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Comparisons of the impacts of disturbance on amphibian species richness in the Chocóan Rainforest, Ecuador

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Reserva Tesoro Escondido is located within the Tumbes-Chocó-Magdalena biodiversity hotspot in north-west Ecuador and is home to approximately 679 amphibian species. This study aimed to investigate the effects of disturbance on amphibian species richness, abundance and assemblage through the use of visual encounter surveys along three study sites within the Reserva Tesoro Escondido. The results from these surveys report 406 observations and 46% of the total known amphibian species. Species evenness and diversity did not significantly vary across three sites sampled in the reserve even when accounting for abiotic factors, resulting in a site-specific species assemblage. Generalised Linear Models (GLM) investigated species richness and abundance relationship to environmental variables, finding altitude as the most significant factor on species abundance and richness. Overall, the results showed great diversity and no trace of species homogenisation across habitats which may be linked to disturbance.

Keywords: Amphibians, species richness, disturbance ecology, Ecuador biodiversity, Chocó

INTRODUCTION

The Tropical Andes (including the Chocó) have been described as one of the most biodiversity-rich areas on the planet due to a high presence of endemic vascular plants and vertebrates, accounting for 6.7% and 5.7% respectively of the global recognised species (Myers et al., 2000; Mittermier et al., 2005; Bax & Francesconi, 2019). Such diversity of organisms can be explained by the structural complexity of the habitats and the tree diversity found within tropical forests (Richards, 1952; Wiens, 2011). Brummitt & Lughadha (2003) consider the North Andean forests to be the top biodiversity hotspot in the world, the distribution of hotspots has been generally attributed to areas with high diversity levels of vascular plants (Mittermier et al., 1998; Myers et al., 2000; Brummitt & Lughadha, 2003).

Many amphibians have complex life cycles in which they spend part of their early life as larvae (being fully aquatic), they then metamorphose and spend the rest of their life as a terrestrial adult (Liedtke et al., 2022). Amphibians are distributed on all continents apart from Antarctica (Duellman, 1999), they are known for their ability to exchange gases and fluids through their skin due to it being a semipermeable membrane (Lindemann & Voute, 1976). The function of their skin can also be considered the "Achilles' heel" of amphibians, making them more vulnerable to threats such as pollution and disease (Clarke, 1997; Blaustein et al., 2003; Ohmer et al., 2015). Their ability to adapt so efficiently can be attributed to the evolution of morphological, biochemical, behavioural and physiological adaptations (Clarke, 1997). In Neotropical forests, amphibians have evolved to survive in fairly stable environments (Pyron & Wiens, 2013), where abiotic factors such as humidity and rainfall do not vary significantly throughout the year (Ron et al., 2019). Amphibians play an irreplaceable role in food webs, ecosystem services and human medicine, thus their conservation is essential for the benefit of ecosystem balance (Angerer, 2011; Hocking & Babbitt, 2014).

Although new species of amphibians are being described every year, globally amphibians are threatened due to a combination of factors (Stuart et al., 2004; Luedtke et al., 2023). Tropical forests are under constant threat due to habitat loss, degradation and fragmentation, which are known to be the major drivers of biodiversity loss (Achard et al., 2002; Fahrig, 2003; Murad & Pearse, 2018). These forest ecosystems have been put under enormous pressure from threats such as the expansion of mineral mining, water resources, agricultural land expansion and the extraction of timber (Roy et al., 2018;

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Bax & Francesconi, 2019). The high levels of biodiversity in the Neotropics are most likely due to a series of historical events that guided evolutionary and ecological processes (Calderón et al., 2004; Ghazoul & Sheil, 2010).

Moritz et al. (2000) proposes that the high level of amphibian diversity (especially within dart frogs; family Dendrobatidae), is due to a combination of palaeogeographic and ecological events such as climate change and riverine barriers (Godinho & da Silva, 2018). Moritz et al. (2000) also indicates that the ability of species to colonise new areas, adapt and diversify within them may also lead to the diversity seen. An opposite theory proposed by Santos et al. (2009) suggests that the strongest influencing factor that dictates species radiation and dispersal in the Neotropics may have been the formation and presence of the Andes. Similar patterns can also be seen in the glass frogs (Castroviejo-Fisher et al., 2014), and Amazonian rocket frogs (Réjaud et al., 2020). When viewed together, these two arguments are complementary to one another. The characteristics discussed subsequently allowed species to radiate and adapt into different niches, thus justifying the biodiversity level observed within Tumbes-Chocó-Magdalena biodiversity hotspot along the Pacific coast of South America (Navas, 2002; 2006; Richter et al., 2009; Rull, 2011).

Ecuador is known to have suffered the highest rates of deforestation in South America (Moslandl et al., 2008). In 2014, the Food and Agricultural Organisation estimated that 62% of the country's original 26 million ha of forest had been lost due to human development (FAO, 2014). Within Ecuador, the Chocó-Darien western rainforest, which is one of the 25 biodiversity hotspots globally, is experiencing one of the highest observed population growth rates (Cincotta et al., 2000). When combining the figures reported above, they highlight the fact that the Chocó requires the implementation of better conservation measures as the aforementioned human activities are decreasing overall biodiversity, including amphibian diversity, across Ecuador (Lips & Donnelley, 2002; Calderón et al., 2004; Bustamante et al., 2005).

Ecuador is a highly diverse country with an estimated total of 679 amphibian species (Frost, 2023). There are likely other amphibian species still awaiting discovery due to factors such as cryptic diversity and a lack of scientific exploration, so this estimate is conservative (Arteaga et al., 2016). Among the amphibians found within Ecuador, 13% are listed as Critically Endangered, 23% as Endangered and 21% as Vulnerable on the IUCN Red List (Ortega-Andrade et al., 2021). Very few species (4%) are listed as Data Deficient whereas 27% are Least Concern, highlighting the importance of conservation and monitoring of Ecuador's amphibians (Ortega-Andrade et al., 2021).

There are a number of factors that may influence amphibian species richness, abundance and assemblage across a landscape. These changes can have a positive or negative impact and the effects are generally well-studied (Hecnar & M'Closkey, 1997; Skelly et al., 2002; Wanger et al., 2009; Blaustein et al., 2010; Galloy & Denoël, 2010). These differences can result in species reacting in contrasting ways to the distinct levels of disturbance depending on the scale of the factor (Wanger et al., 2009; Sirami et al., 2010; Cortés-Gómez et al., 2013). For example, when looking at biotic factors, adult amphibians can be selective in terms of breeding sites depending on the vegetation structure, favouring more complex structure (Ambu et al., 2022). Thus, the presence or absence of a species from environments defined as having a more open or closed canopy, could be a result of this relationship (Kiesecker & Skelly, 2000; Skelly et al., 2002; van Buskirk, 2005). On the other hand, abiotic factors can also have similar effects on amphibians; for example the presence of water can determine the abundance and assemblage of some species that depend on it for reproduction (Werner et al., 2007). The altitudinal gradient and climate also play their role in the presence of amphibians. With an increase in altitude, amphibian species assemblages are negatively affected due to a decrease in air temperature and changes in habitat (Navas, 2002).

This study aims to identify whether disturbance is the key factor influencing amphibian species richness, abundance and assemblage within the Chocóan Rainforest, Ecuador. Amphibians were chosen as the model species as they are one of the most abundant and representative classes of vertebrates found within our study sites. We predict that increasing disturbance would be the most influencing factor on the aforementioned species metrics.

MATERIALS & METHODS

Habitat and site descriptions

The study was conducted during the summer of 2018 in the protected area Reserva Tesoro Escondido (0° 32.371' N, 79° 08.651' W; elev. ~340 m a.s.l.) and completed over a total of 30 days. Data was collected starting on 30 May and ending on 6 July 2018. Reserva Tesoro Escondido (Fig. 1), as its name suggests is a protected area in the province of Esmeraldas and covers approximately 30 km^2 located in north-western Ecuador, situated in the Tumbes-Chocó-Magdalena hotspot (Rodríguez-Mahecha et al., 2004). The area is considered to be a lowland tropical rainforest (Sierra, 1996), a forest type considered characteristic of the neotropics (Sierra, 1999). The vegetation is highly diverse with trees reaching 30–50 m in height, the families Fabaceae, Arecaceae and Moraceae dominate. In addition, there is an abundance in water bodies, ranging from small streams to larger rivers. Combined with an annual mean precipitation of 6,000 mm and high humidity, result in a very moist forest throughout the year (Vargas, 2002; Vazquez & Freile, 2005).

Three sites within Reserva Tesoro Escondido were selected to carry out data collection, providing the ability to survey different altitudinal ranges and habitats. Site 1 (S1) was characterised by having pristine primary forest with no evidence of previous logging. The surveyed altitudinal ranges varied between 196 and 451 m a.s.l., with an average canopy cover of 80%. Site 2 (S2) was

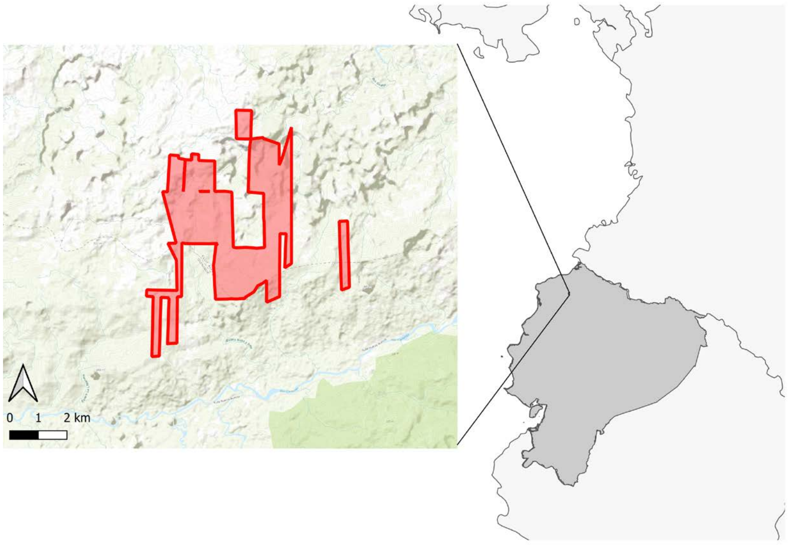

Figure 1. A map showing the location of Reserva Tesoro Escondido within Ecuador. All sites were located within the reserve, however specific site locations have been removed over conservation concerns.

Table 1. Summaries of the different parameters collected at each of the three sites, including the results of the diversity indices we used. CC = Canopy Cover; HL = Herb layer; SL = Sub-canopy layer; and LL = Leaf litter %.

Site	CC (%)	HL (%)	SL (%)	LL (%)	Humidity (%)	Temp (°C)	Rain (mm)	Altitude range (m)	Richness	Abundance	Shannon-Weiner index	Simpson's index	Chao1
S1	80	55.6	61	32.2	90.8	24.7	1.1	196–451	25	212	2.78	0.91	15.64
S2	83	60	58	28.2	91.8	22.4	5.7	297–693	23	82	2.72	0.91	26.5
S3	85	60.8	57.3	34.9	89.612	24.02	1.086	419–546	22	107	2.75	0.92	26.5

located ~6 km away from S1 with an altitudinal range between 297 and 693 m a.s.l, composed mainly of secondary forest with relics of primary forest close to main water bodies; the average canopy cover of 83%. Site 3 (S3) was ~3 km in distance from S2, a matrix of secondary forest, cacao plantations and pasture which provides a mosaic of habitats. Site 3 is considered a highly disturbed area with an average canopy cover of 85%, the altitude ranges between 419 and 546 m a.s.l. The data on altitudinal ranges and canopy cover reported above refer to the areas crossed by transects (Table 1). Transects were selected to optimise coverage of altitudinal gradients available and, equally, distance from water.

Survey protocols

Visual Encounter Surveys (VES) were combined with line transects and point counts in order to standardise data collection, with each of the three sites being sampled for 10 days respectively. The VES methodology was adapted for the study site to improve replicability and overcome constraints imposed by terrain and time limitation from Lips et al. (2001) and Doan (2003).

A total of 30 transects were surveyed, split equally between the three sites. Each transect was 80 m long and was surveyed every day at 15:00 h and 21:30 h. Data collection was carried out on five points along each transect, points were marked with outdoor marking flags and were 20 m apart. A 5 m radius was actively scanned for 25 minutes carefully checking all vegetation layers and leaf litter with the aid of snake hooks. Any amphibians encountered in the five-metre radius were recorded on a waterproof notebook in the correct transect and point number (e.g. Transect 1, Point 1, *Pristimantis achatinus* [1]). At night, weather-resistant head torches (Petzl TIKKA, 200 lumens) and hand torches (Nitecore MT40, 960 lumens) were used in order to detect the presence of amphibians. Each point on the transects was marked with a handheld GPS (Garmin eTrex 30x).

Amphibians encountered at each point were collected and temporarily kept for the day in individual plastic bags filled with vegetation taken from the surrounding area. When back at the field station, each individual was then weighed with a digital scale and measured using vernier callipers (snout to vent for anurans). This process allowed for the completion of surveys on the same transect later at night and avoided any potential pseudo-replication. Identification of individuals was carried out in-situ, any specimen that could not be identified to species level during the survey was done so post-hoc using photos taken previously. Additionally, side view and ventral/inguinal photos of each species (or morph) were taken using a Nikon D3300, to aid in the identification process. Amphibians found on transects that did not fall into the

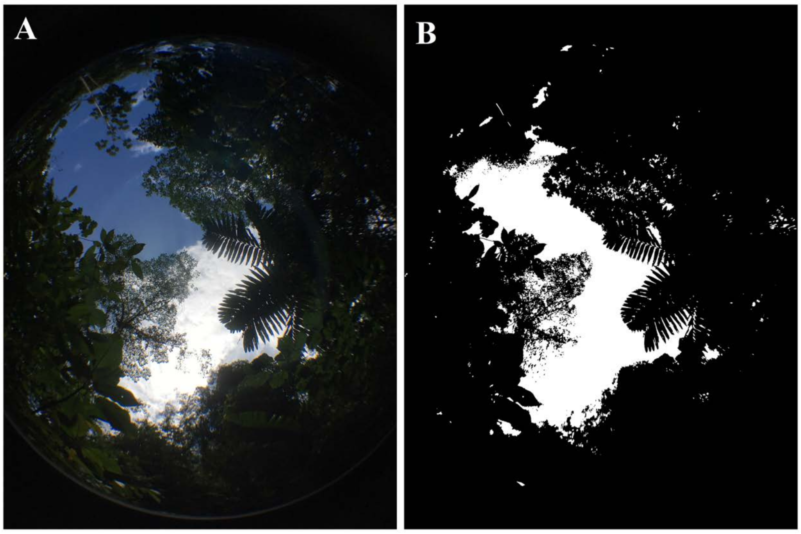

Figure 2. **A.** A photo taken of the canopy cover at one of the survey locations using a fisheye lens, **B.** with the same photo converted to binary using ImageJ. The total area of canopy cover from this site is 83.02%.

5 m radius, were collected and recorded to the nearest 5 m radius. Identification was completed using both Yánez-Muñoz et al. (2010) and Ron et al. (2019).

Environmental variables

A portable weather station (Bresser 5 in 1 Weather Station: model number 7002580) was used for the study, continuously recording temperature, humidity and rainfall for 10 days of each of the expedition phases. The station was mounted in the morning prior to collecting data and dismounted the morning after the last transect was surveyed. This operation was repeated for each site. Altitude was recorded with the aid of a GPS (Garmin eTrex 30x) and the distance from water bodies was estimated using local knowledge, visual or acoustic clues. These last two variables had their own reading for each point on each transect with weather data considered uniform along transects. Vegetation structure data was collected and divided into: canopy cover, sub-canopy layer, shrub layer, herb layer, leaf litter. These factors were visually estimated at a scale from 0–100 percent. Canopy cover was recorded from a stationary location between each point by taking photos using an iPhone 5, looking directly up into the canopy. The iPhone was equipped with a fisheye lens attachment (Olloclip 4-in-1 lens set), allowing for imagery with an 180° field of vision. The images taken were later analysed for the percentage of canopy cover using ImageJ Version 1.53c (Schindelin et al., 2012). Each picture was transposed into binary form allowing for the percentage of vegetation (black pixels) and sky (white pixels) to be calculated within the field of the lens (Fig. 2). Sub-canopy layer was determined as the percent vegetation present from 1.5 m from the ground up until below the tree crown, shrub layer was considered as the percent vegetation coverage between 50 cm to 1.5 m from the ground, the herb layer was determined as percent vegetation coverage between 0–50 cm in height, and finally leaf litter was estimated by looking at its overall coverage on the ground within the surveyed area.

Statistical analysis

Tests for collinearity between predictor variables were conducted via the Variance Inflation Factor (VIF) from the 'usdm' package (Naimi et al., 2014). VIF tests for collinearity through the multiple correlation coefficients of each predictor variable between all other predictor variables (Dormann et al., 2013). VIF values above 10 for any predictor variable were considered collinear and removed. A pairwise correlation was run between all predictor variables to further test for collinearity. We found that both abundance and richness were overdispersed (variance greater than the mean).

We employed Generalised Linear Models (GLM) using the environmental data as independent variables. (R Core Team, 2022). We utilised a Negative Binomial distribution to account for overdispersion in our data. Models were run using the glm.nb() function from the 'MASS' package in R (Ripley et al., 2023). GLMs were run separately for each abundance and richness. We first tested each independent variable alone, and then tested if multiple regression models produced a better fit. Simpson's (Somerfield et al., 2008) and Shannon-Wiener (Shannon & Weaver, 1949) diversity indices were calculated for each site as well as all sites combined using the 'vegan' package (Oksanen et al., 2008). These metrics are commonly used in ecological studies to assess species richness where Simpson's Index (calculated as 1-D) detects dominance of a particular species or group while Shannon-Wiener is sensitive to rarer species (Gotelli & Colwell, 2001). Chao1 is a nonparametric abundance-based estimator for species richness in a community or habitat (Chao, 1984). As species richness tends to underestimate the true number of species, particularly rare ones, Chao1 instead provides a lower bound of species richness including undetected species (Chao & Chiu, 2016). Chao1 was calculated for each site and for all sites combined using the 'fossil' package (Vavrek, 2011).

RESULTS

Of the three amphibian orders, only two were found: Anura and Gymnophiona. Gymnophiona was excluded from analysis as there was only a single observation. The amphibians identified belonged to 7 families and 40 species (46% of the total Chocó species; Ron et al., 2019). 405 observations were recorded over the 30 day survey period across the three sites. A total of 375 people hours of surveys across 11,775 m^2 of the Chocó were scanned between an altitudinal range of 196–693 m a.s.l. Mean amphibian abundance per transect and count point was 13.5 individuals and 2.7 individuals respectively. Mean amphibian richness per transect and count point were estimated at 7.93 species and 3.93 respectively.

Species composition, richness and abundance

Anurans of the family Strabomantidae were the most abundant group found, with 17 species of 178 individuals. The next most species rich families were the Centrolenidae (with 7 species and 45 individuals), Hylidae (6 species and 46 individuals), Bufonidae (4 species and 44 individuals) and Dendrobatidae (with 3 species and 86 individuals). The least rich family was Leptodactylidae (5 individuals of 2 species). Species abundances by site can be found in Table S1 in supplementary materials.

Species evenness and richness calculations can be found in Table 1. For the Shannon-Wiener and Simpson's indices: Site 1 scored 2.78 and 0.91 (respectively); Site 2 scored 2.72 and 0.91. Site 3 scored 2.75 for and 0.92. The total observed species richness between sites did not differ dramatically with 25 species at Site 1, 23 species at Site 2, 22 species at Site 3 and 40 species observed across all sites. The Chao1 values calculated for each site were similar to the observed values with 25.64 for Site 1, 26.5 for Site 2, 26.5 for Site 3 and 40.8 across all sites.

Environmental effects on abundance and richness

Variance Inflation Factor and correlation tests found that temperature was moderate to strongly collinear (VIF = 15.36) with humidity (VIF = 8.75, r = -0.869), rainfall (VIF = 3.42, r = 0.64) and altitude (VIF = 2.18, r = -0.40). The removal of temperature lowered all VIF values to below 1.5 and no further collinearity was detected. As such, temperature was not used for any multivariate analysis, however was still analysed under univariate models. The correlation matrix of observed variables is found in Table S2 in supplementary materials.

For richness the univariate analysis models identified notable associations with sub-canopy layer ($p = 0.048$, $\beta = 0.009$, SE = 0.005), temperature ($p < 0.0001$, $\beta = 0.098$, SE = 0.028), rainfall ($p = 0.029$, $\beta = -0.038$, SE = 0.017) and altitude ($p < 0.0001$, $\beta = -0.003$, SE = 0.0005; Table S3 in supplementary materials). The multiple regression models indicated that the most suitable model incorporated the altitude and sub-canopy layer (richness ~ altitude + sub-canopy layer; y = -0.003 + 0.011). Despite exploring alternative models, none demonstrated statistically significant coefficients (< 0.05) or enhanced model fit. Results are found in Table S4 and Figure S1 in supplementary materials.

For abundance the univariate regression abundance models yielded significant associations with temperature ($p = 0.008$, $\beta = 0.089$, SE = 0.034) and altitude ($p < 0.0001$, $\beta = -0.004$, SE = 0.001). Results are summarised in Table S4 in supplementary materials. While we explored multiple regression models for abundance, they failed to increase explanatory power compared to a univariate model, which only included altitude. Results are found in Table S5 and Figure S2 in supplementary materials.

DISCUSSION

When compared to other studies with a similar methodology elsewhere in the Neotropics (such as the Colombian Chocóan forest), our results outnumber the total species found despite the comparatively low sampling effort (Cortés-Gómez et al., 2013; Ovalle-Pacheco et al., 2019). Although the Reserva Tesoro Escondido is found in an area under multiple socio-economic pressures, overall, the forest is still considered highly biodiverse (Myers et al., 2000), supporting 86 described species of amphibians (Ron et al., 2019), with more likely awaiting discovery or confirmation in the area.

The outputs from the Generalised Linear Models indicate which measured factors contribute to species richness and abundance. We found that altitude and temperature had significant effects on both richness and abundance, while rainfall and sub-canopy layers were significant only for richness. Altitude gradients are well described drivers of amphibian assemblages (Khatiwada et al., 2019; Carvalho-Rocha et al., 2021). These patterns have also been seen in prior studies, whereby as elevation increases species richness and abundance tend to decrease (Khatiwada et al., 2019).

Temperature, rainfall and vegetation cover create unique microhabitat characteristics which certain amphibian families may be able to thrive in (Urbina-Cardona et al., 2006; Rovito et al., 2009). Studies report that some amphibians respond negatively to changes in vegetation, such as canopy cover, due to increased risk of parasitisation, greater fluctuations in environmental variables or the destruction of microhabitat (Kiesecker & Skelly, 2000; Skelly et al., 2002; van Buskirk, 2005). A change in the temperature and/or rainfall may result in modifications to the microhabitat that are less favourable to inhabiting amphibians (Denslow et al., 1998; Greenberg, 2001; Ritter et al., 2005).

Primary forest prevails in most parts of Reserva Tesoro Escondido (Morelos-Juarez et al., 2019), although secondary forest as a result of previous timber extraction and cacao plantations can be found (Calle-Rendón et al., 2016). Despite this, the more disturbed areas of the reserve should still be home to a number of amphibian species based on evidence from other similar locations (Acevedo-Charry & Aide, 2019). Communities around the reserve still rely on cacao farming as a primary source of income, as well as the production of African oil palm and pastures for cattle production (Sierra et al., 2003). This, along with pressures from timber companies (such as Botrosa and Verde Canade) pose a threat to the conservation of the area and the amphibians within (López et al., 2010).

The results of species evenness using the Shannon-Wiener's Index indicated no significant differences between the three study sites. Similar evenness across sites is a common finding in tropical rainforests due to factors such as climatic stability and habitat homogeneity, although species structure and assemblage may change with ecological processes succession (Pearman, 1997; Vargas & Bolaños-L, 1999; Herrera-Montes & Brokaw, 2010). The Simpsons Index indicates low levels of amphibian species diversity, however the results from the Shannon-Weiner Index suggests that diversity is moderate (Roswell et al., 2021). These results are similar to those of Jongsma et al. (2014), demonstrating that although some parts of the forest are severely disturbed, the reserve does not represent homogenised habitat, which can be the case for other anthropogenically disturbed areas within rainforest ecosystems (Cubides & Urbina-Cardona, 2011).

Site 1 being pristine primary forest, Site 2 exhibiting some degree of secondary forest from historical disturbances and Site 3 composed of a mosaic of secondary forest and pastureland. The small differences that we observe in amphibian richness and abundance may be caused by these variations in disturbance as well as altitude (Cortés-Gómez et al., 2013), however further surveys are required to validate these claims. The evidence suggests that both primary and secondary cloud forest are crucial to the survival and conservation of Ecuadorian amphibians. The Chao1 index revealed comparable estimates of species richness across the three different study sites. However, notable differences were observed in the composition of these amphibian assemblages. This incongruity may be attributed to the relatively brief sampling periods, variations in observer effort among sites and other potential sampling biases. Our surveys were only conducted over a short span of time. Extending the survey period as well as surveying a wider diversity of habitats, may increase the number of different species encountered (Barata et al., 2017).

Our results show that species richness was best described by the model including altitude and sub-canopy layer. As Cortés-Gómez et al. (2013) suggest, richness alone may not be a suitable variable for assessing amphibian assemblages across landscapes, as different sites may host species occupying entirely different niches (Guayasamin & Funk, 2009; Herrera-Montes & Brokaw, 2010). For example, more generalist species would be expected to occupy the more disturbed sites, with more specialists in the intact primary rainforest (Riemann et al., 2015; Díaz-García et al., 2017). There is some overlap between the species present in all three sites (see Table S1 in supplementary materials), but many of the habitat specialists are absent from the disturbed sites. The survey methods employed within this study were heavily biased towards those species of amphibians that can be found within the shrub and herb layers.

The presence of five survey points per transect traversing diverse microhabitats could account for some of the observed variability despite the fact that the method has been used elsewhere before (Ovalle-Pacheco et al., 2019). Certain amphibian species are known to be microhabitat specialists, and their occurrence in specific areas may be constrained if their particular needs are not met (Urbina-Cardona et al., 2006; Rovito et al., 2009). It is therefore likely that some amphibians that have specific microhabitats were not observed due to a lack of sufficient coverage of these by the transects, such as arboreal or fossorial species. As the three different sites had varying levels of disturbance, they would have very likely been composed of differing microhabitats.

A small number of individuals from the genus *Pristimantis* could not be identified and should be the focus of future studies to determine if these represent new species, which is highly likely in these environments given the large number of new species described within this genus (Guayasamin & Funk, 2009; Arteaga et al., 2016; Navarrete et al., 2016). There is also the possibility that some of these unidentifiable *Pristimantis* may be ecotypes specific to the habitats in and around Reserva Tesoro Escondido. Furthermore, through the use of visual encounter surveys, additional species of amphibians have since been confirmed to be present within the reserve such as *Hyloscirtus mashpi* (Mattea et al., 2020). This indicates the growing need for additional monitoring to identify all of the amphibian species found within the reserve.

The advent of additional methods to detect the presence of amphibians such as the use of environmental DNA (eDNA) also offers opportunities for novel amphibian species to be identified within the Reserva Tesoro Escondido (Lopes et al., 2017; Quilumbaquin et al., 2023). However, researchers should make themselves aware of the limitations of eDNA before use in the region (Bálint et al., 2018). Further, acoustic sampling of this region may provide records of additional taxa that are difficult to assess via Visual Encounter Surveys, such as taxa higher up in the canopy layer (Measey et al., 2017; Anunciação et al., 2022). Finally, the further protection of the studied habitats in primary and secondary forest may increase the favourable conservation status of the populations of threatened species identified inhabiting them (Ortega-Andrade et al., 2021).

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Author contributions

Conceptualisation, R.G.M & M.P.; formal analysis, D.J. & S.J.R.A.; methodology, R.G.M..; investigation, R.G.M.. & A.M.B.-V.; validation, D.J. & S.J.R.A.; funding acquisition and supervision, M.P; writing original draft, R.G.M.; writing, review and editing, All.

Data accessibility

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Ethical statement

All aspects of fieldwork, including the handling of animals adhered to BHS Ethical Policy (British Herpetological Society, 2017), and ethical approval was granted by the University of Sussex to conduct the research project.

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