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Environmental determinants of group size of mantled howlers (*Alouatta palliata aequatorialis*) in Ecuador

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RESUMEN

Comprender los factores ambientales que influyen en el tamaño del grupo de los aulladores *Alouatta palliata aequatoriales* en el occidente de Ecuador es clave en el diseño de acciones de conservación efectivas para este primate en peligro de extinción. Usando registros de la especie obtenidos en censos de primates locales, regionales y nacionales en la última década, evaluamos la influencia en el tamaño del grupo de variables abióticas (elevación, latitud, precipitación) y bióticas/antropogénicas (productividad primaria, presencia de áreas protegidas, presión de caza, fragmentación de boques, densidad poblacional humana). También evaluamos la influencia de estas variables y del tamaño de grupo en la presencia de individuos solitarios de esta especie. Analizamos los datos con modelos con GLMs, combinando funciones step-wise y multimodelos en R. Nuestros resultados apuntan a la presencia de áreas protegidas y la fragmentación del hábitat como los principales determinantes del tamaño del grupo de los monos aulladores. También encontramos que la densidad poblacional humana tiene un efecto significativo en la presencia de individuos solitarios. Con base en estos resultados, proponemos crear un corredor ecológico para restaurar la conectividad y dispersión de los monos aulladores al suroeste de Ecuador.

Palabras clave: Primates ecuatorianos, demografía, conservación, corredor ecológico

ABSTRACT

Understanding the environmental factors that influence group size in mantled howlers *Alouatta palliata aequatorialis* in western Ecuador is key in the design of effective conservation actions for this Endangered primate. Using records of the species obtained in local, regional and national primate censuses in the past decade, we assessed the influence on group size of abiotic (elevation, latitude, precipitation) and biotic/anthropic variables (net primary productivity, presence of protected areas, hunting pressure, forest fragmentation, human population density). We also assessed the influence of these variables and of group size on the presence of solitary individuals of this species. We analyzed the data with GLMs, combining stepwise and multimodel functions in R. Our results point to the presence of protected areas and habitat fragmentation as the main determinants of mantled howler monkey group size. We also found that human population density has a significant effect on the presence of solitary individuals. Based on these results, we propose to create an ecological corridor to restore the connectivity and dispersal of howler monkeys in southwestern Ecuador.

Key words: Ecuadorian primates, demography, conservation, ecological corridor

Tabla de contenido

INTRODUCTION

Individuals behave adaptively when forming groups because group size has costs related to fitness and energy (Bond *et al.* 2019). The benefits of grouping are organized in four main categories: predator avoidance, territorial competition, foraging advantages and avoidance of conspecific threat; however, group living has disadvantages related to feeding and reproductive competition, as well as epidemiological risks, which increase mortality and lowers reproductive rates depending on the size of the group (Chapman & Chapman 2000, Reyna-Hurtado *et al.* 2016).

Group size and its effects in terms of energy, fitness and behavior have been studied exhaustedly in primates (Majolo *et al.* 2008). It is known that the number of individuals per group can vary within and between populations, since the size of the group is commonly driven by the amount of available resources and the travel capacity of the group (Markham & Gesquiere 2017, Wrangham *et al.* 1993); however, variables such as infanticide, home range or predation risk are also known to influence group size (Marshall 2010, Strier 1992). Evaluation of ecological factors has shown that correlated variables, such as food availability and precipitation, as well as habitat quality and complex canopy structure, have positive impacts on group size (Arroyo-Rodríguez & Mandujano 2006, Marshall 2010).

Studies on the species of the genus *Alouatta* in the Neotropics have shown that human-driven variables such as fragmentation and forest conservation status have a negative effect on the number of individuals per group (Arroyo-Rodríguez & Dias 2010). Forest with higher levels of fragmentation present less canopy structure. Canopy modification negatively effects habitat quality and the availability of food resources since larger trees are no longer present (Arroyo-Rodríguez & Mandujano 2006).

One of the most studied primates of the genus is *Alouatta palliata*, commonly known as mantled howler monkey (Arcos & Ruiz 2007; Cortes-Ortiz et al. 2015). This is a resilient species with flexible feeding strategies and social behavior, which allow it to persist in moderately disturbed habitats. Because of this flexibility, mantled howler monkeys have been reported in forests where other tropical primates such as white-faced capuchins (*Cebus capucinus*) and spider monkeys (*Ateles fusciceps*) no longer occur (Clarke *et al.* 2002). Past studies found that high tree density is key for *A. palliata* in forest patches, so there is higher probability of finding larger populations in bigger and less disturbed forest patches (Cristóbal-Azkarate *et al.* 2005).

This species is distributed from southwestern Mexico to northwestern Peru, but population densities vary widely depending on the country, subspecies and methods used to estimate density. For example, in Ecuador, *A. palliata aequatorialis* population density ranged from 190 to 950 individuals/km^2, depending on forest patch size (Tirira *et al.* 2018), while in Colombia density ranged between 0.7 to 1.5 individuals/km^2 (Cortés-Ortiz *et al.* 2015).

The main threats to *A. palliata aequatorialis* are related to habitat degradation, mainly driven by deforestation and fragmentation, illegal pet trade and hunting, which reduce population density and possibly group size (Papworth & Mejía 2015). The subspecies is considered globally as Vulnerable, but it is Endangered in Ecuador (Tirira 2001, Cortes-Ortíz *et al.* 2015). Ecuadorian mantled howlers are found in ecosystems that are as threatened as they are, such as tropical dry forests which have lost up to 75% of their original cover, and Chocó forests that are threatened mainly by agriculture in the lowlands and mining on the Andean slopes (Gentry & Dodson 1987, Mestanza-Ramón *et al.* 2022).

To improve the conservation status of this species in Ecuador we must have a deeper knowledge of important environmental factors, especially those that determine group size

(Cortes-Ortiz *et al.* 2015). Group size is key to understanding which advantages and constraints individuals are facing. For example, smaller groups may be more vulnerable to predation and easily displaced from vital resources, while larger groups may experience greater intragroup competition that may increase foraging time and home range size (Markham *et al.* 2015). Increased male-male competition in larger groups may also increase the number of solitary males in a population since smaller and weaker males may avoid competition by remaining solitary for a longer time, as reported in Costa Rica by Bolt and collaborators (2021). By affecting individual behavior, these differences in group size may directly influence population dynamics as well (Brouwer *et al.* 2006).

Previous studies of this species have suggested that group size is directly determined by the productivity and continuity of the habitat (Peres 1997, Arroyo-Rodríguez & Mandujano 2006). Forest productivity is influenced by environmental variables, such as latitude, temperature and precipitation, resulting in more productive ecosystems in the tropics. Temperature and precipitation have a positive correlation if productivity is measured in terms of leaf and fruit biomass, which is key for howler's survival (Bicca-Marques 2003, Schuur 2003, Malhi *et al.* 2011, Behie & Pavelka 2015).

In this study, we used general linear models (GLMs) to identify the variables that have the greater influence on group size and presence of solitary individuals of this endangered species. Based on current knowledge, we expected that larger groups and more solitary individuals would be found in larger areas of forest of lower elevation and less anthropogenic perturbations (i.e. hunting and fragmentation), as well as in areas of higher net primary productivity (NPP).

METHODS

Study area

The forests of western Ecuador are among the most threatened ecosystems in the country (Dodson & Gentry 1991). Four main forests types can be found in this area: Tumbes dry scrub and deciduous forest in the south, and Chocó lowland and piedmont rainforest in the north (Ron 2020). Several public and private protected areas are located in this region, being the areas of the National System of Protected Areas, the larger ones (León Yánez *et al.* 2011). The records of mantled howlers were collected both in protected and unprotected forest patches, located in the provinces of Esmeraldas, Manabí, Santa Elena, Guayas, Cotopaxi, Pichincha, El Oro and Loja (Figure 1).

Data collection

Primate surveys were conducted by researchers, trained local guides, park guardians and university students in 2014 and then annually from 2017 through 2022. All the surveyors were previously trained to ensure the correct identification of the species and accurate data recording. The surveys were performed by teams of 2-5 surveyors, early in the morning from 06:30 to 11:00 and in the afternoon from 15:30 to 17:30 (local time). The teams walked at an average speed of 1km/h, in already existing trails. Each trail was surveyed only once per survey year. When a group of howlers was detected, the surveyors followed the animals as long as possible to record their location coordinates and group size.

A total of 172 records of mantled howlers (groups or solitary individuals) were included in the analyses. Most of the records (n=125) from 2017, 2018 and 2019 were obtained in the first regional primate census in western Ecuador (2017, Cervera *et al.* 2018) and the first national primate census (2018-2019). Data from these censuses were used with the permission of the Grupo de Estudio de Primates del Ecuador (GEPE). The remaining records, from 2014 through 2022, were gathered by the team of the USFQ project Primates, Forests and People (research permits 019-17-IC-FAU-DNB/MA, MAE-DNB-CM-2016-0046 to S. de la Torre).

Analytical modeling

Environmental variables.

Temperature (°C) and precipitation (mm) were obtained from historical monthly weather data of WorldClim on a spatial resolution of 21 km^2 approximately (https://www.worldclim.org/data/monthlywth.html#). For our models we selected the most recent raster data (year 2018) and calculated the annual average of each variable.

We downloaded the elevation data at 30-meter resolution from the interface of the Shuttle Radar Topography Mission (https://dwtkns.com/srtm30m/), which produced the highest-resolution digital elevation model of the Earth (Farr *et al.* 2007).

Net Primary Productivity (NPP) was obtained from NASA Earth Observations web page (https://neo.gsfc.nasa.gov/) at a spatial resolution of 1 km^2, these data were calculated based on the MOD17 algorithm, provided by the MODIS Land Science Team (Running *et al.* 1999). To include these data in the models, we calculated the mean value from 2001 to 2021.

We used the GIS application ArcGIS Pro (ver 2.9.1), to match all the data values with each pair of coordinates of the mantled howler records to obtain a single temperature, precipitation, altitude and NPP value per record. We also included latitude (in decimal degrees) as a variable since in western Ecuador the size and number of protected areas increases with latitude, finding larger forest patches in the northern region (Figure 1). Forest type changes with latitude as well, with Chocó rainforests occurring in the north and Tumbes dry deciduous forests occurring in the south. Here, we refer to latitudes below 0 degrees as lower (southern) latitudes and latitudes above 0 degrees as higher (northern) latitudes.

Anthropogenic variables.

We obtained the shapefile of the National System of Protected Areas (http://ide.ambiente.gob.ec/mapainteractivo/) from the interactive map of MAATE (Ministerio del Ambiente, Agua y Transición Ecológica). In our models, the presence of protected areas was included as a binary variable (1 for presence, 0 for absence).

Since primate hunting in western Ecuador is mainly carried out by indigenous communities (Ráez-Luna 1995), we used the presence of indigenous territories, obtained from the CONAIE (Confederación de Nacionalidades Indígenas del Ecuador) webpage (https://conaie.org/), as a proxy of the hunting pressure. In our models, the presence of indigenous territories was also included as a binary variable (1 for presence, 0 for absence). When the protected areas or the indigenous territories did not cover the whole canton (see below), the presence or absence was estimated based on the howler records. If the howler records were inside a protected area or an indigenous territory, then these variables were assumed to be present in the whole canton.

We used the forest fragmentation index (FFI) calculated by Noh *et al.* (2022, Table S2) for Ecuadorian ecosystems based on the MAGAP-MAE ecosystem classification (2015). We used this same ecosystem classification to assign the FFI to each howler record.

Finally, we used the shapefile of human population density from the geographic visor of the Instituto Geográfico Militar (https://www.geoportaligm.gob.ec/visorIEE/composer/).

This shapefile gathers the information from the national census of 2010. We paired the closest density value with each howler record coordinates, using the GIS application ArcGIS Pro (ver. 2.9.1).

Statistical analyses

Considering that the spatial resolution of some of the environmental variables was relatively large (< 10 km^2), to reduce multicollinearity we carried out the analyses at the canton level, using the median and variance of group size and the mean for each environmental variable per canton, when applicable. For solitary individuals, the total number of solitary individuals was calculated at canton level and related to the canton mean for each environmental variable. Two cantons (Eloy Alfaro and Quinindé) showed similar number of howler records inside and outside protected areas, so the data for these cantons were split into two sets, one for the records inside the protected areas and other for the records outside of the protected areas.

We performed correlation matrices to discard from our models those variables that were highly correlated (correlation > 0.8). After this analysis, we discarded the variable temperature (Tables 1 and 2).

Step-wise models

Since we found cantons with similar medians but with different group size ranges, we decided to carry out two GLMs, one with the median and other with the variance of group size as the dependent variables. We used precipitation, elevation, presence of protected areas, presence of indigenous communities, fragmentation index, and human population density as explanatory variables in both models.

We carried out a third GLM with the presence of solitary individuals as the dependent variable. The explanatory variables were the same as in the previous models plus the median of group size. This last variable was included because of the possible correlation between larger group sizes and the presence of more solitary individuals reported in Costa Rica by Bolt and collaborators (2021). To perform these analyses, we used R (ver. 2022.07.2+576).

Multimodels

To complement the results of the stepwise models, we used the R package *glmulti*, to obtain all the possible models with all the possible combinations of predictors and interactions. The best model was selected based on the AIC (Calcagno & Mazancourt 2010). To optimize the runtime, only a subset of all possible models was explored for each dependent variable, this subset option was included in the package.

RESULTS

We analyzed 172 records of mantled howlers from 18 cantons in western Ecuador. The number of records per canton varied considerably as did the median of group size (Table 3). The largest groups were recorded in the canton Manta, whereas the smallest group sizes were recorded in the canton Bolivar. In several cantons, no solitary individuals were recorded (Table 3).

Stepwise models

The only variable that had a significant effect on group size was the presence of protected areas ($p<0.05$), with larger groups found in cantons with protected areas (Table 4).

On the other hand, fragmentation ($p<0.001$), followed by the presence of protected areas ($p<0.01$) and latitude ($p<0.05$) significantly influence the variance of group size (Table 5). There is more variability in the size of the groups in cantons with more forest fragmentation and protected areas, while there is less variability in cantons of northern latitudes.

The presence of solitary individuals is better explained by human population density ($p<0.001$), but group size, NPP and protected areas have also significant effects. More solitary individuals were found in cantons with higher human population density, median group size and NPP. On the other hand, the number of solitary individuals was lower in protected areas (Table 6).

Multimodels

For the median of group size, the best 25 models, out of a total of 320 models, were compared. The best model (AIC=110.5418, $p<0.05$) includes the interaction between latitude and the presence of protected areas. This interaction shows up in more than 80% of the models (Table 7, Figure 2).

For the variance of group size, the best 25 models, out of a total of 390 models, were compared. The sum of the interaction between fragmentation with population density and the interaction of latitude with elevation (AIC=156.7956 $p<0.05$) is shown as the best model that predicts the variance in group size. These predictor variables also show up in more than 80% of the models (Figure 3).

For the presence of solitary individuals, the best 25 models, out of 280 possible models were compared. The best model (AIC=82.54191, $p<0.05$) includes human population density, net primary productivity and the interactions between human population density with group size, indigenous communities with protected areas, and indigenous communities with fragmentation. These predictor variables were found in more than 80% of the models performed (Table 9, Figure 4).

DISCUSSION

Based on the results of previous studies of mantled howlers (eg., Arroyo-Rodríguez & Dias 2010; Bolt *et al.* 2021; Cortés-Ortiz *et al.* 2015) we expected to find larger groups and more solitary individuals in larger areas of forest of lower elevation and less anthropogenic perturbations (i.e. hunting and fragmentation), as well as in areas of higher net primary productivity (NPP), precipitation and temperature. These expectations were partially met since we did find larger groups in larger protected areas; however, we found more solitary individuals in areas with greater human population density (i.e., more disturbed areas).

Our results point to the presence of protected areas as the most important predictor of group size in mantled howlers in Ecuador. The significant effect of the interaction between protected areas and latitude seems to reflect the fact that there are larger protected areas in northern Ecuador (León Yánez *et al.* 2011), suggesting again that protected areas are key for the conservation of this primate. Larger groups of mantled howlers are more commonly found inside protected areas and, although group size is not equivalent to population size or population density, it is possible that population density in these protected areas may also be higher. Future studies should focus on disentangling the relationship between these two demographic variables.

The variation in group size within cantons seems to be mainly affected by a combination of the presence of protected areas and high levels of forest fragmentation. Cantons such as

Puyango, Las Lajas, Puerto López and Manta are the ones with greater variance (Table 3). These cantons have more fragmentated habitats and greater human population density but also have some protected areas (e.g., Bosque Protector Puyango, Parque Nacional Machalilla and Refugio de Vida Silvestre Pacoche). In these scenarios, it seems that mantled howlers could form very large groups (up to 32 individuals) in the larger forest patches, whereas in small forest fragments groups could be considerably smaller (2 individuals). On the other hand, in cantons such as Quinindé, with less fragmentation and larger forest patches, the variance in group size is low (3-7 individuals) and groups have usually less than 10 individuals. This difference could be related to how difficult it may be for an individual to disperse and establish a new group. In areas with high forest fragmentation, individuals may form very large groups because they may not be able to disperse to other forest patches that could be too distant for them to reach. Long term monitoring of some of these groups is certainly needed to understand their dynamics and to assess their viability over time.

The variability of group sizes in Ecuadorian mantled howlers points to the behavioral flexibility of this primate species. Individuals can adjust their behaviors to live in larger or smaller groups depending on the characteristics of the forest patches. A similar variability in group size in this species was reported in Los Tuxtlas Biosphere Reserve - Mexico, where a variation from 6 to 59 individuals per group was found (Asensio *et al.* 2007). In Costa Rica, group size varied between 11 and 25 members per group (Clarke *et al.* 2002), while in Barro Colorado - Panama, there were groups from 5 to 45 individuals (Ryan *et al.* 2008). This variation in group size could affect individual survival and reproduction and, therefore, population dynamics. It is known that shorter groups show less intraspecific competition but are easily displaced from valuable resources (Markham & Gesquiere, 2017; Strier, 1992), while larger groups are able to access to more resources, but may have higher epidemiological risk and infanticide (Crockett 2003; Daviews *et al.* 1991). Strier (1992) also found lower reproductive success in groups of howlers with more females.

Both stepwise and multimodels show a significant effect of human population density on the mantled howler's population structure. The fact that more solitary individuals were found in areas with higher human population density suggests that human activities may be altering the dispersion of individuals, making it more difficult for solitary individuals to join a group.

Although my results don't show evidence of the effect of hunting on group size, more research is needed to better understand the relationship that indigenous communities of northwestern Ecuador have with mantled howlers. Previous studies mentioned the consumption of primates in Awa, Chachi and Épera communities (Tambonero de la Cruz & Añapa-Pianchiche 2013, Cárdenas Villalobos 2016, Villena-Esponera 2016, Villena *et al.* 2018), but it is not clear if mantled howlers are part of their current diets.

Despite sampling limitations that relate to some cantons having only one record of howler monkeys, this is the first region-wide study to assess the environmental factors that affect group size of mantled howlers in Ecuador. Our results highlight the importance of protected areas in the conservation of this endangered primate and of its habitat. Assuming that protected areas not only have larger groups of mantled howlers, as shown in my analyses, but also have more groups and, therefore, higher population densities, the presence of protected areas may contribute to the long-term viability of mantled howler populations. In this scenario, the creation of new protected areas, public or private, should be strongly promoted.

Other conservation strategies could be related to the creation of corridors to facilitate dispersal between forest patches. Indeed, the creation of an ecological corridor might be the best option to restore the connectivity between large groups and solitary individuals in highly fragmented areas like the ones in southwestern Ecuador. We, thus, propose to create a corridor in southwestern Ecuador and northwestern Peru to restore the connectivity between the Arenillas Presa Tahuin and Puyango protected forests, the Arenillas Ecological Reserve and the Cerros de Amotape and Tumbes National Reserve (Figure 5). Although these protected forest fragments are relatively close to each other, ecological restoration projects should be implemented to accelerate the dispersion of species and improve their habitat quality (Beita *et al.* 2021), especially in the Ecuadorian area.

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ANNEXES

Tables

Table 1. Correlation of the variables of the model for group size

	Group size	Elevation	Latitude	Precipitation	Temperature	Protected areas	Population density	Fragmentation	NPP
Group size	1								
Elevation	0.0251	1							
Latitude	-0.3386	-0.1646	1						
Precipitation	-0.0094	0.5870	-0.1039	1					
Temperature	-0.1631	-0.9297	0.0511	-0.5134	1				
Protected areas	0.4118	-0.1539	0.0486	0.0048	0.0669	1			
Population density	-0.2342	-0.3696	0.0875	-0.5358	0.3508	-0.2527	1		
Fragmentation	0.1983	0.0746	-0.1683	0.0283	-0.1437	0.1386	-0.2908	1	
Indigenous Communities	-0.1615	-0.0569	0.1427	0.2092	0.0916	-0.1640	-0.0704	-0.3912	1
NPP	-0.1771	0.6719	0.2874	0.5716	-0.5453	-0.0030	-0.4689	-0.1607	0.1150

Table 2. Correlation of the variables of the model for solitary individuals

	Solitary individuals	Group size	Elevation	Latitude	Temperature	Precipitation	Protected areas	Population density	Fragmentation	NPP
Solitary individuals	1									
Group size	0.2369	1								
Elevation	-0.1292	-0.1112	1							
Latitude	-0.1277	-0.2360	-0.1515	1						
Temperature	0.1625	-0.0821	-0.9281	0.0500	1					
Precipitation	-0.0778	-0.0752	0.5854	-0.0999	-0.5103	1				
Protected areas	0.0249	0.4352	-0.1696	0.0510	0.0748	-0.0030	1			
Population density	0.7665	0.2489	-0.2964	0.0746	0.2323	-0.3171	0.2218	1		
Fragmentation	0.1972	0.1956	0.0835	-0.1739	-0.1490	0.0391	0.1327	0.3248	1	
Indigenous Communities	0.0245	-0.1816	-0.0552	0.1437	0.0910	0.2049	-0.1640	-0.1128	-0.3895	1
NPP	-0.1223	-0.2910	0.6806	0.2821	-0.5442	0.5724	-0.0058	-0.3327	-0.1598	0.1169

Table 3. Number of groups, group size (median and range), and number of solitary individuals of *A. palliata aequatorialis* per canton

Province	Canton	Canton area (km^2)	Number of groups	Group size range	Group size median	Solitary individuals
Cotopaxi	Pujilí	1308	2	5 – 8	6.5	0
El Oro	Las Lajas	297	33	2 – 19	8.2	8
El Oro	Piñas	615	1	6	6	0
Esmeraldas	Eloy Alfaro	4302	10	2 – 9	4.6	2
Esmeraldas	Muisne	1265	14	3 – 14	7.3	2
Esmeraldas	Quinindé	3855	9	3 – 7	4	0
Guayas	Naranjal	2015	4	5 – 11	9.5	0
Loja	Puyango	643	7	2 – 19	7.7	0
Manabí	Bolívar	537	1	2	2	0
Manabí	Jama	575	47	2 – 21	7.3	7
Manabí	Manta	309	22	2 – 32	11.6	6
Manabí	Montecristi	734	12	2	2	1
Manabí	Pedernales	1932	1	4	4	0
Manabí	Puerto López	420	6	6 – 20	14.8	0
Manabí	Sucre	764	1	3	3	0
Pichincha	Distrito Metropolitano de Quito	4183	7	2 – 7	4.2	2
Pichincha	San Miguel de los Bancos	839	1	6	6	0
Tumbes	Zarumilla	745	4	4 – 7	6	1

Table 4. Estimate and p-value of each explanatory variable for the median of group size (* p<0.05)

Variables	Estimate	p-value
Elevation	0.0005653	0.2853
Fragmentation	-0.000698	0.9432
Indigenous communities	0.0025633	0.9895
Latitude	-0.065665	0.3398
NPP	-0.014678	0.2372
Population density	-0.005198	0.2783
Precipitation	-0.006646	0.6517
Protected areas	0.5175601	0.0218 *

Table 5. Estimate and p-value of each explanatory variable for the variance of group size (* p<0.05, **p<0.01, *** p<0.001) using the variance

Variables	Estimate	p-value
Elevation	-0.0005879	0.2443
Fragmentation	0.0568043	2.01e-11***
Indigenous communities	0.0671458	0.7054
Latitude	-0.1096456	0.0466*
NPP	0.0001692	0.9864
Population density	0.0055578	0.1120
Precipitation	0.0138031	0.2686
Protected areas	0.4742247	0.0031**

Table 6. Estimates and p values of each explanatory variable for presence of solitary individuals (* p<0.05, **p<0.01, *** p<0.001)

Variables	Estimate	p-value
Elevation	-0.002597	0.0887
Fragmentation	-0.000520	0.9889
Group size	0.144900	0.0218 *
Indigenous communities	-0.128200	0.8413
Latitude	-0.345200	0.0638
NPP	0.082710	0.0177 *
Population density	0.003527	0.0000074 ***
Precipitation	0.029680	0.4999
Protected areas	-1.458000	0.0437 *

Table 7. Multimodels with the lowest AIC to explain the median of group size

model	aicc	weights
group_size ~ 1 + latitude:protected_area	110.5418	0.11556417
group_size ~ 1 + fragmentation:protected_area + latitude:protected_area	111.2796	0.07991160
group_size ~ 1 + fragmentation:population_density + latitude:protected_area	111.3135	0.07856736
group_size ~ 1 + population_density:protected_area + latitude:protected_area	111.5052	0.07138528
group_size ~ 1 + protected_area + latitude:protected_area	111.8332	0.06059031
group_size ~ 1 + protected_area:precipitation + latitude:protected_area	112.0768	0.05364230

Table 8. Models with the lowest AIC to explain the variance group size

model	aicc	weights
group_size ~ 1 + fragmentation:population_density + latitude:elevation	156.7956	0.17300092
group_size ~ 1 + fragmentation:population_density	157.8451	0.10236501
group_size ~ 1 + fragmentation:population_density + latitude:elevation + latitude:protected_area	159.5452	0.04374907
group_size ~ 1 + fragmentation:population_density + latitude:elevation + NPP:latitude	159.6078	0.04240108
group_size ~ 1 + fragmentation:population_density + latitude:elevation + latitude:precipitation	159.6989	0.04051264
group_size ~ 1 + fragmentation:population_density + latitude:elevation + NPP:population_density	160.0493	0.03400185

Table 9. Models with the lowest AIC to explain the occurrence of solitary individuals

model	aicc	weights
solitary ~ 1 + population_density + latitude + precipitation:group_size + population_density:group_size + latitude:group_size + latitude:communities + NPP:population_density	54.91708	0.46966807
solitary ~ 1 + population_density + latitude + precipitation:group_size + population_density:group_size + fragmentation:group_size + latitude:group_size + latitude:communities + NPP:population_density	58.97786	0.06166013
solitary ~ 1 + population_density + latitude + precipitation:group_size + population_density:group_size + latitude:group_size + latitude:communities + NPP:population_density + NPP:fragmentation	59.07207	0.05882308
solitary ~ 1 + population_density + fragmentation + latitude + precipitation:group_size + population_density:group_size + latitude:group_size + latitude:communities + NPP:population_density	59.29245	0.05268563
solitary ~ 1 + protected_area + population_density + latitude + precipitation:group_size + population_density:group_size + latitude:group_size + latitude:communities + NPP:population_density	59.43501	0.04906108
solitary ~ 1 + population_density + latitude + precipitation:group_size + protected_area:precipitation + population_density:group_size + latitude:group_size + latitude:communities + NPP:population_density	59.76765	0.04154367

Figures

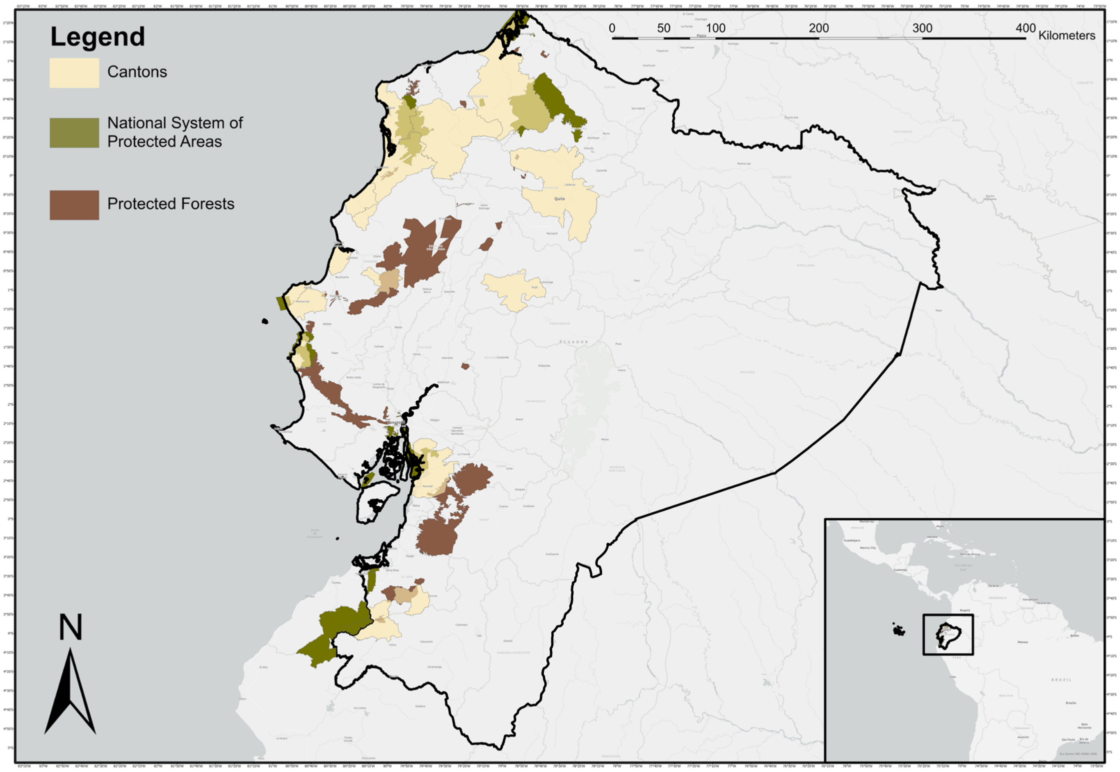

Figure 1. Study area. Map of continental Ecuador highlighting the surveyed cantons (cantons with mantled howler records, in yellow) and the presence of protected areas.

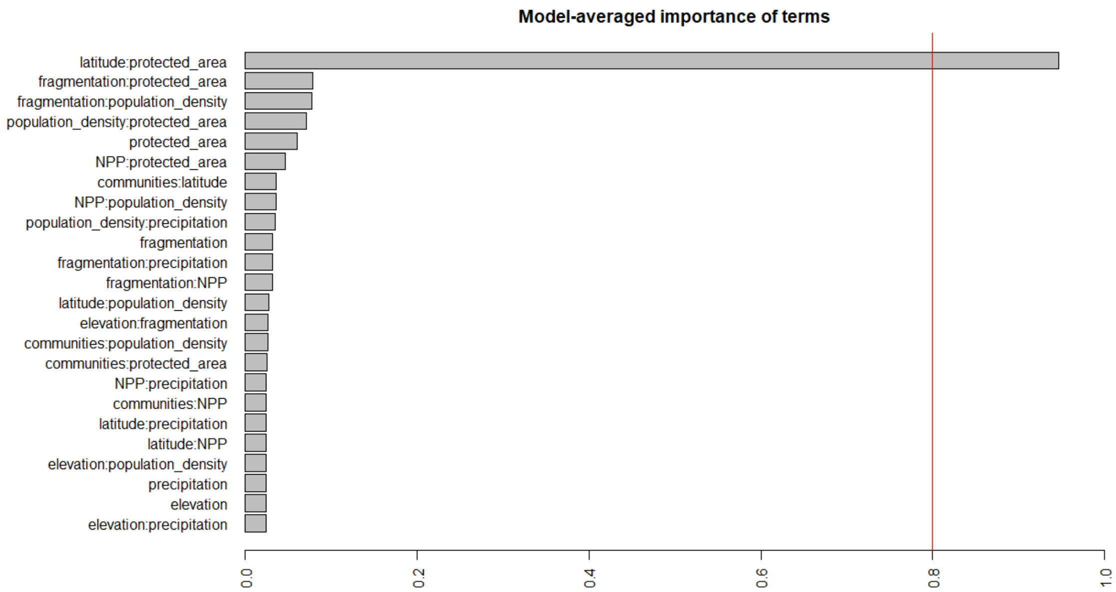

Figure 2. Predictors importance for the median of group size. The X axis represents the proportion of models in which each predictor (Y axis) appears

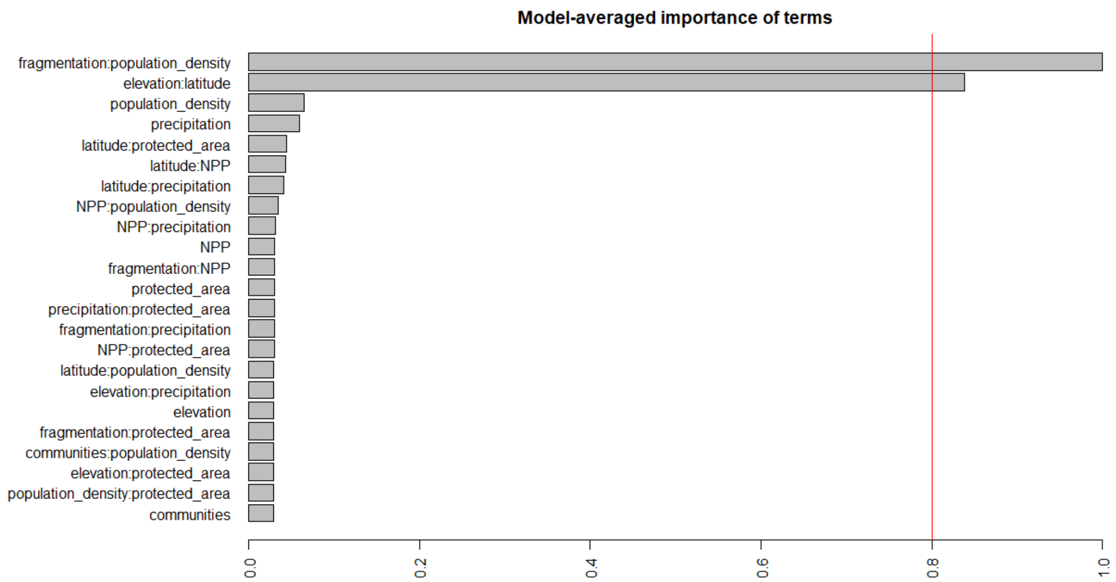

Figure 3. Predictors importance for the variance of group size models. The X axis represents the percentage of models in which each predictor (Y axis) appears

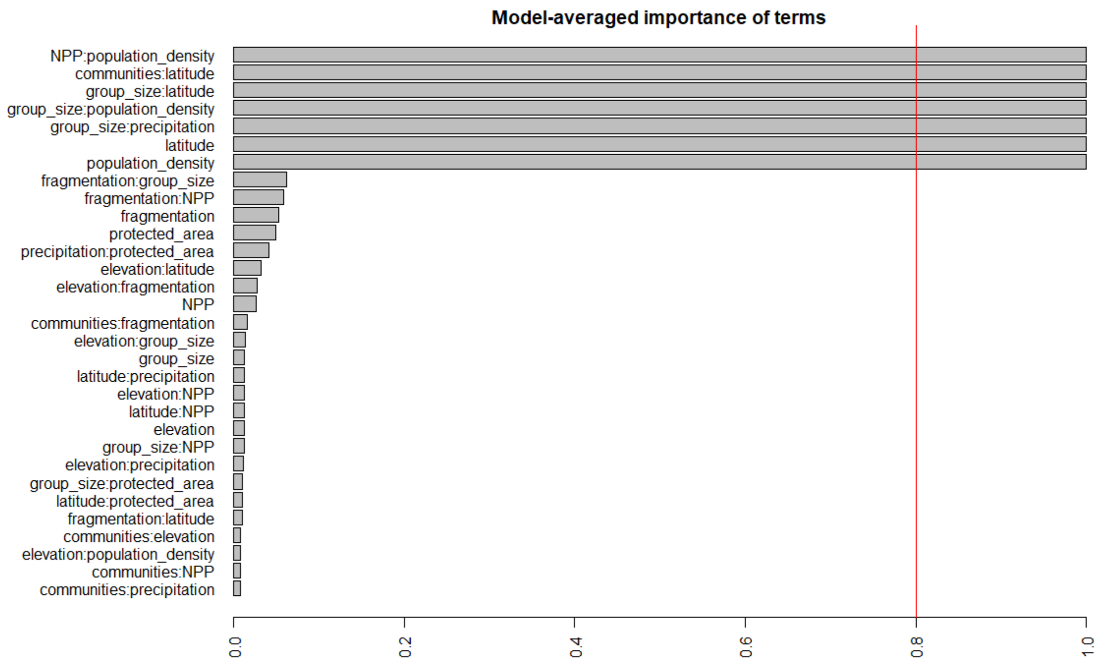

Figure 4. Predictors importance for the occurrence of solitary individuals. The X axis represents the proportion of models in which each predictor (Y axis) appears

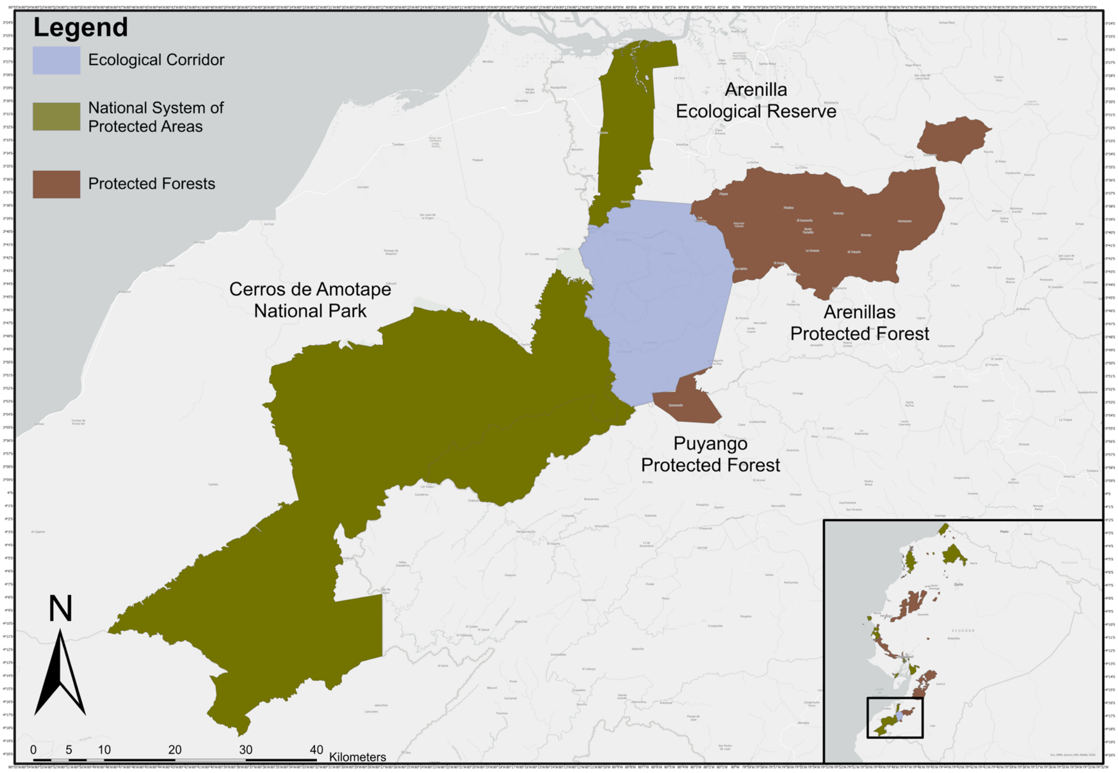

Figure 5. Potential area for an ecological corridor in Southwestern Ecuador