,0,0)	3	LC
<i>Osteocephalus mutabor</i> ³²	—	1	1 (1,0,0)	2	LC
<i>Osteocephalus planiceps</i> ³³	8 (8,0,0)	1	2 (2,0,0)	11	LC
<i>Phyllomedusa tarsius</i> ³⁴	—	—	1 (1,0,0)	1	LC
(Brown-bellied Leaf Frog)					
<i>Phyllomedusa vaillantii</i> ³⁵	—	2	—	2	LC
(White-lined Leaf Frog)					
<i>Scinax garbei</i> ³⁶	—	—	1 (1,0,0)	1	LC
(Eirunepe Snouted Treefrog)					
<i>Scinax ruber</i> ³⁷	4 (4,0,0)	—	—	4	LC
(Red-snouted Treefrog)					
Leptodactylidae					
<i>Adenomera andreae</i> ³⁸	1 (1,0,0)	1	2 (0,2,0)	4	LC
(Lowland Tropical Bullfrog)					
<i>Edalorhina perezii</i> ³⁹	—	1	1 (0,1,0)	2	LC

(Perez's Snouted Frog)					
<i>Engystomops petersi</i> ⁴⁰	4 (2,0,2)	5	9 (5,3,1)	18	LC
(Peter's Dwarf Frog)					
<i>Leptodactylus lineatus</i> ⁴¹	2 (2,0,0)	—	4 (1,2,1)	6	LC
(Gold-striped Frog)					
<i>Leptodactylus mystaceus</i> ⁴²	1 (0,0,1)	—	—	1	LC
(Amazonian White-lipped Frog)					
CAUDATA					
Plethodontidae					
<i>Bolitoglossa cf. peruviana</i> (complex) ⁴³	2 (2,0,0)	3	4 (4,0,0)	9	LC
(Peru Mushroomtongue Salamander)					
SERPENTES					
Boidae					
<i>Boa constrictor</i> ^A	—	—	1 (1,0,0)	1	NE
(Boa Constrictor)					
<i>Corallus hortulanus</i> ^B	—	—	1 (1,0,0)	1	NE
(Amazon Tree Boa)					
Dipsadidae					
<i>Atractus collaris</i> ^C	1 (0,1,0)	—	—	1	NE
(Collared Ground Snake)					
<i>Atractus major</i> ^D	1 (0,1,0)	—	1 (1,0,0)	2	LC
(Brown Ground Snake)					
<i>Dipsas catesbyi</i> ^E	—	—	3 (3,0,0)	3	LC
(Catesby's Snail-eater)					
<i>Dipsas indica</i> ^F	1 (1,0,0)	—	1 (1,0,0)	2	NE
(Neotropical Snail-eater)					
<i>Drepanoides anomalus</i> ^G	2 (2,0,0)	—	—	2	NE
(Black-collared Snake)					
<i>Imantodes cenchoa</i> ^H	—	3	1 (1,0,0)	4	NE
(Blunthead Tree Snake)					
<i>Imantodes lentiferus</i> ^I	—	—	1 (1,0,0)	1	NE
(Amazon Basin Tree Snake)					
<i>Liophis reginae</i> ^J	—	—	1 (0,0,1)	1	NE
(Royal Ground Snake)					
<i>Oxyrhopus melanogenys</i> ^K	2 (1,0,1)	—	1 (1,0,0)	3	LC
(Tschudi's False Coral Snake)					
<i>Oxyrhopus petolarius</i> ^L	—	1	1 (1,0,0)	2	NE
(Calico Snake)					
Typhlopidae					
<i>Amerotyphlops reticulatus</i> ^M	1 (0,1,0)	—	—	1	LC

(Reticulate Worm Snake)					
SAURIA					
Dactyloidae					
<i>Anolis fuscoauratus</i> _N	5 (5,0,0)	3	7 (7,0,0)	15	NE
(Slender Anole)					
<i>Anolis trachyderma</i> _O	—	2	4 (3,1,0)	6	NE
(Roughskin Anole)					
Gymnophthalmidae					
<i>Cercosaura cf. argula</i> _P	2 (0,2,0)	—	2 (0,2,0)	4	LC
(Elegant-eyed Lizard)					
<i>Leposoma parietale</i> _Q	7 (1,6,0)	—	5 (2,3,0)	12	LC
Hopllocercidae					
<i>Enyalioides laticeps</i> _R	1 (1,0,0)	—	1 (1,0,0)	2	NE
(Guichenot's Dwarf Iguana)					
Sphaerodactylidae					
<i>Pseudogonatodes guianensis</i> _S	1 (0,1,0)	—	1 (1,0,0)	2	NE
Teiidae					
<i>Kentropyx pelviceps</i> _T	9 (0,7,2)	—	1 (0,1,0)	10	NE
(Forest Whiptail)					
Tropiduridae					
<i>Plica umbra</i> _U	1 (1,0,0)	—	—	1	NE
(Harlequin Racerunner)					

Appendix 3. Species accumulation curves plotting species by number of individuals observed during plot surveys for (A) forest edge habitat (plot center point at 10 m perpendicular distance from forest edge); (B) intermediate habitat (center point at 50 m); (C) interior forest habitat (center point at 100 m); and (D) all VES records combined across habitats.



Appendix 4. Species accumulation curve for drift fence captures, plotting species by number of individuals recorded.

